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A Revision of the Genus *Orohippus* (Perissodactyla, Equidae)

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INTRODUCTION

The present paper constitutes the second part of a study of the Eocene horses. The first part of the study (Kitts, 1956) dealt with the lower Eocene genus *Hyracotherium*, the most primitive known equid.

Leidy (1870) described the earliest discovered specimen referable to the genus *Orohippus* as later defined. He recognized the true affinities of the specimen, placing it in the genus *Pachynolophys*. In 1872 Marsh erected the genus *Orohippus* and thus recognized the special relationships of the group. He did not, however, put in *Orohippus* all of the species which are today generally recognized as belonging there.

Orohippus and *Hyracotherium* are very similar to each other in almost all known anatomical characters. For this reason, and because the dentition and skeleton of *Hyracotherium* have been described in some detail, frequent reference to the anatomy of *Hyracotherium* is made in the course of the description of *Orohippus*. The two genera differ markedly in the extent of their temporal and geographic distribution. *Hyracotherium* is represented by rather large samples from at least three distinct horizons and nearly a dozen well-separated geographic localities, while *Orohippus* is known only from two distinct horizons and a rather restricted area. Because the distribution of *Orohippus* is so restricted, conclusions regarding taxonomy and evolu-

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tion within the genus are in a number of instances necessarily more tentative than in the case of *Hyracotherium*.

I wish to express my gratitude to Dr. G. G. Simpson of the American Museum of Natural History, Dr. Joseph T. Gregory of the Peabody Museum, Yale University, and Dr. C. Lewis Gazin of the United States National Museum for allowing me complete access to *Orohippus* material included in the collections in their charge, and to Mr. Irwin Gold, who prepared the photographs.

The following abbreviations are used: A.M.N.H. (the American Museum of Natural History); U.S.N.M. (United States National Museum); Y.P.M. (Peabody Museum, Yale University); *N* (number of specimens); *OR* (observed range); *SR* (standard range); *M* (mean); σ (standard deviation); *V* (coefficient of variation). All measurements are in millimeters.

STRATIGRAPHY OF THE EOCENE DEPOSITS IN THE BRIDGER BASIN

It has long been recognized that two distinct mammalian faunas occur in the continental sediments of the Bridger Basin. Wortman (1901) recognized an upper and a lower Bridger on the basis of faunal differences. Matthew (1909) gave upper and lower Bridger faunal lists, and divided the lower beds into horizons A and B and the upper beds into horizons C, D, and E on the basis of lithology. Wood (1934) proposed the name "Black's Fork member" for the lower Bridger beds (A and B of Matthew) and "Twin Buttes member" for the upper beds (C and D of Matthew). In no one locality is the entire section exposed. Matthew was able to provide a map which indicated the areas in which particular horizons are exposed. It has consequently been possible to determine the approximate stratigraphic position of many specimens for which only the geographic locality was recorded at the time of collection. Only those specimens for which the stratigraphic position could be determined or was originally recorded have been considered in this study. Horizons A and E contain only fragmentary mammalian remains, and to my knowledge no specimens certainly referable to *Orohippus* have been found at either.

There are well-marked differences between hyracotheres from the lower and those from the upper beds. There are no apparent differences between specimens collected at different levels within the lower or the upper beds with the exception that one species, *O. agilis*, is possibly restricted to a position rather high in the upper beds.

ORDER PERISSODACTYLA OWEN, 1848

FAMILY EQUIDAE GRAY, 1821

OROHIPPIUS MARSH, 1872

Orohippus MARSH, 1872, p. 207.

Helotherium COPE, 1872, p. 466.

Oligotomus COPE, 1873a, p. 606.

Helohippus MARSH, 1892, p. 353.

TYPE: *Orohippus pumilus*.

TYPES OF SYNONYMS: Of *Helotherium*, *H. procyoninum*; of *Oligotomus*, *O. cinctus*; of *Helohippus*, *H. pumilus*.

DISTRIBUTION: Bridger formation, middle Eocene, Bridger Basin, Wyoming.

DIAGNOSIS: P³ and P⁴ with four major cusps in all species and fully molariform in advanced species. Mesostyle on molars in all species and on P³ and P⁴ in advanced species. Upper molars with well-developed lophs but with intermediate cusps detectable. Ectoloph on molars V-shaped in crown view in all species and on P³ and P⁴ of advanced species. P₄ molariform. Mesolophid sharply oblique. Digits I and V absent in pes.

Marsh (1872) assigned a right maxillary fragment with P³-M² and roots of P¹ and P² to the new genus and species *Orohippus pumilus*, stating simply that *Orohippus* was nearly allied to *Anchitherium*. Later (1873) Marsh further characterized the genus (on the basis of the type specimen of *O. agilis*) as having four functional digits in the manus, the first premolar nearly as large as the second, the skull elongate and equine in proportions, the orbit not closed behind, no ant-orbital fossa, three upper molars, four premolars, the radius and ulna separate, and the ulna stouter than in *Anchitherium*. Marsh (1892) completed his characterization of the genus with the following additional characters; 44 teeth without cement, incisors without pit, canines large, molar teeth with short crowns more or less flattened, no diastema between upper premolars, and P³ and P⁴ similar to molars.

Marsh referred only three species to *Orohippus*. The type of *O. agilis* consists of a fragmentary skull, with a forelimb and vertebrae. It was on this specimen that Marsh largely based his characterization of the genus. The type of *O. pumilus* consists of loose teeth, while that of *O. major* consists of an associated right M² and M³ and a left M². In neither of the latter specimens could any conclusions about a diastema be reached. The ambiguity of the phrase "P³ and P⁴ similar to molars" has resulted in considerable confusion. P³ and P⁴ in the type specimen of *O. pumilus* are much less molariform than those in the type speci-

men of *O. agilis*, and in the type specimen of *O. major* the premolars are lacking.

The genus *Orohippus* as conceived and defined by Marsh would include only two upper Bridger species among those included in the genus in this classification. Marsh's reference of *O. pumilus* and *O. major* to the genus was based on purely negative evidence and was, from his point of view, entirely accidental.

In his description of *Helotherium procyoninum* Cope (1872) stated, "This species is distinguishable from those already known as pertaining to this genus, by its small size, as it did not much exceed the racoon in dimensions." I have not been able to discover any reference to this genus by Cope or any other worker previous to or subsequent to this description. The very brief description is not sufficient to distinguish the form from many other Paleocene and Eocene condylarths and perissodactyls. Cope later (1873a) put this species in *Orohippus*. He gave no explanation of his previous reference.

Cope (1873b) characterized the genus *Oligotomus* as having molars very similar to those of *Hyopsodus* and *Lophiotherium*. He stated that *Oligotomus* differed from these genera and from *Orotherium* "in the possession of but two premolars." The type species of the genus, *O. cinctus*, was the only species subsequently referred to *Orohippus* that was ever referred to *Oligotomus*.

Another Marsh hyracothere genus was *Orotherium*. In the original description (1872) the genus was compared to *Lophiotherium*, and it was stated that its relationship to *Orohippus* could not be determined at that time. Of the species ultimately referred to *Orohippus*, only the type species, *Orotherium uintanum*, was ever referred to this genus. Several species that were later referred to *Eohippus* or *Hyracotherium* were earlier put in *Orotherium*.

Marsh (1892) designated *Helohippus pumilus* as the type of the genus *Helohippus*. The type specimen of this species had originally been referred to *Lophiodon* by Marsh (1871). *Helohippus* was characterized as being structurally intermediate between *Eohippus* and *Orohippus*, because of the combination of a diastema between P¹ and P², and a molariform P⁴. No other species were referred to this genus.

An examination of the specific synonymies will show that many species that were ultimately referred to *Orohippus* were earlier put in a number of other lower Tertiary Perissodactyla genera, both American and European.

Several early described species were referred to European genera (Leidy, 1870; Marsh, 1871; Cope, 1884). These references probably re-

sulted from a lack of European material that could be used for comparative studies. As better American material became available new genera were erected on the basis of these specimens. Most European workers continued to refer these species to European genera. Thus Flower (1876), Flower and Lydekker (1891), and Zittel (1893) referred most of the species which had long been put in distinctly American genera by American workers to *Pachynolophus*.

Trouessart, in contrast to his European colleagues, consistently referred these species either to *Orohippus* or to *Epihippus*.

The current concept of the genus, that is, to include middle Eocene forms with a diastema, dates from Hay (1902), who included all the species included in the genus in this classification except *Lophiodon pumilus* (Marsh, 1871) which was placed in *Orohippus* by Granger (1908).

Reference of the species referred to *Orohippus* in Granger (1908) and in this classification to *Hyracotherium* (Cope, 1877 and 1884; Lydekker, 1886; Matthew, 1899), *Epihippus* (Scott and Osborn, 1890; Trouessart, 1898), and *Pliolophus* (Cope, 1884; Scott and Osborn, 1890) no doubt resulted from the ambiguity of the phrase "P³ and P⁴ similar to the molars" in Marsh's characterization of the genus.

The teeth of *Orohippus* are quite different from those of *Hyracotherium*, but, because the dentition varies considerably from species to species, a detailed description of the teeth accompanies the discussion of each species. At this point it may be said, however, that the teeth of all species of *Orohippus* differ from those of *Hyracotherium* in the characters listed below:

1. P³ and P⁴ with four major cusps of roughly equal size.
2. Upper molars with mesostyle and with ectoloph V-shaped between paracone and metacone.
3. P₃ with entoconid.
4. P₄ with entoconid about as large as other cusps.
5. Heel of M₃ always relatively shorter than in *Hyracotherium*.

Skeletal material pertaining to *Orohippus* consists of the type specimen of *Orohippus agilis* which consists of a skull, a nearly complete forelimb, and a number of vertebrae; a specimen from the Black's Fork member consisting of a skull and nearly complete skeleton (A.M.N.H. No. 12648) which was described by Granger (1908); and a small number of isolated elements. Comparison of the various skeletal elements of *Orohippus* with those of *Hyracotherium* reveals striking similarities; indeed in most cases the bones of the two genera are quite

indistinguishable. For this reason the skeleton of *Orhippus* is not here described in any detail.

