

10. THE EVOLUTION OF OLIGOCENE HORSES

DONALD R. PROTHERO and NEIL SHUBIN

The popular image of Oligocene horses portrays their evolution as a single, orthogenetic lineage grading continuously from *Mesohippus* to *Miohippus*. We find that they are highly speciose, with a "bushy," branched phylogeny that includes at least four valid species of *Mesohippus* (*M. bairdi*, *M. westoni*, *M. exoletus*, *M. barbouri*) overlapping with several species of *Miohippus* (*M. obliquidens*, *M. assiniboensis*, *M. intermedius*, *M. gidleyi*, *M. annectenc*, and ?*M. equinanus*). The two genera are not a continuous intergrading sequence, but instead are marked by a distinctive set of changes in size, dentition, skull and foot 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, and Marsh's 1879 genealogy of American horses were among the first such sequences to lend support to the theory of evolution. Early phylogenies presented the evolution of horses as a single unbranched lineage, but as more information emerged, the phylogeny began to look more branched and "bushy" (Stirton, 1940; Simpson, 1951).

Most horse phylogenies, however, were abstractions based on a few examples from each geological 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 so critical, since to most paleontologists (e.g., Simpson, 1953) horse evolution neatly fit into the prevailing gradualistic neo-Darwinian view. But since the work of Eldredge and Gould (1972), detailed records have become critical in the dispute over the

tempo and mode of speciation. Some authors (e.g., Stanley, 1979) have noticed the "bushiness" of the horse family tree, and the apparent stability of certain taxa (e.g., *Hyracotherium*), and have argued that the horse fossil record supports the punctuational mode of change. Others (e.g., Gingerich, 1980) have interpreted *Hyracotherium* 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 history of *Mesohippus* and *Miohippus*. These 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 fossil horses have excellent stratigraphic documentation for each specimen. The stratigraphic details of the deposits bearing these horses has recently been improved (Prothero, 1982). With the help of magnetostratigraphy, 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 paleontological speciation.

At present, Oligocene horse phylogeny is encumbered by several sources of taxonomic confusion. The early history of horse taxonomy was characterized by extreme typological taxonomic splitting, and "horizontal" taxa that are partially defined by their stratigraphic occurrence. For example, Osborn (1918) distinguished

Mesohippus and *Miohippus* by a stratigraphic boundary, rather than on morphological grounds. Stirton (1940) recorded 20 species of *Mesohippus* and 18 species of *Miohippus*, and did not attempt to synonymize any of them. More recent work (Forstén, 1970a, 1970b) has gone to the other extreme, lumping all species of *Mesohippus* into two species spanning an enormous amount of morphological variability across nearly eight million years. Some workers (e.g., Emry *et al.*, 1987) are not satisfied with this arrangement, either.

The Frick Collection of the AMNH of fossil horses offers an unparalleled opportunity to resolve this dispute. Unlike the samples examined by Forstén, the Frick Collection allows us to place our phylogenetic hypothesis within a finely resolved stratigraphic context. If the diverse morphologies found at the same stratigraphic level by Forstén (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 biostratigraphically, 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, Orellan, and Whitneyan (30-33 Ma). The taxonomy of early and medial Chadronian horses is currently being investigated by Dr. R. J. Emry. 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 satisfactory review of Arikareean horses requires a detailed study of the split between the equine and anchitheriine lineages, which 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.; F:AM,

Frick Collection, AMNH; CM, Carnegie Museum of Natural History, Pittsburgh, Penn.; l.f., local fauna; Ma, million years before present; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; LACM, Los Angeles County Museum of Natural History, Los Angeles, Calif.; NMC, National Museum of Canada, Ottawa; SDSM, South Dakota School of Mines Museum of Geology, Rapid City, S.D.; USNM, United States National Museum, Smithsonian Institution, Washington, D.C.; YPM, Yale Peabody Museum, New Haven, Conn.

Taxonomy and morphology

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Mesohippus Marsh, 1875

Palaeotherium: Leidy, 1850

Anchitherium: Leidy, 1852

Miohippus: Hay, 1902 (in part)

Pediohippus: Schlaikjer, 1935 (in part)

Revised Diagnosis. Small equids (M^{1-3} length = 27-37 mm) with molarized P2/2. I^{1-3} with shallow pitted crowns. Longer face than *Epihippus*, *Orohippus*, or *Hyracotherium*, with extended premaxilla and longer diastema. Angle of jaw posteriorly rounded, without a notch. No contact between the cuboid and third metatarsal. Metacarpal five usually reduced. The genus typically has a very shallow facial fossa.

Type species. *Mesohippus bairdi* (Leidy, 1850).

Included species. *Mesohippus westoni*, *Mesohippus exoletus*, *Mesohippus barbouri*, and several Chadronian species not discussed here.

Distribution. Late Eocene (late Duchesnean, Porvenir l.f., Vieja Group, Texas) to mid-Oligocene (late Orellan, top of the Upper Nodules, Middle *Oreodon* 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.

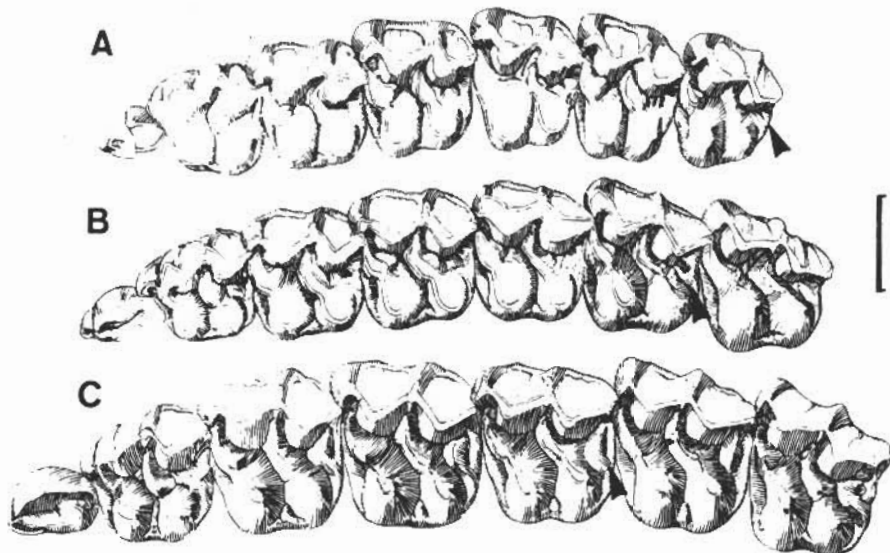


Fig. 10.1. Representative examples of hypostyles in Oligocene horses. Descriptive system modified after Clark and Beerbower (1967, Table 18 key). Type 1 hypostyles (A, *Mesohippus westoni*, F:AM 74023) are thin ridges with almost no cusp or spur projecting anteriorly. Type 2 hypostyles (B, *Mesohippus bairdi*, F:AM 115366) have a small spur projecting anteriorly from the hypostyle ridge on most of the cheek teeth (particularly apparent on P²-M² in this example). Type 3 hypostyles (C, *Miohippus assiniboiensis*, F:AM 116359) have a distinct ovoid or triangular pocket developed between the posterior ridge and the anterior spur of the hypostyle (apparent on P³-M³ in this example). Scale bar = 1 cm.

Discussion. As mentioned in the introduction, the taxonomy of *Mesohippus* has gone from extreme splitting to extreme lumping. Osborn (1904, 1918) named a new species for practically every single variant he encountered in the small collections then available. Many of his "diagnostic features" are impossible to use when the variability of larger samples is considered. In addition, Osborn seldom compared specimens from different stratigraphic levels. For Osborn, each species terminated at a stratigraphic boundary, and stratigraphic position was part of species definition. Virtually no statistical techniques were employed, since biometry was in its infancy in 1918.

Since then, several authors have attempted to analyze larger samples of *Mesohippus*. Clark and Beerbower (1967) established a numerical coding system for various features of the upper teeth, and this system was adopted by Forstén (1970a, 1970b, 1971). We have adopted a similar system, shown in Figure 10.1. Each specimen was encoded for length, width, and five character states for each of the upper cheek teeth. Over 300 skulls, palates, and maxillae have been analyzed. We originally intended to analyze this data matrix by multivariate methods, but such techniques became unnecessary when obvious patterns emerged. Contrary to Forstén (1970a, 1970b), not all the tooth characters

were randomly assorted or useless taxonomically. We found that the condition of the lingual cingulum, hypostyle, metaconule, and occasionally the crochet was quite useful. In addition, we considered other skeletal characters. The Frick Collection of fossil horses contains numerous skulls, and the condition of the facial fossa has proven particularly important in other horses (MacFadden, 1984) and in *Mesohippus* as well. We examined the numerous associated postcranial remains to determine if there were other useful features in the skeleton. We also examined mandibles and lower teeth, but except for size, the lower dentition showed no consistent pattern of diagnostic features. Because only skulls or maxillae with relatively unworn dentitions are identifiable to species, we do not list every *Mesohippus* specimen in the referred material below. The Frick Collection has thousands of specimens of *Mesohippus* and *Miohippus* (particularly lower jaws and postcranials) that cannot be identified to species. Only identifiable material has been cataloged, identified, and listed. We looked for evidence of sexual dimorphism, but found no sign that Oligocene horses show the type of dimorphism found in *Hyracotherium* or many Miocene horses. The completeness and quality of Frick Collection horses has made it possible to reassess the question of how many species of *Mesohippus* are distinct and recognizable.

Mesohippus bairdi (Leidy, 1850)

Fig. 10.1B, 10.2

Palaeotherium bairdii Leidy, 1850, p. 122

Anchitherium bairdii: Leidy, 1852, p. 572

Anchitherium bairdi: Leidy, 1869, p. 303

Mesohippus bairdii: Marsh, 1875, p. 248

Mesohippus bairdii: Osborn and Wortman, 1894, p. 213

Synonym. Mesohippus hypostylus Osborn, 1904, p. 170

Revised Diagnosis. M¹⁻³ length = 30-36 mm. Lingual cusp or partial lingual cingulum on upper premolars and frequently on molars. Hypostyles usually class 2 or class

3 (see Figure 10.1).

Type. USNM 8632, a partial skull, with left M²⁻³, right M¹⁻³, and the posterior half of the cranium. From the head of Bear Creek, Pennington County, South Dakota. Stratigraphic level unknown, but almost certainly Scenic Member of the Brule Formation.

Referred material. LATE CHADRONIAN: Chadron Formation, Big Badlands, S.D.: AMNH 1180 (type specimen of *M. hypostylus*); AMNH 38836; F:AM 74009. Bartlett Ranch, Dawes Co., Neb: F:AM 74036, 116391. Douglas area, Converse Co., Wyo.: F:AM 116378, 116376. Seaman Hills area, Niobrara Co., Wyo.: F:AM 116330, 74060, 74025, 74034, 74029, 74026, 116370, 11636, 11636, 116366, 74033, 74028.

