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INTRODUCTION

THE FIRST SPECIMEN OF *Hyracotherium* to be found in North America was collected by Cope and described by him in 1872. Cope immediately recognized the correct general systematic position of the specimen, referring it to the genus *Lophiotherium*, and later (1884) to *Hyracotherium*. It was Marsh (1876), however, who first recognized that the early Eocene hyracotheres were the ancestors of the modern horse, and he consequently referred them to the new genus *Eohippus*.

With Marsh's recognition of *Hyracotherium* as the ancestor of all the later horses, including *Equus*, the genus became the object of intense scientific and popular interest. Despite this great interest and the fact that the literature on *Hyracotherium* runs to thousands of pages, there has never been a really adequate description of the skeleton, although Cope (1884) briefly described the skull and the skeleton of the type of *H. venticolum*, and many later authors have made brief reference to the morphology of the genus in works on the evolution of the Equidae. In contrast to the neglect of the anatomy of *Hyracotherium*, no fewer than 16 species of the genus have been named, of which 11 were recognized by the most recent reviser (Granger, 1908).

The present study was undertaken in the belief that a detailed morphological description and a systematic revision in the light of new material and a greater knowledge of the stratigraphy of the North American lower Eocene would add materially to our knowledge of the genus *Hyracotherium* and to our understanding of the evolution of the Equidae.

As far as possible the morphology of *Hyracotherium* has been viewed against the background of the morphology of its ancestors, descendants, and closely related contemporaries. In the course of the description comparisons have been made with *Phenacodus* and *Mesohippus*. *Phenacodus* is too specialized in several respects to have been the ancestor of *Hyracotherium*, but it is the best-known representative of the family Phenacodontidae, the group from which the perissodactyls almost certainly arose. *Meso-*

hippus was chosen as a representative of the descendants of *Hyracotherium*, because it is the most primitive equid that has decisively crossed the gap between the primitive cursorial perissodactyl and the horse.

The systematic revision has been based on large samples, wherever such samples were available.

I wish to express my gratitude to Dr. G. G. Simpson for the privilege of studying the abundant material in the collection of the American Museum of Natural History and for his helpful suggestions and encouragement during every phase of the present study. I am indebted to Dr. Bobb Schaeffer for his suggestions concerning the section of this paper dealing with morphology, and to Mrs. Rachel H. Nichols for her help in locating numerous specimens and references. Drs. C. Lewis Gazin of the United States National Museum, Alfred S. Romer of the Museum of Comparative Zoölogy, Harvard College, Glenn L. Jepsen of Princeton University, Joseph T. Gregory of Yale University, Horace E. Wood of Newark College, Rutgers University, Albert E. Wood of Amherst College, Robert P. Sharp of the California Institute of Technology, John A. Wilson of the University of Texas, and Bryan Patterson of the Chicago Natural History Museum have generously allowed me to examine material in the collections in their charge.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History
M.C.Z., Museum of Comparative Zoölogy, Harvard College
P.U., Princeton University Geological Museum
U.S.N.M., United States National Museum

All measurements are given in millimeters. Abbreviations used in tables are:

N, number of measurements included
OR, observed range
SR, span of standard range
M, mean
σ, standard deviation
V, coefficient of variation
L, maximum length
W, maximum width

DESCRIPTION OF THE GENUS *HYRACOTHERIUM*

ORDER **PERISSODACTYLA** OWEN, 1848

FAMILY **EQUIDAE** GRAY, 1821

HYRACOTHERIUM OWEN, 1840

Hyracotherium OWEN, 1840, p. 163; 1841, . 203, pl. 21.
Pliolophus OWEN, 1858, p. 54, pls. 1–4.
Eohippus MARSH, 1876, p. 402.
Protorohippus WORTMAN, 1896, p. 92, figs. 14, 5.

TYPE: *Hyracotherium leporinum.*

TYPES OF SYNONYMS: Of *Pliolophus, P. vulpiceps;* of *Eohippus, E. validus;* of *Proorohippus, P. venticolus.*

DISTRIBUTION: Lower Eocene of Europe and North America.

DIAGNOSIS: Diastema between P^1 and P^2. P^3 never molariform but with well-developed fourth major cusp in advanced species. P^4 with three major cusps. Upper molars with well-developed lophs but with intermediate cusps usually prominent. Mesostyle absent. Diastema between P_1 and P_2. P_4 never fully molariform but with well-developed entoconid in some individuals. Mesolophid of lower molars sharply oblique.

The type of *H. leporinum* consists of a well-preserved anterior portion of a skull with right P^2–M^3 and left P^4–M^3 from the London Clay of Herne Bay, Kent, England. In his original description Owen compared the specimen with *Choeroptemus*. The dention is indistinguishable from certain early Wasatchian upper dentitions in the collection of the American Museum, and the skull is nearly identical in structure with the American *Hyracotherium* skulls described in the section of the present paper devoted to morphology.

Pliolophus vulpiceps was based on a complete skull from the London Clay near Harwick, England. Owen states that *Pliolophus* differed from *Hyracotherium* in having a more distinct metaconule and protoconule, a complete cingulum on the last three premolars and on the molars, and a wider diastema between P^1 and P^2. The type specimen closely resembles the type specimen of *H. leporinum,* and Cooper (1932) believed that they belonged to two closely related species.

P_4 of the type specimen of *P. vulpiceps* has a well-developed entoconid, and Cope (1884) placed American early Eocene hyracotheres with an entoconid on P_4 in this genus. Wortman (1896) regarded *Pliolophus* as a subgenus of *Hyracotherium.* An entoconid on P_4 may apparently be present or absent in different individuals of a single population. Variation of the entoconid is described below under the species.

I do not propose to discuss the question of the synonomy of *Eohippus* and *Hyracotherium* at any length. The two authors to consider the question most recently, Cooper (1932) and Simpson (1952), agree that the European and American lower Eocene hyracotheres are congeneric beyond question. It should be noted that among the earlier workers Cope and Wortman consistently referred Wasatchian hyracotheres to *Hyracotherium.* I have not examined any European specimens of *Hyracotherium,* but my impression based on a study of the casts of the important British specimens is that even specific separation of American and British specimens would be difficult if not impossible.

Wortman (1896) placed *H. venticolum* from the Wind River formation in a separate genus, *Protorohippus,* which he distinguished from *Hyracotherium* on the basis of the following five characters: (1) no vestige of the fifth digit on the pes; (2) outer cusps of the superior molars subcrescentic; (3) rudimentary mesostyle present; (4) rudimentary hypostyle usually present; (5) third superior premolar with four well-developed cusps.

As is pointed out below in the discussion of the foot, in the two hyracothere hind feet known from the Wind River formation the fifth digit is indeed lacking but so is the mesocuneiform. It is entirely possible, therefore, that the lack of a fifth digit in these cases is the result of post-mortem loss. The paracone and metacone of specimens from the Lost Cabin member of the Wind River formation are no more crescent-shaped than those of specimens from the Willwood formation, and there is little or no evidence of a mesostyle and hypostyle in any Wasatchian

specimens. Certain Lost Cabin specimens are readily distinguishable from early Wasatchian specimens on the basis of the character of the P^3 cited by Wortman. Third upper premolars of specimens from the Lysite member of the Wind River formation and equivalents, unknown at the time of Wortman's revision of the early Eocene hyracotheres, are, however, intermediate in structure between those of early Wasatchian specimens and those of Lost Cabin specimens. It now seems more reasonable to regard the presence of a fourth major cusp on P^3 as a specific, rather than a generic, character.

MORPHOLOGY

DENTITION

IN NO SPECIMENS OF *Hyracotherium* known to me are the upper incisors preserved, but in one specimen of *H. angustidens* and one of *H. vasacciense* the alveoli of these teeth are present. In *H. angustidens* (A.M.N.H. No. 15428) there is a short diastema between I^3 and C, and a somewhat longer one between C and P^1. There is also a short diastema between P^1 and P^2. This diastema is slightly shorter than the anteroposterior diameter of P^1. *Hyracotherium vasacciense* (A.M.N.H. No. 4832) resembles *H. angustidens* in that a diastema between P^1 and P^2 is present. The diastema is, however, slightly longer than the anteroposterior diameter of P^1. There is no specimen of *H. craspedotum* in which either the incisors or their alveoli are preserved. In one specimen referable to this species (A.M.N.H. No. 55100) the alveoli for the canines and the complete cheek tooth series are preserved. The diastema between P^1 and P^2 is short as in *H. angustidens*. In *Mesohippus* there is a short diastema between I^3 and the greatly reduced canine, and a much longer one between C and P^1. In *Phenacodus* there are short gaps of about equal length between I^3 and C, and between P^2 and P^3.

In no specimen of *H. angustidens* are the lower incisors and canines preserved. In one specimen (A.M.N.H. No. 15428), however, the entire cheek tooth series is preserved. There is a short diastema between P_1 and P_2 which is shorter than the anteroposterior diameter of P_1. In a specimen of *H. vasacciense* (A.M.N.H. No. 4832) the alveoli of the incisors and the alveoli for the canines are preserved; there is a short diastema between I_3 and C and a somewhat longer one between C and P_1. The diastema between P_1 and P_2 is somewhat longer than the anteroposterior diameter of P_1. In no specimen of *H. craspedotum* are the lower teeth anterior to P_2 preserved. In *Mesohippus* there is a very short diastema between I_3 and C and a much longer one between C and P_1. In *Phenacodus* there are short gaps between I_3, C, P_1, P_2, and P_3.

P^1 is single-cusped and mediolaterally compressed. The anterior edge of the tooth is convex, and the longer posterior edge is slightly concave.

In *H. vasacciense* P^2 consists of two conical, well-separated cusps of about equal size, and an internal cingulum which is wider posteriorly than anteriorly. In *H. angustidens* and *H. craspedotum* the anterior lateral cusp is much larger than the posterior, and the internal cingulum is narrow posteriorly.

In *H. angustidens* and *H. craspedotum* the crown of P^3 is roughly triangular in shape. The anterior angle is usually more acute than the posterior. The protocone is conical and prominent, with a strong protoloph running from its anterolateral portion obliquely to the anterior end of the ectoloph. A slight thickening of the ectoloph representing the protoconule may be present, but it is variable in its development and is frequently absent. In some specimens there is a very weak crest running from the protocone posterolaterally towards the metacone, but this structure is also frequently absent. The paracone and the metacone are conical and about equal in height to the protocone. They are close together and are joined by a weak ectoloph which continues anteriorly to join the lateral end of the protoloph and posteriorly to the posterior corner of the tooth. The cingulum is weak and may be absent along the anterior border. At the anterolateral corner of the tooth the cingulum is raised into a prominent sharp parastyle. In *H. vasacciense* the protocone is distinct and prominent and is located well anterior to a line connecting the protocone and the paracone. Apparently the protoconule migrates anteromedially to form the protocone of the molariform P^3 as suggested by Granger (1908).

In *H. angustidens* and *H. vasacciense* the crown of P^4 is shaped like an isosceles triangle with the base external and roughly parallel to the midline. The large protocone is steeply conical and is located at the extreme internal angle. A prominent protoloph runs obliquely
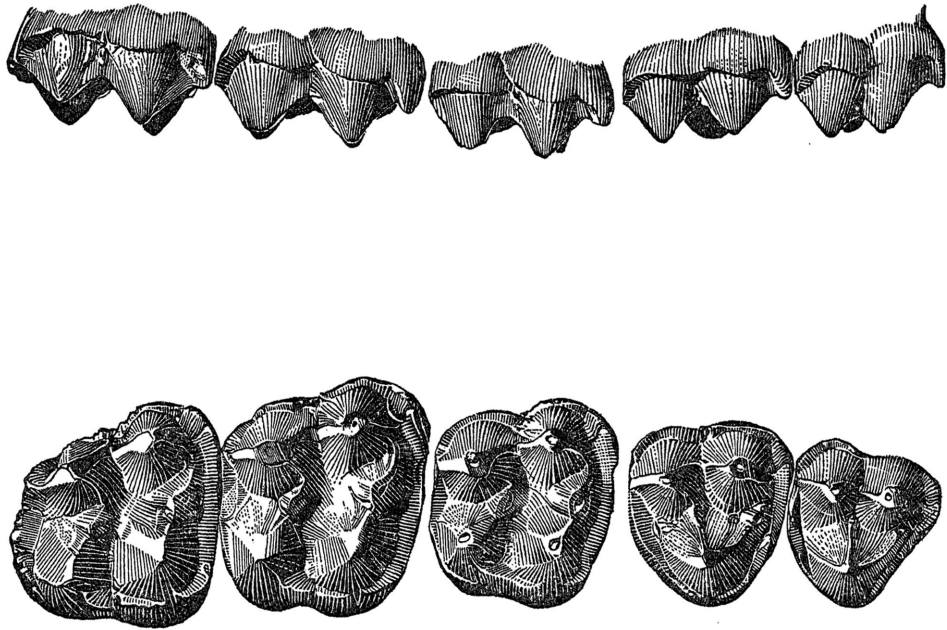
FIG. 1. *Hyracotherium angustidens* (Cope), A.M.N.H. No. 48018, right
P^2-M^3. Crown and lateral views. ×3.

from the protocone and terminates in a small paraconule which is located immediately antero-internally of the paracone. A weak crest runs between the protocone and the metacone. A small cuspule is sometimes present on the crest, but its development is variable, and it may be entirely absent. The paracone and hypocone are farther apart than in P^3, and the protoloph is somewhat stronger. The cingulum is weak and may be absent at the internal angle. The parastyle is strong. In *H. craspedotum* the protocone is elongated anteroposteriorly and often shows an incomplete division into two cusps. The postero-internal portion of the tooth is usually produced posteriorly to form a flat shelf of variable area. It is doubtful that the postero-internal cusp was added to P^4 in the equids by a direct splitting of the protocone, but an examination of primitive species of *Orohippus* shows clearly that the fourth major cusp was added at the postero-internal corner of the tooth, apparently by a migration of the posterior intermediate cusp. The interior cusps of P^3 and P^4 are thus not homologous as pointed out by Granger (1908) and more recently by Butler (1952).

