10. THE EVOLUTION OF OLCIGOCENE HORSES

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The popular image of Oligocene horses portrays their evolution as a single, orthogonally linearizing grade coming continuously from Miocene to Holocene. We find that the more recent view, a "tightly" branched phylogeny that includes at least seven valid species (e.g., M. nodi, M. xenotho, M. ephippus, M. arvensis, M. antiquus, M. canadensis, and M. equus), represents the two genera are not a continuous integrating lineage, but instead are marked by a distinctive set of changes in size, dental and tooth features, and overlap by about 5 million years.

Introduction

The evolution of horses has traditionally been among the best-documented examples of an evolutionary sequence in the fossil record. Huxley's 1870 series of European horses, andMarsh's 1879 genetics of American horses were among the first such sequences to lend support to the theory of evolution. Early paleontologists presented the evolution of horses as a single unbranched lineage, but as more information emerged, the phylogeny began to look more branched and "tightly" branched (Huxley, 1870; Prothero, 1984). Most horse phylogenies, however, were abstractions based on a few examples from each geographic level. Until recently, very little work had been done on the detailed geometry of the phylogenetic pattern of horses. In the past, this may not have been as critical, since most work in paleontology (e.g., Simpson, 1950) horse evolution usually falls under the subject of Oligocene view. But since the work of El- Trego and Gould (1972), detailed records have become critical in the dispute over the temps and mode of speciation. Some authors (e.g., Stanley, 1970) have noticed the small size of the modern horse family tree, and the apparent stability of certain taxa (e.g., Eohippus), and have argued that the horse fossil record supports the punctuational mode of change. Others (e.g., Curren, 1980) have interpreted Hyaenoho in a gradualistic framework. Since only a small portion of the horse fossil record has been examined in detail, the dispute is far from settled.

One of the more fossiliferous portions of the horse record is the Oligocene fauna, especially in Wyoming. Horses are quite abundant and well preserved in localities such as the Big Badlands of South Dakota. Not only are specimens very abundant, but in the Frick Collection of the AMNH, the most horses have excellent stratigraphic documentation for each specimen. The stratigraphic details of the deposits hosting these horses have recently been improved (Prothero, 1982). With the help of micrornematography, greater precision of correlation and time control are also available. With this data base, it is now possible to examine the details of horse phylogeny during the Oligocene, and compare it to the two competing models of palaeontologic speculation.

At present, horse phylogeny horse phylogeny is encumbered by several sources of taxonomic confusion. The early history of horse evolution is characterized by a hyper- typological taxonomic splitting, and "artificial" taxa that are partially defined by their stratigraphic occurrence. For example, Oeben (1910) distinguished Mesotherium and Miohippus by a stratigraphic boundary, rather than on morphological grounds. Sitter (1940) recorded 20 species of Mesotherium and 18 species of Miohippus, and did not attempt to syn-onymize any of them. More recent work (Fossey, 1970a, 1970b) has gone to the other extreme, lumping all species of Mesotherium into two species spanning an enormous amount of morphological variability across nearly eight million years. Some workers (e.g., Ewen et al., 1967) are not satisfied with this arrangement, either.

The Frick Collection of the AMNH of fossil horses offers an unparalleled oppor- tunity to resolve this dispute. Unlike the samples examined by Fossey, the Frick Collection allows us to place our phylogenetic hypothesis within a finely resolved stratigraphic context. If the diverse mor- phologies found at the same stratigraphic level by Fossey (and thus placed in the same species by her) have drastically different geographic and stratigraphic ranges, they may represent more than one species. If each of these morphologies has a distinctive and unique distribution in time and space, they are also useful biogeographi- cally, and should, as a heuristic tool, be recognized as valid species. Thus, the systematic details of Oligocene horse evolution are important for evolutionary biology as well as for stratigraphy.

We have restricted this study to horses from the latest Chadronian, Orellian, and Whitneyan (30-33 Ma). The taxonomy of early and medial Chadonian horses is corre- sponding to be investigated by Dr. R. J. Ewen. We have excluded Arikareean and later horses from this study, since they are not germane to the details of horse evolution in the more fossiliferous Oligocene. Also, a satisfilactory review of Arikareean horses requires a detailed study of the split between the equine and antilophine lin- eages that is beyond the scope of the present report. Abbreviations used in this paper are as follows: AMNH, American Museum of Natural History, New York, N.Y.; FAM, Frick Collection, AMNH; CM, Carnegie Museum of Natural History, Pittsburgh, Penn.; I.F., local fauna; M.A., million years before present; MCZ, Museum of Comparative Zoology, Harvard University, Cam- bridge, Mass.; LACM, Los Angeles Country Museum of Natural History, Los Angeles, Calif.; NMC, National Museum of Canada, Ottawa; SOSM, South Dakota School of Mines Museum of Geology, Rapid City, S.D.; USNM, United States National Museum, Smithsonian Institution, Wash- ington, D.C.; YPM, Yale Peabody Museum, New Haven, Conn.

Taxonomy and morphology

Order Perissodactyla Owen, 1846
Family Equidae Gray, 1821
Mesohippus Marsh, 1879
Palaeohippus Leidy, 1881
Mesotherium Leidy, 1852
Miohippus Hay, 1902 (in part)
Palaxippus Schlatter, 1935 (in part)

*Rediaded Diagnost. Small equids (4-5 length = 27-37 mm) with molarized P2/2.
(1-9) with shallow pitted crowns. Longer face than Equus, Orydhipus, or Hya- othecium, with extended premaxilla and longer diastema. Angle of jaw posteriorly rounded, without a notch. No contact between the cuboid and third metatarso-

Metacarpal five usually reduced. The genus typically has a very shallow facial fossa.