EARLY ORELLAN: Lower Nodules, Lower Scenic Member, Big Badlands, S.D.: AMNH 39131, 39133, 38857, 39030, 38936, 39005, 38855, 38935, 39004, 1188, 9769, 39447, 11864; F:AM 74006, 74004, 74003, 74010, 74014, 74043, 116404, 11639, 74008. Little Badlands, Stark Co., N.D.: F:AM 74040. Geike Ranch, Sioux Co., Neb.: F:AM 7403, 74035. Munson Ranch, Sioux Co., Neb.: F:AM 116390, 116388, 116364, 74039.

LATE ORELLAN: Top of Upper Nodules, Middle *Oreodon* Beds, Big Badlands, S.D.: F:AM 74013, 116403, 116397, 116396, 74044.

Horizon and localities. Late Chadronian to late Orellan, North and South Dakota, Nebraska, Wyoming, and Colorado.

Discussion. The most common horse in the White River Group is *Mesohippus bairdi*. Although the type specimen (Figure 10.2) is very poorly preserved, it clearly shows upper molars with slight lingual cingula and with class 2 hypostyles. Some specimens of *Mesohippus bairdi* show a few hypostyles of class 3. Occasionally (Forstén, 1970a, 1970b), crochets appear on the upper teeth, but they are extremely rare. The facial fossa is well displayed on many skulls, and shows the typical *Mesohippus* condition. Scott (1941) gave a thorough description of *Mesohippus bairdi*, so no further description is needed here. We

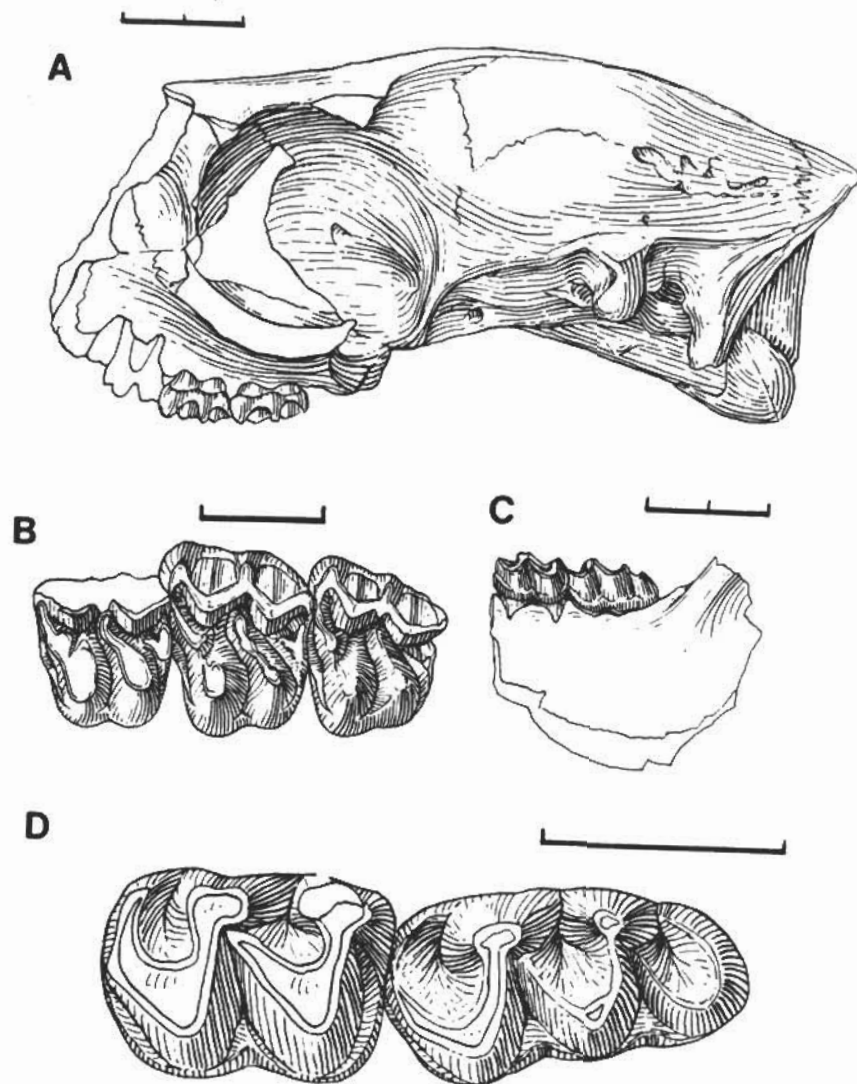


Fig. 10.2. *Mesohippus bairdi*, USNM 8632, type specimen of genus and species, in (A) left lateral view; (B) left M¹⁻³; (C) lower jaw fragment with M₂₋₃; (D) crown view of M₂₋₃. Scale bars in cm.

consider *Mesohippus hypostylus* to be a junior synonym of *Mesohippus bairdi*. In size (Tables 10.1, 10.2) it lies completely within the range of variation of *Mesohippus bairdi*, and the type of *Mesohippus hypostylus* (AMNH 1180) comes from deposits that also contain *Mesohippus bairdi*.

Osborn (1904, 1918) distinguished *Mesohippus hypostylus* from *Mesohippus bairdi* as follows: "Distinguished . . . from *Mesohippus bairdii* by more rudimentary hypostyle and less elevated crests. Metalph sharp; metaconule not defined at base. P¹ small. Skull with pre-orbital fossa apparently deeper than in *Mesohippus bairdii*."

Of these features, none appears to be valid. The hypostyles on AMNH 1180 are all class 2, as is seen on the type specimen of *Mesohippus bairdi*. Their condition is not more "rudimentary," since both the type and most of the referred material have this kind of hypostyle. The elevation of the crests is highly variable and not taxonomically significant. The metaconules of *Mesohippus hypostylus* and *Mesohippus bairdi* are typically class 2 on P²⁻³, class 3 on P⁴ and M¹⁻³. The condition of the facial fossa on AMNH 1180 is difficult to judge, since the specimen has been dorsoventrally crushed. However, judging from most referred skulls, the condition of the fossa in *Mesohippus hypostylus* and *Mesohippus bairdi* is identical. Thus, *Mesohippus hypostylus* is clearly a junior subjective synonym of *Mesohippus bairdi*.

Clark and Beerbower (1967) referred most of the mid-sized Chadronian horses to *Mesohippus hypostylus*. We suspect that many of these specimens are referable to *Mesohippus bairdi*, but that others are referable to other species. Forstén (1970a, 1970b) placed *Mesohippus hypostylus* in synonymy with *Mesohippus bairdi*. We agree, although for different reasons than she gave.

Mesohippus westoni (Cope, 1889)
Fig. 10.1A, 10.3

Anchitherium westoni Cope, 1889, p. 3
Mesohippus westoni: Osborn 1904, p. 169
Mesohippus westoni: Lambe 1905a, p. 243
Mesohippus westonii: Russell 1975, p. 637

Synonym. *Mesohippus montanensis* Osborn, 1904

Revised Diagnosis. M¹⁻³ length = 30-36 mm. Lingual cingula or circular cusps on upper cheek teeth are very faint or absent. Hypostyles usually absent or class 1, rarely class 2. No crochets.

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

Referred material. MIDDLE CHADRONIAN: Pipestone Springs, Jefferson Co., Montana: AMNH 9662 (type specimen of *M. montanensis*); AMNH 9663.

LATE CHADRONIAN: Chadron area, Dawes Co., Neb.: F:AM 74055, 74048, 116342, 116336. Douglas area, Converse Co., Wyo.: F:AM 116375, 116380, 116334. Seaman Hills, Niobrara Co., Wyo.: F:AM 111744, 74057, 74058, 74059, 74063, 74054, 74053, 74045, 116386, 116374, 116372, 116365, 116341, 116340, 116339, 116338, 116337, 116335, 74052.

EARLY ORELLAN: Lower Nodules, Scenic Member, Big Badlands, S.D.: F:AM 74020, 116348, 116345, 116344, 74023, 74046. Munson Ranch, Sioux Co., Neb.: F:AM 74039.

LATE ORELLAN: Upper Nodules, Middle Oreodon beds, Big Badlands, S.D.: F:AM 116350, 116347, 116346, 116343.

Horizon and locality. The type is from the early Chadronian Cypress Hills fauna, Saskatchewan. Referred material from many other Chadronian localities, and from early to late Orellan localities in Wyoming, Nebraska, and South Dakota.

Discussion. *Mesohippus westoni* is easily distinguished from similar-sized *Mesohippus bairdi* by the absence of lingual cingula and by its rudimentary hypostyles. It is distinguished from *Mesohippus celer* by its slightly larger size and larger M³. The type of *Mesohippus westoni* is very poor, and normally the name would be considered indeterminate. However, Russell (1975) described additional

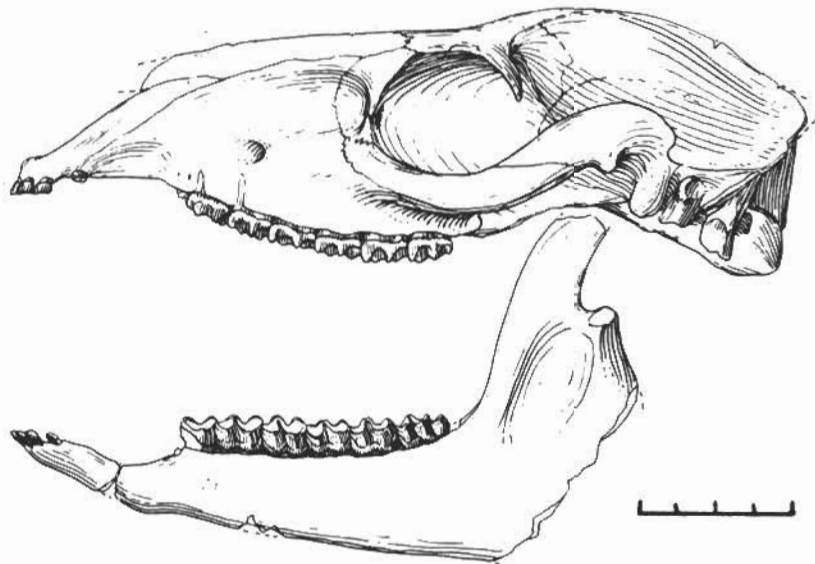


Fig. 10.3. *Mesohippus westoni*, F:AM 74023. Referred skull and mandible in left lateral view. Scale bar in cm.

topotypic material of *Mesohippus westoni* from Cypress Hills that clearly establishes the morphology of this species. As Lambe (1908) and Russell (1975) pointed out, the two diagnostic features of *Mesohippus westoni* (vestigial lingual cingulum and rudimentary hypostyle) are features that are true of Osborn's species *M. montanensis* from Pipestone Springs. The specimens referred to *M. westoni* 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 *westoni* is the senior synonym for Chadronian-Orellan *Mesohippus* larger than *M. celer* with rudimentary hypostyles, and faint or absent

lingual cingula.