The crown of M^1 is quadrate. It is broader than long and tapers slightly internally. The anterior border is considerably longer than the posterior. The internal border is parallel to the midline, and the external border is consequently oblique, forming an angle of about 20 degrees with the midline. This angle is, however, highly variable. The protocone and hypocone are steeply conical, of about equal height, and are located at the extreme antero-internal and postero-internal angles of the tooth, respectively. The paracone and metacone are about equal in height to the protocone and the hypocone and are equidistant from the lateral border, the paracone thus being more lateral than the metacone. The two cusps are connected by an ectoloph which continues anteriorly to join the lateral end of the protoloph and posteriorly to the postero-external angle of the tooth. The protoloph runs obliquely from the lateral side of the protocone and joins the ectoloph immediately anterior to the paracone. The protoconule is usually present as a thickening of the protoloph and is highly variable in its development. The metaloph is weaker than the protoloph. It runs obliquely from the hypocone and may not quite reach the anteromedial quarter of the metacone. The

metaconule is highly variable in its development and is usually less prominent than the protoconule. A narrow cingulum may completely surround the tooth but is frequently absent at the antero-internal angle. The parastyle is prominent and sharp.

M^2 is virtually identical to M^1 in structure but is larger. M^3 is generally similar in structure to the other two upper molars. The external border is usually more oblique, however, and in many individuals the cingulum along the posterior border is broad and forms a prominent shelf.

P_1 is mediolaterally compressed. The single cusp is convex anteriorly and concave posteriorly.

P_2 is also mediolaterally compressed. There are two cusps, a large anterior one and a much smaller posterior one.

P_3 is long and slender, with a steeply conical protoconid and a smaller metaconid immediately postero-internal to it. A weak metalophid runs from the anterior cusps directly posterior to a small, centrally located hypoconid.

The crown of P_4 is roughly rectangular in shape, but the talonid is low, and the entoconid never is so large as the other cusps

and may be absent. The development of the entoconid is of no apparent taxonomic importance in *Hyracotherium*, as in each population the entoconid shows about the same range of size variation. The protoconid and metaconid are steeply conical and close together, with the protoconid slightly more anterior. The paralophid runs anteriorly and then medially across the anterior margin of the tooth. The hypoconid is considerably lower than the protoconid and metaconid. The hypoconulid varies greatly in size. The size of the hypoconulid is correlated positively with the size of the entoconid. A very low ridge runs medially from the hypoconid in specimens in which the entoconid is large. A weak cingulum is present along the lateral border of the tooth.

The crown of M_1 is nearly rectangular but usually somewhat narrower anteriorly than posteriorly. The protoconid and metaconid are steeply conical, with the protoconid somewhat more anterior. In unworn teeth there is always at least a slight indication of the twinning of the metaconid. A high protolophid runs between the protoconid and the metaconid. The paralophid runs anteromedially and then medially across the an-
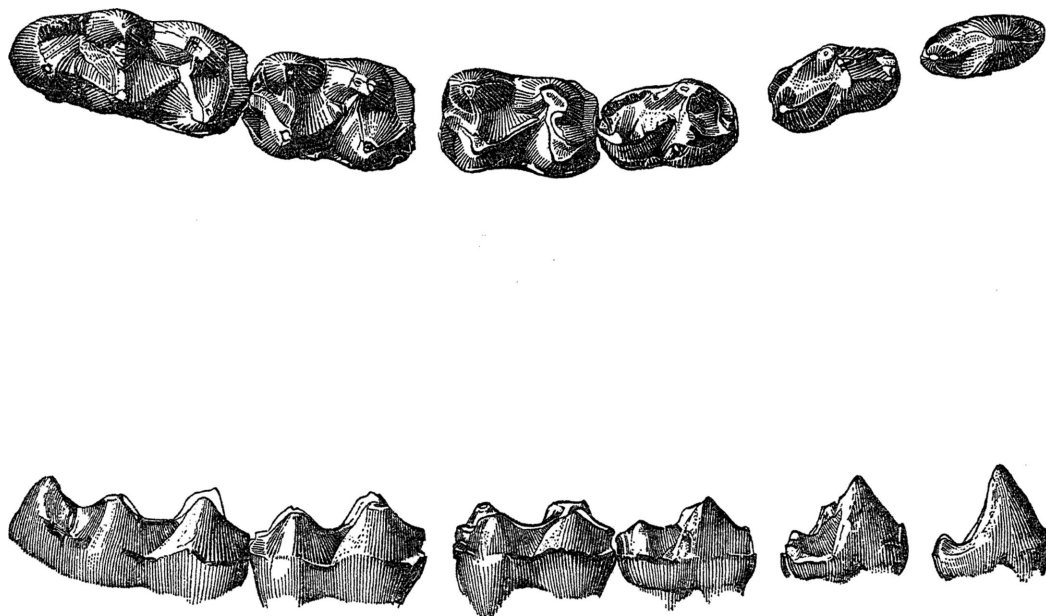

FIG. 2. *Hyracotherium angustidens* (Cope), A.M.N.H. No. 48015, right P_2–M_3. Crown and lateral views. ✕3.

terior border of the tooth from the protoco-
nid. The hypoconid and entoconid are a
little farther apart and somewhat lower than
the protoconid and metaconid. The hypocon-
id is slightly more anterior than the pro-
toconid. The hypolophid is variable in its
development, but it is never so high as the
protolophid. The metalophid runs diagonally
across the tooth from the hypoconid and usu-
ally joins the protolophid near its medial
end. The hypoconulid is between and im-
mediately posterior to the hypoconid and
the entoconid. A sharp crest runs from the
hypoconulid to the hypoconid. The cingulum
is absent on the medial side of the tooth. It
is present and of variable width on the lateral
side and may be absent beneath the meta-
conid and entoconid.

The structure of M_2 is identical with that
of M_1 except for its larger size.

The form and arrangement of the major
cusps are the same in M_3 as in M_1 and M_2.
The hypolophid is, however, lower, and the
hypoconulid is produced posteriorly into the
prominent heel. The hypoconulid is offset
laterally, and a crest runs from it directly
forward to join the hypolophid near the
hypoconid. Another irregular crest runs from
the hypoconulid around the postero-internal
angle of the tooth. Small cuspules are fre-
quently present along the crest. The heel is
extremely variable in size and shape but
tends to be short and broad in *H. angustidens*
and *H. craspedotum*, and long, narrow, and
anteriorly constricted in *H. vasacciense*. In
well-worn teeth the heel may assume the
form of a smooth, shallow basin.

In two specimens (A.M.N.H. Nos. 164 and
15658), one from the Lysite and one from the
Gray Bull, which show DP^3 and DP^4, DP^4 is
identical in structure to M^1 except that it is
smaller in size. DP^3 has four distinct cusps,
but differs from the molars in being longer
than wide. The cusps are well separated,
with the anterior ones closer together than
the posterior.

DP_2 is relatively very long and narrow.
There is a small anterior cusp followed by a
barely separate protoconid and metaconid.
The hypoconid is large and directly posterior
to the protoconid and metaconid.

DP_3 is relatively long and narrow. The
protoconid and metaconid are close together,

with the metaconid well anterior. The paralo-
phid is produced anteriorly and terminates
in a small distinct cusp. There is a small
cuspule at the lateral edge of the tooth be-
hind the protoconid.

DP_4 is like M_1 but is smaller and relatively
less wide.

For a complete description of the milk
dentitions of perissodactyls, including *Hyra-
cotherium*, see Butler (1952).

The teeth of the Phenacodontidae show,
in general, the characters one would expect
to find in the ancestors of *Hyracotherium*. In
almost all respects the teeth of the phenaco-
dontids are more primitive than the teeth
of *Hyracotherium*. The intermediate cusps
are distinct, and there is little tendency
towards loph formation in M^1 and M^2. M^3
is always smaller than M^1 and M^2 and lacks
a distinct hypocone. M_3 is also relatively
small, and the entoconid and hypoconulid
are often united by a strong crest and are
quite indistinguishable as distinct cusps.
None of the premolars is fully molariform,
although in the more specialized genera there
may be a distinct entoconid on P_4.

All the phenacodontids except *Desmato-
claenus* are more specialized than *Hyraco-
therium* in having a distinct mesostyle on at
least M^1 and M^2. The presence of a mesostyle
does not, of course, absolutely exclude any
genus from the ancestry of *Hyracotherium*.
The possession of a mesostyle was, however,
apparently of distinct selective advantage in
conjunction with a number of different tooth
patterns, under different conditions and at
different times, because it eventually appears
in all phyla of condylarths and perissodac-
tyls. It seems unlikely, therefore, that the
mesostyle would appear in the ancestor of
Hyracotherium, then disappear, only to re-
appear in *Orohippus*.

There are prominent internally placed
paraconids on the lower molars of *Des-
matoclaenus*. The cusp is greatly reduced in
the other genera of the family, and in these
genera the paralophid is also greatly reduced.
I have examined no specimens pertaining to
Desmatoclaenus, but from Gazin's description
(1941) I can see no character that would
exclude *Desmatoclaenus* from the ancestry of
Hyracotherium. *Desmatoclaenus* is known
from the Wagonroad and Dragon faunas of

Puercan and Dragonian age, respectively, which allows sufficient time for the evolution of *Hyracotherium*. The complete absence of forms structurally intermediate between *Desmatoclaenus* and *Hyracotherium* in the relatively well-known North American Paleocene fauna suggests, however, that the evolution of the perissodactyls from condylarth ancestors took place elsewhere.

As mentioned above, the other genera of the family, including *Tetraclaenodon*, *Gidleyina* (not examined, description from Simpson, 1935), *Phenacodus*, and *Ectocion*, are all more specialized than *Hyracotherium* in the possession of a mesostyle. Only in *Ectocion* are the lophs of the upper molars developed to a noticeable extent, and even in this late and specialized genus the intermediate cusps are prominent.

SKULL AND LOWER JAW

The description of the skull is based largely on the specimens listed below. They are referred to in the subsequent discussion as specimens 1, 2, and 3, respectively. In the summer of 1953 a field party from the American Museum of Natural History working in the Huerfano Basin discovered a number of nearly complete *Hyracotherium* skulls and postcranial skeletons. Preparation of this material had not been finished at the time of the completion of the present study. Dr. G. G. Simpson has very kindly offered to allow me to study the specimens when preparation has been completed. A study of the new material will no doubt reveal details not preserved in the present, rather limited but nearly complete, material.

1. A.M.N.H. No. 4831: A nearly complete but badly crushed skull from the Lost Cabin member of the Wind River formation. This specimen was described and figured by Cope (1884).

2. A.M.N.H. No. 4832: A skull from the Lost Cabin, complete except for the larger portions of the maxillae, but fragmented and somewhat distorted. This skull is associated with a nearly complete postcranial skeleton. The specimen was described by Cope (1881 and 1884) and selected by him as the type of *Hyracotherium venticolum*.

3. A.M.N.H. No. 14810: A skull fragment from the Lost Cabin consisting of the rostrum, orbital walls, and palate with much of the bone lacking.

The skulls above have been compared with skulls of *Phenacodus copei* (A.M.N.H. No. 4378) and *Phenacodus primaevus* (A.M.N.H. No. 4369 and P. U. No. 14864) from the Big Horn Basin, and with many skulls of *Mesohippus* from various horizons and localities.

Viewed from above the skull has a rather long, narrow rostrum which expands evenly posteriorly. The width across the zygomata is less than twice the width of the rostrum at the interior borders of the orbits. The dorsal surfaces of the frontals are broad and flat, and the short supraorbital processes are followed by a sharp cranial constriction. The brain case is moderately expanded. There is a strong postcranial constriction just posterior to the zygomatic processes of the squamosals, and the skull flairs posteriorly into the lambdoidal crests. In *Mesohippus* the dorsal portion of the rostrum is constricted to form the facial fossae, and the cranial constriction is not so sharp as in *Hyracotherium*. The brain case of *Mesohippus* is much more expanded than that of *Hyracotherium*, and there is little or no postcranial constriction. In *Phenacodus* the dorsal surfaces of the nasals and frontals are broad and flat, and the orbits are relatively more anteriorly located. The cranium shows almost no expansion. The lambdoidal crests of *Phenacodus* are more pronounced than those of *Hyracotherium*.

In lateral view the dorsal surface of the skull is convex posteriorly, and slopes gently and is nearly flat from the supraorbital process anteriorly. The lateral edge of the occiput is inclined slightly, and the basioccipital is inclined at an angle of about 150 degrees with the tooth row. The external nares extend posteriorly into the rostrum to the level of the canine. The zygomatic arch is narrow and is gently curved. In lateral view the skull of *Mesohippus* is very similar to that of *Hyracotherium*. The basioccipital, however, is somewhat more sharply inclined than that of *Hyracotherium*, the dorsal surface of the cranium is more convex, and the

external nares do not extend so far posteriorly. The skull of *Phenacodus* differs strikingly from that of *Hyracotherium* in lateral view. The rostrum of *Phenacodus* is very deep and short, and the basioccipital is nearly parallel to the tooth row. The brain case of *Phenacodus* is very shallow.

The nasal is of uniform width anteriorly and slightly expanded posteriorly. It extends posteriorly to the level of the anterior border of the orbit and meets the lacrimal narrowly. Its dorsal surface is transversely convex, more so anteriorly than posteriorly. It projects anteriorly well beyond the ascending ramus of the premaxilla. The frontal, maxillary, and premaxillary sutures are straight and simple. Posteriorly the nasal of *Mesohippus* is more laterally expanded than that of *Hyracotherium*. In *Phenacodus* the nasal extends posteriorly to a point above the center of the orbit. The posterior third of the nasal is greatly expanded laterally. Anteriorly it tapers almost to a point and extends only a short distance beyond the premaxilla.

In lateral view the body of the maxilla is narrow. The ascending ramus is rather broad and flat and of uniform width. It is inclined posteriorly at an angle of about 45 degrees. The maxillary and nasal sutures are simple. In no specimen examined is the palatal process complete, but in specimen 2 the palatal process is preserved to the lateral borders of the anterior palatal foramen. The foramen apparently extended well posterior to the maxillary suture and was very narrow. In *Mesohippus* the ascending ramus of the premaxilla is not so wide anteroposteriorly as that of *Hyracotherium*. The ascending ramus of the premaxilla of *Phenacodus* is very narrow anteroposteriorly and relatively longer than that of *Hyracotherium* because of the relatively greater depth of the muzzle.

The facial portion of the maxilla is broad and flat except for the sharp facial crest, a continuation of the inferior border of the zygomatic arch, which extends to the infraorbital foramen directly above P⁶. The dental plate of the maxilla forms the floor of the orbit. The maxillo-palatine suture coincides roughly with the angle between the floor and the lateral wall of the orbit. The zygomatic root is long, extending from opposite M^1 to opposite M^3, but is not strong. The jugal extends forward to the lacrimal which it narrowly meets. Posteriorly the jugal is narrow and of uniform width, and forms both the inner and outer faces of the zygoma. In no specimen is the zygomatic arch preserved posterior to M^3. In general shape and proportions the facial portion of the maxilla of *Mesohippus* is similar to that of *Hyracotherium*. There is in *Mesohippus*, however, a facial fossa which is variable in its form and extent, and the infraorbital foramen is relatively smaller than that of *Hyracotherium*. In *Phenacodus* the facial portion of the maxilla is very broad dorsoventrally in conjunction with the deep muzzle, and there is no facial crest. The infraorbital foramen of *Phenacodus* is relatively much larger than that of *Hyracotherium*.