Type species, Mesohippus baradii (Leidy, 1850).

*Oligocene species.

*Mesotherium xenotho, Mesohippus ephippus, Mesotherium antiquus, Miohippus baradii, and several Chadronian species not dis- cussed here.

*Distribution. Late Eocene (late Duchesnian, Parvus I.); Vojna Group, Texas Intro to mid-Oligocene (late Orellian, top of the Upper Nodules, Middle Orellan beds). Known from the White River Group in South Dakota, North Dakota, Nebraska, Wyoming, Colorado, and from White River equivalents in Montana, Saskatchewan, Texas, and possibly Florida.
DISCUSSION

As mentioned in the introduction, the taxonomy of Mesotherium has gone from extreme splitting to extreme lumping. Osborn (1906, 1910) named a new species at practically every single quarry encountered in the fossil collections than available. Many of the diagnostic features are impractical to use when the variability of larger samples is considered. In addition, Osborn trained comparable specimens from different stratigraphic levels. For Orski, each species named a stratigraphic position was part of species definition. Virtually no statistical techniques were employed, since biostratigraphy was in its infancy in 1910.

Since then, several authors have attempted to analyze larger samples of Mesotherium. Clark and Bebeau (1967) established a numerical coding system for various features of the upper teeth, and this system was adopted by Forsin (1970a, 1970b). We have adopted a similar system, shown in Fig. 10.1. Each specimen was encoded for length, width, and five characteristic zones of each of the upper cheek teeth. Over 300 skulls, palates, and maxillae have been analyzed. We originally intended to analyze the data matrix by multivariate methods, but such techniques became unnecessary when obvious patterns emerged. Contrary to Forsin (1970a, 1970b), not all the tooth characters were randomly assorted or useless taxonomically. We found that the condition of the lingual cingulum, hypsylale, metacrista, and occasionally the premaxilla was quite useful. In addition, we considered other skeletal characters. The Přívrat Collection of fossil horses contains numerous skulls, and the condition of the facial fossa has proven particularly important in Miocene horses (MacFadden, 1980) and in Miocene as well. We examined the numerous associated postcranial remains to determine if they were other useful features in the skeletons. We also examined mesials and lower teeth, but except for age, the lower dentition showed no consistent pattern of diagnostic features. Because only skulls and mandibles with relatively unweathered dentitions are identifiable to species, we do not list every Miocene specimen in the reported material below. The Přívrat Collection has thousands of specimens of Mesotherium and Mesotherium (particularly lower jaws and postcranial) that cannot be identified to species. Only identifiable material has been catalogued, identified, and listed. We looked for evidence of sexual dimorphism, but found no sign that Oligocene horses show the type of dimorphism found in Hyaenodon or many Miocene horses. The completeness and quality of the Přívrat Collection horses have made it possible to reassess the question of how many species of Mesotherium are distinct and recognizable.

Mesotherium barid (Leidy, 1859)


Residual Diagnosis: M1-3 length: 50.3-50.3 mm. Lingual cusp or partial lingual cingulum employed, since biostratigraphy was in its infancy in 1919.
consider *Mesophius hypostylus* to be a junior synonym of *Mesophius baeri*. In view (Tables 10.1, 10.2) it lies etymologically within the range of variation of *Mesophius baeri*, and the type of *Mesophius hypostylus* (AMNH 1190), comes from a deposit that also contains *Mesophius baeri*. Osborn (1904, 1915) distinguished *Mesophius hypostylus* from *Mesophius baeri* as follows: "Distinguishes . . . from *Mesophius baeri* by more rudimentary hypostyle and less inflated crest. Metabolism sharp; metacorm not defined at base. P3 small. Skull with preoral fossa very slightly deeper than in *Mesophius baeri*."

Of these features, none appears to be valid. The hypostyle on AMNH 1190 are all class 2, as is seen on the type specimen of *Mesophius baeri*. Their tradition is not truly "rudimentary," since both the type and most of the referred material have this kind of hypostyle. The elevation of the crown is highly variable and not taxonomically significant. The metacorms of *Mesophius hypostylus* and *Mesophius baeri* are typically class 2 on P3-5, class 3 on P4 and M1-2. The condition of the fascial fossa on AMNH 1190 is difficult to judge, since the specimen has been dorsoventrally crushed. However, judging from most referred skulls, the condition of the fossa in *Mesophius hypostylus* and *Mesophius baeri* is identical. Thus, *Mesophius hypostylus* is clearly a junior subjective synonym of *Mesophius baeri*.

Clark and Zechar (1967) referred most of the mid-sized Chasmosaurines to *Mesophius hypostylus*. We suspect that many of these specimens are referable to *Mesophius baeri*, but that others are referable to other species. Fiskes (1970a, 1970b) placed *Mesophius hypostylus* in synonymy with *Mesophius baeri*. We agree, although for different reasons than the gave.

*Mesophius* (Cope, 1889)  
*Fig. 103A, 103B, 103C, 103D*

Archichasmosaurus l Watson, Cope 1889, p. 5  
Mesophius mancosensis. Osborn 1904, p. 109  
Mesophius intermedius. Lambe 1905a, p. 243  
Mesophius underwoodi. Russell 1973, p. 837  
*Symposium* Montanensis Osborn 1904

**Retract Diagnosis.** M1-3 length = 30-36 mm. Lingual ridges or circular cusps on upper cheek teeth are very large or absent. Hypostyles usually absent or class 1, rarely class 2. No crests.