Osborn (1904, p. 40) distinguished *M. montanensis* from *M. westoni* by "sharp elevation of crests and absence of internal cingulum." Now that larger samples are known, these species cannot be distinguished by these features. The shape of molar crests is highly variable and greatly affected by wear. The lingual cingulum on the type of *Mesohippus westoni* is a little stronger than on the type of *Mesohippus montanensis*, but Russell (1975) has shown that there is some variation in this feature in topotypic samples of *Mesohippus westoni*. We have seen similar variation in the strength of the lingual cingulum in Frick Collection samples from the later Chadronian and Orellan. There appears to be no grounds for distinguishing *Mesohippus montanensis* Osborn, 1904, and it is here considered a junior synonym of *Mesohippus westoni* (Cope, 1889).

Clark and Beerbower (1967, p. 48) considered *Mesohippus montanensis* a junior synonym of *Mesohippus hypostylus* and Forstén (1970b) considered it a junior synonym of *Mesohippus bairdi*. As shown previously, *Mesohippus hypostylus* cannot be distinguished from *Mesohippus bairdi*, but *Mesohippus montanensis* (= *westoni*) can. Although the two species intergrade very slightly, there does appear to be a separation between horses with no lingual cingula and rudimentary hypostyles (*Mesohippus westoni*) and horses with stronger lingual cingula and well-developed hypostyles (*Mesohippus bairdi*). The two groups can be readily identified with well-preserved upper dentitions; they are not indistinguishable, as implied by Forstén (1970a, 1970b).

Other characters of these two species vary randomly, but the two characters discussed above are clearly associated. *M. westoni* and *M. bairdi* are diagnosable 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 *Mesohippus westoni*, yet coeval deposits in the High Plains contain both species. Cypress Hills contains *Mesohippus westoni* but no *Mesohippus bairdi*. Both species appear to become extinct at the end of the Orellan (top of the Middle Oreodon Beds), although Whitneyan collections are so sparse that their ranges may extend into younger deposits.

Mesohippus exoletus (Cope, 1874)

Fig. 10.4

Anchitherium exoletum Cope, 1874, p. 496

Mesohippus exoletus: Osborn, 1918, p. 47

Synonyms. *Mesohippus trigonostylus*

Osborn, 1918, pp. 47-48; *Pedohippus trigonostylus* Schlaikjer, 1935, p. 141.

Revised Diagnosis. M¹⁻³ length = 32-36 mm. Lingual cingula on nearly all upper cheek teeth. Hypostyles 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, tibia, 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.: F:AM 116351. Seaman Hills, Niobrara Co., Wyo.: F:AM 116356.

EARLY ORELLAN: Lower Nodules, Scenic Member, Big Badlands, S.D.: AMNH 674 (type of *M. trigonostylus*, *Metamynodon* beds); F:AM 74016, 116353, 74001; AMNH 39149. Little Badlands, Stark Co., N.D.: F:AM 116406, 116354. Munson Ranch, Sioux Co., Neb.: F:AM 116389.

LATE ORELLAN: Upper Nodules, Middle Oreodon Beds, Big Badlands, S.D.: F:AM 74019, 116402, 116401, 116393, 116394, 116395, 116400, 116358, 11635, 116355, 116352. Fitterer Ranch, Stark Co., N.D.: F:AM 116405.

Horizon and localities. Known from the late Chadronian to late Orellan (top of Middle Oreodon beds), in Colorado, Wyoming, Nebraska, South and North Dakota.

Discussion. Osborn (1918, p. 47) reported the type of *Anchitherium exoletum* lost, and this was cited by Scott in 1941. Since Cope's description was inadequate and the specimen was not figured, Osborn considered the species *exoletus* to be indeterminate. Since 1941, however, the type of *M. exoletus* (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 hypostyles so characteristic of *Mesohippus trigonostylus*. In size (Table 10.2), AMNH 6298 also falls within the *M. trigonostylus* population. *M. exoletus* appears to be the a senior

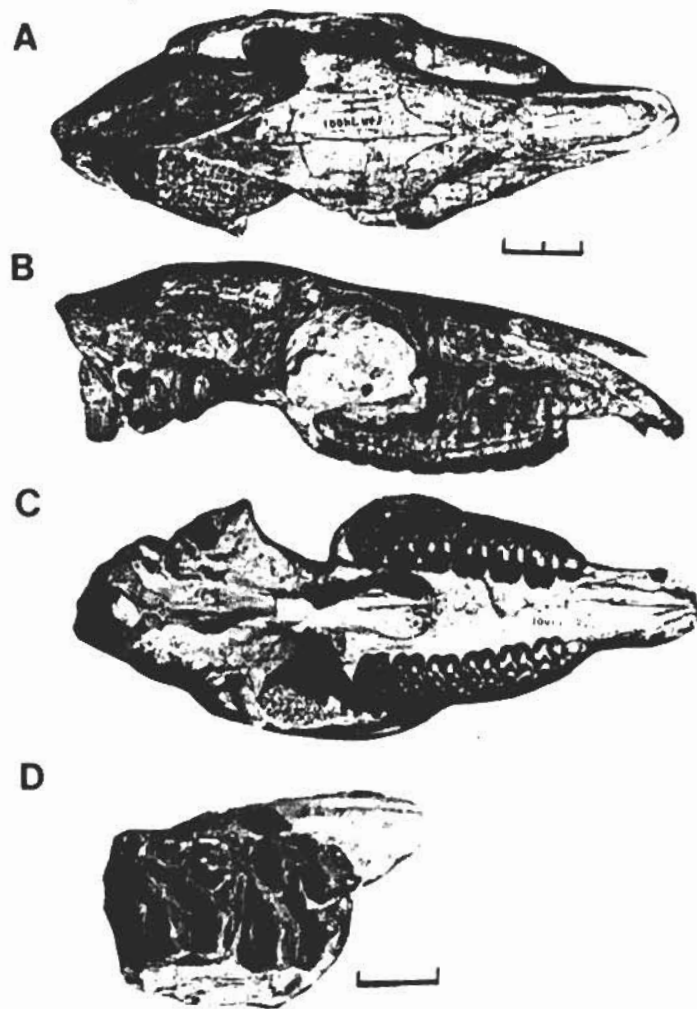


Fig. 10.4. *Mesohippus exoletus*. F:AM 74001, referred skull in (A) dorsal, (B) right lateral, and (C) ventral views. (D) AMNH 6298, type specimen. Scale bars in cm.

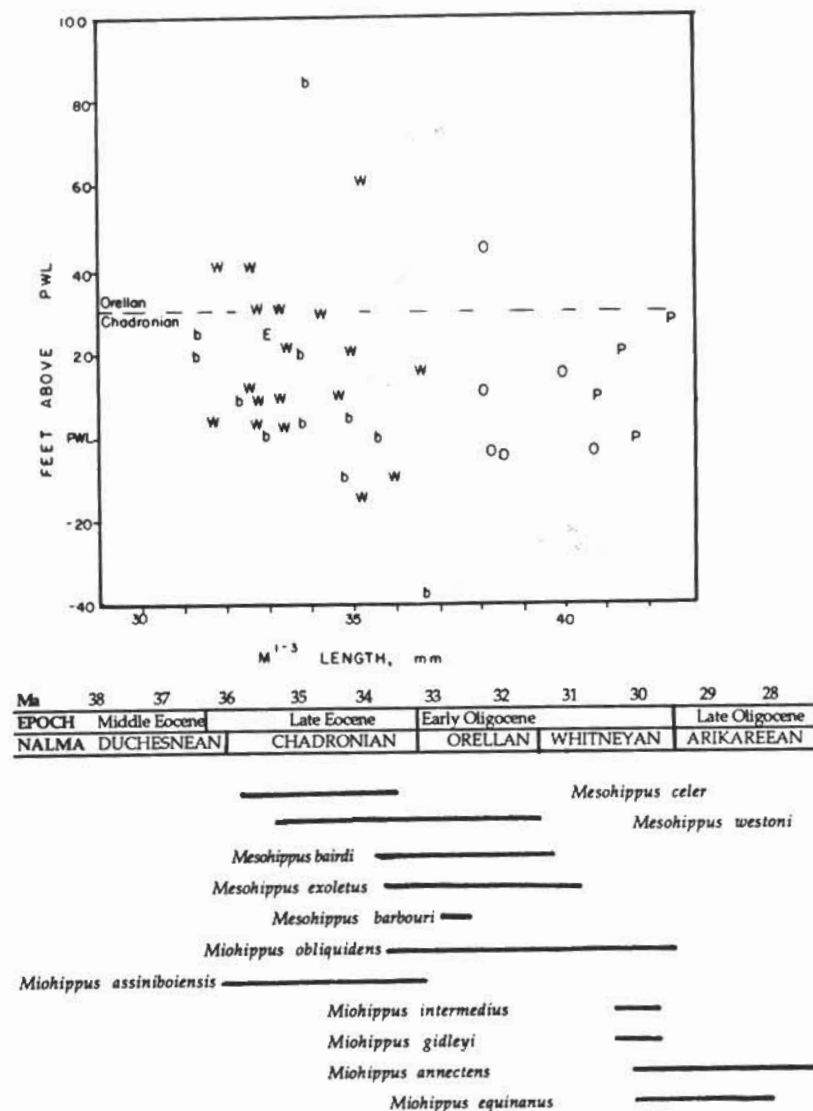


Fig. 10.5A. (top) Stratigraphic distribution versus size of horse specimens from the late Chadronian-early Orellan deposits in the Seaman Hills, near Lusk, Wyoming. Symbols as follows: b = *Mesohippus bairdi*; e = *Mesohippus exoletus*; o = *Miohippus obliquidens*; p = *Miohippus assinibiensis*; w = *Mesohippus westoni*. All five species occur at a level about 20 feet below the Persistent White Layer (PWL). Fig. 10.5B (bottom). Temporal ranges of the equid species discussed in this chapter. NALMA = North American land mammal "age." Timescale is recalibrated to reflect new dates and correlations of the North American sections (see Chapter 28).

subjective synonym of *M. trigonostylus*.

Mesohippus exoletus can be distinguished from *Mesohippus bairdi* and *Mesohippus westoni* in its slightly larger size and especially by its distinctive class 3 triangular hypostyles on all upper cheek teeth. In all remaining skull, jaw, and skeletal features, *Mesohippus exoletus* and *Mesohippus bairdi* are very similar.

In the later Orellan, *Mesohippus exoletus* is generally more abundant than other species of *Mesohippus*. *M. exoletus* occurs with *M. bairdi* and *M. westoni* in deposits near the Chadronian-Orellan boundary as well, although in much smaller numbers (Fig. 10.5A).