The palatal process of the maxilla extends from a point opposite the canine to a point opposite M^3. The palate along the midline is not preserved in any specimen, but in specimen 1 the maxillary palatine suture runs along the medial side of M^3 and M^2 and then diverges anteromedially. In the British specimen described by Simpson (1952) the sutures meet at the midline opposite P^4. As nearly as can be determined from the material at hand, the palatal processes of the maxillae of *Mesohippus* and *Phenacodus* are essentially similar to the process in *Hyracotherium*.

The palatal process of the palatine is poorly preserved in all specimens. The left lateral border of the choanae is preserved in specimens 2 and 3. The choanae apparently extend at least as far forward as M^2, a character in which they differ from those of the British specimen described by Simpson, in which they extend only as far forward as M^3. The palatine is narrowly and sharply ridged along the border of the choanae. The palatal process of the palatine of *Phenacodus* is relatively longer than that of *Hyracotherium*, and consequently the anterior border of the choanae is farther posterior than in *Hyracotherium*, being opposite M^1.

The fronto-palatine suture runs irregularly but generally horizontally and parallel to the maxillo-palatine suture. A large foramen pierces the palatine bone near its anterior end, and immediately posterior and some-

what ventral to it is another, somewhat smaller foramen. These foramina correspond exactly to those in the British specimen of *Hyracotherium* identified by Simpson as the maxillary and spheno-palatine foramina. In *Equus* these foramina are contained partly within the maxilla, but in *Mesohippus* they are entirely within the palatine as they are in *Hyracotherium*. A smaller, more posterior foramen present in the palatine of the British specimen is lacking, apparently as a result of breakage, in all American specimens. In *Mesohippus* the palatine and its foramina are virtually identical in structure to those of *Hyracotherium*. In *Phenacodus* the palatine is relatively broader than in *Hyracotherium*. The maxillo-palatine and fronto-palatine sutures run posteroventrally from the lacrimal, roughly paralleling each other at an angle of about 45 degrees. Approximately in the center of the palatine is a large, bilobed foramen which apparently represents the confluent maxillary, spheno-palatine, and posterior palatine foramina.

The lacrimal is small and shows little facial expansion either dorsoventrally or antero-posteriorly. The fronto-lacrimal suture runs almost vertically across the anterior portion of the orbital wall. The foramen is large and is located just beneath the anterior border of the orbit. In *Mesohippus* the lacrimal extends farther dorsally than it does in *Hyracotherium*. In *Phenacodus* the lacrimal is less anteroposteriorly and more dorsoventrally expanded than that of *Hyracotherium*. The anterior portion of the orbit of *Phenacodus* is deeply excavated anteriorly. The orbital portion of the lacrimal is entirely within this excavation and is not visible in lateral view.

The fronto-sphenoid suture ascends irregularly, but roughly vertically across the orbital wall immediately anterior to the cranial constriction. Just anterior to this suture, at about the mid-height of the orbital wall, is a small circular foramen which is apparently directed medially into the brain case. This foramen is almost certainly the ethmoidal which occurs in this region in *Equus*, though partly within the frontal. In *Mesohippus* the fronto-sphenoid suture is more posteriorly located, and the ethmoidal foramen is more ventral. In *Phenacodus* the fronto-sphenoid suture runs posterodorsally

at an angle of about 45 degrees. The ethmoidal foramen of *Phenacodus* is located as in *Hyracotherium*, just within the frontal.

In the posteroventral corner of the orbital facies of the sphenoid is a large oval foramen which in specimen 3 completely perforates the skull. Two symmetrical, paramedian grooves run directly posterior from this foramen into the brain case. Immediately posterolateral to this foramen in specimen 2 is a deep, posteriorly directed groove which apparently represents the remains of a canal, the lateral wall of which has been broken away. This groove terminates posteriorly in a small, fragmented area where the endocranial matrix is exposed.

As Simpson has pointed out in connection with the British specimens, the optic nerve must have passed through the large anterior foramen. It is, however, probably too large to be considered as a separate optic foramen, and Simpson has suggested that it represents the confluent optic foramen and foramen lacerum anterius and thus carried cranial nerves II, III, IV, V, and VI. In view of the large size of this foramen and the absence of a small anterior foramen in the sphenoid, it is very probable that Simpson's suggestion is correct.

The lateral groove then would represent the anterior opening of the foramen rotundum which passed into the brain case somewhere in the broken area. In the British specimen the lateral wall of this groove is intact, and lateral to it is another groove which evidently represents the medial wall of another passage, probably the alar canal. In a complete but poorly preserved skull from the Gray Bull beds (A.M.N.H. No. 15428) the posterior opening of the alar canal is apparently present just anteromedial to the glenoid surface. There is no evidence of a foramen ovale separate from the foramen lacerum medium in this specimen, nor is there in specimen 2. In specimen 2 there is a broad bridge of bone between the foramen lacerum medium and the area from which the brain case is missing. A separate foramen ovale could almost certainly not have been so far anterior as to be included in this area. In specimen 1 there is a slit in the anterior border of the foramen lacerum medium which corresponds closely in position with the incisura ovalis of *Equus*. This may well

represent the transitional condition between a separate foramen ovale and one confluent with the foramen lacerum medium. It is interesting to note that specimen 2, in which no such slit exists, belongs to a more advanced species than specimen 1.

In *Mesohippus* the foramina of the cranial nerves are essentially as they are in *Equus*. The separate optic foramen, foramen lacerum anterius, foramen rotundum, and anterior opening of the alar canal are close together and located beneath a flange of the sphenoid. In *Phenacodus* there is a small optic foramen posteroventral to the ethmoidal foramen, and in the posteroventral corner of the orbital facies of the sphenoid, a large, kidney-shaped foramen which apparently represents the confluent foramen lacerum anterius, foramen rotundum, and the anterior opening of the alar canal.

The dorsal surface of the frontal is nearly flat. Anteriorly it meets the nasal along a straight, transverse suture. The parietal runs anterolaterally from the midline and then downward to the squamosal. The supraorbital process is short and pointed and directed posteriorly. A sharp, low crest runs from the supraorbital process to the sagittal crest, joining it at a point where the parietal sutures meet. In *Mesohippus* the frontals extend anteriorly for a short distance between the nasals. The dorsal surface of the frontal of *Mesohippus* is otherwise similar to that of *Hyracotherium*. In *Phenacodus* the dorsal portion of the frontal is very short medially owing to the posterior extension of the nasals. Laterally it extends farther anteriorly around the orbit narrowly to meet the lacrimal.

The parieto-squamosal suture is not visible, but judging from the position of the fronto-squamosal suture it must have been high on the cranium. The parietals apparently broaden somewhat posteriorly and then narrow sharply and come almost to a point just anterior to the nuchal crest. The squamosal is thus greatly expanded dorsally, forming most of the lateral wall of the cranium and part of the cranial roof. The position of the parieto-squamosal suture is variable in *Mesohippus*, but it is apparently always lower on the cranial wall than in *Hyracotherium*, as it is in *Phenacodus*.

The glenoid cavity is shallow and faces directly downward, and the postglenoid process is short and blunt. The zygomatic process of the squamosal is sharply crested dorsally in a continuation of the lambdoidal crest. In all specimens the zygomatic process of the squamosal is broken off close to its base. Both the mastoid and paramastoid processes are short and blunt. The glenoid cavity in *Mesohippus* is deeper, and the postglenoid process is longer, than in *Hyracotherium*. In *Phenacodus* the glenoid cavity is very shallow, and the postglenoid process is somewhat longer than in *Hyracotherium*. The zygomatic process of *Mesohippus* is more sharply crested dorsally, while in *Phenacodus* this process extends farther laterally and is not so sharply crested dorsally.

The occipitals are so crushed and distorted in all specimens that little can be said except that the complex is very high and narrow, and was concave dorsally and laterally, and centrally narrowly convex. The foramen magnum was apparently almost round. The occipitals of *Mesohippus* are like those of *Hyracotherium*, while in *Phenacodus* they are broader and flatter dorsally.

The basioccipital is columnar as is the basisphenoid. *Mesohippus* resembles *Hyracotherium* in this respect, while the basioccipital of *Phenacodus* is relatively broader and flatter laterally.

The hypoglossal foramen is rather large and is located immediately anterior to the slightly convex anterior border of the occipital condyle. In *Mesohippus* and *Phenacodus* the anterior border of the condyle is convex laterally and concave medially.

The tympanic bullae are partially preserved in specimen 1. They were apparently oval in shape and moderately inflated.

The lateral aspect of the mandible tapers rather evenly anteriorly from the level of the P_2 and is very shallow at its anterior extremity. From the level of P_2 to M_3 the mandible is of uniform depth. The symphysis extends posteriorly to the level of P_1. The dorsal border is slightly concave, while the ventral border is slightly convex. Just posterior to M_3 the ventral border is concave for a slight distance and then continues convex to the angle. The ascending ramus is very broad. Its anterior border is slightly convex and nearly vertical, while the posterior border is strongly convex ventrally and extends well posterior to the condyle. The

coronoid process is broad and slightly inclined posteriorly and is well separated from the condyle by a broad shallow mandibular notch. The thickness and depth of the ramus have been cited by earlier authors as characters distinctive of species. These characters are variable, and, as Wortman (1896) pointed out, the thickness and depth of the ramus apparently increase with age, because it is usually shallow and thin in specimens with unworn teeth and deep and thick in specimens with well-worn teeth. The mandible of *Mesohippus* tapers gradually from the angle anteriorly to the level of P_2 and then sharply to the anterior end. The posterior border of the ascending ramus is not so sharply convex as in *Hyracotherium*, and the coronoid process is relatively higher and more posteriorly inclined. In *Phenacodus* the mandible is not so shallow anteriorly and is thicker.

POSTCRANIAL SKELETON

MATERIAL

The description of the postcranial skeleton is based on three partial skeletons in the collection of the American Museum (A.M.N.H. Nos. 4832, 15428, and 15820) and a large number of isolated bones and fragments from various horizons and localities. The first skeleton is the Lost Cabin specimen described by Cope and mentioned above. The other two skeletons are from the Gray Bull beds and are undescribed. Two of the three species recognized in the present work are thus represented by nearly complete specimens, the third being represented only by skeletal fragments. The postcranial skeletons of the three species differ from one another only in the size and proportions of the various bones (see tables 1 and 2).

The three skeletons of *Hyracotherium* have been compared with a mounted skeleton of *Mesohippus bairdi* (A.M.N.H. No. 1492) from the middle Oreodon beds and isolated bones of *Mesohippus* from various horizons and localities, and with a mounted skeleton of *Phenacodus copei* (A.M.N.H. No. 4378) from the Big Horn Basin.

VERTEBRAL COLUMN

The description of the vertebrae is based largely on the relatively well-preserved vertebral column of A.M.N.H. 15820. There are 17 thoracic and seven lumbar vertebrae.

CERVICAL VERTEBRAE: The axis and atlas are so poorly preserved that almost no statement concerning their morphology is possible. The spinous process of the axis was, however, broad and rounded rather than spinous as in *Phenacodus*. The remaining cervical vertebrae are also poorly preserved.

The centra resemble those of *Mesohippus* except for being relatively shorter and in having less sharply convex and concave anterior and posterior faces. In *Phenacodus* the cervicale are relatively shorter than those of *Hyracotherium*, and the faces of the centra are less sharply convex and concave.

THORACIC VERTEBRAE: The fifth thoracic vertebra is well preserved. The anterior face of the centrum is roughly semicircular in shape with the dorsal, flat side forming the ventral border of the vertebral foramen. The face is slightly convex in all directions. The posterior face is similar in shape to the anterior, but is concave. The centrum is constricted and very bluntly keeled ventrally. The anterior zygapophyses consist of two very short, anteriorly projecting processes. The greater part of the anterior articular facet lies on the body of the neural arch. It is laterally slightly convex and faces almost directly dorsally but is inclined very slightly cranially. The distal portion of the neural spine is lacking. The base is inclined sharply in the posterior direction. The oval, slightly concave posterior articular facet lies beneath the laterally expanded posterior portion of the base of the spine. It faces largely ventrally and somewhat posteriorly. The transverse processes project dorsolaterally at an angle of about 45 degrees. On their ventrolateral surfaces are the facets for the tubercles of the ribs. These facets face anteroventrally at an angle of about 25 degrees. They are anteroposteriorly slightly concave and mediolaterally very slightly convex. The half facets for the articulation of the head of the ribs project laterally from the dorsal halves of the anterior and posterior faces of the centrum. The anterior half facets face

TABLE 1

MEASUREMENTS OF SKULL AND SKELETAL ELEMENTS IN TWO SPECIES OF *Hyracotherium*

	H. vasacciense A.M.N.H.No. 4832	*H. angustidens* A.M.N.H. No. 15428
Skull		
Basal length	136.5	179.5
Distance from anterior extremity of nasals to anterior border of orbit	63.0	94.0
Distance, alveolus I^1 to M^3	80.0	110.5
Humerus		
Greatest length	97.5	130.0
Least anteroposterior diameter of shaft	7.5	—
Least transverse diameter of shaft	9.0	—
Radius		
Greatest length	96.5	112.5
Least anteroposterior diameter of shaft	5.0	6.5
Least transverse diameter of shaft	10.0	10.0
Ulna		
Greatest length	119.0	141.0
Least anteroposterior diameter of shaft	7.0	9.0
Least transverse diameter of shaft	5.0	5.5
Metacarpal II		
Greatest length	47.0	55.0
Least transverse diameter	6.0	7.0
Metacarpal III		
Greatest length	52.0	—
Least transverse diameter	5.5	—
Metacarpal IV		
Greatest length	45.0	54.0
Least transverse diameter	4.5	6.5
Metacarpal V		
Greatest length	40.0	45.5
Least transverse diameter	4.5	6.0
Femur		
Greatest length	131.0	174.0
Least anteroposterior diameter of shaft	11.5	16.5
Least transverse diameter of shaft	10.0	12.5
Tibia		
Greatest length	121.0	166.5
Least anteroposterior diameter of shaft	8.0	11.0
Least transverse diameter of shaft	9.5	12.0
Fibula		
Greatest length	111.0	150.0
Least anteroposterior diameter of shaft	4.0	5.0
Least transverse diameter of shaft	4.5	4.0
Metatarsal II		
Greatest length	62.0	—
Least transverse diameter	5.0	—
Metatarsal III		
Greatest length	65.5	82.5
Least transverse diameter	6.5	9.0

TABLE 2

LIMB INDICES IN *Phenacodus, Mesohippus,* AND TWO SPECIES OF *Hyracotherium*

	Phenacodus	H. angustidens	H. vasacciense	Mesohippus
Humerus/radius	79	100	95	102
Humerus/metacarpus	31	55	53	64
Femur/tibia	110	110	101	101
Femur/metatarsus	37	51	56	57

anterolaterally at an angle of about 45 degrees and are slightly concave. The posterior half facets face posteroventrally at an angle of about 10 degrees and are more deeply concave than the anterior half facets.