The basicranial region of the skull in the two genera apparently differs somewhat. In no specimen of *Orohippus* are the foramina of the orbital region preserved, but an examination of the fragmented basicranial region of A.M.N.H. No. 12648 suggests that the foramen ovale was confluent with the foramen lacerum (see Edinger and Kitts, 1954). In *Hyracotherium* the condition of the foramen ovale could not be certainly determined, but in one specimen (A.M.N.H. No. 4831) it appeared to be in a condition transitional between separation from, and confluence with, the foramen lacerum (see Edinger and Kitts, 1954; and Kitts, 1956). In no other preserved parts do the skulls of *Hyracotherium* and *Orohippus* differ.

The manus and the pes of *Orohippus* differ from those of *Hyracotherium* in that the central digit, that is, the third, is in each case relatively larger. In the pes, furthermore, there is no vestige of a first or fifth digit, as indeed there may not have been in late Wasatchian species of *Hyracotherium*.

Perhaps the most significant differences between *Orohippus* and *Hyracotherium* from a functional point of view are quite minor ones in the structure of the articular grooves of the tibia and the trochlear crests of the astragalus. In *Hyracotherium* the trochlear crests of the astragalus are roughly parallel to the long axis of the foot, and the articular grooves of the tibia are oriented with their axis about parallel to the sagittal plane. In *Orohippus* and in all later horses the trochlear crests are inclined at an angle to the long axis of the foot, the distal ends of the crest being more lateral, and the axis of the articular grooves of the tibia are oriented at an angle to the sagittal plane, the anterior ends being more lateral. In *Orohippus* the angle of offset in each case is perhaps 6 or 8 degrees, while in *Equus* it may be as great as 35 degrees. The functional consequence of this arrangement is that the entire foot moves medially during flexion and laterally during extension. This movement does not affect the foot during the propulsive phase, as the tarso-tibial joint is almost fully extended during all the time that the foot is in contact with the ground.

In *Equus* the long collateral ligaments of the tarso-tibial joint are tense during extension. The tension results largely from a moving apart of the origins and insertions of these ligaments in a sagittal plane during extension of the joint. This tension serves to bind and stabilize the joint during the propulsive phase when the foot is in contact with the ground. The origins and insertions of the short collateral ligaments

are not appreciably farther apart in a sagittal plane during flexion when the ligaments are tense than they are during extension. The origins and insertions of the short collateral ligaments do move apart during extension, however, particularly in the case of the medial ligament, in a transverse plane as a result of the medial movement of the foot. The canted trochlear crests and articular grooves of the tibia may thus simply provide a mechanism for increased tension of the short collateral ligaments and consequent stabilization of the tarso-tibial joint during flexion. The stabilization of the joint during flexion may, at first thought, seem to be of little advantage, but it must be borne in mind that in *Equus* the tarso-tibial joint is very sharply flexed and the limb is swung very rapidly anteriorly during the recovery phase in running.

Orohippus major Marsh, 1874

Orohippus major MARSH, 1874, p. 248.

Pliolophus major (Marsh), OSBORN, 1890, in Scott and Osborn, p. 544.

TYPE: Y.P.M. No. 11270, fragment of right maxilla with M² and M³, and loose M² from Millersville, Bridger Basin, Wyoming.

HYPODGM: The type specimen, Y.P.M. No. 11620, and A.M.N.H. Nos. 11633 and 11634.

KNOWN DISTRIBUTION: Bridger formation, southwestern Wyoming, Black's Fork and Twin Buttes members (horizons B, C, and D).

DIAGNOSIS: Length of M², 9.3 mm. Mean length of M₃, 12.90 mm. (two specimens). Mesostyle weak. Heel of M₃ broad and relatively long.

In the original description *O. major* was distinguished from other species of the genus on the basis of its large size and because, in the words of Marsh, "the intermediate lobes of the molars are less well developed and the antero-posterior buttress is more elevated."

Granger (1908) emphasized the primitive characters of the type specimen, including the weakness of the mesostyle and the resemblance to *Hyracotherium* in the general shape of the molars. Granger referred two specimens consisting of lower molars, one from the lower beds and one from the upper beds, to this species because of their large size (A.M.N.H. No. 11633 and No. 11634).

The type specimen could be included in the species *Orohippus pumilus* without doing great violence to the tooth-size distribution of that species, but the specimen has, as Granger pointed out, a number of distinct morphological characters which in conjunction with its larger size seems to indicate that it represents a species distinct from *Orohippus pumilus*.

The type specimen is, in general, quite similar to the upper molars

of *Hyracotherium*, particularly to those of *H. craspedotum*. It does, however, show a few relatively advanced characters that serve to distinguish it from specimens referable to *Hyracotherium*. Between the paracone and the metacone the cingulum is slightly elevated to form a distinct mesostyle. The mesostyle is much more pronounced on M^2 than on M^3 . The ectoloph, both between the parastyle and the paracone and between the paracone and the metacone, is relatively higher and sharper than in *Hyracotherium*. In addition, in crown view it is V-shaped, with the point of the V directed externally. The internal angle formed is very slightly obtuse. A vertical ridge extends from the point of the V nearly to meet the point of the mesostyle.

The lower teeth referred to this species are distinctly larger than others in either the upper or the lower beds and must have been associated with upper teeth at least as large as the type specimen. These molars are in no way distinguishable from the molars of *Hyracotherium craspedotum* from the late Wasatchian deposits. They may be distinguished from those of other species of *Orohippus* on the basis that the heel of M_3 is rather broad and stout and relatively long.

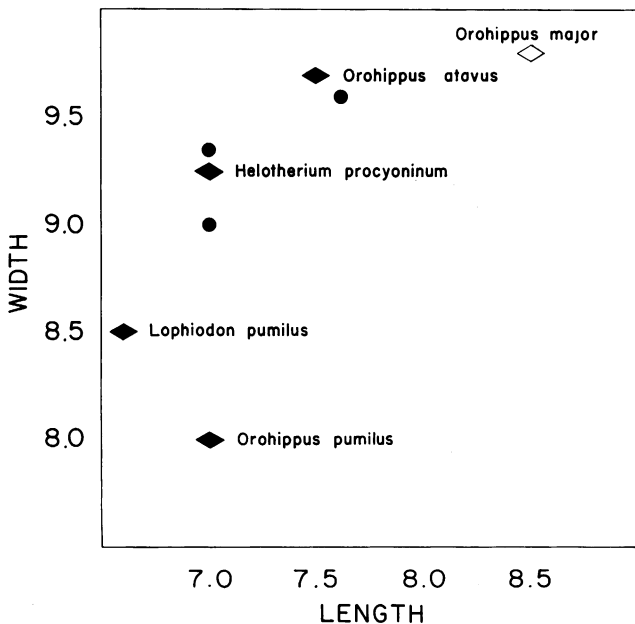


FIG. 1. Scatter diagram of length and width of M^1 of sample from Black's Fork member. Symbols: Solid, specimens referable to *Orohippus pumilus*; in outline, specimen referable to *O. major*; diamonds, type specimen and types of synonyms.

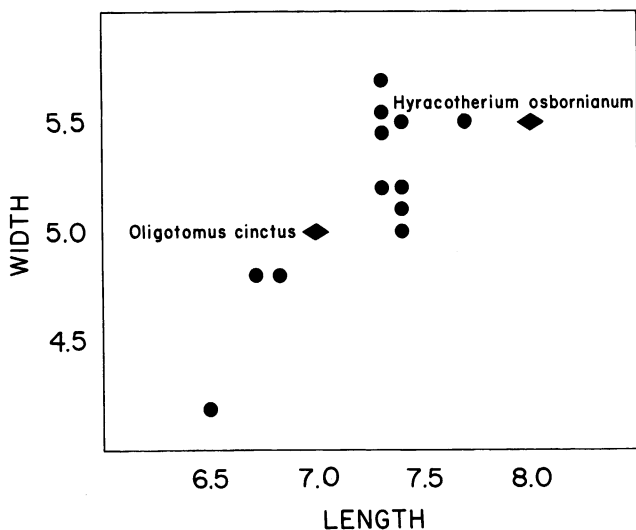


FIG. 2. Scatter diagram of length and width of *M*₁ of sample from Black's Fork member. All specimens are referable to *Orohippus pumilus*. Types of synonyms are indicated by diamonds.

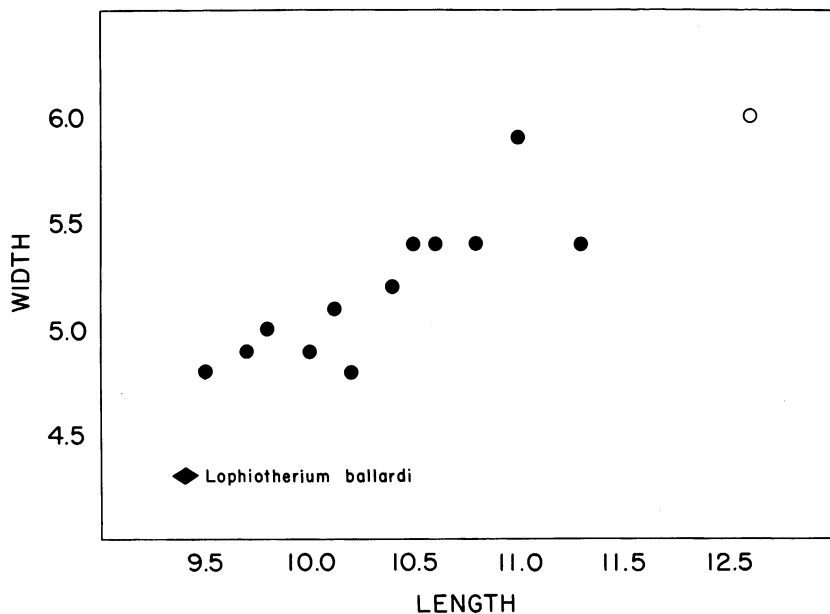


FIG. 3. Scatter diagram of length and width of *M*₃ of sample from Black's Fork member. Symbols: Solid, specimens referable to *Orohippus pumilus*; in outline, specimen referable to *O. major*; diamond, type of synonym.