Some may object to designating three similar-sized species of *Mesohippus* (plus two of *Miohippus*) from the same deposits (e.g., the Lusk area 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 speciose. Many localities in the Miocene have four or five species of closely related horses, and a few quarries have over a dozen. For example, Skinner and Johnson (1984, p. 276) report eight genera of horses in Railway Quarry A of the Valentine Formation, and 12 species were reported by Schultz (1977) from the Clarendonian of Texas. Even today, two or more species of zebra can be found together in East Africa. Morphologically, these *Mesohippus* species can be unambiguously distinguished, and have distinctive stratigraphic and geographic ranges. If 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. Instead, we find three distinct clusters of morphology. These clusters have clear biostratigraphic and biogeographic definition and utility. We cannot agree with Forstén (1970a, 1970b), who places all

medium-sized *Mesohippus* from the Orellan in a single species.

Mesohippus barbouri Schlaikjer, 1931
Fig. 10.6

Miohippus antiquus: Forstén, 1974 (in part)

Revised Diagnosis. M¹⁻³ length = 34-36 mm. Metaconules reduced. No lingual cingula. Unusually short rostrum and pinched diastema, causing a flaring symphysis. Upper incisors circular and deeply cupped. Humerus and femur relatively short with respect to metapodial length.

Type. MCZ 17641, a complete skeleton, from the late Orellan of the Big Badlands, South Dakota.

Referred material. EARLY ORELLAN: Lower Nodules, Scenic Member, Big Badlands, S.D.: F:AM 116324, 116325, 74074. Harvard Fossil Reserve, Goshen Co., Wyo.: MCZ 2781, 2792.

LATE ORELLAN: Upper Nodules, Middle Oreodon Beds, Big Badlands, S.D.: F:AM 116322, 116323.

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

Description and discussion. *Mesohippus barbouri* was thoroughly described by Schlaikjer (1932). It is a very distinctive horse, with a peculiarly short face and unusually rounded, deeply cupped incisors (Fig. 10.6A-C). The upper incisors of most primitive horses are more oval in cross-section, and have only shallow pits on the crowns.

Schlaikjer (1935) referred some specimens from Harvard Fossil Reserve, Goshen County, Wyoming, to *Mesohippus barbouri*. Forstén (1974) placed these specimens in *Miohippus antiquus*. However, the two smaller specimens from Harvard Fossil Reserve (MCZ 2781 and MCZ 2792) are clearly within the size range of *Mesohippus barbouri*, and too small for *Miohippus obliquidens*, which is the most common horse from this quarry. The ratio of dental specimens of *Mesohippus barbouri* to *Miohippus obliquidens* in this quarry is 2:10. Interestingly, Forstén (1974) reported that the

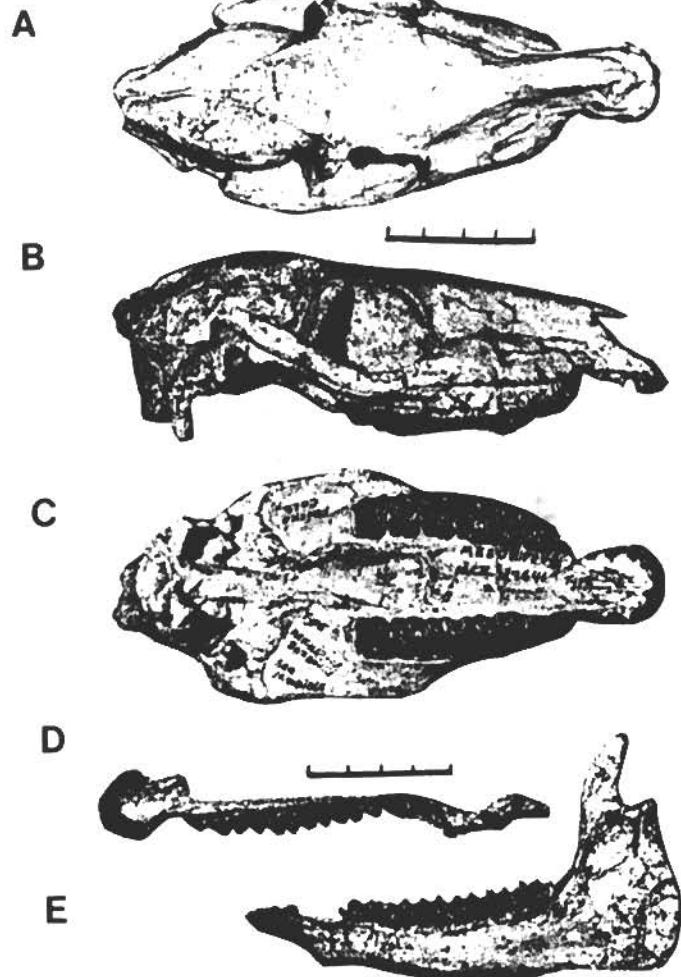


Fig. 10.6. *Mesohippus barbouri*, MCZ 17641, type skull in dorsal (A), right lateral (B), and ventral (C) views; type mandible in crown (D) and left lateral (E) views. Scale bars in cm.

ratio of metatarsals III without a cuboid facet (the *Mesohippus* condition) to those with a cuboid facet (the *Miohippus* condition) is 2:9. Thus, we would associate these two metatarsals III without cuboid facets with the dentitions that can be referred to *Mesohippus barbouri*.

Miohippus Marsh, 1874

Anchitherium: Leidy, 1870, p. 113

Miohippus Marsh, 1874, p. 249

Mesohippus: Osborn, 1904, p. 177 (in part)

Pediohippus: Schlaikjer, 1935, p. 141

Revised Diagnosis. Small to medium sized equids (M^{1-3} length = 34-50 mm) with a slightly longer skull than *Mesohippus*, large, well developed hypostyles (usually class 3), and a deeper, more anteriorly expanded facial fossa. Facet between the third metatarsal and cuboid.

Type species. *Miohippus annectens* Marsh, 1874.

Included species. *Miohippus obliquidens*, *Miohippus assiniboensis*, *Miohippus intermedius*, *Miohippus gidleyi*, ?*Miohippus equinanus*, and a number of exclusively Arikareean species not discussed here.

Distribution. Mid-Chadronian (Cypress Hills) to Arikareean of Saskatchewan, Montana, Oregon, Wyoming, Nebraska, Colorado, and North and South Dakota.

Discussion. The distinction between *Mesohippus* and *Miohippus* has always been controversial. Marsh (1874) created the taxon *Miohippus* for horses from the Arikareean John Day beds of Oregon. Osborn (1918) made the genus a strictly horizontal taxon for all horses from the late Whitneyan through most of the Arikareean. Osborn's diagnosis of *Miohippus* 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 hypostyles, the longer face, and the deeper facial fossa are all characters that distinguish *Miohippus* from *Mesohippus*. The cuboid-third metatarsal articulation in particular has served

as a useful derived feature signaling the appearance of *Miohippus*, since this character is a result of the broadening of the third metatarsal with increased monodactyly.

Schlaikjer (1935, p. 141) created a new genus *Pediohippus* for a number of *Miohippus* specimens which had rudimentary crochets on the upper cheek teeth. Scott (1941) adopted Schlaikjer's generic taxonomy. Forstén (1974) synonymized *Pediohippus* with *Miohippus* by showing that the crochet was a highly variable feature within populations, and not taxonomically useful. Our studies confirm this conclusion. Although weak crochets occasionally occur in *Miohippus*, they are irregularly developed on adjacent teeth, and sometimes are not even symmetrically developed on both sides of the same skull. The presence of crochets alone is not diagnostic, let alone sufficient justification of a new genus.

Stirton (1940) considered *Pediohippus* to be a junior synonym of *Miohippus*. Stirton (1940) and Simpson (1951) thought that *Mesohippus* and *Miohippus* intergraded in the Orellan. Lillegraven (1970) expressed doubt that *Mesohippus* and *Miohippus* could be distinguished at all. However, in our examination of the Frick Collection of fossil horses, a clear distinction between the two genera became apparent. *Miohippus* is a significantly larger horse, with a longer face. Its facial fossa is deepest just anterior to the orbit and tapers anteriorly, becoming shallower toward the rostrum. The fossa terminates at about the level of P^2 . There is almost no overlap or intergradation between these two morphologies, yet they overlap considerably in temporal range (Fig. 10.5B).

All *Miohippus* specimens that have associated tarsals clearly show the cuboid-metatarsal III articulation. This is never seen in *Mesohippus*. The definition of *Miohippus* is unambiguous. This genus now includes a number of derived but early horses that had previously been referred to *Mesohippus* on purely stratigraphic grounds.

Table 10.1. Skull and mandible measurements (in mm)

	I^1-M^3	Pmax-Occip.	W. zyg.	Pmax-Anter. Orbit	Ant. orb.-Occ.	Occip. W.	Occip. Ht.	Jaw Depth at P_2	Jaw Depth at M_3	I_1 -Angle
<i>M. bairdi</i> (type) USNM 8632					111	59	47			
<i>M. bairdi</i> AMNH 1477	108	200	85	105	93	56	46	19	32	
<i>M. bairdi</i> AMNH 1492	106	178	81	102	84	54	44	18	25	
<i>M. bairdi</i> F:AM 74029	110	176	75	92	111			21	31	152
<i>M. westoni</i> F:AM 74052	109	178	75	97	96	57	46	18	30	149
<i>M. westoni</i> F:AM 74063	114	184		93	104		49	18	29	156
<i>M. exoletus</i> F:AM 7400	107	175	79	87	102	55	49			
<i>M. barbouri</i> (type) MCZ 17451	111	182	85	90	101	50	47	28	39	149
<i>M. barbouri</i> F:AM 116325	111	171	83	81	99	38	39	16	30	158
<i>M. obliquidens</i> (type) AMNH 668					108		46	21	27	148
<i>M. obliquidens</i> (type of <i>ofmeteuolophus</i>) AMNH 1210	118	205		110	117	59	54	20	28	163
<i>M. assiniboensis</i> F:AM 116359	132	199		106	108	69	55	17	28	170
<i>M. assiniboensis</i> F:AM 116361	119	192	81	98	111		50	17	29	161
<i>M. intermedius</i> (type) AMNH 1196	140	220	98	114	124	68	55	17	28	170
<i>M. gidleyi</i> (type) AMNH 1192					88	55				
<i>M. gidleyi</i> (type of <i>validus</i>) AMNH 680	135	229	96	120	122	72	63			
<i>M. annectens</i> (type) YPM 12230	165	208	114	151	154	72	67			

Table 10.4. Postcranial measurements (in mm)

	<i>M. bairdi</i> AMNH 1477	<i>M. bairdi</i> AMNH 1492	<i>M. bairdi</i> F:AM 74026	<i>M. westoni</i> F:AM 74052	<i>M. westoni</i> F:AM 74063	<i>M. exoletus</i> F:AM 74001
Atlas length	37	33	35	36		35
Atlas width	36		36	36		36
L. axis centrum	51	42				
Axis width	32	26				
Scapula length	142	131	148		142	
Scapula width	99	83	78		66	
Length humerus	130	117	129	116	129	131
Humerus prox W	38	25	34		30	36
Humerus dist W	30	26	32		28	27
Radius length	146	128	133	119	134	32
Radius prox W	26	23	23		24	25
Ulna length			134			134
McII length	84	73	79			88
McII width	10		9			9
McIII length	85	78	81	97		91
McIII width	14		13	10		11
McIV length	77	68	76			84
McIV width	11		8			10
Femur length		157	196		179	177
Femur prox W	51			39		45
Femur dist W	39	35	31		34	39
Tibia length	197	170	205	177	189	187
Tibia prox W	40	34	35	33	37	38
Tibia dist W	28	24	26	21	23	25
Astragalus L	22		24	22	27	23
Astragalus W	21	21	19	18	18	20
Calcaneum L	54	45	50	45	53	51
Calcaneum W	21	18	23	23	22	24
MtII length	105	85	100		103	106
MtII width	12		8		10	11
MtIII length	109	94	109	99	111	112
MtIII width	12		10		13	14
MtIV length	106	86		94	105	
MtIV width	12			8	9	

Table 10.4 (continued).