The thoracic and lumbar vertebrae of *Mesohippus* are apparantly almost identical in structure to those of *Hyracotherium.* The fifth thoracic vertebra of *Phenacodus* differs from that of *Hyracotherium* in having a broader neural arch and broader articular surfaces. The transverse processes are longer than those of *Hyracotherium* and project farther laterally, and the facets for the heads of ribs are less deeply concave.

As nearly as can be determined from the poorly preserved material, the next four thoracic vertebrae are similar to the fifth vertebra. The tenth thoracic vertebra is well preserved and also similar to the fifth except that the facets for the tubercles of the ribs are considerably smaller and are slightly convex in all directions.

The last three thoracic vertebrae are markedly different from the other thoracic vertebrae. The posterior zygapophyses project farther caudally, and the articular surfaces are fully separate and sharply convex mediolaterally, with laterally and ventrally directed faces. The anterior articular facets are borne partially on the inner surfaces of the transverse processes and thus have a dorsally and medially facing surface. The spine of the sixteenth thoracic vertebra is vertical and thus anticlinal.

The posterior thoracic vertebrae of *Phenacodus* are like those of *Hyracotherium* except that the neural arches are narrower.

LUMBAR VERTEBRAE: The centra of the lumbar vertebrae are sharply keeled ventrally. The articular surfaces are, in general, very poorly preserved, but the posterior

articular surface of the fifth is intact. Its surface is nearly semicircular mediolaterally, and its most dorsal portion faces dorsally, indicating that the anterior zygapophysis of the following vertebra must have embraced it. In *Mesohippus* the zygapophyses of the second to fifth lumbar vertebrae are embracing, and the posterior articular surfaces are identical to the one preserved in *Hyracotherium.* It is thus highly probable that some of the zygapophyses of the lumbar vertebrae of *Hyracotherium* were embracing. The presence of embracing zygapophyses greatly restricts movement between vertebrae. The thoracic vertebrae of *Phenacodus* are similar to those of *Hyracotherium,* but in none are the zygapophyses embracing. The posterior articular surfaces face ventrally and laterally, but never dorsally.

Slijper (1946) has shown that with decreasing mobility of the body axis in the heavier ungulates, the spinal insertion of the longissimus muscle shows a tendency to shift backward. Correlated with the decreasing importance of this muscle is the tendency of
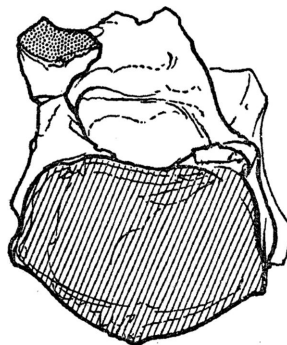

FIG. 3. *Hyracotherium angustidens* (Cope), A.M.N.H. No. 15820 (part), fragment of lumbar vertebra. Posterior view showing articular facet. ×1.

the neural spines of the lumbar vertebrae to become less cranially or even caudally inclined.

In *Equus* the longissimus muscle is relatively important, being inserted into the neural spines from the fourteenth thoracic vertebra to the third sacral vertebra. The neural spines of the lumbar vertebrae are slightly cranially inclined. They are, however, less cranially inclined than in cursorial animals with a very flexible spine, such as *Canis*, and less so than in *Phenacodus*.

Slijper states that in *Hyracotherium* the lumbar neural spines are vertical. He cites as authority for this statement Romer (1936) and Scott (1929). No mention of *Hyracotherium* could be found in papers by these authors for the dates cited. An examination of the literature has led me to conclude that Slijper meant to refer to text figures in Romer (1933) and Scott (1937). In the collections of the American Museum there is only one lumbar neural spine of *Hyracotherium* of which the angle can be determined, and that angle is exactly the same as that of the homologous spine of *Equus*.

The evidence bearing on this point is far from conclusive, but apparently the longissimus muscle was less important in *Hyracotherium* than in *Phenacodus*, indicating a less flexible spine.

SACRAL VERTEBRAE: The sacrum consists of five fused vertebrae. The distal portions of the neural spines are missing, but apparently they were well separated. The wings are moderately expanded dorsally, and the auricular surface is relatively long. The lateral borders converge slightly posteriorly. The sacrum of *Mesohippus* is very similar to that of *Hyracotherium*. The sacrum of *Phenacodus* consists of only three vertebrae. The wings extend just beyond the parallel lateral borders.

CAUDAL VERTEBRAE: There are, as far as I have been able to determine, no caudal vertebrae of *Hyracotherium* in any American collection.

RIBS

As nearly as can be determined from the fragmentary material at hand, the ribs of *Hyracotherium* present no remarkable feature and are virtually identical in structure to those of *Mesohippus*. The ribs of *Phenacodus* are slightly more robust and relatively less compressed than those of *Hyracotherium* and have heads that are less sharply convex.

SCAPULA

The scapula of *Hyracotherium* has usually been restored to resemble that of later horses, that is, with the blade relatively narrow and with the coracoid, glenoid, and vertebral borders more or less straight. In the collection of the California Institute of Technology are a partial skull and nearly complete postcranial skeleton from the Gray Bull beds of the Big Horn Basin of Wyoming. Both scapulae are virtually complete and are to my knowledge the only ones in existence with the blade intact. I have examined casts of both scapulae. They are far more dog-like than horse-like. The coracoid border is straight, and the vertebral and glenoid borders are continuous and strongly convex. The spine is high and sharp, and the acromion process is nearly or quite as large as in *Canis*. The neck is constricted, and the glenoid cavity is oval and shallowly concave. The tuber scapulae is located at the posterior border of the glenoid surface. The infraspinous fossa is somewhat smaller than the supraspinous fossa, while in the dog they are about equal in area. The areas of muscle insertion on the medial side of the scapula are, as nearly as can be determined from the cast, almost exactly as they are in *Canis*. In *Mesohippus* the vertebral border is straight and the acromion process is relatively much smaller than in *Hyracotherium*. I have examined no specimen of *Phenacodus* in which the acromion process has not been broken away. The scapular blade of *Phenacodus* was relatively less broad than that of *Hyracotherium*.

HUMERUS

Posteriorly the head of the humerus is sharply and rather evenly convex. Anteriorly it is nearly flat and merges anteriorly into the narrow greater tuberosity and anterolaterally into the bicipital groove. The bicipital groove is broad and shallow and more or less evenly convex proximodistally. It is not divided into two separate grooves, as it is in most later horses. This broad, simple,

bicipital groove apparently allowed transverse movement of the biceps muscle within the groove and hence considerable rotation of the humerus relative to the scapula. In *Mesohippus* the proximal part of the bicipital groove consists of a narrow, horizontal, shelf-like, anteromedial continuation of the head which overhangs a depression on the anteromedial side of the proximal end of the humeral shaft. There is no apparent division of the groove into two separate parts. In *Phenacodus* the groove is essentially like that of *Mesohippus*, but in addition a low ridge runs longitudinally in its approximate center.

The greater and lesser tuberosities are rather narrow, and there is no medially projecting attenuation of the greater tuberosity such as is found in *Mesohippus*.

The shaft of the humerus is mediolaterally flattened, and in dorsal view it tapers evenly and is slightly curved, the convex side being anterior. In *Mesohippus* the shaft does not taper so sharply, while in *Phenacodus* it is essentially as in *Hyracotherium*. The deltoid ridge, which is prominent and rather sharp in *Mesohippus* and *Phenacodus*, is low and blunt.

The condyles are smaller relative to the head than they are in either *Mesohippus* or *Phenacodus*. The lateral condyle is very shallowly grooved longitudinally, a feature undoubtedly restricting lateral movement between the humerus and the radius. The epicondyles are small. The partition between the olecranon and coronoid fossae is absent, resulting in a perforation of the bone at this point. In *Mesohippus* the lateral condyle is deeply grooved and the partition between the olecranon and coronoid fossae is present. In *Phenacodus* a supracondyloid foramen is present, the epicondyles are prominent, and the lateral condyle is ungrooved, although there is a very slight depression at its dorsolateral margin.

RADIUS

The humeral articular surface of the radius is mediolaterally expanded and is divided into two distinct surfaces. The surface for the articulation of the lateral condyle of the humerus consists of a relatively broad, medial, mediolaterally convex groove and a lateral anteriorly inclined surface. Divided from this surface by a low ridge is the surface for the articulation of the medial condyle of the humerus. It is flat mediolaterally and very slightly concave anteroposteriorly and is inclined medially at an angle of about 10 degrees. In *Mesohippus* the humeral articular surface of the radius is very similar to that of *Hyracotherium* except that the medial surface is less medially inclined and is slightly concave in all directions. In *Phenacodus* the lateral surface is a simple, shallowly concave groove, and the medial surface is flat and somewhat more medially inclined.

The shaft is anterolaterally compressed and slightly bowed, with the concave side posterior. The groove for the tendon of the extensor carpi radialis muscle is relatively deep, while in *Mesohippus* it is broad and shallow. In *Phenacodus* the shaft is twisted so that this groove lies on the lateral surface.

The scaphoid facet is poorly preserved but was apparently much as it is in *Mesohippus*, that is, anteriorly anteroposteriorly concave and posteriorly anteroposteriorly convex. The lunar facet is anteroposteriorly concave and mediolaterally slightly concave, as it is in *Mesohippus*. In *Phenacodus* both facets are concave in all directions, and in correlation with the twisted shaft the lunar facet is posterolateral rather than directly lateral to the scaphoid.

ULNA

The medial surface of the olecranon is concave, while the lateral surface is slightly convex. The olecranon is essentially similar in all three genera, but in *Phenacodus* it is relatively much larger than in *Hyracotherium* or *Mesohippus*.

The articular surface of the semilunar notch laps back onto the lateral and medial surfaces of the olecranon, particularly the distolateral portion which is expanded and faces anterolaterally. This condition indicates that a considerable amount of rotation of the radius and ulna relative to the humerus was possible. The semilunar notch of *Mesohippus* is similar to that of *Hyracotherium*, but the distolateral portion of the articular surface is less expanded. In *Phenacodus* the area of the articular surface on the lateral and medial surfaces of the olecranon is somewhat greater than in *Hyracotherium*.

The small, flat, radial facet is virtually confluent with the articular surface of the semilunar notch, being separated from it only by a low ridge. In *Mesohippus* the radial facet is more distally located and separated from the articular surface of the semilunar notch, while *Phenacodus* resembles *Hyracotherium*, although the facet is relatively larger.

The shaft is mediolaterally flattened and curved to fit the curve of the radius. Near its distal end the shaft tapers suddenly and sharply to the small distal extremity. The cuneiform facet is oval, with the long axis running anteroposteriorly. It is mediolaterally convex and anteroposteriorly slightly concave. The small vertical pisiform facet is very slightly convex in all directions. In *Mesohippus* the shaft tapers gradually and is very thin at its distal end. The confluent cuneiform and pisiform facets are very small. In *Phenacodus* the shaft tapers very little, and its posterodistal edge projects medially well beyond the radius. The cuneiform and pisiform facets, however, are not notably larger than in *Hyracotherium*.

MANUS

The manus of *Phenacodus* is so different from that of *Hyracotherium* that a detailed comparison has not been made. The carpus of *Phenacodus* is serial in arrangement, that is, each distal element of the carpus bears, with one exception, upon a single proximal element, although there is a narrow lunar-unciform contact. In *Tetraclaenodon*, a Paleocene form possibly ancestral to *Phenacodus*, the carpus is alternating, there being a lunar-unciform and lunar-magnum contact. The alternating carpus may thus be the primitive condition in this group, the serial arrangement being a specialized feature secondarily derived in *Phenacodus*.

In no specimen is the carpus well preserved. The description is based on the complete, but poorly preserved carpus of A.M.N.H. No. 4832 and the carpus of A.M.N.H. No. 15428, which lacks the trapezium, trapezoid, and unciform. There are apparently no specific differences in the carpus.

The lunar, which tapers somewhat distally, occupies the central position of the carpus. Lateral to it the cuneiform curves plantarly and slopes distally. Medial to it the scaphoid curves plantarly. The trapezium, roughly square in shape, is very small, and its position is well plantar to the other elements. The trapezoid is also small and square. The magnum is very small and in dorsal view is irregularly oval. It bears broadly upon the scaphoid and very narrowly upon the lunar and extends a little farther distally than does the trapezoid. The unciform is large and extends farther distally than the magnum. It is borne narrowly by the lunar and broadly by the cuneiform.

The second metacarpal is borne largely by the trapezoid but apparently also by the trapezium. The third metacarpal is borne broadly by the magnum and narrowly by the unciform, which also bears the fourth and fifth metacarpals. The third metacarpal is a little longer than the second and fourth which are of about equal length. The first metacarpal is very short and is without phalanges. The metacarpals are closely applied to each other throughout their length. The fifth and second metacarpals are somewhat plantar to the fourth and third.

The carpus of *Mesohippus* is high and narrow in dorsal view, owing to the more plantar position of the cuneiform, unciform, and trapezoid. The magnum is the central element of the carpus and is borne about equally by the scaphoid and the lunar. The third metacarpal is borne entirely by the magnum. The unciform, which is borne somewhat more broadly by the cuneiform than by the lunar, is much longer proximodistally than the magnum, while the trapezoid is somewhat shorter. The metatarsals thus articulate at three different levels. The second and fourth metacarpals are closely applied and mostly plantar to the third.