Orohippus pumilus Marsh, 1871

- Lophiodon pumilus* MARSH, 1871, p. 38.
Helohippus pumilus MARSH, 1892, p. 353.
Orohippus pumilus (Marsh), GRANGER, 1908, p. 247.
Lophiotherium ballardi MARSH, 1871, p. 39.
Pachynolophus ballardi (Marsh), ROGER, 1896, p. 170.
Orohippus ballardi (Marsh) HAY, 1902, p. 611.
Helotherium procyoninum COPE, 1872, p. 476.
Orohippus procyoninus COPE, 1873a, p. 606.
Hyracotherium procyoninum COPE, 1877, p. 262.
Orohippus pumilus MARSH, 1872, p. 207.
Pachynolophus pumilus (Marsh), ROGER, 1896, p. 170.
Oligotomus cinctus COPE, 1873b, p. 2.
Pliolophus cinctus COPE, 1884, p. 653.
Pachynolophus cinctus (Cope), ROGER, 1896, p. 170.
Orohippus cinctus (Cope), WORTMAN, 1896, p. 103.
Hyracotherium osbornianum COPE, 1884, p. 630.
Orohippus osbornianus (Cope), TROUESSART, 1898, p. 774.
Orohippus typicus GRANGER, 1908, p. 249.
Orohippus atavus GRANGER, 1908, p. 253.

TYPE: Y.P.M. No. 11336, fragment of right maxilla with P^3 - M^2 and roots of P^1 and P^2 from Marsh's Fork, Bridger Basin.

TYPE SPECIMENS OF SYNONYMS: *Lophiotherium ballardi*: Y.P.M. No. 13328, fragment of left ramus with M_2 - M_3 from Grizzly Buttes, Bridger Basin. *Helotherium procyoninum*: A.M.N.H. No. 5052, right M^3 from Cottonwood Creek, Bridger Basin. *Orohippus pumilus*: Y.P.M. No. 11306, isolated right P^3 , right M^3 , and fragments of upper molars, probably not all of the same individual, from Grizzly Buttes, Bridger Basin. *Oligotomus cinctus*: A.M.N.H. No. 5050, fragment of right ramus with broken P_4 and M_1 from Cottonwood Creek, Bridger Basin. *Hyracotherium osbornianum*: A.M.N.H. No. 5051, fragment of right ramus with M_1 and roots of M_2 and M_3 from Black's Fork, Bridger Basin. *Orohippus atavus*: A.M.N.H. No. 11625, fragmentary skull and portions of hind limb from the mouth of Cottonwood Creek, Bridger Basin.

HYPODIGM: The type specimen, the type specimens of the synonyms, and the following specimens: Y.P.M. Nos. 11619, 13305-2, 13309, 13310-2, 13311-2, 13326, 13327, 13328, 13348; U.S.N.M. Nos. 13402, 13404, 17852, 17856, 17877; A.M.N.H. Nos. 11624, 11626, 11629, 12121, 12648, 12657, 19223, 19224.

KNOWN DISTRIBUTION: Bridger formation, southwestern Wyoming, Black's Fork member (Bridger B).

DIAGNOSIS: Diastema between P^1 and P^2 . P^2 with lobe-like postero-

internal shelf. P^3 with acute ($50-55^\circ$) antero-external angle and obtuse ($125-130^\circ$) antero-internal angle. Mesostyle very weak or absent on P^3 and P^4 . Anterior and posterior borders of P^4 parallel and protocone distinctly more medial than hypocone. Mesostyle moderate on molars. P_4 may be pointed anteriorly. Heel of M_3 narrow and sharply constricted anteriorly.

In the original description the type specimen of *Lophiodon pumilus* was compared with that of *Lophiodon nanus* (later referred to *Helaletes*). Later Marsh (1892) designated the species as the type of the new genus *Helohippus*, characterized by the presence of a diastema between P^1 and P^2 , and P^4 similar to the molars. The type species was the only one ever referred to the genus. Granger (1908) placed the species in *Orohippus*, distinguishing it from other species of the genus because of the greater anterior-posterior compression of the molars.

With the exception of the few specimens referable to *Orohippus major*, specimens from the lower beds constitute a remarkably homo-

TABLE 1
NUMERICAL DATA ON *Orohippus major* FROM THE BLACK'S
FORK AND TWIN BUTTES MEMBERS

	<i>N</i>	<i>OR</i>	<i>M</i>
M^2			
L	1		9.3
W	1		10.5
M^3			
L	1		8.5
W	1		9.8
M_1			
L	1		9.5
W	1		6.8
M_2			
L	3	8.4-9.5	8.97
W	3	6.3-7.1	6.73
M_3			
L	2	12.1-13.7	12.90
W	2	6.0-6.8	6.40

TABLE 2
MEASUREMENTS OF TYPE SPECIMEN AND TYPE SPECIMENS OF SYNONYMS OF *Orohippus pumilus*

	<i>Lophiotherium ballardi</i>	<i>Oligotomus cinctus</i>	<i>Hyracotherium obsornianum</i>	<i>Lophiodon pumilus</i>	<i>Helotherium procyoninum</i>	<i>Orohippus pumilus</i>	<i>Orohippus alatus</i>
P ₃	—	—	—	—	—	—	—
L	—	—	—	—	—	—	—
W	—	—	—	—	—	—	—
P ₄	—	6.3	—	—	—	—	—
L	—	5.0	—	—	—	—	—
W	—	—	—	—	—	—	—
M ₁	—	7.0	8.0	—	—	—	—
L	—	5.0	5.5	—	—	—	—
W	—	—	—	—	—	—	—
M ₂	6.7	—	—	—	—	—	—
L	4.7	—	—	—	—	—	—
W	—	—	—	—	—	—	—
M ₃	9.3	—	—	—	—	—	—
L	4.4	—	—	—	—	—	—
W	—	—	—	—	—	—	—

TABLE 2—(Continued)

<i>Lophiotherium ballardi</i>	<i>Oligotomus cinctus</i>	<i>Hyracotherium obsornianum</i>	<i>Lophiodon pumilus</i>	<i>Helotherium procyonium</i>	<i>Orohippus pumilus</i>	<i>Orohippus atavus</i>
P ³	—	—	—	—	—	—
L	—	—	—	—	—	—
W	—	—	—	—	—	—
P ⁴	—	—	—	—	6.6	6.3
L	—	—	—	—	8.0	8.0
W	—	—	—	—	—	—
M ¹	—	—	6.2	—	—	7.6
L	—	—	7.4	—	—	9.5
W	—	—	—	—	—	—
M ²	—	—	6.2	—	—	8.0
L	—	—	8.4	—	—	10.0
W	—	—	—	—	—	—
M ³	—	—	6.6	7.0	—	7.6
L	—	—	8.5	8.3	—	8.6
W	—	—	—	—	—	—

TABLE 3
NUMERICAL DATA ON *Orohippus pumilus* FROM THE
BLACK'S FORK MEMBER

	<i>N</i>	<i>OR</i>	<i>SR</i>	<i>M</i>	σ	<i>V</i>
P ³						
L	2	7.1-7.2		7.15	—	—
W	2	6.3-8.4		7.35	—	—
P ⁴						
L	3	6.2-6.3		6.27	—	—
W	3	7.2-8.0		7.70	—	—
M ¹						
L	4	6.2-7.9		7.25	—	—
W	4	7.4-9.5		8.75	—	—
M ²						
L	4	6.2-8.0		7.12	—	—
W	4	8.4-10.0		9.02	—	—
M ³						
L	7	6.6-8.0	3.15	7.26 \pm 0.18	0.49 \pm 0.13	6.69 \pm 1.79
W	7	8.0-9.0	2.31	8.46 \pm 0.13	0.36 \pm 0.09	4.22 \pm 1.13
P ²						
L	3	6.2-6.3	—	6.27	—	—
W	3	3.0-3.4	—	3.20	—	—
P ₃						
L	7	6.2-7.6	3.62	6.77 \pm 0.21	0.56 \pm 0.15	8.26 \pm 2.21
W	7	4.0-4.7	1.62	4.23 \pm 0.09	0.25 \pm 0.07	5.91 \pm 1.58
P ₄						
L	14	6.3-7.3	2.42	6.95 \pm 0.10	0.37 \pm 0.07	5.38 \pm 1.02
W	14	4.3-5.6	2.24	5.00 \pm 0.09	0.34 \pm 0.06	6.90 \pm 1.30
M ₁						
L	15	6.5-8.0	2.42	7.24 \pm 0.10	0.37 \pm 0.07	5.17 \pm 0.94
W	15	4.2-5.7	2.51	5.18 \pm 0.10	0.39 \pm 0.07	7.49 \pm 1.37
M ₂						
L	13	6.7-7.9	2.03	7.45 \pm 0.09	0.31 \pm 0.06	4.21 \pm 0.82
W	13	4.7-5.9	2.28	5.36 \pm 0.07	0.35 \pm 0.07	6.57 \pm 1.29
M ₃						
L	13	9.3-11.3	3.85	10.25 \pm 0.16	0.59 \pm 0.12	5.79 \pm 1.13
W	13	4.4-5.9	2.48	5.12 \pm 0.11	0.38 \pm 0.07	7.48 \pm 1.47

geneous sample. The coefficients of variation for the linear dimensions of the teeth are consistent with the hypothesis that a single population is represented. In the case of tooth length, for no tooth does V exceed 7.00 (see table 3). The distributions of tooth dimensions approach the normal distribution when a sample of reasonable size is available, as, for example, in the case of M_3 (see fig. 3).

In the case of tooth structure also, there is remarkably little variation. In the few cases of appreciable variation discussed below, there is more or less continuous variation in structure between extreme morphological types.

There is a diastema between P^1 and P^2 . In most specimens this diastema is about as long as the anterior-posterior diameter of P^2 . In one specimen (A.M.N.H. No. 12648), however, the diastema is shorter than this on one side and almost absent on the other.

P^2 consists of two well-developed external cusps of about equal size and a prominent lobe-like projection or shelf at the postero-internal corner of the tooth. The internal edge of this shelf is somewhat crenulated, but no distinct cusp is present upon it.

P^3 and P^4 are more advanced towards molariformity than the corresponding teeth in any species of *Hyracotherium*. P^3 has four well-developed cusps of roughly equal size. The protocone and the hypocone are somewhat closer together than are the paracone and the metacone. The ectoloph is straight and rather low, and the paraconule and metaconule are very distinct. The cingulum is weak and sharply constricted between the paracone and the metacone. In most specimens there is the slightest suggestion of a mesostyle. In the particular specimen mentioned above (A.M.N.H. No. 12648) the mesostyle is quite strong. The parastyle is strong and located relatively far anterior. This character in conjunction with the relative closeness of the protocone and the hypocone results in an acute antero-external angle ($50-55^\circ$). The antero-internal angle is obtuse ($125-130^\circ$) while the posterior angles are about 90 degrees each.