	<i>M. barbouri</i> MCZ 17641	<i>M. obliquidens</i> F:AM 74066	<i>M. obliquidens</i> F:AM 74067	<i>M. assiniboensis</i> F:AM 116359	<i>M. assiniboensis</i> F:AM 74077	<i>M. gidleyi</i> AMNH 1218
Atlas length					39	
Atlas width					41	
L. axis centrum						
Axis width						
Scapula length	134	135			156	
Scapula width		92			92	
Length humerus	117					163
Humerus prox W						
Humerus dist W	24				32	44
Radius length	130	134		131		
Radius prox W	25	22		26		32
Ulna length				134		
McII length	96			90		89
McII width				9		9
McIII length	102			93		96
McIII width	12			12		12
McIV length	91			82		91
McIV width				9		10
Femur length	157	173		183		188
Femur prox W	33			42		54
Femur dist W		32		38		38
Tibia length	182	187		183		208
Tibia prox W		29		38		41
Tibia dist W		22		25		26
Astragalus L				25		25
Astragalus W				19		22
Calcaneum L		46		53		59
Calcaneum W		23		26		23
MtII length	113			101		109
MtII width				9		6
MtIII length	117	102		110		115
MtIII width	15	12		15		6
MtIV length	109			103		98
MtIV width				8		9

Miohippus obliquidens (Osborn, 1904)
new combination
Fig. 10.7

Mesohippus obliquidens Osborn, 1904, p. 173

Synonymy. *Mesohippus eulophus* Osborn, 1904, p. 173; *Mesohippus meteulophus* Osborn, 1904, p. 174 (= *Miohippus meteulophus* Osborn, 1918, p. 51); *Pediohippus antiquus* Schlaikjer 1935, p. 141 (= *Miohippus antiquus* Forstén, 1971, p. 404); *Mesohippus brachystylus* Osborn, 1918, p. 53 (= *Pediohippus brachystylus* Schlaikjer, 1935, p. 144).

Revised Diagnosis. M¹⁻³ length = 34-39 mm. Molar crests complete with metaconules weak or absent. Molar crests more obliquely oriented than in any other species (Fig. 10.7F).

Type. AMNH 668, a badly crushed juvenile skull, with DP²⁻⁴ and M¹⁻², and both lower rami (Fig. 10.7A). DP²⁻⁴ have been prepared away by Morris Skinner, revealing permanent P³⁻⁴. From the late Orellan (middle *Oreodon* beds) of the Big Badlands, South Dakota.

Referred material. LATE CHADRONIAN: Chadron Formation, Big Badlands, S.D.: F:AM 116329. Chadron area, Dawes Co., Neb.: F:AM 74073, 74047, 74067. Douglas area, Converse Co., Wyo.: F:AM 74076, 74072, 116383, 116381, 116377, 17597, 116326, 116327, 116328. Seaman Hills, Niobrara Co., Wyo.: F:AM 74071, 74064, 74066, 116412, 116387, 116384, 116368, 116333.

EARLY ORELLAN: Lower Nodules, Scenic Member, Big Badlands, S.D.: F:AM 74021; AMNH12290, 39115. Harvard Fossil Reserve, Goshen Co., Wyo.: MCZ 2790 (holotype of *P. antiquus*); MCZ 2791, MCZ 2942 (*P. antiquus* paratypes), MCZ 2789, 2785, 2788, 2783, 2786, 2779, 2782.

LATE ORELLAN: Fitterer Ranch, Stark Co., N.D.: F:AM 116408. Upper nodules, Middle Oreodon beds, Big Badlands, S.D.: F:AM 116398, 116392.

EARLY WHITNEYAN: Upper *Oreodon*

beds, Big Badlands, S.D.: F:AM 116363. Vista Member, Cedar Creek area, Weld Co., Colo.: AMNH 8791 (type of *M. eulophus*).

LATE WHITNEYAN: *Leptauchenia* nodules, Big Badlands, S.D.: AMNH 1210 (type of *M. meteulophus*); AMNH 11860 (type of *M. brachystylus*); AMNH 1043; F:AM 116409. Rainey Butte, Slope Co., N.D.: AMNH 12846.

Horizon and localities. Late Chadronian to late Whitneyan, Wyoming, Colorado, South and North Dakota, and Nebraska.

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 typical *Mesohippus*. In just two pages, Osborn (1904, p. 173-174) named three species (*obliquidens*, *eulophus*, *meteulophus*) that are nearly identical in size and morphology (Fig. 10.8). We consider them 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 *obliquidens* has already been established in the literature by Schlaikjer (1935) and Scott (1941), and has priority over *eulophus* and *meteulophus*. It is therefore the senior synonym of the three.

Schlaikjer (1935) proposed the name *Pediohippus antiquus* for part of the late Orellan horse sample from Harvard Fossil Reserve. He also reported *Mesohippus obliquidens* and *Mesohippus barbouri* from this quarry. Forstén (1974) demonstrated that most of the larger horses referred to *Pediohippus antiquus* could not be distinguished from *Miohippus obliquidens*, and she synonymized the two species. However, the species *obliquidens* has 31 years' priority over *antiquus*, so she should have utilized the name *Miohippus obliquidens* rather than the name *Miohippus antiquus*.

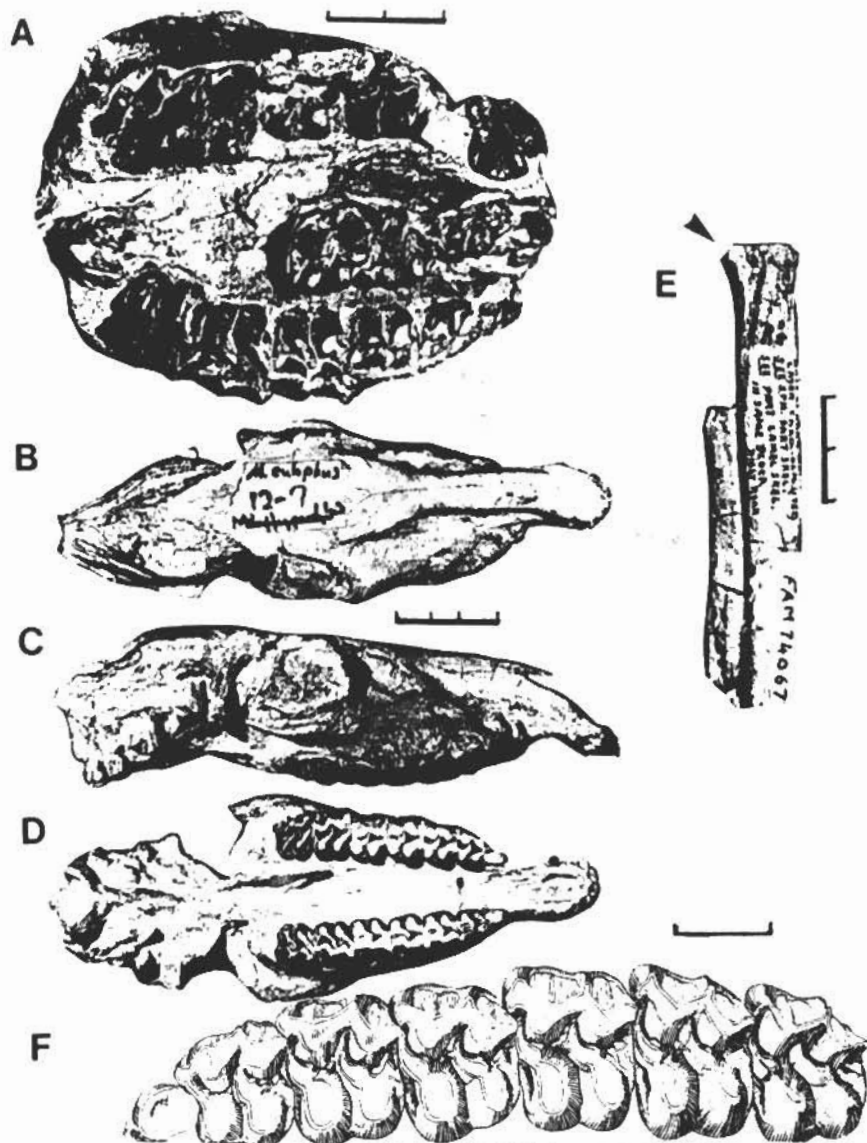


Fig. 10.7. *Miohippus obliquidens*. (A) AMNH 668, type specimen, in palatal view. Right deciduous premolars removed by Morris Skinner to show unerupted permanent premolars not previously illustrated. Referred skull, F:AM 116328, in dorsal (B), right lateral (C), and ventral (D) views. (E) Third metatarsal, F:AM 74067, showing distinct cuboid facet (arrow). (F) Referred left upper dentition, F:AM 116412. Scale bars in cm.