The scaphoid is high and narrow in dorsal view. The lateral aspect is rectangular. The radial facet is roughly oval in shape and largely flat. Along its dorsomedial border, however, it is narrowly convex. Joining the radial facet at its dorsolateral edge and perpendicular to it is the small, flat, proximal, cuneiform facet. The facet for the magnum is rectangular and mediolaterally concave. It occupies only the most dorsal portion of the distal end of the scaphoid. The distal cu-

neiform facet meets the lateral edge of the facet for the magnum. Plantarly it narrows sharply and runs along the mediodistal border of the bone. The trapezoid facet is mediolaterally concave and is inclined medially at an angle of about 45 degrees. The scaphoid of *Mesohippus* is quite strikingly different from that of *Hyracotherium*. The dorsal portion of the radial facet is slightly dorsoplantarly convex, while the plantar portion is dorsoplantarly concave. The facets for the magnum and the trapezoid are relatively much larger than in *Hyracotherium*, and the trapezoid facet is directed distally rather than obliquely. The distal cuneiform facet does not continue distally. There is, however, a small cuneiform facet at the plantar corner.

The lunar tapers somewhat distally in dorsal view. Dorsally the radial facet is dorsoplantarly convex. Plantarly it tapers into a narrow heel which is separated from the broad dorsal portion by a shallow transverse groove. Although poorly preserved, this area is apparently also dorsoplantarly convex. The flat, vertical, proximal, scaphoid facet joins the dorsomedial margin of the radial facet. The facet for the magnum is narrow dorsally and broadens plantarly. It is concave in all directions and faces somewhat laterally. The distal scaphoid facet runs along the lateral edge of the facet for the magnum, narrowing plantarly. The unciform facet is narrow and dorsoplantarly concave. It extends the entire dorsoplantar length of the lunar. The flat proximal cuneiform facet is inclined somewhat laterally. It extends less than half of the dorsoplantar length of the lunar, while the narrow distal cuneiform facet runs nearly the entire dorsoplantar length along the distolateral border. In *Mesohippus* the radial facet is less sharply concave dorsally and broader distally. The facet for the magnum is relatively much larger than it is in *Hyracotherium*. The proximal scaphoid facet is narrow and the cuneiform bears upon most of the lateral surface of the lunar.

The unciform is irregularly oval in dorsal view. The magnum-cuneiform facet is dorsoplantarly convex and mediolaterally nearly flat. The facet for the fourth metacarpal is flat. Plantolaterally it rises rather sharply, forming the facet for the fifth metacarpal.

The unciform apparently touches the magnum at three or four points, but no distinct facets are visible on either the unciform or the magnum. This is probably because of poor preservation. A distinct tuberosity extends distolaterally from the lateral side. In *Mesohippus* there are small facets marking the contact with the magnum along the proximomedial border, and at the distodorsomedial and distoplantomedial corners.

The pisiform is greatly flattened mediolaterally. It is hooked in a medial direction; that is, the medial surface is dorsoplantarly concave, while the lateral surface is dorsoplantarly convex. The cuneiform facet is triangular in shape and is dorsoplantarly slightly convex. The adjoining ulnar facet is slightly concave in all directions. The pisiform of *Mesohippus* is relatively more robust throughout and is more markedly hooked.

The dorsal aspect of the cuneiform is high and narrow. It is dorsoplantarly rather long. The ulnar facet is dorsoplantarly concave and mediolaterally slightly convex. Behind the ulnar facet and separated from it by a low ridge is the pisiform facet which is dorsoplantarly concave and flat plantarly. The proximal and distal lunar facets are flat and are confined to the dorsal half of the bone. The latter is considerably narrower than the former. The unciform facet is broad and dorsoplantarly concave. It forms a continuous surface with the unciform facet of the lunar. The cuneiform of *Mesohippus* is very similar to that of *Hyracotherium* except for the smaller size of the ulnar facet.

In dorsal view the magnum is irregularly oval in shape and very small. In proximal view it is broad dorsally and tapers into a narrow heel plantarly. The scaphoid facet is slightly convex and tapers somewhat plantarly. The lunar facet is flat and narrow. It is nearly vertical and thus almost perpendicular to the scaphoid facet. The facet for the third metacarpal is dorsoplantarly concave and mediolaterally slightly convex. The small oval facet for the second metacarpal is slightly concave in all directions. It faces medially at an angle of about 30 degrees. As mentioned above there are no facets in the specimens at hand to mark the contact of the magnum and unciform. In *Mesohippus* the lunar facet is relatively broader than in *Hyracotherium*,

and its face is nearly horizontal. Facets marking the contact with the unciform are present on the lateral surface.

The trapezoid is small and prism shaped and is square in dorsal view. The scaphoid facet is mediolaterally concave and dorsoplantarly flat. The facet for the second metacarpal is flat. Nearly all the lateral surface is in contact with the magnum. The trapezoid of *Mesohippus* is nearly identical in structure to that of *Hyracotherium*.

The trapezium is poorly preserved. It is very small and apparently touches the scaphoid, trapezoid, and second metacarpal. In *Mesohippus* the trapezium is further reduced and touches only the trapezoid and the second metacarpal.

Proximally the third metacarpal is triangular in cross seciton. Distally it becomes oval and dorsoplantarly compressed. The facets for the magnum and unciform are mediolaterally concave and dorsoplantarly flat. Along the proximomedial and proximolateral edges are narrow facets for the second and fourth metacarpals. The head is smooth dorsally and prominently keeled plantarly. The third metacarpal of *Mesohippus* is like that of *Hyracotherium*, but is relatively much larger.

The fourth metacarpal is not so dorsoplantarly compressed as the third. The facet for the unciform is dorsoplantarly convex and mediolaterally flat. In *Mesohippus* the second and fourth metacarpals are reduced, mediolaterally very compressed, and closely applied to the third.

Proximally the second metacarpal is mediolaterally compressed. Distally it curves medially and is less compressed. The facet for the trapezium is deeply dorsoplantarly concave.

The fifth metacarpal is compressed mediolaterally and diverges laterally somewhat. The facet for the trapezium is dorsoplantarly convex and inclined medially. In *Mesohippus* the fifth metacarpal is reduced to a short vestige.

The first phalanges are all similar, but the lateral and medial ones are somewhat less dorsoplantarly compressed than the third. They taper slightly distally. The proximal articular surface is concave in all directions. The distal articular surface is convex dorsoplantarly and slightly concave mediolater-

ally and extends well back onto the plantar surface.

The second phalanges are similar to the first but are relatively much shorter.

The terminal phalanx of the third digit is hoof-like. It is somewhat longer than the second phalanx. The plantar surface is flat, and the dorsal surface is mediolaterally convex. The facet for the second phalanx is oval and slightly concave in all directions. The terminal phalanges of the second, fourth, and fifth digits are slightly shorter and much narrower than the terminal phalanx of the third.

For a complete discussion of the function of the digital ligaments of *Hyracotherium* and of all later horses, see the excellent paper of Camp and Smith (1942).

PELVIS

The pelvis is horse-like in that the ventral portion of the blade of the ilium diverges anterolaterally and the dorsal portion extends almost vertically to a point above the spines of the sacral vertebrae. The functional significance of the dorsally expanded ilium is not entirely clear. It is found to a greater or lesser degree in almost all cursorial ungulates and never in cursorial carnivores. The possible functional significance of the character suggests itself if one considers the action of the pelvis and the femur in the horse and dog during running. At maximum flexure the angle between the femur and the horizontal plane is approximately the same in the horse and the dog. In the horse, however, the angle of the pelvis relative to the horizontal plane changes very little and probably never exceeds 45 degrees during locomotion, and consequently the angle between the pelvis and the femur is much more acute than in the dog, in which the pelvis may assume a nearly vertical position at maximum flexure. The dorsally expanded ilium affords a more dorsal insertion for the gluteus medius muscle and an angle of application that approaches 90 degrees at the beginning of the propulsive phase.

The blade of the ilium is concave dorsally, and the crest is concave. The anterolaterally extending portion forms a relatively narrow, tapering process. The tuber sacrale is missing from all specimens examined. In *Mesohippus*

the dorsal portion of the blade near the tuber is narrow and is rounded anteriorly and nearly flat posteriorly. The ventral portion is gently concave. The ventral portion of the ilium of *Phenacodus* is somewhat produced anteriorly but not laterally. The dorsal portion of the blade is low and rounded, and the crest is almost straight. The lateral surface of the blade is very slightly concave and almost perpendicular to the horizontal plane.

The shaft of the ilium is very short, broad, and flat. In *Mesohippus* it is much longer, narrower, and relatively thicker, while in *Phenacodus* is it similar to that of *Hyracotherium*.

The acetabulum is almost perfectly circular and deep and has projecting borders. The acetabular fossa is broad and shallow. In *Mesohippus* the acetabulum is oval and the dorsal surface is mediolaterally flat, as is the head of the femur.

The tuber ischii projects posterior to the posterior border of the ischium as it does in *Mesohippus*, while in *Phenacodus* it is more anteriorly located.

FEMUR

The head of the femur is nearly hemispherical and is well offset from the shaft. The depression for the ligamentum teres is broad and rather shallow. The neck is slightly constricted and is inclined to the long axis of the shaft at an angle of about 45 degrees. In *Mesohippus* the head is not so far offset from the shaft, and the proximal part of the articular surface is nearly flat mediolaterally, a feature that undoubtedly contributed to a restriction of the lateral movement of the limb. In *Phenacodus* the head is hemispherical but is not so far offset as in *Hyracotherium*.

The great trochanter extends far above the head and is medially inclined. This expansion of the great trochanter, which is nearly or quite as marked as it is in any of the later horses, indicates a forceful action of the gluteus medius muscle. The medial inclination of the great trochanter apparently reduced the rotating action of the gluteus medius. In *Phenacodus* the trochanter extends well beyond the head but is not so high as in *Hyrachotherium*.

The trochanteric crest is high and sharp and is parallel to the long axis of the shaft.

The trochanteric fossa in *Hyracotherium* and *Mesohippus* is not nearly so deep as it is in *Phenacodus*, perhaps reflecting a decrease in importance of the obturator externus muscle as the limb became more specialized for movement in a single plane.

The lesser trochanter is strong and is triangular in shape. The third trochanter is relatively as large as in later horses, and the tip is characteristically hooked in an anterior direction. The third trochanter of *Phenacodus* is nearly as strong as it is in *Hyracotherium*, but it is more distally located and it is flat.

There is no trace of the supracondyloid fossa which is present in *Phenacodus* and *Mesohippus* as a shallow depression. The condyles and epicondyles present no remarkable features and are closely similar to those of both *Phenacodus* and *Mesohippus*. The trochlear crests are sharp and the articular groove is narrow and rather shallow. In *Mesohippus* this groove is a little broader and deeper than in *Hyracotherium*.

TIBIA

The lateral and medial condyles are close together, and the intercondyloid eminence is high. The intercondyloid tubercles are high, and the articular surfaces consequently rise sharply internally. The lateral intercondyloid tubercle is higher than the medial, while in *Mesohippus* they are of about equal height. In later horses it is the medial tubercle which is higher. The proximal end of the tibia of *Phenacodus* differs rather strikingly from the condition described above. The intercondyloid tubercles are very low, and there is almost no intercondyloid eminence. There is, consequently, no sharp internal rise of the articular surfaces, but the medial surface is depressed at its center.

The spine is prominent but is not so convex anteriorly as it is in *Mesohippus* and later horses. Furthermore, in none of the specimens examined is the prominent, laterally projecting tuberosity so characteristic of later horses present. The absence of this tuberosity in *Hyracotherium* and its presence in later horses are almost certainly connected with the increasing importance of various patellar ligaments, particularly the lateral.

The proximal third of the shaft of the tibia is triangular in cross section. The antero-

lateral and the posterior faces are deeply concave, resulting in sharp crests at the medial and lateral posterior borders. At the proximal end of the posterolateral crest, directly beneath the lateral condyle, is the concave facet for the fibula. The distal part of the shaft is roughly triangular in cross section, but the surfaces are convex rather than concave.

The lateral articular groove is slightly concave, and it faces distolaterally at an angle of about 45 degrees. The medial articular surface has nearly vertical sides and is narrow and deep. The grooves run parallel to the sagittal plane. In *Mesohippus* the distal end of the fibula is fused to the tibia, the astragalar facet thus forming the lateral, vertical side of the lateral articular groove of the tibia. The articular grooves of *Mesohippus* form an angle of about 30 degrees with the sagittal plane, the posterior ends being more medial. The articular grooves of *Phenacodus* are similar to those of *Hyracotherium* but are wider and shallower in correlation with the blunter, lower trochlear crests. The groove for the tendon of the lateral digital extensor is much longer than in *Mesohippus*. This groove is apparently not present in *Phenacodus*.

FIBULA

The shaft of the fibula is circular in cross section and expanded at its proximal and distal ends. The tibial facet faces proximally and is circular and slightly convex in all directions. The distal extremity is closely applied to the tibia. The astragalar facet is nearly vertical and proximodistally slightly concave. The fibula of *Mesohippus* differs from that of *Hyracotherium* only in being somewhat smaller relative to the tibia and in having its distal third fused to the tibia. In *Phenacodus* the fibula is considerably larger than that of *Hyracotherium* and is less broadly in contact with the tibia.

PES

The description of the hind foot is based on four more or less complete specimens. Two of these (A.M.N.H. Nos. 15428 and 15820) are from the Gray Bull beds of the Willwood formation and are referable to *H. angustidens*. The other two (A.M.N.H. Nos.

4832 and 4848) are from the Wind River formation.

The tarsus as a whole is high and narrow in dorsal view. The trochlear crests are parallel to the long axis of the foot, and the lateral crest is directly beneath the body of the calcaneum. The navicular facet of the astragalus is slightly offset medially and is proximal to the cuboid facet of the calcaneum. The cuboid is long and narrow in dorsal view, and the navicular, which bears narrowly on the calcaneum, is proximodistally compressed. The dorsal aspect of the ectocuneiform is square, and it occupies a central position beneath the lateral half of the navicular. It extends farther distally than the cuboid and the mesocuneiform. The mesocuneiform is much smaller than the ectocuneiform. It is slightly plantar to the ectocuneiform as is the cuboid. The small, mediolaterally flattened entocuneiform is located largely plantar, but somewhat medial to the mesocuneiform. Its dorsal edge bears about equally on the mesocuneiform and the second metatarsal.

The third metatarsal is borne entirely by the ectocuneiform. The slightly shorter second and fourth metatarsals are closely applied to the third proximally, but distally diverge laterally and a little plantarly.

The first phalanx is nearly as broad and about one-fourth as long as the metatarsal. The second phalanx is narrower and about one-half as long as the first. The terminal phalanx is a littler narrower and somewhat longer than the second.