In P^4 the protocone is more medial than the hypocone but the anterior-posterior distances between the protocone and the hypocone, and between the paracone and the metacone, are about equal. The anterior borders of the tooth are approximately parallel, and the external angles are roughly 90 degrees each. The antero-internal angle is acute ($55-60^\circ$) and the postero-internal angle is obtuse ($120-125^\circ$). The ectoloph is not V-shaped. The paraconule and metaconule are prominent. The cingulum is weak and moderately constricted between the paracone and the metacone. The parastyle is somewhat weaker than

in P^3 and not so far anterior, and the mesostyle is a little stronger than in P^3 .

The upper molars of *O. pumilus* differ from those of *O. major* in that the ectoloph is relatively higher and sharper, both between the parastyle and the paracone, and between the paracone and the metacone. The ectoloph is perhaps slightly more sharply V-shaped than in *O. major*, but the interior angle formed is still very slightly obtuse. The point of the V is very close to the mesostyle which is considerably stronger than in *O. major*.

No P_1 is known but, if one can judge from the alveolus present in a few specimens, a diastema about as long as the anterior-posterior diameter of P_2 was present.

P_2 is relatively larger than in *Hyracotherium* and relatively broader. The posterior cusp is relatively larger than in *Hyracotherium* but still considerably smaller than the anterior cusp. A low crest, absent in *Hyracotherium*, runs between the two cusps.

P_3 is like that of *Hyracotherium* in the possession of a large protoconid and a much smaller metaconid. In contrast to *Hyracotherium* the hypoconid is fully as large as the protoconid, and a small but obvious entoconid is present. The tooth is usually quite narrow anteriorly, but there is some variation in the distance of forward projection of the paralophid.

P_4 is essentially molariform in that an entoconid comparable in size to the other major cusps is present. In some individuals P_4 is, except for its smaller size, indistinguishable from M_1 . In others, however, the protoconid and metaconid are rather closely applied to each other, and the paralophid is long and projects quite far anteriorly. These characters give the tooth a rather primitive aspect reminiscent of *Hyracotherium*. P_4 's of the species cannot be divided into two distinct groups on the basis of this character, as there is a nearly continuous series of intergrades between the extremes described above. P_4 is the most variable tooth in the dentition, as it is in *Hyracotherium*. In *Hyracotherium* an entoconid is sometimes present, but it is never comparable in size to the other major cusps.

M_1 and M_2 of *O. pumilus* are nearly identical in structure to those of *Hyracotherium*. The major cusps are perhaps a little higher relatively and the cingulum is more sharply constricted between the protoconid and the hypoconid.

M_3 differs markedly from that of *Hyracotherium* only in the structure of the heel. It is relatively somewhat shorter than in *Hyracotherium*, and it is narrower and more sharply constricted anteriorly.

In his original description Marsh (1871) compared the type specimen of *Lophiotherium ballardi* with the type of *Lophiotherium sylvaticum* (Leidy, 1871) which was also later referred to *Orohippus* (Trouessart, 1898). The species was distinguished from *Lophiotherium sylvaticum* because of its smaller size. Granger (1908) recognized the species but stated that it might prove to be identical with *Orohippus pumilus* when more complete material was known. The type specimen consists of the smallest M_2 and the smallest M_3 known from the lower Bridger beds. Examination of figure 1 will show, however, that it is only slightly smaller than other teeth in the sample. This may simply represent another example of the quite common practice, particularly among earlier workers, to select extreme variants as type specimens.

Cope (1872) characterized the species *Heliotherium procyoninum* in the words, "This species is distinguished from those already known as pertaining to this genus by its small size, as it did not much exceed the raccoon in dimensions." As mentioned in the discussion of generic synonymy, no author had referred any species to this genus previous to the above description nor has any species been referred to it since. Later Cope (1873a) put the species in *Orohippus* and again characterized it by its small size. Marsh (1873) and Granger (1908) tentatively synonymized the species with *O. pumilus*.

Orohippus pumilus is the type species of the genus. A discussion of the original description is included under the generic synonymy.

Granger (1908) recognized *O. pumilus*, but as he had referred *Lophiodon pumilus* (Marsh, 1871) to *Orohippus* it was necessary to designate the species by a new name; Granger chose *O. typicus*. He considered the two species to be very similar, even though all previous writers had referred them to different genera. He stated that they could be distinguished only on the basis of the greater anterior-posterior diameter of the molars in the type specimen of *Lophiodon pumilus* and in the slightly different form of P^3 and P^4 in the two types. As the two specimens differ very little in the anterior-posterior diameter of the upper molars (0.4 mm. in the case of M^3), I assume that Granger referred to the difference in relative anterior-posterior diameter. In the type specimen of *Orohippus pumilus* the ratio of the length to the width is 0.78, while in the type specimen of *Lophiodon pumilus* it is 0.88. It is difficult to evaluate this considerable difference. The character is highly variable in species of *Hyracotherium*, and the same appears to be true in species of *Orohippus*, although there are too few specimens of upper teeth of any one species to allow an adequate analysis of the variation. That Granger actually placed little

stock in the taxonomic value of the character is indicated by the fact that he placed the type specimen of *Hyracotherium procyoninum*, in which the ratio is 0.85, in *Orohippus typicus*.

P⁴ in the two type specimens is nearly identical in structure.

Cope (1884) placed *Oligotomus cinctus*, the type species of *Oligotomus* (see discussion under generic synonymy), in the genus *Pliolophus*. He distinguished the species from the others that he had referred to *Pliolophus*, that is, *P. cristonensis*, *P. vulpiceps*, *P. loevii*, *P. sylvaticus*, and *P. uintanus*, the former three of which were ultimately placed in *Eohippus* (Granger, 1908), on the basis of its size and the acute angles of the "external V's." The type specimen is quite worn and the "external V's" apparently represent the worn surface of the hypoconulid, hypoconid, and the metalophid; and the protolophid, protoconid, and paralophid. This character appears to show very little variation from specimen to specimen. Granger (1908) tentatively synonymized this species with *Orohippus ballardi*.

Cope (1873a) had referred the specimen later designated as the type of *Hyracotherium osbornianum* to *Orotherium sylvaticum*. Later (1884) he stated that the specimen differed from the type specimen of *O. sylvaticum* in its narrower P₄, the absence of an intermediate tubercle on M₁, and the presence of a double anterior internal cusp on M₁, and designated the specimen as the type of the species *Hyracotherium osbornianum*. The separation of the two species is followed in the present classification, and the difference in width of P₄ is regarded as a valid specific character. It should be pointed out, however, that in no unworn dentition referable to *Orohippus* is the twin metaconid not perfectly obvious, and this character is detectable in the relatively well-worn molars of the type specimen of *Orotherium sylvaticum*.

Granger (1908) referred the species to *Orohippus* as had Trouessart (1898). Granger stated simply, "The type of this species exhibits but few characters for comparison, but it represents a medium sized form from the lower horizon and does not appear to be referable to any previously described member of the genus." He referred an associated skull, lower jaw, and partial skeleton (A.M.N.H. No. 12648) to *O. osbornianum*. This specimen differs somewhat from the morphology of *Orohippus pumilus* as described above in that there is almost no diastema between P¹ and P², and P₄ is relatively broad posteriorly. This specimen may have important bearing on the specific evolution within the genus and is considered at some length in the section of this paper devoted to evolution.

Granger (1908) characterized *O. atavus* as a medium-sized species from the lower beds, which is, with the exception of *O. major*, the most primitive of the genus. The primitive character cited is the structure of P^3 which he stated shows little advance over that of *Eohippus craspedotum*. The structure of P^3 is indeed primitive, but it falls well within the rather narrow limits of variation for this character among specimens from the lower beds.

Orohippus progressus Granger, 1908

Orohippus progressus GRANGER, 1908, p. 250.

TYPE: A.M.N.H. No. 12120, fragmentary skull from Twin Buttes, Bridger Basin, Wyoming.

HYPODIGM: The type specimen and U.S.N.M. Nos. 17854, 17866, 17867, 17871.

KNOWN DISTRIBUTION: Bridger formation, southwestern Wyoming, Twin Buttes member (horizons C and D).

DIAGNOSIS: Size small. Mean length of M_3 , 9.25 mm. (four specimens). Mean length of P^4 , 6.37 mm. (three specimens). Disastema between P^1 and P^2 . P^4 narrower internally than externally, with hypocone nearly as far internal as protocone. Protoconid and metaconid usually closer together than hypoconid and entoconid on P_4 and lower molars. P_4 , M_1 , and M_2 usually narrower anteriorly than posteriorly.

The type specimen of *Orohippus progressus* consists of a fragmentary skull with P^1 – M^3 . Granger (1908) characterized the species as a small form from the upper beds, comparable in size to *O. typicus*, but differing from that species in the greater development of the parastyle and mesostyle and in the less-rounded outline of the last molar. The type differs from all known lower Bridger specimens in the degree of development of the parastyle and mesostyle, a fact pointed out by Granger, and in a few other characters, particularly in the structure of P^3 and P^4 . The type and three other similar specimens can be easily

TABLE 4
MEASUREMENTS OF TYPE SPECIMEN OF *Orohippus progressus*

P^3		P^4		M^1		M^2		M^3	
L	W	L	W	L	W	L	W	L	W
6.9	7.2	6.9	7.0	7.1	8.8	7.3	8.6	7.0	8.5

TABLE 5
NUMERICAL DATA ON *Orohippus progressus* FROM THE TWIN BUTTES MEMBER

	<i>N</i>	<i>OR</i>	<i>M</i>
P ³			
L	4	6.1-7.0	6.68
W	4	6.1-7.2	6.70
P ⁴			
L	3	6.5-6.9	6.37
W	3	6.9-7.2	7.02
M ¹			
L	1		7.0
W	1		8.7
M ¹			
L	2	6.3-6.5	6.40
W	2	4.4-5.0	4.70
M ₂			
L	2	7.0-7.0	7.0
W	2	4.7-5.4	5.05
M ₃			
L	4	9.2-9.3	9.25
W	4	4.4-5.1	4.62

distinguished from the remainder of the specimens from the upper beds by morphological criteria. These four dentitions have a significantly smaller mean size than upper dentitions of other structural type, although there is slight overlap in this character.

The type specimen is not associated with a lower dentition nor are any of the upper dentitions of similar structural type which have been assigned to this species. Assignment of lower teeth to the species must be based largely on size. There is a group of small lower teeth from the upper beds which, if one can judge from the comparative sizes of associated upper and lower teeth in other species of *Orohippus* and in *Hyracotherium*, would have been associated with upper teeth in the size range of the type specimen and the other upper dentitions which have been referred to the species. The distributions of the linear dimensions of this group of lower teeth does not overlap the distributions of

teeth assigned to other upper Bridger species. The distinctness of this distribution must be regarded as spurious, as the size distribution of the upper teeth assigned to the species overlaps that of other species. In addition to the size there is a fairly distinct structural character that serves to distinguish the lower teeth assigned to the species.