**Type.** NMC 6289, a left upper molar missing the labial portion of the ectocrone.

**Referred Material.** MCM 22, CHAS- 

**DREXELIAN: Phaseolite Springs, Jefferson Co. Montana. AMNH 9660 (type specimen of M. montanensis); AMNH 9661.**

**LATE ULCERODROMIAN: Chadron area, Dawes Co., Neb.:** AM 7422, 7432, 76059, 76070, 74050, 74057, 74063, 74064, 74050, 74052, 74036, 74039, 74042. **Southern Hills, Niobrara Co.:** AM 7163, 74059, 76059, 76030, 76025, 74050, 74057, 74050, 74055, 74057, 76032, 76032, 76032, 76032, 76032, 76032, 76032, 76032, 76032. **EARLY OREGILLIAN: Lower Nukodes, Seven Mile Member, Big Badlands, S.D.:** AM 74030, 76030, 76030, 76030, 76030, 76030, 76030, 76030, 76030, 76030, 76030.

**Hornum and Holotype.** The type is from the early Chadronian Cypress Hills fauna, Saskatchewan. Referred material from many other Chadronian localities, and from early to late Orellanian localities in Wyoming, Nebraska, and South Dakota.

**DREXELIAN: Mesophius intermedius** is easily distinguished from similar Mesophius baeri by the absence of lingual cingula and by its rudimentary hypostyle. It is distinguished from Mesoph- pian by its slightly larger size and larger helix. The type of Mesophius intermedius is very poor, and normally the name would be considered indeterminate. However, Russell (1973) described additional
Fig. 10.3. Mesophyes serratus, FAM 7427. Referred skull and mandible in left lateral view. Scale bar in cm.

topotypic material of Mesophyes serratus from Cypress Hills that clearly establishes the morphology of this species. As Lambe (1908) and Russell (1975) pointed out, the two diagnostic features of Mesophyes serratus (vestigial lingual cingulum and rudimentary hypoptyl) are features that are true of Osborn's species M. montanensis from Pipestone Springs. The specimens referred to M. serratus from the Cypress Hills, Pipestone Springs, and from the localities mentioned above are identical in size (Russell, 1975; see Table 10.2). Thus, it appears that the name serratus is the senior synonym for Chadronian-Orellanian Mesophyes larger than M. color with rudimentary hypoptyl, and faint or absent lingual cingulum.

Osborn (1918, p. 40) distinguished M. montanensis from M. serratus by 'sharp elevation of crest and absence of internal cingulum.' Now that larger samples are known, these species cannot be distinguished by these features. The shape of molars is highly variable and greatly affected by wear. The lingual cingulum on the type of Mesophyes serratus is a little stronger than on the type of Mesophyes montanensis, but Russell (1975) has shown that there is some variation in this feature in topotypic samples of Mesophyes serratus. We have seen similar variation in the strength of the lingual cingulum in a Czech Collection sample from the later Chadronian and Orellan. There appears to be no grounds for distinguishing Mesophyes montanensis Osborn, 1904, and it is here considered a junior synonym of Mesophyes serratus (Cope, 1884).

Clark and Bebber (1967, p. 40) considered Mesophyes montanensis a junior synonym of Mesophyes hypotylostylus and Forstel (1907) considered it a junior synonym of Mesophyes bairdi. As shown previously, Mesophyes hypotylostylus cannot be distinguished from Mesophyes bairdi, but Mesophyes montanensis (sensu lato) can. Although the two species intergrade very slightly, there does appear to be a separation between horses with no lingual cingula and rudimentary hypoptyl (Mesophyes serratus) and horses with stronger lingual cingula and well-developed hypoptyl (Mesophyes bairdi). The two groups can be readily identified with well-preserved upper dentitions; they are not indistinguishable, as implied by Forstel (1907a, 1907b).

Other characteristics of these two species vary randomly, but the two characters discussed above are clearly associated. M. serratus and M. bairdi are diagnostic morphological clusters and deserve recognition as species. They also have different geographic and temporal ranges, which provides further evidence that they are distinct species. For example, the Pipestone Springs Main Pocket locality contains only Mesophyes serratus, yet coeval deposits in the High Plains contain both species. Cypress Hills contains Mesophyes serratus but no Mesophyes bairdi. Both species appear to become extinct at the end of the Chadron (top of the Middle Creeden Beds), although Whitneyan collections are too sparse that their ranges may extend into younger deposits.

Mesophyes soralus (Cope, 1874)

Archbishop Cope, 1874, p. 466.
Mesophyes soralus: Osborn, 1918, p. 47.

Synonyms: Mesophyes trigonostylus


Retained Diagnosis. M1-L3 length = 32-36 mm. Lingual cingula on nearly all upper cheek teeth. Hypoptyl all class 3 (triangular in shape). No crochets.

Type: AMNH 6298, a left maxilla with M1-2 and the base of zygomatic arch, with associated fragments of a scapula, ischium, and metapodials (Fig. 10.4D). From the Cedar Creek area, Logan County, Colorado (Orellan, according to Galbreath, 1953).

Referred material: LATE CHADRONIAN: 5 feet below top of Chadron Formation, Red Shirt Table, Shannon Co., S.D.: FAM 114351, Spearman Hills, Niobrara Co., Wyo.: FAM 116356.


LATE ORELLAN: Upper Nodules, Middle Creeden Beds, Big Badlands, S.D.: FAM 74019, 116400, 116401, 116493, 116395, 116400, 116358, 116353, 116354, 116352; Patterson Ranch, Stark Co., N.D.: FAM 116405.

Habitat and localities. Known from the late Chadronian to late Orellanian (top of Middle Creeden beds), in Colorado, Wyoming, Nebraska, South and North Dakota.