The tarsus of *Mesohippus* is lower and broader than that of *Hyracotherium* owing to the proximodistal compression of the distal elements. The trochlear crests form an angle of about 10 degrees with the long axis of the foot, the proximal ends being more internal. The navicular is greatly broadened and occupies a position almost directly beneath the astragalus. The ectocuneiform occupies a central position beneath the navicular, with the cuboid and mesocuneiform somewhat lateral but largely plantar to it. The mesocuneiform does not extend quite so far distally as the ectocuneiform. The distal facets of the cuboid and the ectocuneiform are at the same level. The third metatarsal of *Mesohippus* is relatively much larger than

in *Hyracotherium*, and the second and fourth metatarsals are closely applied and largely plantar to it. The second phalanx is relatively shorter than in *Hyracotherium*.

In *Phenacodus* the trochlear crests are parallel to the calcaneal tuber as in *Hyracotherium*, but the navicular facet of the calcaneum is more offset medially. The navicular and the cuboid are more proximodistally compressed than in *Hyracotherium* and the ectocuneiform somewhat less so. The facets for the metatarsals on the cuboid, ectocuneiform, and entocuneiform are about on a level with one another, while the facet of the mesocuneiform is considerably proximal to them. All five digits are present, with the first and the fifth greatly reduced, the fifth somewhat more so than the first. There is considerable interlocking of the proximal ends of the metatarsals, but distally they diverge sharply.

The tibial trochlea of the astragalus is quite deep, and the trochlear crests are well defined and sharp. The crests are parallel to the long axis of the articulated foot. The trochlear crests of *Mesohippus* are higher and sharper than those of *Hyracotherium* and are oriented at an angle of about 10 degrees with the long axis of the foot, the proximal ends of the crests being more medial than the distal. In *Phenacodus* the trochlear crests are lower and less sharp than in *Hyracotherium*.

The neck of the astragalus is short and slightly constricted and diverges medially at an angle of about 10 degrees. In *Mesohippus* there is almost no neck, as the dorsal edge of the navicular facet meets the distal end of the medial trochlear crest. In *Phenacodus* the neck is quite long and is more constricted than in *Hyracotherium* and is more offset medially.

The navicular facet, which is offset from the body owing to the angle of the neck, is oval in shape and is dorsoplantarly convex and laterally slightly concave. The dorsal portion of the facet curves slightly onto the dorsal surface of the neck. At the plantar edge of the facet is a slight projection which fits into a depression at the plantar edge of the astragalar facet of the navicular, restricting movement between the two elements. At the plantolateral edge of the navicular facet and separated from it by a low ridge is the small, flat, cuboid facet. At the lateral

edge of the cuboid facet is the vertical distal astragalar facet. The navicular facet of *Mesohippus* is very similar to that of *Hyracotherium*, while in *Phenacodus* it is strongly convex in all directions. There is no contact between the astragalus and cuboid in *Phenacodus*.

The sustentacular facet is oval, with its long axis parallel to the trochlear crests. It is slightly convex distally and proximally curves up under the overhanging medial trochlear crest. The proximal and distal portions are perpendicular to each other. In *Mesohippus* this facet is essentially as described above, while in *Phenacodus* the distal portion is broader and more convex.

The astragalo-calcaneal facet is broadly oval, with its proximal half lying beneath the overhanging lateral trochlear crest and its distal half lying on the body. The two faces are approximately perpendicular to each other. There is a very small distal extension of this facet. The astragalo-calcaneal facet of *Mesohippus* is very similar to that of *Hyracotherium*, while in *Phenacodus* it is shallowly and evenly concave.

The calcaneal tuber is mediolaterally compressed and expanded at its distal end to form a prominent tuberosity. There is no groove for the tendon of Achilles which is present in *Phenacodus*. The area of insertion for this tendon is large, covering nearly half of the area of the proximal end of the tuber. The plantaris muscle apparently inserted just dorsal to the insertion of the tendon of Achilles, their relationship thus having been essentially as it is in *Equus*.

The sustentaculum is broad proximodistally, and the slightly concave sustentacular facet is oval and is slanted plantarly at an angle of about 30 degrees. In *Phenacodus* this facet is nearly round and somewhat more concave than in *Hyracotherium*.

The astragalo-calcaneal facet is deeply and sharply concave distally. Proximally the facet extends onto the dorsomedial portion of the tuber. Just proximomedial of this are two small pits which receive projections on the distal end of the tibia when the limb is extended. This compound facet in its articulation with the astragalo-calcaneal facet of the astragalus virtually prevents movement in the sagittal plane between these two

elements. In *Phenacodus* this facet is broadly
and evenly convex.

The cuboid facet is semicircular in shape,
with the flat side medial. Dorsally it is flat,
while plantarly it is slightly concave. Joining
the medial edge of this facet is the flat,
vertical, distal, astragalar facet. The cuboid
facet of *Phenacodus* is square in outline and
is flat plantarly and concave dorsally.

The calcaneum of *Mesohippus* differs from
that of *Hyracotherium* only in that the tuber
is relatively shorter and dorsoplantarly
broader.

The cuboid is high and narrow in both
dorsal and lateral views and is somewhat
mediolaterally flattened. The convex cal-
caneal facet covers almost the entire proximal
end of the bone. The small astragalar facet
is confluent with the calcaneal facet and is
located at its dorsomedial corner. The dorsal
half of the distal end of the cuboid is covered
by the flat facet for the fourth metatarsal.
Plantar to this facet and projecting somewhat
distal to its surface is the prominent tuber-
osity for the attachment of the plantar liga-
ment. On the medial surface of the cuboid is
a prism-shaped projection. The proximal
surface of this projection bears a small, flat,
navicular facet, while the distal surface bears
a similar facet for the cuneiform. In *Phena-
codus* the cuboid and the astragalus do not
meet. The proximal facet is consequently
somewhat smaller than in *Hyracotherium*.
The calcaneal facet is moderately concave,
and there is no distinct navicular facet. The
cuboid of *Mesohippus* differs from that of
Hyracotherium in being markedly more
proximodistally compressed and in having
a much larger tuberosity for the attachment
of the plantar ligament.

The navicular is slightly compressed proxi-
modistally. The astragalar facet is dorso-
plantarly concave and laterally slightly con-
vex, and there is a slight depression at its
plantar margin which fits the projection on
the navicular facet of the astragalus men-
tioned above. The mesocuneiform facet is
nearly flat and covers the dorsal half of the
distal end of the bone. The slightly convex
entocuneiform is smaller, covering only the
medial portion of the plantar half, and is
separated from the mesocuneiform facet by
a low ridge. At the plantar edge of the medial

surface is the flat, vertical, cuboid facet. The
navicular of *Mesohippus* is much more
proximodistally compressed than that of
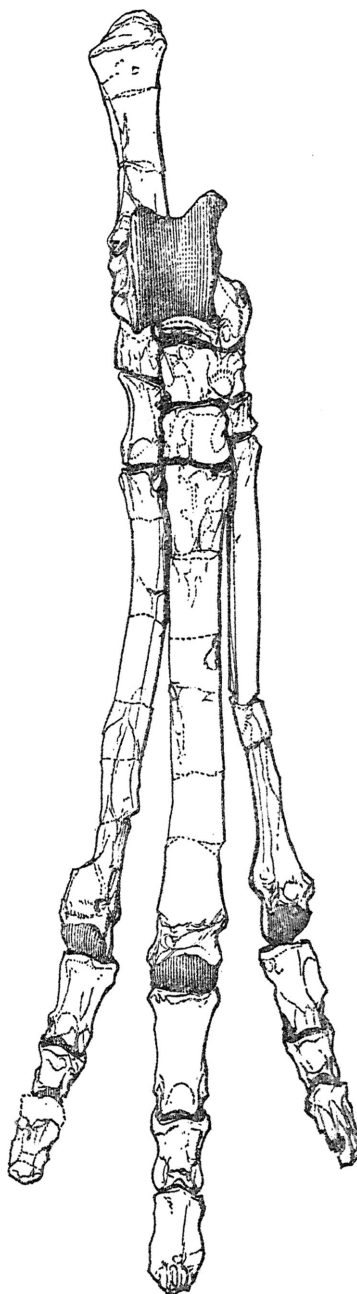*Hyracotherium*. Laterally the astragalar facet

FIG. 4. *Hyracotherium angustidens* (Cope),
A.M.N.H. No. 15820 (part), right hind foot.
Anterior view. ×1.

is slightly concave but is mediolaterally flat for most of its width. In *Mesohippus* the ectocuneiform and entocuneiform have fused, and the navicular bears upon the ecto-portion of the bone. There is consequently an addition to the mesocuneiform facet forming one continuous, strongly convex facet. The navicular of *Phenacodus* is proximodistally markedly compressed. The astragalar facet is deeply convex in all directions. The distal surface of the bone is slightly convex in all directions, and the facets are apparently continuous. There is a prominent tuberosity on the plantar surface.

The ectocuneiform is square in dorsal view. The navicular facet is triangular in shape, with the base dorsal, and is dorsoplantarly slightly concave and laterally nearly flat. The small cuboid facet is located at the plantolateral edge of the navicular facet. The facet for the third metatarsal is oval in shape, with a narrow, plantarly extending heel, and is laterally mediolaterally slightly convex and medially mediolaterally concave. The ectocuneiform of *Mesohippus* is like that of *Hyracotherium* but is much more proximodistally compressed. In *Phenacodus* the navicular facet of the ectocuneiform is flat, while the facet for the third metatarsal is dorsoplantarly concave. A very prominent grooved hook for the insertion of the tendon of the peroneus longus muscle originates from the proximal half of the plantar edge of the bone.

The mesocuneiform is a simple, prism-shaped bone, nearly square in dorsal aspect. The facets for the navicular and the second metatarsal are flat. In *Mesohippus* the mesocuneiform and ectocuneiform are fused. The dorsal portion of the resulting bone is proximodistally compressed, but its plantar portion flares sharply proximally and distally. The facets for the navicular and second metatarsal are thus flat dorsally and respectively upturned and downturned plantarly. The mesocuneiform of *Phenacodus* closely resembles that of *Hyracotherium* except that the facets are dorsoplantarly concave.

Of the four hind feet examined, one specimen of *H. angustidens* (A.M.N.H. No. 15820) has an entocuneiform and a greatly reduced fifth metatarsal. The other three specimens show no trace of these elements, and in all

three the mesocuneiform is missing, apparently as a result of post-mortem loss. It is clear that in these cases the lack of the metatarsal may also be the result of post-mortem loss rather than phylogenetic reduction.

In A.M.N.H. No. 15820 the ectocuneiform is oval and mediolaterally compressed. It bears about equally on the mesocuneiform and the fourth metatarsal. The fifth metatarsal is mediolaterally compressed and tapers to a point distally.

The third metatarsal is triangular in cross section proximally. Distally it becomes oval in cross section, the long axis of the oval running mediolaterally. The proximal facet fits the navicular facet precisely, and apparently little movement was possible at this contact. The dorsal surface of the head is smoothly rounded, while the plantar surface is prominently keeled. In *Mesohippus* the third metatarsal is similar to that of *Hyracotherium* except for its much greater relative size.

The fourth metatarsal is mediolaterally compressed and slightly curved laterally and plantarly. The proximal facet is oval and flat, and the head is very much narrower than that of the third metatarsal. The head is grooved on its plantolateral side rather than keeled centrally. The second metatarsal is similar to the fourth except for the plantarly directed facet for the ectocuneiform. The mesocuneiform facet is very small. The second and fourth metatarsals of *Mesohippus* are similar to those of *Hyracotherium* except that they are relatively smaller and not so curved, as they are more closely applied to the third metatarsal.

The first phalanx of the third digit is about one-fourth as long as the metatarsal. The shaft is constricted and dorsoplantarly compressed. The plantar surface is flat, while the dorsal surface is mediolaterally convex. The facet for the metatarsal is nearly circular and shallowly convex in all directions. The facet for the second phalanx faces posteroplantarly and is mediolaterally concave and dorsoplantarly convex. The first phalanx of the second and of the fourth digits is slightly shorter than that of the third and is mediolaterally compressed. The facets for the metatarsals are dorsoplantarly

concave and mediolaterally nearly flat. The facets for the second phalanges are similar to the facet of the third digit, but are much narrower. The second phalanges closely resemble the first but are much shorter.

The terminal phalanges of the hind foot are identical in structure to those of the fore foot.

In *Mesohippus* the phalanges are similar to those of *Hyracotherium*. The second phalanges of all the digits are, however, relatively reduced, and the terminal phalanx of the third digit is relatively much broader.

All the differences between the tarsus of *Hyracotherium* and that of *Phenacodus* are differences that contribute to the increased stability and decreased mobility of the former, necessary as the stability imparted by multiple digital contact with the ground is lost. Thus, in *Hyracotherium*, there are three contacts in the tarsus which are not present in the tarsus of *Phenacodus*. These are the contacts between the astragalus and the cuboid, the distal ends of the astragalus and the calcaneum, and the navicular and the cuboid (the navicular and the cuboid are closely applied to each other in *Phenacodus*, but their contact is not marked by a distinct facet). Further reduction of mobility in the tarsus of *Hyracotherium* has been accomplished by a change in form of the facets, particularly a mediolateral flattening, resulting in a restriction of lateral movement. The most remarkable change of this sort is in the navicular facet of the astragalus. In *Mesohippus* mobility of the tarsus has been further reduced by a greater flattening of the facets and by the proximodistal compression of the distal elements.

COMPARISON WITH OTHER LOWER EOCENE PERISSODACTYLA

As Wood (1934) has pointed out, already in the early Eocene the teeth of perissodactyls showed a definite evolutionary dichotomy into a horse-palaeothere-titanothere complex on the one hand and a tapir-rhinoceros complex on the other. In the postcranial skeleton, however, the lower Eocene perissodactyls are strikingly similar to one another and are probably not divisable into suborders on the basis of any known skeletal character.

The teeth of the genus *Homogalax* are so similar to those of *Hyracotherium* that a consideration in some detail of the differences between them is warranted. In *Homogalax* the lateral borders of the upper molars are usually more oblique than those of *Hyracotherium*, and the major cusps and the parastyle are relatively higher. The protoloph and metaloph are high and sharp in contrast to those of *Hyracotherium*, and there is little or no trace of a distinct paraconule and metaconule. In P[4] the protoloph is strong, with no trace of a distinct protoconule, and the metaloph is weak. P[3] is similar to P[4], but the metaloph is weak or even absent. In the lower molars of *Homogalax* the metalophid runs almost directly anterior, or at most only slightly medially, from the metaconid, while in *Hyracotherium* the metalophid runs obliquely across the tooth to join the protolophid near its junction with the metaconid. In addition to this difference, the hypolophid in *Homogalax* is equal in height to the protolophid, while in *Hyracotherium* it is always lower.