P¹ is preserved only in the type specimen. It is a simple tooth with a single laterally compressed cusp. There is a diastema between P¹ and P² which is about as long as the anterior-posterior diameter of P². This character alone serves to distinguish specimens that pertain to this species from all others collected from the Twin Buttes member.

P³ is very similar to that of *O. pumilus*. The protocone and the hypocone are, however, about equidistant from the external border of the tooth, and the parastyle is less anteriorly located, giving the tooth a more distinctly quadrate aspect. There is the faintest trace of a mesostyle on P³.

P⁴ differs from that of *O. pumilus* in that the hypocone is nearly as far internal as the protocone, and the protocone and hypocone are closer together than the paracone and metacone. The tooth is consequently somewhat narrower internally than externally, and the posterior borders are not parallel. The parastyle is a little stronger than in *O. pumilus*, and in all specimens there is at least a trace of a mesostyle. In one unworn specimen (A.M.N.H. No. 13109) the mesostyle is quite strong, and the ectoloph is distinctly V-shaped.

The upper molars differ from those of *O. pumilus* only in that the ectoloph is a bit higher and the parastyle and mesostyle are stronger. The point of the ectoloph V and the crest of the mesostyle nearly merge.

Lower teeth referable to this species are, with the exception of a single M₃, well worn. The only distinct morphological character of the lower teeth is in the heel of M₃. The heel is relatively very short and narrow, and it is not constricted anteriorly. The general shape of the lower molars is like that of other species found in the upper beds in that the protoconid and metaconid tend to be closer together than the hypoconid and entoconid, and the tooth is in some cases narrower anteriorly than posteriorly. There appears to be considerable variation in this character.

No teeth anterior of P₄ are known.

Orohippus sylvaticus (Leidy), 1870

Lophiotherium sylvaticum LEIDY, 1870, p. 126.

Pliolophus sylvaticus (Leidy), COPE, 1884, p. 631.

- Pachynolophus sylvaticus* (Leidy), ROGER, 1896, p. 170.
Orohippus sylvaticus (Leidy), TROUESSART, 1898, p. 773.
Orotherium uintanum MARSH, 1872, p. 217.
Pliolophus uintanus (Marsh), COPE, 1884, p. 651.
Pachynolophus uintanus (Marsh), ROGER, 1898, p. 170.
Epihippus uintanus (in part) (Marsh), TROUESSART, 1898, p. 777.
Orohippus uintanus (Marsh), MATTHEW, 1899, p. 45.

TYPE: U.S.N.M. No. 3753, fragment of left ramus with P_4-M_3 from Henry's Fork, Bridger Basin, Wyoming.

TYPE SPECIMEN OF SYNONYM: *Orotherium uintanum*: Y.P.M. No. 11314, fragment of right ramus with P_2-M_3 from Henry's Fork, Bridger Basin, Wyoming.

HYPODIGM: The type specimen, the type specimen of the synonym, and Y.P.M. Nos. 11314, 11322, and U.S.N.M. Nos. 13403, 17849, 17850, 17851, 17861, 17862, 17864, 17869, 17874, 17876.

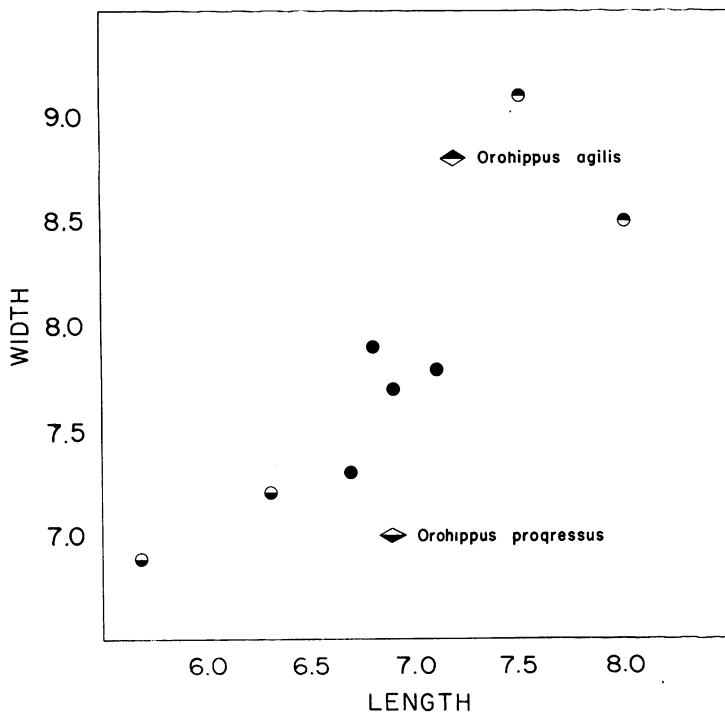


FIG. 4. Scatter diagram of length and width of P^4 of sample from Twin Buttes member. Symbols: Solid, specimens referable to *Orohippus sylvaticus*; solid below, specimens referable to *O. progressus*; solid above, specimens referable to *O. agilis*; diamonds, type specimens.

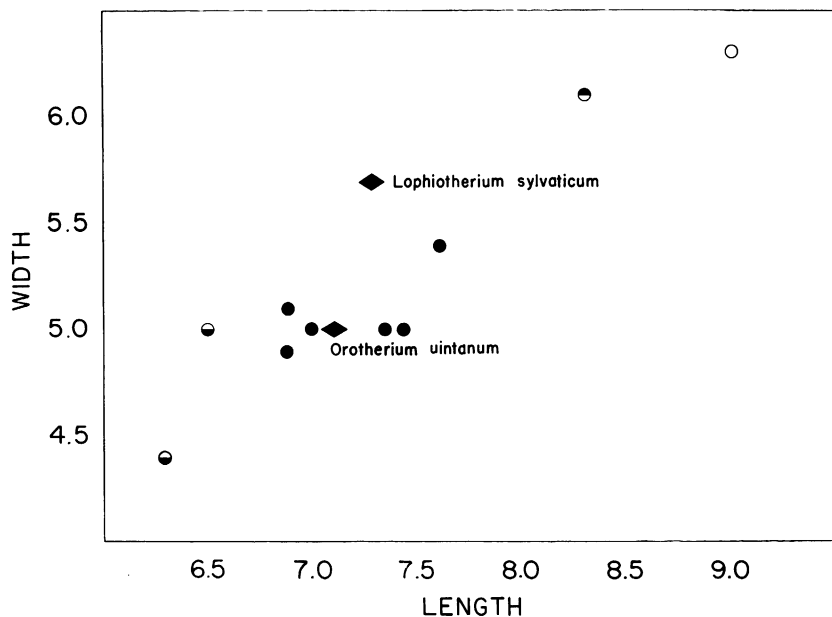


FIG. 5. Scatter diagram of length and width of M_1 of sample from Twin Buttes member. Symbols: Solid, specimens referable to *Orohippus sylvaticus*; solid below, specimens referable to *O. progressus*; solid above, specimens referable to *O. agilis*; in outline, specimen referable to *O. major*; diamonds, type specimen and type of synonym.

KNOWN DISTRIBUTION: Bridger formation, southwestern Wyoming, Twin Buttes member (horizons C and D).

DIAGNOSIS: No diastema between P^1 and P^2 . P^2 triangular. Antero-external angle of P^3 more acute than in *O. pumilus*. Protocone of P^3 slightly external of hypocone. P^4 molariform but slightly narrower internally than externally. Ectoloph on molars rises nearly to crest of external cusps. Parastyle and mesostyle strong. No diastema between P_1 and P_2 . Protoconid and metaconid closer together than hypoconid and entoconid in P_4 and lower molars. P_4 and M_1 and often M_2 and M_3 distinctly narrower anteriorly than posteriorly. Heel of M_3 relatively long and narrow and unconstricted anteriorly.

The type specimen of *O. sylvaticum* consists of a fragment of the left ramus with P_4 – M_3 . The majority of the lower teeth that have been found in the upper Bridger beds are probably assignable to the same species as this type. They are similar in size, and, although these specimens vary considerably in shape and structure, there is continuous variation between extremes and at least one distinct morphological

character which all of these teeth have in common. There is, in my opinion, no associated upper and lower dentition referable to this species. Granger (1908) assigned an associated upper and lower dentition (A.M.N.H. No. 12648) to *O. sylvaticum*. Although the lower dentition resembles that of the type specimen of *O. sylvaticum* in a number of respects, it differs from this type and from the other upper Bridger lower dentitions in other striking respects. In the present classification this specimen is referred to *O. agilis* and is discussed in the next section. The reference of upper molars to the species must, as in the case of the lower molars of *O. progressus*, be indirect. There is a small group of upper teeth of distinct morphological type the size of which is compatible with their being associated with the type specimen of *O. sylvaticum* and with the majority of other upper Bridger lower dentitions, and they have been assigned to this species.

P¹ is not present in any specimen referred to this species, but the alveolus of this tooth is presented in several specimens. There was no diastema between P¹ and P².

As in *O. pumilus* and *O. progressus* P² consists of two external cusps of roughly equal size. The internal portion of the tooth is formed by a shelf which is narrow anteriorly and broadens evenly posteriorly. It is not lobate posteriorly as it is in *O. pumilus* and *O. progressus*. The tooth as a whole has the form of a narrow triangle, with the base posterior. Located along the internal edge of the shelf are two small cuspules more closely spaced than are the external cusps.

TABLE 6

MEASUREMENTS OF TYPE SPECIMEN AND TYPE SPECIMEN OF SYNONYM OF
Orohippus sylvaticus

	P ₂		P ₃		P ₄		M ₁		M ₂		M ₃	
	L	W	L	W	L	W	L	W	L	W	L	W
<i>Lophiotherium</i>												
<i>sylvaticum</i>	—	—	—	—	6.8	5.2	7.6	5.7	—	—	10.8	5.2
<i>Orotherium</i>												
<i>uintanum</i>	—	—	6.9	4.5	6.9	5.0	7.1	5.0	7.7	5.4	11.3	5.0

In general aspect the crown view of P³ is very similar to that of *O. pumilus*. The protocone is, however, somewhat external of the hypocone, and the parastyle is a little farther anterior, giving the tooth an even more narrowly pointed anterior aspect than that of *O. pumilus*.