Discussion. Osborn (1918, p. 47) reported the type of Anototherium cattilatum lost, and this was cited by Scott in 1941. Since Cope's description was inadequate and the specimen was not figured, Osborn considered the type to be indeterminate. Since 1941, however, the type of M. creedeni (AMNH 6298) has reappeared. Although the type (Fig. 10.4D) consists of only M1-2, these teeth clearly show good examples of class 3 triangular hypoptyl so characteristic of Mesophyes trigonostylus. In size (Table 10.2), AMNH 6298 also falls within the M. trigonostylus population. M. creedeni appears to be the a senior
Fig. 10.4. *Makhipus*, AMNH 74031, referred skull in (A) dorsal, (B) right lateral, and (C) ventral views. (D) AMNH 298, type specimen. Scale bars in cm.

Fig. 10.5A. Stratigraphic distribution (orages) of horse species from the upper Chedronian.

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THE EVOLUTION OF PERISSODACTYLS

Mesotherium castellaneum can be distin-
guished from M. hardyi and M. echinatum on its relatively short tooth.
In all remaining skulls, jaw, and skeletal features, Mesotherium castellaneum
is very similar. In the larger Orellan, M. castellaneum is generally more abundant
than other species of Mesotherium. M. castellaneum occurs with M. hardyi and M. echinatum in
deposits near the Chadronian-Orellan boundary as well, although in much smaller
numbers (Fig. 10.3A).

Some may object to designating this
classification of Mesotherium plus
two of Mesotherium from the same deposits
(e.g., the Devonian of Wyoming). It might
be argued that under a biological species
concept, these forms would be ecologically
equivalent and thus would have to be the
same biological species. However, we are
persuaded that separate species, rather
than a series of intergrading subspecies, are
preferable. Horses are notoriously specious.
Many localities in the Miocene have four or
five species of closely related horses, and a
few quarries have over a dozen. For exam-
ple, Skinner and Johnson (1984, p. 276) re-
port eight genera of horses in the Railway
Canyon of the Valentine Formation, and 12
species were reported by Schultz (1977) from
the Clarnes quadrangle of Texas. Even to-
day, two or more species of redbone can be
found together in East Africa. Morphologi-
cally, these Mesotherium species can be
unambiguously distinguished, and have dis-
tinctive stratigraphic and geographic ranges.
These taxa are to be stratigraphically useful, they cannot be lumped
into a common species. It is conceivable that they are end members of a biological
continuum, but our data do not support this.
Indeed, we find three distinct clusters of morphology. These clusters have clear
biogeographic and biogeographic defini-
tion and utility. We cannot agree with
Forsin (1970a, 1970b), who places all
medium-sized Mesotherium from the Orell-
lan in a single species.

Mesotherium barbouri Schlaikjer, 1931
Fig. 10.4
Mesotherium barbouri, Forsin, 1974 (in part).
Recent Diagnoses. M1-3 length = 34-
36 mm. Metacarpals reduced. No bacular
cubita. Usually short and slightly
pinched diaphyses, causing a flaring sym-
dysis. Upper incisors circular and deeply
cupped. Holmem and femur relatively
short with respect to metapodial length.

Type. M.C. 1764, a complete skeleton,
from the late-Orellan of the Big Badlands, South Dakota.

References: WATER: EARLY ORELLAN:
Lower Redhorn, Scenic Member, Big Bad-
lands, S.D.: P.A. 11632, 11635, 76074.
Upper Redhorn, Scenic Member, Big Badlands, S.D.: P.A.
11632, 11635.

Horton and localities. Early to late
Orellan, South Dakota and Wyoming.

Description and discussion. Mesother-
um barbouri was thoroughly described by
Schlaikjer (1931). It is a very distinctive
horse, with a peculiarly short face and uni-
ually small, deeply cupped incisors (Fig. 10.3A-C). The upper incisors of most
primitive horses are more oval in cross-
section, and have only shallow pits on the
crowns.

Schlaikjer (1931) referred some spec-
imens from the Harvard Fossil Reserve, Golden
County, Wyoming, to Mesotherium barbouri.
Forsin (1974) placed these specimens in
Mesotherium aequalis. However, the two
smaller specimens from this Harvard Fossil Re-
serve (M.C. 2581 and M.C. 2792) are clearly
within the size range of Mesotherium bar-
bouri, and too small for Mesohippophius obe-
latis, which is the most common horse
from this quarry. The ratio of dental spec-
imens of Mesotherium barbouri to Mesohippo-
phius obelites in this quarry is 2:10. Inter-
estingly, Forsin (1974) reported that the

OLIGOCENE HORSES

Fig. 10.4. Mesotherium barbouri, M.C. 1764; type skull in dorsal (A), right lateral (B), and ventral (C) views; type mandible in crown (D) and left lateral (E) views. Scale
bars in mm.
ratio of metatarsals II (without a cuboid facet) to the Metapodials condition to those with a cuboid facet (the Metapodials condition) is 1:4. Thus, we would associate these two metatarsals III with cuboid facets with the dentition that can be referred to Metapodius barthorum.

Metapodius Marth, 1874

Archithorax Leidy, 1880, p. 113 Metapodius Marth, 1874, p. 129 Metapodius Osborn, 1906, p. 177 (in part)

Pedopodius Schauzky, 1935, p. 141

Rutiodus Dyalus. Small to medium sized eights (1/2-2/3 sagittal, 30-40 mm) with a slightly longer skull than Metapodius, large, well developed hypaxial (usually class 3), and a deepened, laterally expanded facial fossa. Face between the first metatarsal and cuboid.