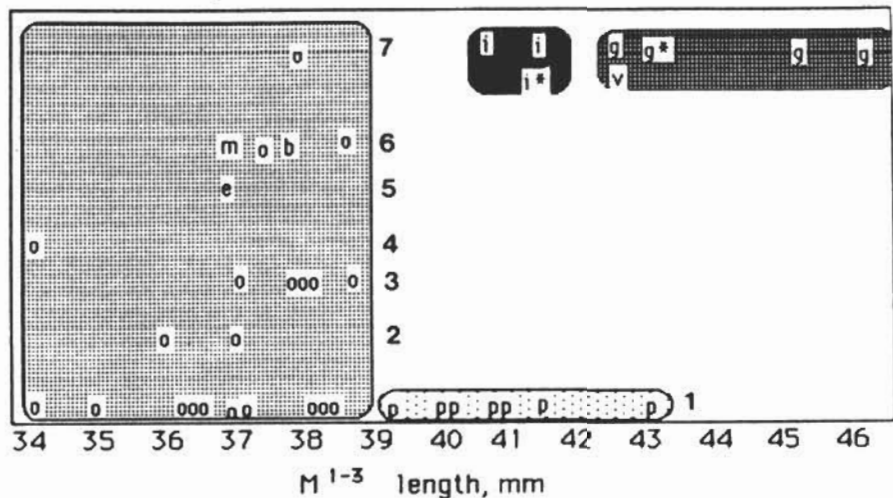


Fig. 10.8. Stratigraphic distribution versus size of specimens of *Miohippus*. Symbols as follows: b = type of *M. "brachystylus"*; e = type of *M. "eulophus"*; g = *M. gidleyi*; g* = type of *M. gidleyi*; i = *M. intermedius*; i* = type of *M. intermedius*; m = type of *M. "meteulophus"*; o = *M. obliquidens*; p = *M. assiniboensis*; v = type of *M. "validus."* Shaded areas indicate range of size and stratigraphic variation of *M. assiniboensis* (light dots), *M. obliquidens* (medium dots), *M. gidleyi* (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 Orellan); 3) Harvard Fossil Reserve, near Torrington, Wyoming (middle Orellan); 4) Upper Nodules, Big Badlands, South Dakota (late Orellan); 5) Upper *Oreodon* beds, Big Badlands, South Dakota (early Whitneyan); 6) *Leptauchenia* beds, Big Badlands, South Dakota (middle Whitneyan); 7) *Protoceras* beds, Big Badlands, South Dakota (late Whitneyan).

We do not agree with Forstén that all of the horses from this quarry are one species. At least two individuals are referable to *Mesohippus barbouri* (see earlier).

M. obliquidens is clearly referable to *Miohippus*, since several specimens (e.g., F:AM 74047, 74067) consist of partial skeletons that show an articulation between the cuboid and third metatarsal (Fig. 10.7E). We consider this articulation a diagnostic feature of *Miohippus*. In addition, most of the Harvard Fossil Reserve horses (here referred to *Miohippus obliquidens*) have this articulation. A number of uncrushed skulls of *M. obliquidens* (such as F:AM 116328, 116327, 116326, AMNH 1210)

clearly show the typical *Miohippus* facial fossa. Osborn (1904, 1918) diagnosed *obliquidens* as lacking a facial fossa, but this is based on the type specimen, in which the facial region is crushed and impossible to interpret.

Miohippus assiniboensis (Lambe, 1905b),
new combination
Figs. 10.1C, 10.9

Mesohippus assiniboensis Lambe, 1905b, p. 50.

Mesohippus assiniboensis: Russell, 1975
Synonyms. Mesohippus planidens
Lambe, 1905b, p. 49; *Mesohippus grandis*

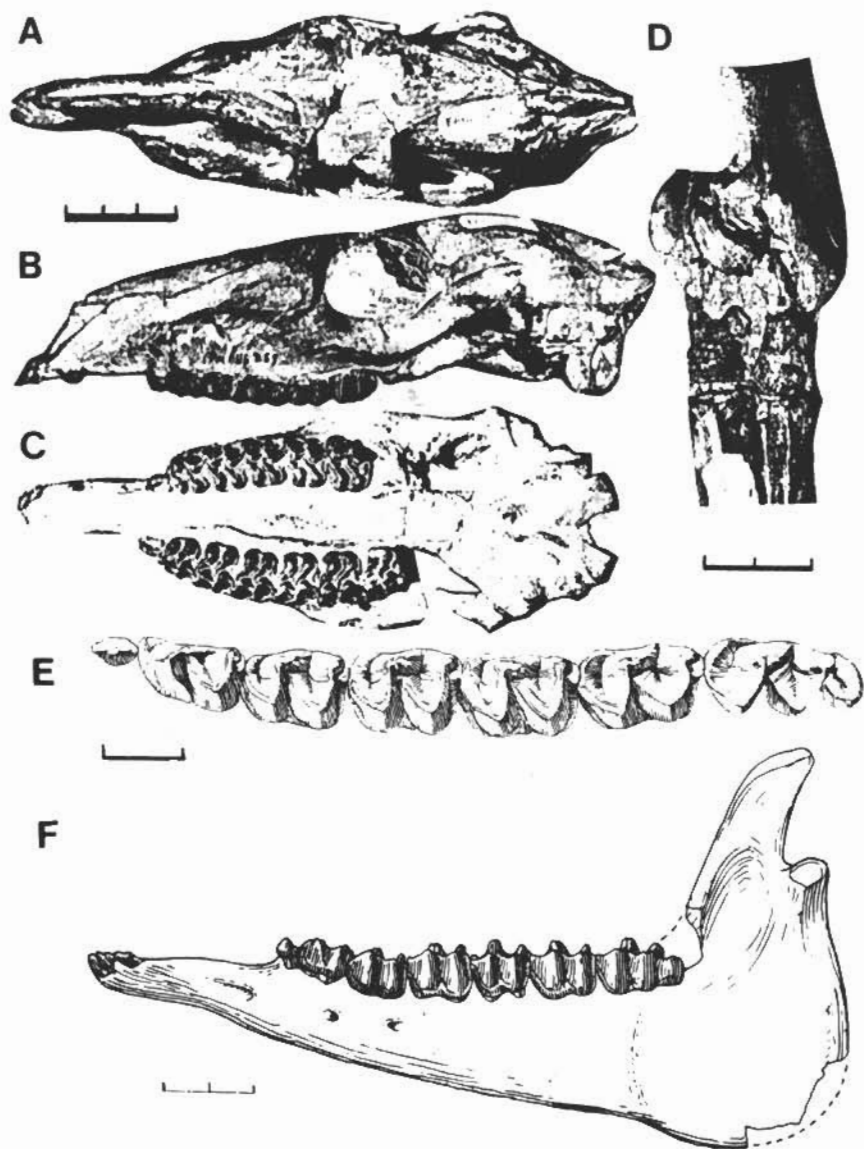


Fig. 10.9. *Miohippus assiniboensis*. F:AM 116359, referred specimen, skull in dorsal (A), left lateral (B), and ventral (C) views, (D) articulated ankle with cuboid-Mt III contact (arrow), and mandible in dorsal (E) and left lateral (F) views. Scale bars in cm.

Clark and Beerbower, 1967

Revised Diagnosis. M¹⁻³ length = 38-42 mm. Skull longer than *Miohippus obliquoidens*, but shorter than *Miohippus intermedius*. Hypostyles all class 3. Crochets frequently present.

Type. NMC 6305, right P² from the Chadronian of Cypress Hills, Saskatchewan.

Referred Material. Seaman Hills, Niobrara Co., Wyo.: F:AM 74077, 74078, 116332, 116359, 116360, 116361, 116362, 116371, 11637. Douglas area, Converse Co., Wyo.: F:AM 116379. Little Badlands, Stark Co., N.D.: F:AM 116407.

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 latest Chadronian horse that is known from a nearly complete skeleton (F:AM 116359, Fig. 10.9). The uncrushed skull shows the distinctively long facial fossa and longer, more slender rostrum that distinguishes it from *Miohippus obliquoidens*. The upper incisors have deep pits in the crowns, and are oval in cross section. The cheek teeth are large relative to the size of the skull (Tables 10.1, 10.2). They have well-defined lophs with almost no metaconules, except on P². The hypostyles are mostly class 3 (Fig. 10.1C), but are much thicker and higher than the hypostyles found in *Mesohippus exoletus*. The upper cheek teeth lack a lingual cingulum, but a faint cingular cusp occurs in the valley between the lophs. On some specimens, however, a faint cingulum can be seen. The mandible (Fig. 10.9E, F) of F:AM 116359 shows a long, pinched symphysis. The incisors are spatulate, with flattened tips. In the lower cheek teeth, the metaconid and metastylid are well separated. The hypoconulids on P₂-M₂ are also very prominent.

The postcranial skeleton of F:AM 116359 includes an atlas, two cervical vertebrae, a pelvis, and most of both hind limbs. In most features, they are identical

to *Mesohippus*, except that they are larger (Table 10.4). The tarsus (Fig. 10.9D) clearly shows the cuboid-metatarsal III articulation, diagnostic of *Miohippus*. This is also seen in F:AM 74077 and several other specimens referable to *Miohippus assiniboiensis*.

In all its preserved features, it is clear that this species must be referred to *Miohippus*. Yet this species is known only from the Chadronian, and it occurs in the same deposits as three species of *Mesohippus* and *Miohippus obliquoidens* (Fig. 10.5A). The oldest species name that appears applicable to this horse is *Mesohippus assiniboiensis* Lambe, 1905b. Lambe's type (NMC 6305) is a very poor specimen, with few diagnostic features. But Russell (1975) referred a topotypic sample from the Cypress Hill to *Mesohippus assiniboiensis*, and this material is a good match in size and morphology (Fig. 10.9) with F:AM 116359 and other horses of this size and morphology such as F:AM 74077 (compare Russell, 1975, with Tables 10.1, 10.2).

Lambe (1905b, p. 49) described another species of horse from the same locality, which he called *Mesohippus planidens*, because it had a flattened ectoloph. We find that the only preserved ectoloph (M²) on the type is no more flattened than is typical for these horses. Russell (1975, p. 648) considered *Mesohippus planidens* to be indeterminate, or possibly a synonym of *Mesohippus assiniboiensis* Lambe 1905b. The larger topotypic samples from Cypress Hills include many specimens referred to *Mesohippus assiniboiensis* that are indistinguishable from the type of *Mesohippus planidens*, except for the ectoloph. Since the slightly flattened ectoloph is not a valid character separating the two species, we suggest that the names *assiniboiensis* and *planidens* refer to the same horse. In this case, the first reviser (Russell, 1975) has established the priority of *assiniboiensis* (Lambe 1905b, p. 50) over the name *planidens* (Lambe 1905b, p. 49), even though the type specimen of *assiniboiensis* is not very diagnostic. It appears that the horses

called *Mesohippus assiniboiensis* by Russell (1975) are in fact referable to *Miohippus assiniboiensis*.

Clark and Beerbower (1967, pp. 48-49) described the species *Mesohippus 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 distinguishes it from other late Chadronian horses is its unusually large size. However, the type and referred specimens of *M. grandis* match *M. assiniboiensis* closely in size, and in morphology (Table 10.3). Both large horses are known from the latest Chadronian. Since *M. assiniboiensis* has priority over *M. grandis*, we consider Clark and Beerbower's taxon to be a junior subjective synonym.