TABLE 7

NUMERICAL DATA ON *Orohippus sylvaticus* FROM THE TWIN BUTTES MEMBER

	<i>N</i>	<i>OR</i>	<i>SR</i>	<i>M</i>	σ	<i>V</i>
P ²						
L	2	6.3-6.2		6.50		
W	2	4.0-4.5		4.25		
P ³						
L	2	6.8-7.0		6.90		
W	2	6.3-6.7		6.50		
P ⁴						
L	4	6.7-7.1		6.85		
W	4	7.3-7.9		7.67		
M ¹						
L	3	7.0-7.6		7.40		
W	3	8.4-8.8		8.57		
P ₂						
L	1			5.9		
W	1			3.0		
P ₃						
L	5	6.3-6.9		6.48		
W	5	3.8-4.6		4.18		
P ₄						
L	8	6.3-6.9	1.46	6.62 ± 0.08	0.23 ± 0.06	3.41 ± 0.85
W	8	4.5-5.2	1.31	4.91 ± 0.07	0.20 ± 0.05	4.11 ± 1.03
M ₁						
L	8	6.9-7.6	1.70	7.20 ± 0.09	0.26 ± 0.07	3.65 ± 0.91
W	8	4.9-5.7	1.76	5.14 ± 0.10	0.27 ± 0.07	5.29 ± 1.32
M ₂						
L	5	7.5-7.7		7.62		
W	5	5.2-5.6		5.36		
M ₃						
L	7	10.0-11.3	3.02	10.57 ± 0.18	0.47 ± 0.12	4.41 ± 1.18
W	7	5.0-5.2	0.54	5.16 ± 0.03	0.08 ± 0.02	1.63 ± 0.44

The ectoloph between the paracone and the metacone is V-shaped, and there is a distinct mesostyle which merges with the vertical ridge extending dorsally from the point of the ectoloph V.

P⁴ is to all intents and purposes molariform. It differs from M¹ only in that the protocone and hypocone are a little closer together than the paracone and metacone and that the tooth is consequently a little narrower internally than externally.

The ectoloph of M¹ is high and sharp and extends nearly to the points of the paracone and metacone. It thus forms a nearly continuous external ridge, with peaks at the paracone and metacone. Both the parastyle and mesostyle are stronger than they are in *O. progressus*. No M² or M³ referable to this species has ever been found.

Although no P₁ is known, the alveolus of this tooth is present in a few specimens. There was no diastema between P₁ and P₂.

P₂ and P₃ are structurally indistinguishable from those of *O. pumilus*. They are perhaps relatively a little larger and more massive.

P₄, M₁, and M₂ of *O. sylvaticus* are characterized by the fact that the protoconid and metaconid are distinctly closer together than are the hypoconid and entoconid, and that the tooth is nearly always markedly narrower anteriorly than posteriorly. As noted above, this character is also present in *O. progressus*, but in *O. sylvaticus* it shows a more extreme development in some individuals. Both of these characters show considerable variation. In some individuals they are scarcely noticeable, while in others the anterior cusps are very closely applied to one another and the posterior end of the tooth is broad, with a distinct, laterally projecting lobe. Almost all conceivable variations between these two extremes are to be found in lower teeth assigned to this species, and it is quite impossible to divide them into two, or even into three or four, distinct groups on the basis of these characters.

M₃ is like the other molars in that the anterior cusps are closer together than the posterior cusps. The heel relatively is long and unrestricted anteriorly.

Orotherium uintanum is the type species of the genus *Orotherium*. Marsh (1872) in his original description stated that the genus differed from *Lophiotherium* in the possession of a prominent tubercle on P₂, and in the slightly bifid character of the anterior inner cone of the lower molars. He pointed out that the type specimen resembled the types of *Lophiotherium sylvaticum* and *Lophiotherium ballardi*, and that both of these species should be referred to *Orotherium*.

Granger (1908) recognized *Orohippus uintanus* as a valid species, citing as specific characters, particularly as separating it from *O. syl-*

vaticus, the slenderness of M_3 , the wide separation of the anterior pair of cusps, and the comparatively weak entoconid on P_3 . The relative slenderness of various teeth I have found to be a character that varies widely within what appear to be single populations. The fact that the closeness of the protoconid and the metaconid is an extremely variable character is pointed out above. Granger based much of his characterization of *O. sylvaticus* on a specimen (A.M.N.H. No. 12649) which is referred to *O. agilis* in this classification. In this specimen the protoconid and the metaconid are much closer together than they are in the type specimen of *O. sylvaticus* or in any specimen referred to that species here, and it differs from all of these in a number of other very striking characters discussed under *O. agilis*. Although the type specimens of *O. uintanum* and *O. sylvaticus* differ in the proximity of the protoconid and metaconid, neither specimen represents the extreme of variation in that character among the specimens that I have assigned to *O. sylvaticus*. Granger's characterization of P_3 is based on the above-mentioned specimen, as the type of *O. sylvaticus* contains no P_3 .

Orohippus agilis Marsh, 1873

Orohippus agilis MARSH, 1873, p. 407.

Hyracotherium agilum (Marsh), COPE, 1877, p. 267.

Epihippus agilis (Marsh), OSBORN, 1890, in Scott and Osborn, p. 506.

TYPE: Y.P.M. No. 1268, fragmentary skull, forelimb, and vertebrae from Henry's Fork, Bridger Basin, Wyoming.

HYPODIGM: The type specimen and A.M.N.H. Nos. 12649 and 12127.

KNOWN DISTRIBUTION: Bridger formation, southwestern Wyoming, Twin Buttes member (horizons C and D).

DIAGNOSIS: No diastema between P^1 and P^2 . P^2 triangular, with small internal cusp. P^4 fully molariform but with lateral border parallel to edge of palate. P^3 like P^4 but narrower internally than externally. Paraconule and metaconule of molars less prominent than in other species. Mesoloph strong. Ectoloph rises to points of external cusps. Ectoloph V about 90 degrees. P_4 and lower molars with anterior cusps much closer together than posterior cusps. P_4 , M_1 , and M_2 wider posteriorly than anteriorly. P_4 widest tooth of lower series. Heel of M_3 short and relatively broad.

Marsh (1873) distinguished this species from *O. pumilus* by the fact that the inner cones of the upper molars are more nearly of equal size and that each has a distinct basal ridge. The two types are assigned to different species in this classification. The minor differences cited by Marsh, however, would scarcely seem to justify specific separation.

Granger (1908) recognized the species. He separated it from *O. sylvaticus* because of its weaker parastyle and mesostyle and because the last molar was probably more quadrate in outline (only the root of the last molar is preserved in the type). As the type specimen of *O. sylvaticus* consists of lower teeth, the comparison is based on the associated upper and lower dentition assigned by Granger to *O. sylvaticus* (A.M.N.H. No. 12649). The lower teeth of this specimen are described in some detail because of their crucial taxonomic importance and because they are the only lower teeth referred to *O. agilis* in this classification. The upper teeth of this specimen are very similar in every respect to those of the type specimen of *O. agilis*. The type of *O. agilis* is well worn, and as the parastyle and mesostyle are subject to rapid size reduction as a result of abrasion, the fact that these elements are smaller than they are in the virtually unworn referred specimen does not appear to be crucial. The shape of the last molar, which incidentally differs very little in the two specimens, is extremely variable. It is unusual to find any two specimens that are precisely alike in this character.

P¹ consists of a single, laterally compressed cusp. There is no diastema between P¹ and P². P² has, in addition to two lateral cusps of about equal size, a smaller, but well-developed internal cusp about midway between the lateral cusps. The tooth is roughly triangular in crown view.

TABLE 8
MEASUREMENTS OF TYPE OF *Orohippus agilis*

P ³		P ⁴		M ¹		M ²		M ³	
L	W	L	W	L	W	L	W	L	W
6.9	7.2	6.9	7.0	7.1	8.8	7.3	8.6	7.0	8.5

In general outline P³ differs from the molars only in that the external border is parallel to the edge of the palate and that the tooth is somewhat narrower internally than externally. The ectoloph is less sharply V-shaped, and the mesostyle is weaker than in the molars.

P⁴ is fully quadrate but differs from the molars in that it is relatively smaller and that the lateral border is nearly parallel to the edge of the palate. The ectoloph is slightly less sharply V-shaped than in the molars, and the mesostyle, although stronger than in P³, is weaker than in the molars.

TABLE 9
NUMERICAL DATA ON *Orohippus agilis* FROM THE TWIN BUTTES MEMBER

	<i>N</i>	<i>OR</i>	<i>M</i>
P ²			
L	1		6.8
W	1		5.4
P ³			
L	2	7.4-8.0	7.70
W	2	7.8-8.7	8.25
P ⁴			
L	2	7.5-8.0	7.75
W	2	8.5-9.1	8.80
M ₁			
L	3	7.8-8.7	8.17
W	3	9.5-10.5	10.00
M ²			
L	2	8.1-9.2	8.65
W	2	10.4-11.0	10.70
M ³			
L	2	7.8-7.9	7.85
W	2	9.8-10.5	10.01
P ₃			
L	1		7.5
W	1		5.2
P ₄			
L	1		7.6
W	1		6.2
M ₁			
L	1		8.3
W	1		6.1
M ₂			
L	1		8.4
W	1		6.3
M ₃			
L	1		10.4
W	1		5.4

TABLE 10

RATIO OF TRANSVERSE DIAMETER OF P_4 MEASURED ALONG LINE DEFINED BY PROTOCONID AND METACONID TO TRANSVERSE DIAMETER MEASURED ALONG LINE DEFINED BY ENTOCONID AND HYPOCONID

	<i>N</i>	<i>OR</i>	<i>M</i>
<i>Orohippus sylvaticus</i>	4	0.89-0.95	0.92
Type specimen of <i>O. sylvaticus</i>	1		0.90
Type specimen of <i>Orotherium uintanum</i>	1		0.92
<i>Orohippus agilis</i> (A.M.N.H. No. 12649)	1		0.83

TABLE 11

RATIO OF LENGTH OF M_3 TO LENGTH OF M_1-M_2

	<i>N</i>	<i>OR</i>	<i>M</i>
<i>Hyracotherium</i> (various species, horizons, and localities)	63	0.39-0.44	0.41
<i>Orohippus</i> (all species except <i>O. agilis</i>)	8	0.40-0.43	0.41
Type specimen of <i>O. sylvaticus</i> , U.S.N.M. No. 3753 (also included in above)	1		0.41
<i>Orohippus agilis</i> , A.M.N.H. No. 12649	1		0.38
Type specimen of <i>Ephippus parvus</i> , A.M.N.H. No. 2038	1		0.38

Only in this species of *Orohippus* are the paraconule and metaconule distinctly less prominent than they are in *Hyracotherium*. Both of these cusps, but particularly the metaconule, tend to be merged with the lophs with which they are associated. The ectoloph V forms a sharper angle than in the other species of the genus, being just about 90 degrees. The mesostyle is slightly stronger than in *O. sylvaticus*.