Type species: Metapodius avunculus Marth, 1874.

Included species: Metapodius obliviens, Metapodius amphithea, Metapodius intermedius, Metapodius giliey, Metapodius quadripartus, and a number of exclusively Arktico-american species not discussed here.

Distribution: Mid-Charadriiform (Cypreus Hill) to Arktico-american of Saskatchewan, Montana, Oregon, Wyoming, Nebraska, Colorado, and North and South Dakota.

Discussion: The distinction between Metapodius and Metapodius has always been controversial. Marsh (1884) created the taxon Metapodius for horses in the Arktico-american John Day beds of Oregon. Osborn (1918) made the genus a strictly hor- izontal taxon for all horses from the late White Riverian through most of the Arktico-american. Osborn’s diagnosis of Metapodius included a number of invalid, highly variable characters, but a few of these characters have stood the test of time. The articulation between the cuboid and third metatarsal, the larger hypaxial region, the longer face, and the deeper facial fossa are all characters that distinguish Metapodius from Metapodius. The cuboid-third meta- tarsal articulation in particular has served as a useful chiroetrical feature signaling the appearance of Metapodius, since this character is a result of the broadening of the third metatarsal with increased monodactyly.

Sclater (1935, p. 141) created a new genus Pedopodius for a number of Metapodius specimens which had rudimentary condyles on the upper cheek teeth. Scott (1931) adopted Sclater’s generic taxonomy. (Since their 1970s synthesis, Pedopodius with Metapodius is recognized by that the condition was a polyphyletic feature within pedopodius, and not taxonomically useful. Our studies confirm this conclusion. Although weak crests are occasionally found in Metapodius, they are irregularly developed on adjacent teeth, and sometimes are not even symmetrically developed on both sides of the same skull. The presence of condyles is not diagnostic, let alone sufficient justification of a new genus.

Stouton (1940) considered Pedopodius to be a junior synonym of Metapodius. Stouton (1940) and Stouton (1951) thought that Metapodius and Metapodius were intergraded in the Cheval. Lilliegreen (1970) expressed doubt that Metapodius and Metapodius could be distinguished at all. However, in our examination of the Price Collection of fossil horses, a clear distinction between the two genera became apparent. Metapodius is a significantly larger horse, with a longer face. Its facial fossa is deepest just anterior to the orbit and tapers abruptly, becoming shallower toward the nostril. The fles of the region, approximately the level of P2. There is no overlap or integration between these two morphologies, they overlap considerably in temporal range (Fig. 162B).

All Metapodius specimens that have associated teeth clearly show the cuboid- metatarsal II articulation. This is never seen in Metapodius. The definition of Metapodius is problematic. This genus now includes a number of genera and was not an early horse that had previously been referred to Metapodius on purely morphological grounds.
Table 10.2. Measurements of upper teeth
Mean ± standard deviation in mm, sample size given in parentheses ( )

<table>
<thead>
<tr>
<th>M. baini</th>
<th>M. salemi</th>
<th>M. colubris</th>
<th>M. larosae</th>
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<td>P1 Length 11.607.1 (31) 11.407.1 (31) 11.706.0 (14) 11.614.0 (5)</td>
<td>P1 Length 12.906.0 (22) 12.710.8 (22) 11.806.4 (14) 12.721.9 (5)</td>
<td>P1 Length 11.708.0 (33) 11.608.8 (22) 11.908.5 (13) 12.303.9 (5)</td>
</tr>
<tr>
<td>M1 Length 18.406.0 (33) 18.611.1 (22) 18.611.1 (15) 12.050.4 (5)</td>
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</tr>
<tr>
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<td>P Width 14.712.1 (33) 14.501.0 (9) 14.401.0 (13) 14.712.0 (9)</td>
<td>P Width 15.212.0 (33) 15.251.0 (60) 15.221.0 (13) 15.220.5 (5)</td>
<td>P Width 14.920.9 (32) 14.411.0 (55) 14.212.0 (13) 14.391.1 (40)</td>
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<td>M1 Width 34.621.9 (38) 33.813.7 (22) 32.815.1 (11) 33.752.2 (11)</td>
<td>M1 Width 34.610.2 (39) 34.625.3 (26) 33.718.1 (12) 34.615.5 (3)</td>
<td>M1 Width 46.325.1 (32) 33.813.7 (22) 34.615.5 (3)</td>
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<th>M. ptychognathus</th>
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<td>M1 Width 46.325.1 (32) 33.813.7 (22) 34.615.5 (3)</td>
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Table 10.3. Measurements of lower teeth (in mm)

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<tr>
<th>M. horridi</th>
<th>M. baini</th>
<th>M. salemi</th>
<th>M. colubris</th>
<th>M. larosae</th>
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<td>P3 Length 46.325.3 (32) 33.813.7 (22) 34.615.5 (3)</td>
<td>P3 Length 46.325.3 (32) 33.813.7 (22) 34.615.5 (3)</td>
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<td>M1 Length 46.325.3 (32) 33.813.7 (22) 34.615.5 (3)</td>
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## Table 10.4. Postcranial measurements (in mm)

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<th>M. hallae</th>
<th>M. intermedius</th>
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## Table 10.4 (continued).

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</table>
**Oligocene Horses**

The Evolution of Perissodactyls

*Miohippus obliquus* (Osborn, 1908) new combination

Figs. 10.2


*Synonymy.* *Mathohippus* californicus Osborn, 1904, p. 175; *Mathohippus metrallapos Osborn, 1908, p. 174; *Mathohippus metrarhopus.* Osborn, 1918, p. 510; *Palaeohippus* an-

*fragatus* Schlegel, 1930, p. 111; *Mathohippus antiquus* Frazer, 1971, p. 403; *Mathohippus brachyurus* Osborn, 1918, p. 53; *Le Palaeo-

*hippus* brachyurus* Schlegel, 1930, p. 140.