Miohippus intermedius
(Osborn and Wortman, 1895)
Fig. 10.10

Mesohippus intermedius Osborn and Wortman, 1895, p. 354

Miohippus intermedius: Osborn, 1918, p. 54
Pediohippus intermedius: Schlaikjer, 1935, p. 145

Revised Diagnosis. M¹⁻³ length = 40-41 mm. Skull slightly larger than *Miohippus assiniboiensis*, and slightly smaller than *Miohippus gidleyi*. Distinguished from *Miohippus gidleyi* by shallower facial fossa, stronger metalophs, and by lack of metaconules.

Type. AMNH 1196, a nearly complete skeleton from the late Whitneyan *Protoceras* channels of the Big Badlands, South Dakota (Fig. 10.10A-C).

Referred material. F:AM 116418 (55 feet below Upper Whitney Ash, 66 Mountain, Phinney Ranch, Goshen Co., Wyoming) (Fig. 10.10D-E).

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

Discussion. *Miohippus intermedius* is indeed intermediate in size between *Miohippus assiniboiensis* and *Miohippus gidleyi*. Since it occurs with *Miohippus gid-*

leyi and falls on the small end of the size range (Fig. 10.8), it might be synonymized with *Miohippus gidleyi* (in which case *intermedius* would have priority). However, we feel that the deeper facial fossa, the distinctively primitive metaconules and metalophs of *Miohippus gidleyi*, 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 extremely small, so it is difficult to make a final assessment of the variability of horses in the Whitneyan.

Miohippus gidleyi (Osborn, 1904)
10.11A-B

Mesohippus gidleyi Osborn, 1904, p. 178
Miohippus gidleyi Osborn, 1918, p. 56
Pediohippus gidleyi Schlaikjer, 1935, p. 145

Synonyms. *Miohippus validus* Osborn, 1904, p. 177; *Mesohippus grallipes* Sinclair, 1925, p. 55.

Revised Diagnosis. M¹⁻³ length = 42-46 mm. Skull slightly larger than in *Miohippus intermedius*. Facial fossa much broader and deeper than in *Miohippus intermedius*. Metaconules and lingual cingula more distinct than in *Miohippus intermedius*.

Type. AMNH 1192, a dorsoventrally crushed skull, from the *Protoceras* channels, Big Badlands of South Dakota (Fig. 10.11A-B).

Referred material. AMNH 680 (type of *M. validus*); AMNH 1193, 1218; F:AM 116413, 116414, 116415, 116416, 116417.

Horizon and localities. Known only from the late Whitneyan *Protoceras* channels, South Dakota.

Discussion. As pointed out above, *M. gidleyi* is distinguished from contemporaneous *Miohippus intermedius* by its slightly larger size, deeper facial fossa, broader cheek teeth, stronger lingual cingula, and more distinct metaconules. It is the dominant late Whitneyan horse.

Miohippus validus (Osborn, 1904) is

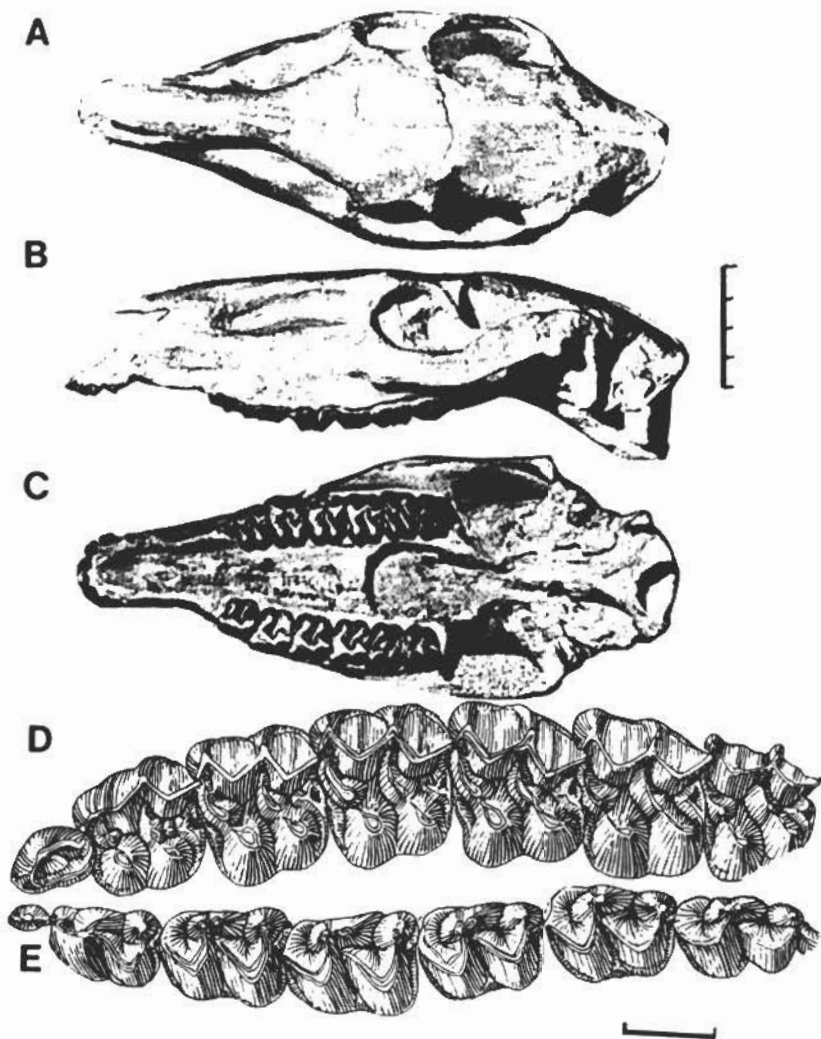


Fig. 10.10. Caption on next page.

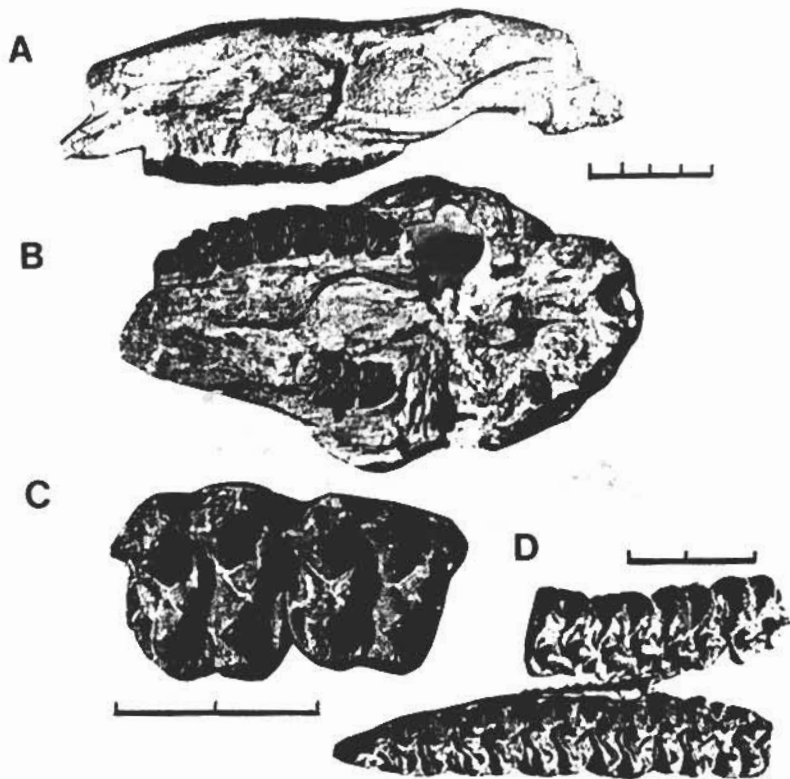


Fig. 10.10. (preceding page) *Miohippus intermedius*, AMNH 1196, type specimen. Skull in dorsal (A), left lateral (B), and ventral (C) views. Referred specimen, F:AM 116418, crown views of upper (D) and lower (E) teeth. Scale bars in cm.

Fig. 10.11. *Miohippus gidleyi*, AMNH 2611, type skull in left lateral (A) and ventral (B) views. (C) *Miohippus "crassicuspis"* (= *annectens*), AMNH 1683, type specimen. (D) *Miohippus equinanus*. F:AM 116421 (upper specimen) compared with type, AMNH 12912 (lower specimen).

here referred to *Miohippus gidleyi*. The distinctive features of *Miohippus validus* listed by Osborn serve to distinguish it only from *Miohippus intermedius*, and Osborn never compared *M. validus* with *Miohippus gidleyi* in print. The type specimen (AMNH 680, not AMNH 1218, as listed by Osborn, 1918) falls within the size range of *Miohippus gidleyi* (Fig. 10.8). The crowns of the upper teeth of the type are too worn to make detailed comparisons with *Miohippus gidleyi*, but in the preserved features they match quite well. The only possible distinguishing feature of *Miohippus validus* is a slight dorsoventral ridge subdividing the facial fossa of the type skull. However, this feature is not known in any other specimen referred to *Miohippus validus*, so it is probably due to individual variation or postmortem deformation of the type specimen. In our opinion, it does not justify the separation of *M. validus* as a distinct species.

Miohippus annectens Marsh, 1874
Fig. 10.11C

Synonym. *Miohippus crassicuspis* Osborn, 1904, p. 178.

Revised Diagnosis. M¹⁻³ length = 47-50 mm.

Type. YPM 12230, a skull with associated limb material, John Day Formation, Arikareean of Oregon.

Referred material. AMNH 683, type of *Miohippus crassicuspis*, plus much Arikareean material not considered here.

Horizon and locality. Late Whitneyan *Protoceras* channels, Big Badlands of South Dakota, and John Day beds, Arikareean of Oregon.

Discussion. *Miohippus crassicuspis* (AMNH 683) is a large *Miohippus* with remarkably distinct protoconules and metaconules (Fig. 10.11C), well-developed class 3 hypostyles, but no crochets. It is clearly much larger than, and morphologically distinct from, any other White River horse, but no previous author has reported comparing it with Arikareean horses. We

find that it is a very good match in size and morphology with the type specimen of *Miohippus annectens* from the John Day beds of Oregon. The type skull of *Miohippus annectens* (YPM 12230) shows very distinct conules and well developed class 3 hypostyles. The lingual cingula are weak or expressed as intervallic cusps, as in the type of *Miohippus crassicuspis*. Reluctance to assign John Day and White River horses to the same taxa need not be a systematic barrier. The John Day and upper White River deposits are now considered so closely similar in age (Tedford *et al.*, 1987; Prothero and Rensberger, 1985) that it does not seem remarkable that a late Whitneyan High Plains horse should also continue into the Arikareean of Oregon.