The only lower teeth referred to *O. agilis* in this classification consist of P_3-M_3 associated with P^3-M^3 (A.M.N.H. No. 12649) which Granger referred to *O. sylvaticus* and on which he based much of his characterization of that species. The lower dentition of this specimen does, in some respects, resemble that of the type specimen of *O. sylvaticus*. The most striking of these resemblances is in the proximity of the anterior cusps of P_4 and the molars, and in the relatively great

posterior width of the teeth, particularly P_4 . It was noted in the discussion of *O. progressus* and *O. sylvaticus* that these characters are common in upper Bridger hyracotheres. In the specimen under consideration these characters are much more extreme than in any specimen referred to these species in this classification (see table 10). The probability that this specimen represents an extreme variant referable to *O. sylvaticus* or *O. progressus* is very remote. Owing to the extreme posterior width of P_4 , this tooth is actually the widest tooth of the lower series, which is not true of any other specimen found in the Bridger formation.

A character that even more strikingly distinguishes this specimen from all other Bridger hyracothere specimens and one that was apparently overlooked by Granger is the relative shortness of M_3 in relation to the length of the molar series. In this character the specimen differs from all known specimens of *Hyracotherium* and *Orohippus* and closely resembles *Epihippus* from the Uintan deposits (see table 11). Again it can be said that the probability that this represents simply an extreme variant referable to some other upper Bridger species is exceedingly remote.

The character of greater posterior width is much less pronounced in M_1 and M_2 than in P_4 , although in all the molars the anterior cusps are decidedly closer together than are the posterior cusps. The heel of M_3 is short and relatively broad.

DISCUSSION

The fact that advanced species of *Hyracotherium* and primitive species of *Orohippus* resemble one another so closely clearly indicates that *Hyracotherium* was the immediate ancestral form and that the transition might well have occurred in a relatively short time. There is, I believe, at least some evidence that bears on the question of which particular species of *Hyracotherium* was the progenitor of the genus *Orohippus*.

Granger (1908) remarked on the primitive aspect of the type specimen of *O. major* and on the similarity in shape of the molars between this specimen and the type specimen of *H. craspedotum*. It is also true that the lower teeth assigned to *O. major* resemble the lower teeth of *H. craspedotum* very closely. Very few specimens of *O. major* are found in either the upper or lower Bridger beds, which suggests that the species occupied an ecological niche rather distinct from that of the species with which it is found associated. *Hyracotherium craspedotum* is usually found to be outnumbered by other species of *Hyracotherium*

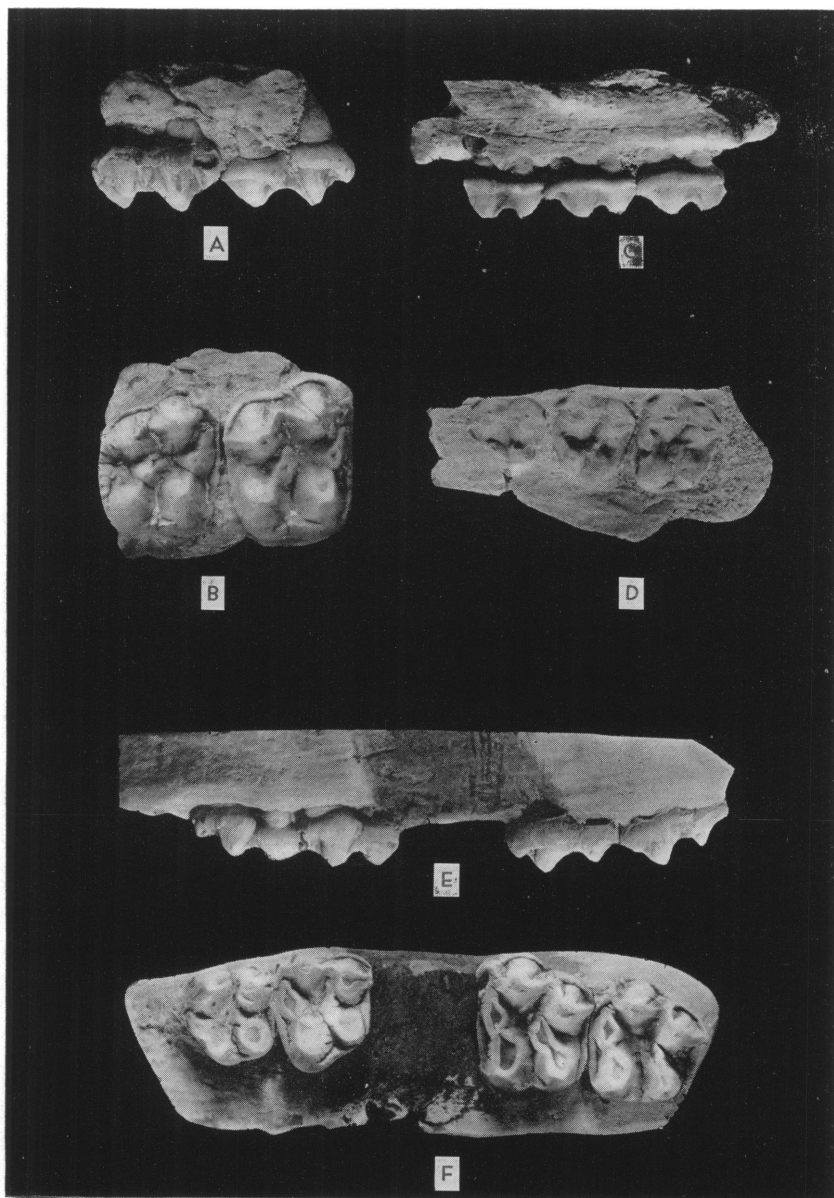


FIG. 7. A, B. *Orohippus major* Marsh. Type, Y.P.M. No. 11270, fragment of right maxilla with M² and M³. A. Lateral view. B. Crown view. $\times 2$. C, D. *Orohippus progressus* Granger. U.S.N.M. No. 17866, fragment of left maxilla with P²-P⁴. C. Lateral view. D. Crown view. $\times 2$. E, F. *Orohippus pumilus* (Marsh). A.M.N.H. No. 11629, fragment of left maxilla with P², P⁴, M², and M³. E. Lateral view. F. Crown view. $\times 2$.

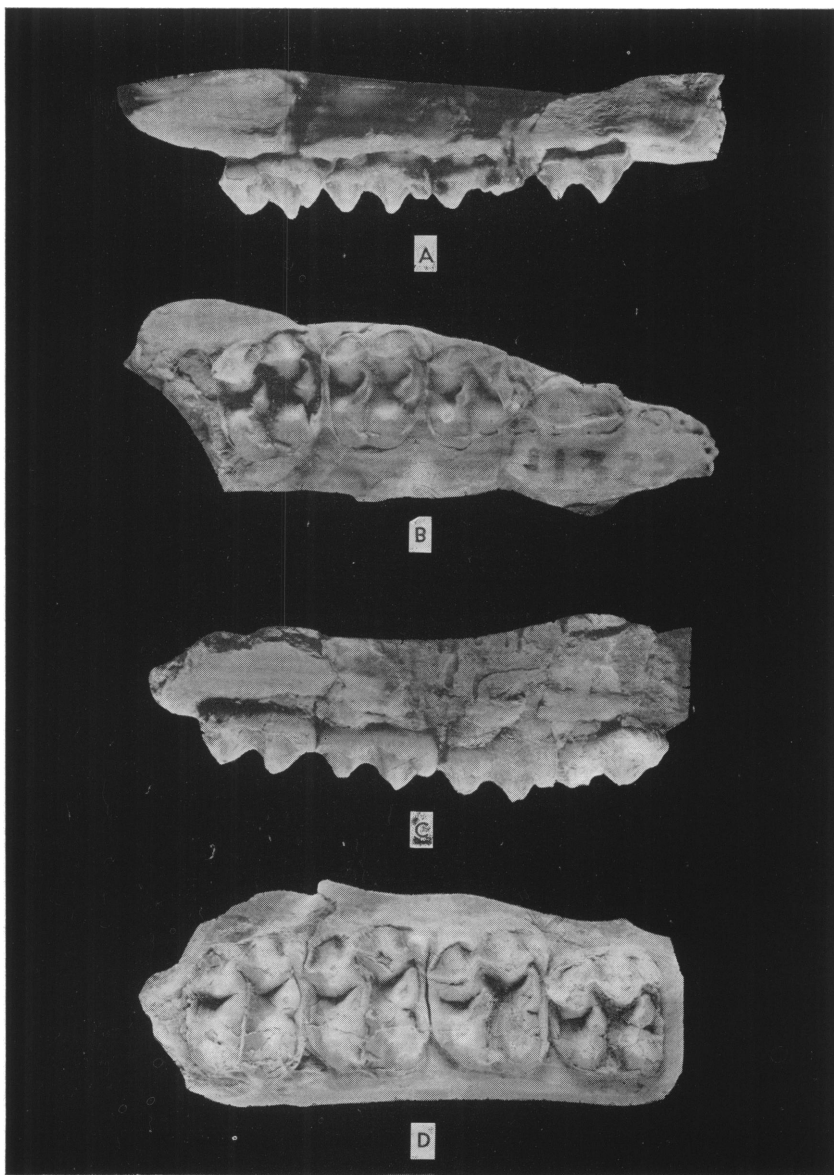


FIG. 8. A, B. *Orohippus sylvaticus* (Leidy). Y.P.M. No. 11322, fragment of right maxilla with P^2 - M^1 . A. Lateral view. B. Crown view. $\times 2$. C, D. *Orohippus agilis* Marsh. A.M.N.H. No. 12127, fragment of right maxilla with P^4 and M^1 . C. Lateral view. D. Crown view. $\times 2$.