Recent Diagnosis. M1-3 length = 34.3 mm. Molar crown complete with insta-

conules weak or absent. Molar crown more obliquely oriented than in any other species (Fig. 10.7).

Type. AMNH 666, a badly crushed ju-

venil skull, with dP3 and m1-2, and both lower rami (Fig. 10.7A). dP3-4 have been pre-

pared away by Morris Skinner, revealing permanent p3-4. From the late Oligo-

*Inidae* (middle Ora
dean) beds of the Big Badlands, South Dakota.

Referenced material. LATE CHA-

ROWIAN: Chadron Formation, fig. Badlands, S.D.: FM 116392. Chadron area, Duvle-

Co., Neb.: FM 74075, 74084, 74087, 74089, 74096, 74105, 74106, 74108, 116363, 116377, 11739, 116236, 116327, 116328, Seanum Hill, Nihi-

na Co., Wy.: FM 74071, 74084, 74096, 116417, 116385, 116384, 116385, 116232. EARLY ORELLIAN: Lower Nodules, Scenic Member, Big Badlands, S.D.: FM 74021, AMNH 112296, 3915. Harvard Fossil Re-

serve, Goshen, Co., Wy.: MCZ 2790 (holotype of *P. majoris*), MCZ 2791, MCZ 2900 (f. antiquus paratype), MCZ 2798, 2799, 2800, 2801, 2799, 2799.

LATE ORELLIAN: Foyrer Ranch, Stark Co., N.D.: FM 116404. Upper nodules, Mio-

hippus Orellian beds, North Dakota. AMNH 116399, 116392.

EARLY WEHMEYAN: Upper Ora-

dean beds, Big Badlands, S.D.: FM 116363. Vista Member, Cedar Creek area, Weld Co., Colo.: AMNH 8791 (type of *M. antigu-

us*).

LATE WEHMEYAN: Leptacotus nod-


Habitat and distribution. Late Chado-

*Inidae* to late Oligocene, Wyoming, Col-

orado, South and North Dakota, and Neo-

braska.

Discussion. Large White River horses with slightly advanced dentitions have been given a plethora of names. In size (Table 10.1), these horses differ very little, although they are clearly larger than typal *Mathohippus.* In just two pages, Osborn (1904, p. 172-174) named three species: (obliquus), *Mathohippus* metrarhopus* that are nearly identical in size and morphology (Fig. 10.5). We consider these all the same species since all of the differences Osborn cited are very slight and mainly due to intraspecific variation. It is clear that the main reason for his separation of these species is the fact that they come from successively higher stratigraphic levels. The name *obliquus* has already been established in the litera-

ture by Schlegel (1930) and Scott (1974), and has priority over *metrarhopus* and *brachyoerus.* It is therefore the senior syno-

nym of the three.

Schlegel (1930) proposed the name *Palaeohippus antiquus* for part of the Late Orellian horse sample from Harvard Fossil Reserve. He also reported *Mathohippus* antiquus* and Mathohippus antiquus* from this quarry. Forsten (1974) demonstrated that most of the larger horses referred to *Palaeohippus antiquus* could not be distin-

guished from *Mathohippus obliquus,* and the synonym cyt the two species. How-

ever, the species *obliquus* has 31 years' priority over *antiquus,* so it should have been utilized the name *Mathohippus antiquus* rather than the name *Mathohippus antiquus.*

Fig. 10.7. *Mathohippus obliquus.* (A) AMNH 666, type specimen, in palatal view. Right deciduous premolars removed by Morris Skinner to show unruptured permanent premolars. Referred skull, FM 116328, in dorsal (B), right lateral (C), and ventral (D) views. (E) Third molar, FM 74067, showing distinct cuspid facet (arrow). (F) Referred left upper molar, FM 116412. Scale bars in cm.
We do not agree with Forstn that all of the horses from this quarry are one species. At least two individuals are referable to *Miohippus barbouri* (see earlier).

*M. obliquus* is clearly referable to *Miohippus*, since several specimens (e.g., FAM 76097, 76097) consist of partial skeletons that show an articulation between the condyle and third metatarsal (Fig. 10.7B). We consider this articulation a diagnostic feature of *Miohippus*. In addition, most of the Harvard Fossil Reserve horses (here referred to *Miohippus obliquus*) have this articulation. A number of described skulls of *M. obliquus* (such as FAM 116328, 116327, 139526, AMNH 17120) clearly show the typical *Miohippus* facial fossa. Oliver (1906, 1918) diagnosed *obliquus* as lacking a facial fossa, but this is based on the type specimen, in which the facial region is crushed and impossible to interpret.

*Fig. 10.8. Stratigraphic distribution versus size of specimens of *Miohippus*. Symbols as follows: b = type of M. *brachyples*; c = type of M. *calyptraeus*; g = M. *galleyi*; g' = type of M. *galleyi*; i = M. *intermedius*; i' = type of M. *metalephas*; M. *obliquus*; p = M. *sauvagei*; x = type of M. *sulphus*. Shaded areas indicate range of size and stratigraphic variation of M. *sauvagei* (light dots), M. *obliquus* (medium dots), M. *galleyi* (heavy dots) and M. *intermedius* (black). Numbered stratigraphic sampling levels are as follows: 1) near Persistent White Layer, Lusk area, Wyoming (late Chadronian); 2) Lower Nodules, Big Badlands, South Dakota (early Orellian); 3) Harvard Fossil Reserve, near Torrington, Wyoming (middle Orellian); 4) Upper Nodules, Big Badlands, South Dakota (late Orellian); 5) Upper Orellian beds, Big Badlands, South Dakota (early Whitneyan); 6) Leptauchenia beds, Big Badlands, South Dakota (middle Whitneyan); 7) Proteinco beds, Big Badlands, South Dakota (late Whitneyan).