?*Miohippus equinanus* Osborn, 1918
Fig. 10.11D

Revised Diagnosis. Small horse (M¹⁻³ length = 31 mm) with relatively advanced, bilophodont dentition and class 3 or 4 hypostyles.

Type. AMNH 12912, a palate with left and right dP¹-M³, from the early Arikareean "Rosebud Formation" (= Sharps Formation; Macdonald, 1963), 5 miles above Manderson, Wounded Knee Creek, South Dakota.

Referred material. AMNH 39028 (*Leptauchenia* nodules, 6 miles east of Oelrichs, Fall River Co., S.D.); F:AM 116411 (Base of Upper *Oreodon* beds, Kodak Point, Big Badlands, S.D.). There is much additional Arikareean material from the type locality in the AMNH, LACM, and SDSM collections, as listed by Macdonald (1963, 1970).

Horizon and localities. Late Whitneyan and early Arikareean, South Dakota.

Discussion. This tiny Arikareean horse is now known from the late Whitneyan. The size and morphology of this taxon is distinctive. It is far smaller than any contemporary horse (Tables 10.2, 10.3), and far more advanced in dental morphology than

any earlier form of comparable size. The reference of this species to *Miohippus* is still questionable, since it is presently known only from upper dentitions. No skulls or postcrania have been found that could show whether it has the diagnostic features of *Miohippus*. Only the relatively derived dentition justifies its assignment to *Miohippus*, and this may change when more complete material is found.

Stirton (1940) made *M. equinanus* "ancestral" to *Archaeohippus*. Although these horses are similar in their diminutive size, they do not match in detail. *Archaeohippus* is much more derived in having the metaloph completely attached to the ectoloph by a high, continuous crest and a strong medicrista. It also has a very high-crowned triangular hypostyle. *M. equinanus* has none of these derived features of *Archaeohippus*. Until more complete skull material is available for *M. equinanus*, reference to *Archaeohippus* is based strictly on size and is therefore questionable.

A note on "*Mesohippus longipes*"

Osborn and Wortman (1894, p. 214) described a nearly complete right hind limb (AMNH 684) from the Whitneyan (Lower Poleslide Member) of South Dakota. They compared this specimen to horses and hyracodonts, and decided that it was equid. On this basis, they named the specimen *Mesohippus longipes*. In the following year, Osborn and Wortman (1895, p. 366) changed their minds and referred this specimen to the tapiroid *Colodon*. Their justification for this was the following: 1) the ectal and sustentacular facets of the astragalus were continuous, as in rhinos and hyracodonts, but not in horses; 2) the ectocuneiform had great vertical depth; 3) there was no cuboid-MT III contact.

Scott (1940, pp. 940-941) reassigned this specimen to *Mesohippus*. He claimed that the astragalus is similar to that of horses, not tapirs, but he gave no justification for this statement. Nevertheless, he admitted that the large size and the lack

of cuboid-MT III articulation make it difficult to refer this specimen to the Equidae.

We examined this specimen, and it is clear that it is not equid. Although the limb is very similar in size to some specimens of *Miohippus gidleyi* (e.g., F:AM 109853), it is a much better match for *Colodon occidentalis* (e.g., AMNH 658). The sustentacular facet of the astragalus of "*M. longipes*" and *C. occidentalis* both have a distinct ventrolateral spur not found on any equid astragalus. The limb proportions are a little too slender for *Miohippus gidleyi*. As noted by previous authors, the ectocuneiform is too deep. The "connection" between the ectal and sustentacular facets is due to plastic deformation of AMNH 684. Most of the facets appear unusually rounded and indistinct. Besides, this "connection" is not found in either tapiroid or horses. It is clear that "*Mesohippus longipes*" Osborn and Wortman, 1894, is not a horse at all, but a hind limb of *Colodon occidentalis* (Leidy, 1868). The former name is here relegated to junior synonymy with *Colodon occidentalis*.

Phylogeny

A phylogenetic hypothesis for the Oligocene Equidae and their sister taxa is shown in Fig. 10.12. Most of the derived characters are dental, but characters of the skull and postcranial skeleton are used where appropriate. The temporal ranges of the species of Oligocene horses are shown in Fig. 10.5B. It is immediately apparent that Oligocene horses are characterized by a rather "bushy" branching phylogeny, and not the single "trunk" portrayed by Stirton (1940) and Simpson (1951). At any given interval of time, at least two or three species of horses existed, and frequently all can be found in the same deposits. Indeed, the pattern seen in Oligocene horses is nearly comparable in species diversity to that seen in the Neogene, except that only two genera are present. In addition, the popular myth that *Mesohippus* imperceptibly grades into a successional genus *Miohippus* is not supported. *Miohippus* appears in the mid-Chadronian, and

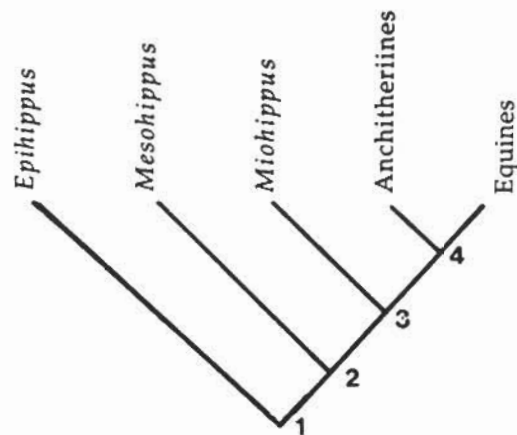


Fig. 10.12. Hypothesis of relationships of Oligocene horses and their sister-taxa. Characters at the numbered nodes as follows: 1) P^2 submolariform; P_1 single rooted; 2) I^{1-3} with pitted crowns; $P^2/2$ molariform; metacarpal V reduced; extended premaxilla; longer diastema; angle of jaw posteriorly rounded without notch; 3) cuboid-metatarsal III contact; deeper, more elongate facial fossa; longer facial region; 4) metaloph connected to ectoloph.

Mesohippus does not become extinct until the early Whitneyan. The two genera overlap by at least four million years.

Patterns of evolution

Since Huxley (1870) and Kowalevsky (1873), horses have been used as one of the classic cases of evolution in the fossil record. The early European lineages connected four successive forms (*Palaeotherium-Anchitherium-Hipparion-Equus*) in the first attempt at a horse phylogeny. In 1876, Huxley visited North America and discovered that O.C. Marsh had a much more complete sequence of horses in this continent. The European "phylogeny" was in fact composed of a non-equid (*Palaeotherium*) and three successive immigration events from North America. Most subsequent horse phylogenies were strictly orthogenetic, with one continuous intergrading lineage and few or no side branches. This long-obsolete picture still appears in much of the popular literature.

Stirton (1940) and Simpson (1951) began

to present a more complex, branching phylogeny of horses. They proposed cladogenic splitting events that led to the anchitherines, the hipparionines, the equines, and many other side branches. The paraphyletic nature of the genus *Merychippus* became apparent. The earlier part of horse family tree was, however, still treated as a single, unbranched "trunk," with *Mesohippus* and *Miohippus* represented as one continuous intergradational lineage. A strong gradualistic bias was evident in these phylogenies, influencing the way in which species were delineated, and their relationships interpreted. For example, Simpson (1951, p. 127) wrote, "*Mesohippus* and *Miohippus* intergrade so perfectly and the differences between them are so slight and variable that even experts find it difficult, at times nearly impossible, to distinguish them clearly." Naturally, this gradualistic bias also finds its way into the popular literature. As recently as 1980, Lewin (1980, p. 884) wrote, "A classic example of... a trend is the evolution of the

modern horse, whose distant ancestor *Hydracotherium* [sic] was a three-toed [sic—it had four toes in the manus] creature no bigger than a dog. The fossil record shows an apparent steady 'progress' through time, with gradual changes in body size and form leading to the familiar *Equus*."

In recent years, however, paleontologists have been challenged to examine their biases with regard to the delineation of species, the construction of phylogenies, and the tempo of evolution (Eldredge and Gould, 1972; Gould and Eldredge, 1977). Eldredge (1979) points out that a gradualistic bias will lead to a "transformational" view of species, which are treated as arbitrary slices of a gradualistic continuum. By contrast, a "taxic" approach will recognize species as diagnostic clusters of morphology without attempting to fit them into an *a priori* bias for intergradational, stratigraphically-defined horizontal taxa. With a less arbitrary, more objective concept of species, it should be possible to assess whether they do in fact intergrade continuously, or show other patterns. One of the patterns recognized with the "taxic" approach is the sympatric persistence of closely related species through long periods of time. Stanley (1975, 1979) has used information of this kind to support the hypothesis of species selection for long-term macroevolutionary trends. The view of species as discrete, non-arbitrary units with their own intrinsic properties leads to many other fruitful hypotheses (e.g., Vrba and Eldredge, 1984).

Recent work on Neogene horses (MacFadden, 1984, 1985, 1988) has clearly shown that horses are very speciose with many genera living sympatrically in the late Miocene of North America. Skinner and Johnson (1984, p. 276) reported eight genera of horses from the late Barstovian Railway Quarry A of the Valentine Formation of Nebraska, and Schultz (1977) reported 12 species of horses from the Clarendon Beds of Texas. Unfortunately, the North American terrestrial Neogene

record gives few examples of continuous fossiliferous sequences which might be used to test whether these species arise gradually or by splitting events (MacFadden, 1984, 1985, 1988). But the Paleogene record does have such continuous, fossiliferous sequences. For example, in the continuous sections of the Eocene of the Bighorn Basin of Wyoming, Gingerich (1980) has reported at least two lineages of *Hydracotherium* living sympatrically with the slightly larger ceratomorph *Homogalax*, which is indistinguishable from *Hydracotherium* in most features.

The new systematic analogies, combined with a robust stratigraphic context, allow us to approach several aspects of the tempo and mode of horse evolution. Three patterns in particular emerge: 1) most horse species do not intergrade morphologically; 2) advanced and primitive species lived sympatrically, and, 3) morphological stasis predominates in horse evolution. These points are elaborated below:

1. Most Oligocene horse species do not intergrade

In our studies of the White River horses, we first attempted to determine if diagnosable clusters of morphology could be recognized in *Mesohippus* and *Miohippus*. Non-arbitrary distinctions between species were indeed possible. It seems that the difficulty of distinguishing species discussed by Simpson (1951) was simply an artifact of small sample size and inadequate stratigraphic data. Taking isolated specimens from each stratigraphic level, a single orthogenetic lineage could be constructed. Larger sample sizes have clearly shown that non-arbitrary distinctions can be made between the various species of *Mesohippus* and *Miohippus*. These distinctions result in diagnosable, non-overlapping clusters of morphology that deserve to be recognized as species in the paleontological sense of the word. Admittedly, there are some specimens that appear to be intermediate or transitional between these clusters, but these are relatively few. In addition, these

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