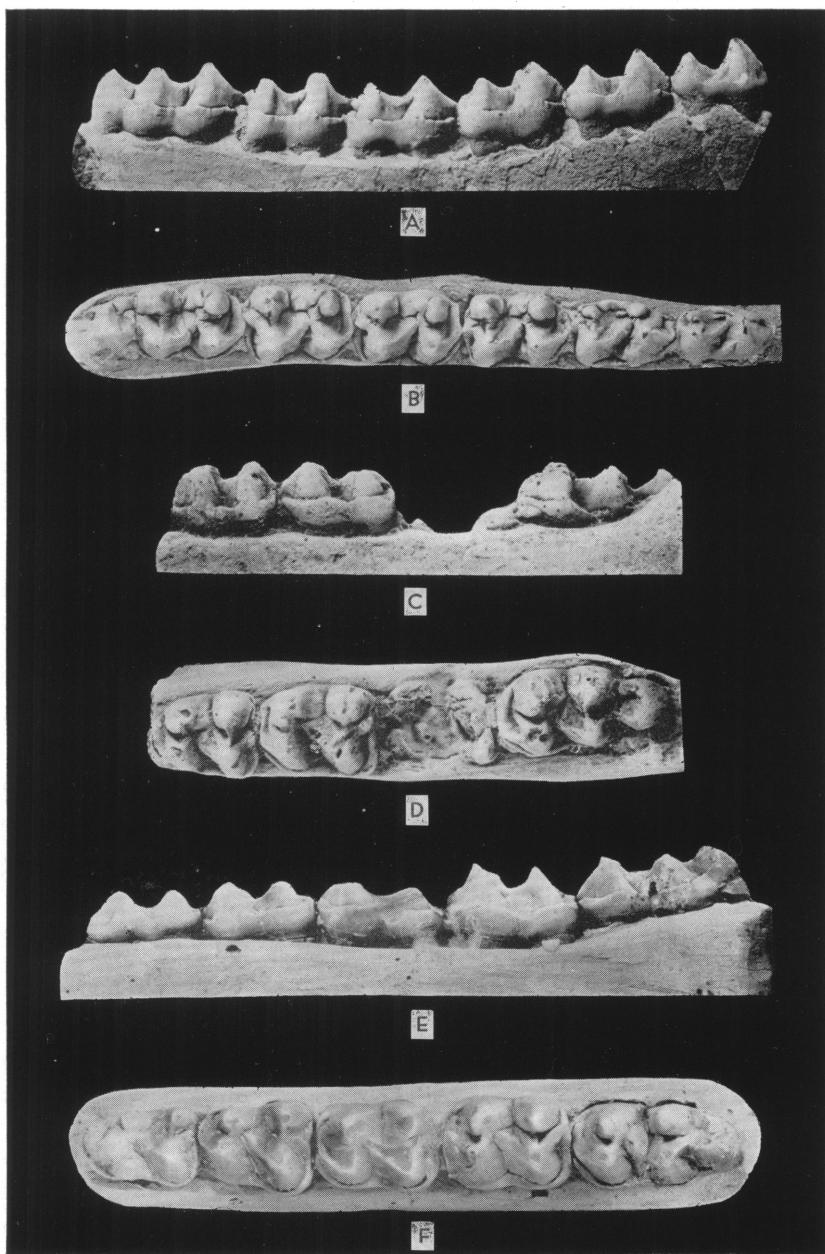


FIG. 9. A, B. *Orohippus pumilus* (Marsh). U.S.N.M. No. 13402, fragment of right mandibular ramus with P_2 - M_3 . A. Lateral view. B. Crown view. $\times 2$. C, D. *Orohippus sylvaticus* (Leidy). Cast of type. U.S.N.M. No. 3753, fragment of left mandibular ramus with P_4 - M_3 . C. Lateral view. D. Crown view. $\times 2$. E, F. *Orohippus agilis* Marsh. A.M.N.H. No. 12649, P_2 - M_3 . E. Lateral view. F. Crown view. $\times 2$.

with which it is associated. These possibly very superficial resemblances are far from conclusive evidence of a direct ancestral descendant relationship between the two species, but they perhaps suggest such a relationship. As P^3 and P^4 of *H. craspedotum* are quite distinctive, discovery of these teeth referable to *O. major* might throw considerable light on this question.

Orohippus pumilus is quite like *H. vasaccienne*, the other late Wasatchian hyracotherid. In P^4 of *H. vasaccienne* what appears to be an enlarged protoconule is located well anterior of a line between the paracone and the protocone. Apparently the protoconule exhibits a phylogenetic anteriomedial migration to give the tooth a distinctly quadrate rather than triangular aspect. In some specimens of *H. vasaccienne* one or more small cuspules are located along a ridge which runs anteromedially from the enlarged protoconule. A very slight anteromedial migration of the protoconule of *H. vasaccienne* and an enlargement of one of the cuspules would produce a tooth identical in structure to P^3 of *O. pumilus*. P^4 of *H. vasaccienne* exhibits no trace of a fourth major cusp. P^4 of *O. pumilus* has, of course, a well-developed hypocone, but it can be said, I think, that P^4 is less advanced towards a molariform condition than P^3 in this species because of the relatively external position of the hypocone.

In *H. craspedotum* P^4 is not in the least molariform, being simply triangular, with no trace of a fourth major cusp. P^4 is rather peculiar in its structure. A prominent shelf-like projection is located at the postero-internal corner of the tooth, and, although the metacone is somewhat anteroposteriorly elongated, this projection is devoid of a cusp. It appears unlikely that a tooth of such structure is related to the origin of P^4 of *O. pumilus*.

A further point of similarity between the two species is the fact that in most individuals of *Hyracotherium vasaccienne* the heel of M_3 is constricted anteriorly, although this character is never so pronounced nor constant in this species as it is in *Orohippus pumilus*. Neither *Hyracotherium craspedotum* nor *O. major* exhibits this character to the slightest degree.

If the two species of lower Bridger hyracotheres were derived from two different species of late Wasatchian hyracotheres, and, I repeat, the evidence for this is far from conclusive, at least two characters that are found in *Orohippus* and not in *Hyracotherium* were separately derived. These characters are the presence of a mesostyle and the V-shaped ectoloph. The parallel derivation of these characters presents no par-

ticular problem as they are known to have arisen independently in a number of condylarth and perissodactyl phyla.

All the upper Bridger species might well have been derived from *O. pumilus*. *Orohippus progressus* appears to be a relatively conservative line emanating from *O. pumilus*. Although the species is advanced over *O. pumilus* in some respects, it retains the diastema between P¹ and P² and the relatively primitive upper molars and premolars.

Orohippus sylvaticus and *O. agilis* resemble each other and differ from *O. pumilus* and *O. progressus* in the lack of a diastema between P¹ and P², in the high degree of molariformity attained in P⁴, and in the strength of the mesostyle and ectoloph. This led Granger (1908) to erect the subgenus *Aminippus* to include the species *O. sylvaticus*, *O. agilis*, and *O. uintanus*, a procedure that I consider perfectly valid and have abandoned only because I do not consider it entirely necessary.

The skull, jaws, and partial skeleton referred to *O. osbornianus* (A.M.N.H. No. 12648) by Granger (1908) and tentatively referred to *O. pumilus* in the present classification may have important bearing on the problem of the origin of *O. sylvaticus* and *O. agilis*. In this specimen P₄ shows the closeness of the anterior cusps and the greater posterior width so characteristic of upper Bridger specimens. The specimen further resembles upper Bridger specimens in that the diastema between P¹ and P² is very short on one side, while on the other side the diastema is virtually absent. On the other hand P³ and P⁴ are not in the least more molariform than they are in typical specimens referable to *O. pumilus*, and the heel of M₃ is constricted anteriorly as it is in that species. All of this strongly suggests that *O. sylvaticus* and *O. agilis* were derived from *O. pumilus* without passing through a stage in which the dentition was similar to that of *O. progressus*, that is, with a diastema and premolars somewhat more molariform than in *O. pumilus*. It is quite possible that *O. sylvaticus* and *O. agilis* were derived from *O. pumilus* separate from *O. progressus*.

In *O. agilis* the essential molariformity of P³ and P⁴, the strength of the mesostyle, the nearly crescentic form of the exterior cusps of the upper molars, and the relative shortness of M₃ clearly mark the species as the most advanced of the genus and the probable ancestor of *Epihippus*.

If it is assumed that the reference of particular specimens from the Twin Buttes member to one of three different species is correct, then the calculated coefficients of variation are rather low for the linear dimensions of the teeth in each species, lower in any case than similar

figures for *O. pumilus*. This fact is understandable on the basis that individuals that are intermediate in character between competing species tend to be eliminated by selection.

Only three specimens referable to *O. agilis* have ever been found. The type specimen, according to J. Heisy, one of Marsh's collectors, was found on Henry's Fork (see Granger, 1908) and is therefore probably from horizon D, although it could have come from horizon C. A.M.N.H. No. 12127 was also found somewhere along Henry's Fork and is labeled "Horizon D₄." This distribution suggests the possibility that *O. agilis* lived rather late in upper Bridger time. It is clear that specimens of this species are absent from relatively very fossiliferous beds in the C horizon. A recent collection by Gazin from Twin Buttes and the area north of Cedar Mountain contains 10 specimens of *Orohippus*, but none of *O. agilis*.

Of the eight specimens referable to *O. progressus*, six are from the C horizon, while two are from the D horizon. Of the specimens assigned to *O. sylvaticus* there are about an equal number from the C and D horizons. In neither species is there any detectable difference between specimens from the two horizons.

A relatively late occurrence of *O. agilis* is consistent with the advanced structure of the species. It is quite possible that *O. sylvaticus* gave rise to *O. agilis*, and it may be that some specimens assigned to *O. sylvaticus* but which particularly resemble those assigned to *O. agilis* represent the remains of an intermediate form.

SUMMARY

The genus *Orohippus*, known only from the Bridger formation of southwestern Wyoming, closely resembles *Hyracotherium*, its probable Wasatchian ancestor. The dentition of *Orohippus* differs from that of *Hyracotherium* largely in the progressive molarization of the premolars in the former genus. A rather minor, but functionally significant, structural character of the ankle joint of the equids, which appears for the first time in *Orohippus*, is discussed. Of the 12 named species that have been referred to the genus, five (*O. major*, *O. pumilus*, *O. progressus*, *O. sylvaticus*, and *O. agilis*) are recognized. The specific evolution within the genus and the relationships to species of *Hyracotherium* are discussed.

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