In *Heptodon* the upper molars show no trace of a protoconule or metaconule. In the lower molars the protolophid and hypolophid are stronger than in *Homogalax*, and the anteriorly directed metalophid is weak. The heel of M[3] is greatly reduced.

The postcranial skeleton of *Homogalax* is almost unknown. The limb bones of *Heptodon*, except for their relatively greater length, are almost identical to those of *Hyracotherium*. The astragalus and calcaneum of both *Homogalax* and *Heptodon* are more condylarth-like than those of *Hyracotherium*. The astragalo-calcaneal facet of the astragalus consists of a single, evenly convex face rather than two flat, more or less distinct faces perpendicular to each other as in *Hyracotherium*. Correlated with the evenly concave form of the astragalo-calcaneal facet of the astragalus is the evenly convex face of the proximal portion of the astragalo-calcaneal facet of the calcaneum. It is evident that in *Homogalax* and *Heptodon*, as in

Phenacodus, more movement in the sagittal plane between the astragalus and calcaneum was possible than in *Hyracotherium*.

The teeth of *Hyrachyus* have been described and compared to those of *Hyracotherium* and other Eocene perissodactyls by Wood (1934). The postcranial skeleton of *Hyrachyus* shares the generalized perissodactyl pattern with *Hyracotherium*. A few differences such as the relatively stouter limbs and less medially offset femur head in *Hyrachyus* are undoubtedly correlated with the larger body size of individuals of this genus. The astragalo-calcaneal facets of the astragalus and calcaneum are similar to those of *Homogalax* and *Heptodon*, and the tibial trochlea is broad and shallow, differing little from that of *Phenacodus*.

The teeth of *Lambdotherium* are more specialized than those of *Hyracotherium*, but in general pattern they are very similar. In *Lambdotherium* there is a well-developed mesostyle on the upper molars and a weak one on P³ and P⁴. The paracone and metacone are ribbed externally. The lower molars are more lophiodont than those of *Hyracotherium* but are otherwise very similar.

The postcranial skeleton of *Lambdotherium* is poorly known. Two calcanea in rather doubtful association with *Lambdotherium* molars in the collection of the American Museum of Natural History are indistinguishable from those of *Hyracotherium*. The fact of doubtful association and the fact that in *Eotitanops* the calcaneum is like that of *Hyrachyus* suggest that the calcanea in question are actually referable to *Hyracotherium*.

GENERAL DISCUSSION OF THE MORPHOLOGY

The dentition of *Hyracotherium* is very primitive. It differs little from the dentition of the most primitive ungulates. There is little indication of the molariformity of the premolars and the lophiodonty which is so characteristic of the later equids. On the basis of the morphology of the teeth there is no particular reason to believe that *Hyracotherium* was fully herbivorous rather than omnivorous.

Hyracotherium is, in almost all characters of the skull, closer to *Mesohippus* than to *Phenacodus*. The differences between the skulls of *Hyracotherium* and *Mesohippus* on the one hand and the skull of *Phenacodus* on the other can nearly all be correlated with the relatively elongate and expanded muzzle in the former genera. In the few characters of the skull in which *Hyracotherium* differs markedly from *Mesohippus*, such as in the arrangement of the orbital foramina, it also differs from *Phenacodus*. The skull of *Hyracotherium* represents a definite departure from the condylarth cranial morphology in the direction of the later horses.

The vertebrae are more or less intermediate in character between those of *Phenacodus* and those of *Mesohippus*. In the possession of embracing zygopophyses, the inclination of the lumbar neural spines, and the character of the sacrum, however, *Hyracotherium* is very similar to *Mesohippus*.

The fore limb is, on the whole, remarkably little specialized. The scapula is clearly more primitive than the scapula of *Phenacodus*. The humerus differs little from that of *Phenacodus* except in lacking an epicondyloid foramen, and the ulna is somewhat relatively reduced in comparison with that of *Phenacodus*. The radius shows some specialization in the mediolateral broadening of the humeral and carpal articular surfaces. The foot, although definitely mesodactyl, is digitigrade and relatively primitive. It is interesting that in *Mesohippus*, although the foot is far more specialized than in *Hyracotherium*, the scapula, humerus, radius, and ulna closely resemble those of *Hyracotherium* and are consequently different from those of *Equus*. The humeroradial index of two species of *Hyracotherium* approaches that of *Mesohippus* and is considerably greater than that of *Phenacodus* (see table 2). The humerometacarpal index of *Hyracotherium* is about midway between that of *Phenacodus* and that of *Mesohippus*.

The hind limb shows most of the fundamental equid specializations. The pelvis differs from that of *Phenacodus* and is strikingly similar to that of the later horses in
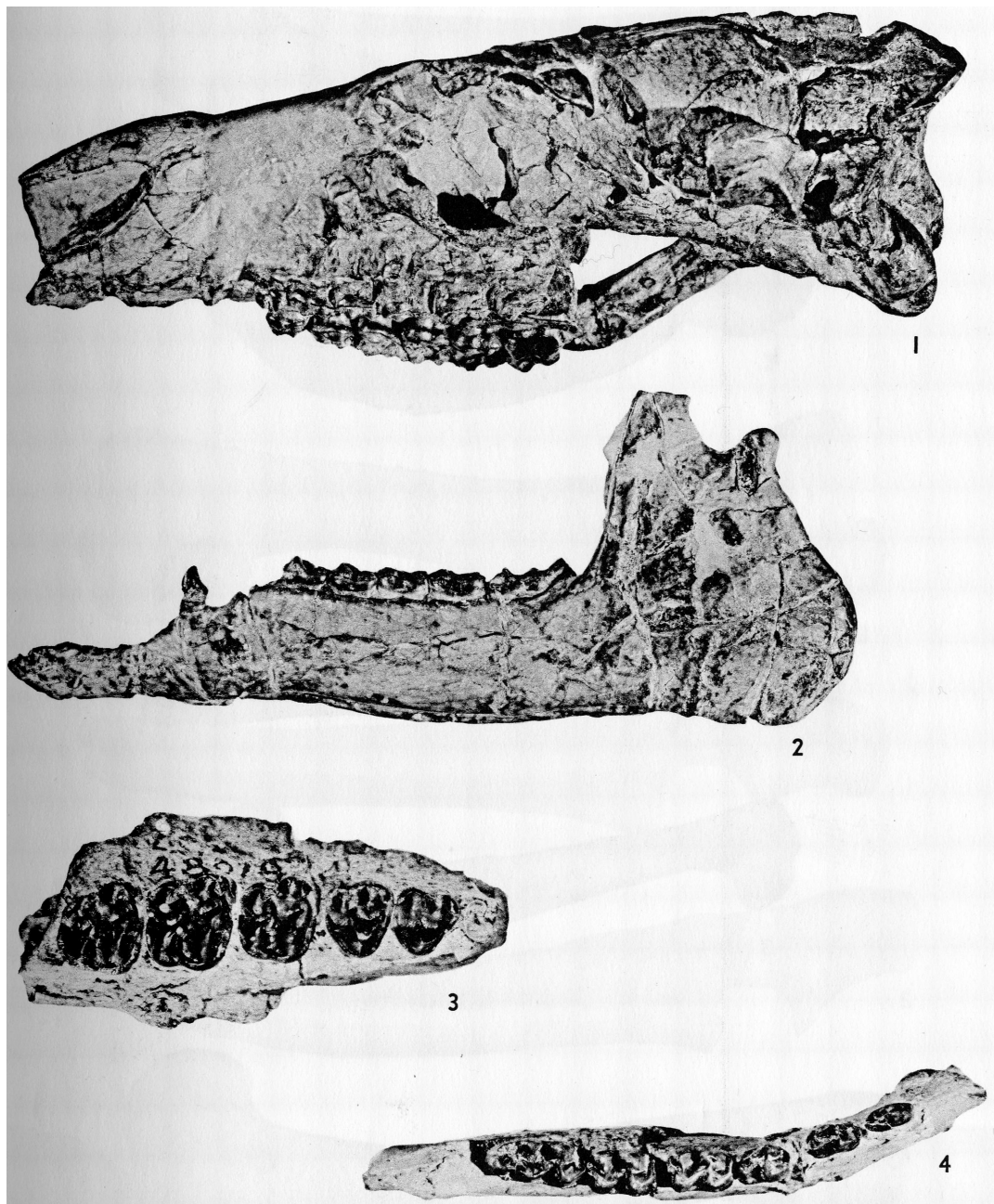
1, 2. *Hyracotherium vasacciense* Cope, A.M.N.H. No. 4832. 1. Skull. 2. Lower jaw. Left lateral views. × 1

3. *Hyracotherium angustidens* Cope, A.M.N.H. No. 48018, left upper jaw with P³-M³. Crown view. × 3/2

4. *Hyracotherium vasacciense* Cope, A.M.N.H. No. 48015, right lower jaw with P₂-M₃. Crown view. × 3/2

1. *Hyracotherium angustidens* Cope, cast of California Institute of Technology specimen, left scapula. Lateral view. × 1

2. *Phenacodus copei* Granger, A.M.N.H. No. 4378, left humerus. Anterior view. × 1

3. *Hyracotherium angustidens* Cope, A.M.N.H. No. 15436, left humerus. Anterior view. × 1

4. *Mesohippus* sp., A.M.N.H. No. 39001, left humerus. Anterior view. × 1
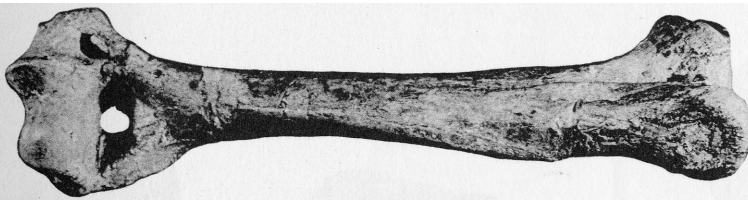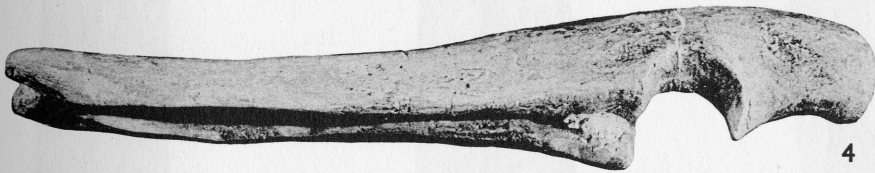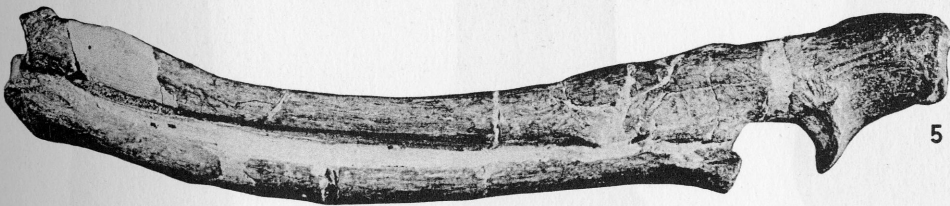
1. *...us copei* Granger, A.M.N.H. No. 4378, left humerus. Medial view. × 1
2. *...rium angustidens* Cope, A.M.N.H. No. 15436, left humerus. Medial view. × 1
3. *...us* sp., A.M.N.H. No. 39001, left humerus. Medial view. × 1
4. *...us copei* Granger, A.M.N.H. No. 4378, right radius and ulna (partly restored). Lateral view. × 1
5. *...rium angustidens* Cope, A.M.N.H. No. 15428, right radius and ulna. Lateral view. × 1
6. *...us bairdi* Leidy, A.M.N.H. No. 8223, right radius and ulna. Lateral view. × 1
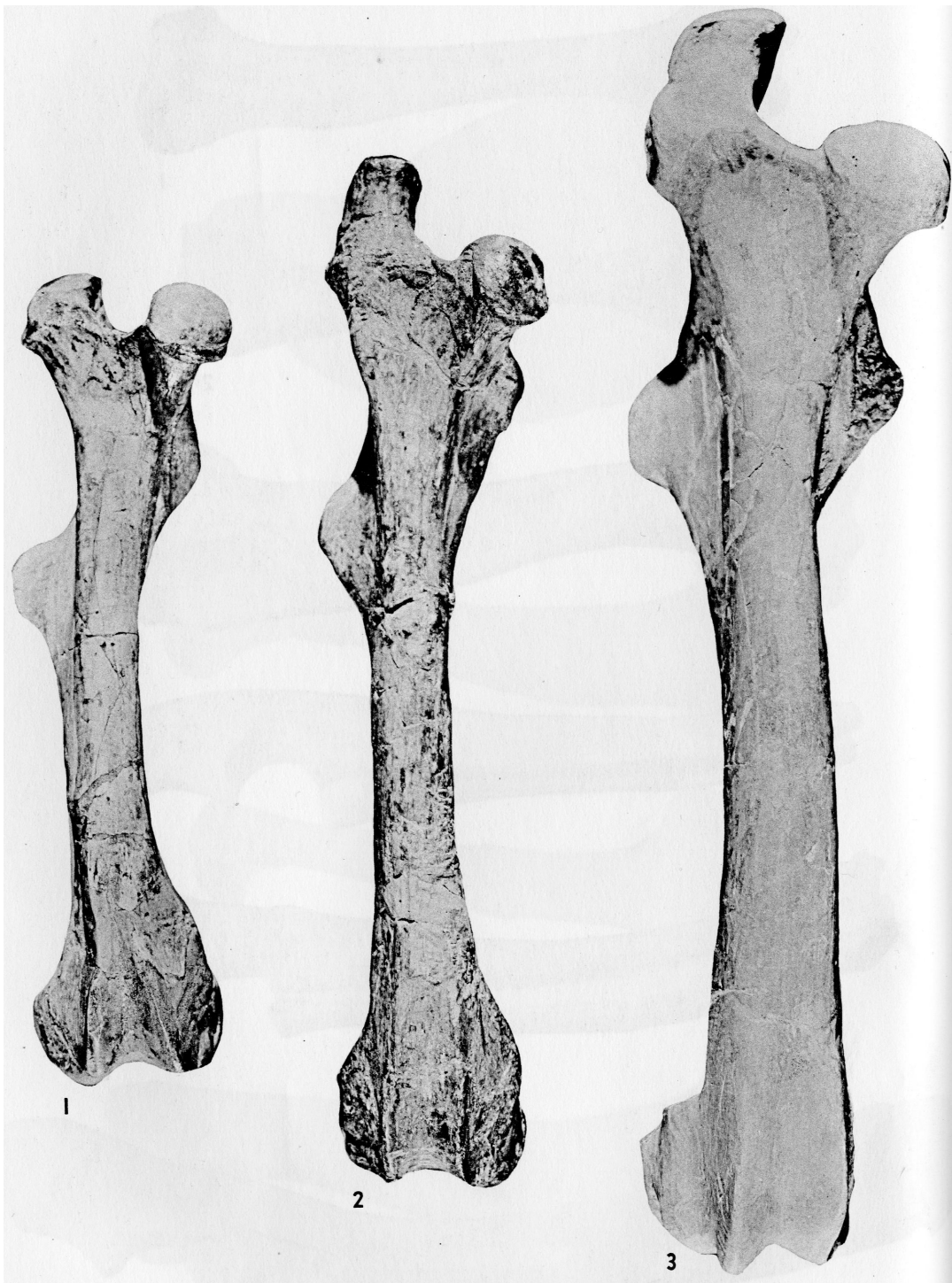
Right femora. Anterior views. ×1
1. *Phenacodus copei* Granger, A.M.N.H. No. 4378
2. *Hyracotherium angustidens* Cope, A.M.N.H. No. 15428
3. *Mesohippus bairdi* Leidy, A.M.N.H. No. 9770