Fig. 10.9. *Miohippus* antonini. FAM 116399, referred specimen, skull in dorsal (A), left lateral (B), and ventral (C) views, (D) articulated ankle with cuboid-M3 III, condyle (arrow), and mandible in dorsal (E) and left lateral (F) views. Scale bars in cm.
The Evolution of Perissodactyls

Clark and Beevor, 1967

Revised Diagnosis, M-1c length = 30.42 mm. Skull longer than Miohippus oblongus, but shorter than that of Miohippus

hyohippus. Hypohippines all class 3. Crochets frequently present. 

Type: NMC 3350, right 2' from the Chadronian of Cypress Hills, Saskatchewan.

Referer Material: Seanam Hills, Noorth Wy. Wyo. FAM: 74077, 74078, 116359, 116358, 116357, 116357, Douglas area, Convexi- 


Horizon and locality: Middle to late Chadronian, Saskatchewan, Wyoming, and North and South Dakota.

Description and discussion: In the Frick Collection, there is a distinctive large lat- 

east Chadronian horse that is known from a nearly complete skeleton (FAM 116359, 

Fig. 10). The unracked skull shows the distinctivc long facial fossa and longer, more oval eris or cross section. The upper incisors are deep set in the crowns, and are oval or cross section. The upper teeth are large relative to the size of the skull (Tables 18, 110). They have well- 

defined hypsids with no molariforms, except on 2' and 3'. The hypohippines are mostly class 3 (Fig. 10.1C), but are much thicker and higher than the hypohippines found in Miohippus easteri. The upper cheek tooth 

lengths are relatively small (Fig. 10.1E, F) of FAM 116359 shows a long, 

principhty incisors. The incisors are spatulate, with flattened upper and lower cheek teeth, the metacynial and metaconid are well separated. The hypocisid on T-3 and M-3 are very prominent.

The postcranial skeleton of FAM 116359 includes an atlas, two cervical vert- 

ebrae, a pelvis, and most of both hind limbs. In some respects, they are identical to Miohippus; except that they are larger than Miohippus oblongus. The characteristic of Miohippus is 

seen in FAM 74077 and other specimens referred to Miohippus asso- 

ciates. In all its preserved features, it is clear that this specimen must be referred to Mi- 

ohippus. Yet this species is known only from the Chadronian, and it occurs in the same 

deposit as three species of Mesotherium, and other hypohippines that are known. 

The oldest of these species is that appears applicable to this horse is Mesotherium asso- 

ciates. Sherman, 1960. It has a very poor specimen, with few diagnostic features. But Russell (1975) described a scapular sample from the Cypress Hill to Mesotherium associates, and this material is a good match in size and morphology (Fig. 10.9) with MAM 116359 and other horses of the same horizon and in morphology such as FAM 74077 compare Russell, 1973, with Tables 10.1, 10.2)

Lamb (1950b, p. 49) described another specimens of M. asso- 

ciates from the same locality, which he called M. nothohippines placentas, because it had a flattened ectoloph. We find that the only preserved ectoloph (M-2) on the type is no more flattened than is characteristic for these horses. Russell (1975, p. 640) considered Mesotherium placentas to be a valid species, or possibly a synonym of Mesotherium assciates. 

Lamb 1950b. The larger hypsids specimens from Cypress Hills include many specimens referred to Mesotherium asso- 

ciates, and the type of the species is a typical Mesohippus placentas. It is a valid character separating the two species, we suggest that the names asso- 

ciates and platelops refer to the same horse. In addition, in this case, the first reviser (Russell, 1975) specifically referred to Mesotherium asso- 

ciates. However, the proposed for the priority of Mes- 

ohippus (Lamb 1950b, p. 50) over the name 

platelops (Lamb 1950b, p. 49), even though the type specimen of asso- 

ciates is not very diagnostic. It appears that the horses 

called Mesotherium asso- 

ciates by Russell (1975) are in fact referable to Miohippus oblongus. 

Clark and Beevor, 1939, 48-49, 

described the species Mesotherium grandis based on some lower jaws from the late Chadronian of the Big Badlands of South Dakota. Since the taxon is known only from lower jaws, the only feature that distinc- 

guishes it from other late Chadronian horses is its unusually large size. However, 

the type and refered specimens of M. grandis, is extremely small, so it is difficult to make a 

final assessment of the variability of horses in the Whitneyan.

Mesotherium intermedius (Osborn and Wortman, 1895) 

Fig. 10.10

Mesotherium intermedius Osborn and Wortman, 1895, p. 354

mesotherium intermedius: Osborn, 1918, p. 54

Palaeohippus intermedius: Schaller, 1935, p. 165

Revised Diagnosis, Mi-1 length = 40.41 mm. Skull slightly longer than Miohippus intermedius. 

Facial fossa much broader and deeper than in Miohippus intermedius. 

Metacynial and metaconid of insectus more distal than in Miohippus intermedius. 

Type: AMNH 1192, a dorsoventrally 

crushed skull, from the Proteroceras channels, Big Badlands of South Dakota (Fig. 10.11-A).

Referer Material: FAM 116418 (55 feet below Upper Whitney Ash, 64 tomato, Pinney Ranch, Goshen Co., Wyoming) (Fig. 10.10-B).

Horizon and locality: Late Whitneyan of South Dakota and Wyoming.

Discussion: Mesotherium intermedius is an intermediate in size between 

Miohippus associates and Mesotherium grandis. Since it occurs with Mesotherium 

gradi and fails on the small end of the size range (Fig. 10.8), it might be synonymized with Mesotherium gradi (in which case asso- 

iates would have priority). However, we feel that the deeper facial fossa, the distinctive primitive metacynials and metaconids of Mesotherium gradi, as well as its slightly wider upper teeth (Table 10.2) warrant separation of the two 

species for the present.

Even with the Frick Collection, the sample of Whitneyan fossil horses is still too small to make a 

final assessment of the variability of horses in the Whitneyan.

Mesotherium intermedius (Osborn, 1904) p. 178

Mesotherium intermedius: Osborn, 1904, p. 177, Mesotherium intermedius: Sinclair, 1925, p. 35

Revised Diagnosis: M-1c length = 42.46 mm. Skull slightly longer than in Miohippus intermedius. 

Facial fossa much broader and deeper than in Miohippus intermedius. 

Metacynial and metaconid of insectus more distal than in Miohippus intermedius. 

Type: AMNH 1192, a dorsoventrally 

crushed skull, from the Proteroceras channels, Big Badlands of South Dakota (Fig. 10.11-A).

Referer Material: FAM 116418 (55 feet below Upper Whitney Ash, 64 tomato, Pinney Ranch, Goshen Co., Wyoming) (Fig. 10.10-B).

Horizon and locality: Late Whitneyan of South Dakota and Wyoming.

Discussion: Mesotherium intermedius is an intermediate in size between 

Miohippus associates and Mesotherium grandis. Since it occurs with Mesotherium 

gradi and fails on the small end of the size range (Fig. 10.8), it might be synonymized with Mesotherium gradi (in which case asso- 

iates would have priority). However, we feel that the deeper facial fossa, the distinctive primitive metacynials and metaconids of Mesotherium gradi, as well as its slightly wider upper teeth (Table 10.2) warrant separation of the two 

species for the present.

Even with the Frick Collection, the sample of Whitneyan fossil horses is still too small to make a 

final assessment of the variability of horses in the Whitneyan.

Mesotherium intermedius (Osborn, 1904) is
Fig. 10.10. (succeeding page) Miohippus intermedius, AMNH 1096, type specimen. Skull in dorsal (A), left lateral (B), and ventral (C) views. Refered specimen, FAM 116417. Crown views of upper (D) and lower (E) teeth. Scale bars in cm.

Fig. 10.11. Miohippus gen. sp., AMNH 2611, type skull in left lateral (A) and ventral (B) views. (C) Miohippus "crassiceps" (neotype). AMNH 5683, type specimen. (D) Miohippus squamiceps. FAM 116421 (upper specimen) compared with type, AMNH 12912 (lower specimen).
have been referred to *Micropius galleyi*. The distinctive features of *Micropius galleyi* based on Osborn's account distinguish it only from *Micropius agassizii* previously described by Osborn, and the species have not been considered to be conspecific. The type of *Micropius galleyi* is a fragment of a lower jaw with four teeth, lacking the upper teeth. The only positive distinguishing feature of *Micropius galleyi* is a groove on the palate which divides the hard palate from the soft palate. However, the feature described by Osborn is not known in any other specimen referred to *Micropius galleyi*, so it is probably due to individual variation or some other factor.

In the opinion of Osborn, it does not justify the separation of *M. galleyi* as a distinct species.

*Micropius agassizii* Marsh, 1874

*Type*. YM 1230, a skull with associated lower teeth, John Day Formation, Oregon.

*Referred material*. AMNH 6960, type locality.

*Description*. *Micropius galleyi* (Osborn, 1918) is a small, lightly built species with distinctive features. The genus *Micropius* is characterized by a large size and a robust skull. The type specimen, YM 1230, is a fragment of a lower jaw with four teeth, lacking the upper teeth. The only positive distinguishing feature of *Micropius galleyi* is a groove on the palate which divides the hard palate from the soft palate. However, the feature described by Osborn is not known in any other specimen referred to *Micropius galleyi*, so it is probably due to individual variation or some other factor.

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*Micropius agassizii* Marsh, 1874

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In the opinion of Osborn, it does not justify the separation of *M. galleyi* as a distinct species.
Fig. 10.12. Hypotheses of relationships of Oligocene horses and their sister-taxon. Characters as the numbered nodes as follows: 1) P4 - sub-rectangular; 2) single-rooted; 2') single-rooted, P1, P4, 2 microchores; 3) P4 with 2 roots; 4) P4, 2 roots; 5) P4 with 3 roots; 6) P4, 3 roots; 7) P4 with 4 roots. The 4-terminal specimen of *Mesantohippus* from the oldest Lagerstätte is not included in this diagram. The *Mesantohippus* specimen from the youngest Lagerstätte is not included in this diagram.

**Patterns of evolution**

Since Husky (1970) and Kowalewsky (1977), horses have been used as one of the classic cases of evolution in the fossil record. The early Eocene lineages connected four successively formed Paleocene to the first appearance of a horse. The best-known lineages in the Eocene are the *Hyrachyus* and *Eohippus* lineages. These lineages are characterized by flattened and elongated nasal bones, reduced size, and a more diverse range of body sizes and habitats.

**Mesantohippus** does not become extinct until the early Oligocene. The two genera overlap by at least four million years.

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The Evolution of Perissodactyls


OLIGOCENE HORSES