Right tibiae and fibulae. Lateral views. × 1
1. *Phenacodus copei* Granger, A.M.N.H. No. 4378
2. *Hyracotherium angustidens* Cope, A.M.N.H. No. 15428
3. *Mesohippus bairdi* Leidy, A.M.N.H. No. 9770

Right tibiae and fibulae. Posterior views. × 1
1. *Phenacodus copei* Granger, A.M.N.H. No. 4378
2. *Hyracotherium angustidens* Cope, A.M.N.H. No. 15428
3. *Mesohippus bairdi* Leidy, A.M.N.H. No. 9770

1. *Hyracotherium angustidens* Cope, A.M.N.H. No. 15820, pelvis. Left lateral view. × 4/5
2. *Hyracotherium* sp., A.M.N.H. No. 4848, right fore foot. Dorsal view. × 1
3. *Hyracotherium* sp., A.M.N.H. No. 4848, left hind foot. Dorsal view. × 1

the expanded wing of the ilium, and the great and third trochanters are nearly identical in structure with those of *Mesohippus*. The tibia and fibula are condylarth-like in being unfused but resemble t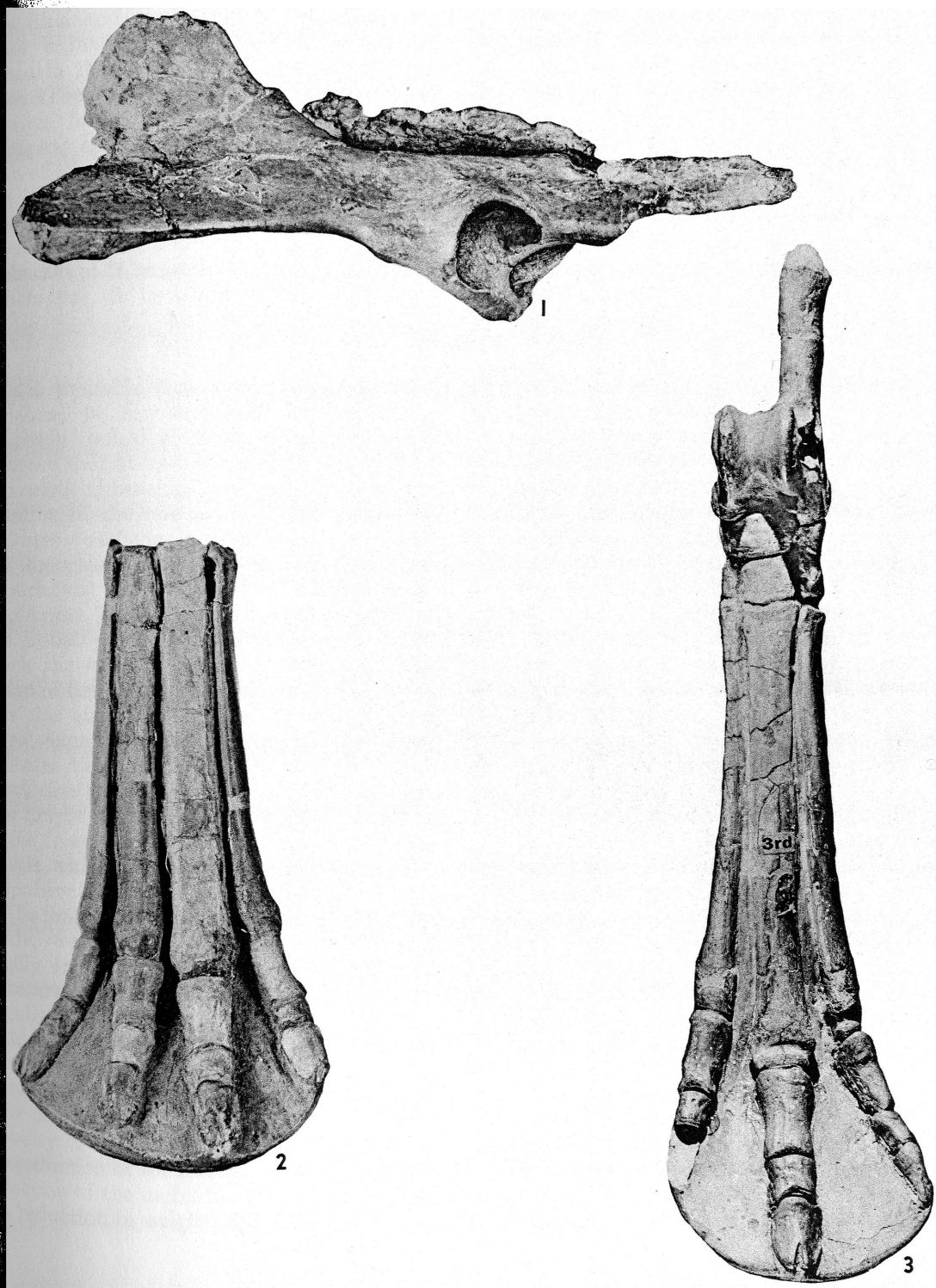hose of the horses in the structure of the articular surfaces. The tarsus shows the fundamental features found in all horses, such as the astragalar cuboid contact and the distinctive form of the navicular facet of the astragalus, and in these features differs strikingly from *Phenacodus*. The femorotibial index of *H. angustidens* is the same as that of *Phenacodus*, while that of *H. vasacciense* is equal to that of *Mesohippus*. In both species the metatarsus is relatively more elongate than that of *Phenacodus* and approaches that of *Mesohippus*.

Hyracotherium is relatively primitive in its morphology, but in almost every structure and bone it reveals fundamental likenesses to *Mesohippus* and the later horses. The resemblances to *Phenacodus* are numerous but on the whole much less striking. It must be borne in mind, however, that *Phenacodus* is obviously specialized in many respects and must have been much more specialized than the form, perhaps *Desmatoclaenus*, which was the common ancestor of both *Phenacodus* and *Hyracotherium*.

LOCOMOTION

It is probable that the series of lumbar vertebrae in *Hyracotherium* constituted a relatively inflexible unit. There is good evidence that at least some of the zygopophyses were embracing, and the angle of inclination of the one neural spine preserved indicates that the longissimus muscle was less important than in *Phenacodus* and the cursorial carnivores and about as important as in *Equus*. The action of the back in running was probably very much as it is in *Equus*, in which the lumbar series bends only in the region of the last two vertebrae.

If the above inferences are correct, the dorsal expansion of the wing of the ilium indicates that the femur was sharply flexed in relation to the relatively immobile pelvis. The height of the great trochanter testifies to the forceful action of the gluteus medius muscle which probably provided the major propulsive force as it does in *Equus*.

The limb as a whole, and consequently the stride, were long in *Hyracotherium* owing largely to the great relative length of the metatarsals and the assumption of a nearly unguligrade pose of the foot. In connection with the latter character, the lateral digital elements are reduced, and the loss of the stability once provided by these elements has been compensated for by a decrease in the mobility of the tarsus. A further corollary of the reduction of the lateral elements, and the reduction of the mobility of those remaining, is a reduction in weight of the distal portions of the limbs, allowing faster movement during the recovery phase.

Although the general action of the hind limb of *Hyracotherium* was apparently similar to that of *Equus*, the action of the foot, particularly the phalanges, must have been quite different. In both *Hyracotherium* and *Mesohippus* there was probably an elastic, median, digital pad. The work of Camp and Smith (1942) has shown that *Hyracotherium* and *Mesohippus* retained the paired interosseous muscles attached to the pairs of proximal sesamoid bones. In later horses the interosseous ligament degenerates and gives rise to the elastic interosseous tendon which imparts the automatic springing action to phalanges of *Equus*.

It has been suggested that the inflexibility of the lumbar series in some ungulates is to be correlated with the mechanical difficulties involved in the maintenance of a flexible axial skeleton in animals of large size. Large size, however, cannot account for the possession of an inflexible lumbar series by *Hyracotherium*, nor by small antelopes in which the spine is rendered almost completely immobile by embracing zygopophyses.

What is the adaptive advantage of the type of locomotion found apparently in *Hyracotherium* over that in which the stride is lengthened by a sharp flexure of the back and a considerable proportion of the propulsive strength is provided by the straightening of the back? The cursorial ungulates, which

all run more or less in the manner postulated for *Hyracotherium*, differ from cursorial carnivores not in being able to attain higher speeds but in being able to maintain high speeds for longer periods of time. The mode of locomotion of cursorial ungulates seems to be less fatiguing than that of the cursorial carnivores. It is not unreasonable to suppose that this difference results from the fact that while in ungulates movement is restricted largely to the limbs, in carnivores the whole body is flexed at each stride. It is, however, by no means certain that the differences in stamina between the two groups can be so easily explained. Factors such as the differences in the proportion of "red" and "white" muscle fibers must also be taken into consideration. If it is assumed that the difference in stamina is partly the result of the different modes of locomotion, then it is perfectly clear why selection has not produced predators with greater staying power. The ungulate mode of locomotion requires above all a sacrifice of skeletal flexibility which no predator can afford to make. The predator would have great difficulty in bringing down its prey while moving its limbs only in the sagittal plane.

In all cursorial animals, particularly in horses, almost all the propulsive force is provided by the hind limbs, the fore limbs serving primarily as supports upon which the body is borne during the recovery phase of the hind limbs. Thus the fore limb serves no unique function in the cursorial ungulate mode of locomotion. This may account for the fact that the fore limb was more conservative in the evolution of the Equidae, that is, slower to aquire the specializations characteristic of *Equus*, than was the hind limb. Modification of the fore limb was not necessary, because it served the same function as it had in the ancestors of the Equidae. The fore limb specializations which appear in later horses, particularly the modifications of the articular surfaces, are probably largely to be correlated with increase in body size rather than with any particular mode of locomotion.

THE WORD "SPECIES" in the following dis-
cussion is used to indicate a group of speci-
mens that is distinguishable from other
groups of specimens on the basis of one or
more morphological characters. In cases
where an adequate sample is available from
a rather restricted horizon, I believe that
paleontological species defined in the above
way will in many cases be biologically
equivalent to recent species, that is, they
will be composed of specimens that are the
remains of individuals that were included
in the same reproductively isolated popula-
tion during life. For example, the two mor-
phologically distinct forms of which the re-
mains are found side by side in late Wasatch-
ian deposits and which were apparently de-
scended from the same early Wasatchian
ancestor are specifically distinct in a genetic
sense. The early Wasatchian ancestor, on the
other hand, was genetically continuous
through time with each of the descendent
species and is consequently not, in a genetic
sense, specifically distinct from either of
them. It is, however, a nearly universal
paleontological convention to term such
ancestral-descendent types "species" if they
differ morphologically to about the same
degree as do genetic species.

The term "subspecies" has been introduced
into the following discussion to distinguish
groups of specimens that exhibit overlapping
ranges of particular morphological characters,
but of which the group means for the particu-
lar character are significantly different. Some
of the groups so distinguished clearly repre-
sent different morphological stages on a
single ancestral-descendent line, while others
may represent contemporaneous geographic
subspecies.

From each Wasatchian mammal-bearing
horizon and locality as large samples as
possible were assembled. Many specimens
from various collections were excluded from
samples because of insufficient stratigraphic
or locality data. Each sample was examined
to determine the morphological characteris-
tics and range of variation. The samples were
then compared with one another and it was
determined whether or not there were
significant differences between them. Finally
the type specimens were compared with the
samples from their respective horizons and
localities.

Hyracotherium angustidens (Cope)

Orohippus angustidens COPE, 1875, p. 20.
Hyracotherium angustidens COPE, 1877, p. 265.
Eohippus angustidens (Cope) Marsh, KING, 1878, p. 377.
Orohippus cuspidatus COPE, 1875, pp. 20, 22.
Hyracotherium cuspidatum COPE, 1877, p. 267.
Eohippus cuspidatus (Cope) Marsh, KING, 1878, p. 377.
Eohippus validus MARSH, 1879, p. 401.
Orotherium cristonense COPE, 1877, p. 254.
Pliolophus cristonense COPE, 1884, p. 651.
Hyracotherium (Pliolophus) cristonense Cope, WORTMAN, 1896, p. 102, figs. 11, 12.
Pliolophus cristonensis Cope, HAY, 1902, p. 610.
Eohippus cristonensis (Cope), GRANGER, 1908, p. 237, fig. 5.
Orotherium loevii COPE, 1877, p. 257.
Pliolophus loevii COPE, 1884, p. 651.
Systemodon etsagicus COPE, 1884, pl. 56, fig. 5.
Eohippus etsagicus (Cope), GRANGER, 1908, p. 239.
Hyracotherium cristatum WORTMAN, 1896, p. 96, fig. 6.
Hyracotherium (Eohippus) cristatum Wortman, MATTHEW, 1899, p. 33.
Eohippus cristatus (Wortman), HAY, 1902, p. 609.
Hyracotherium index (in part) Cope, WORT-MAN, 1896, p. 99, figs. 9, 10.
Hyracotherium (Eohippus) index (in part) Cope, TROUESSART, 1898, p. 771.
Hyracotherium (Pliolophus) montanum WORT-MAN, 1896, p. 103.
Pliolophus montanus (Wortman), HAY, 1902, p. 610.
Eohippus montanus (Wortman), GRANGER, 1908, p. 239.
Eohippus resartus GRANGER, 1908, p. 240.
Eohippus borealis GRANGER, 1908, p. 242, fig. 4, pl. 15, fig. 3.

TYPE: U.S.N.M. No. 1079, fragment of
lower jaw with M_{1-3}, from the Almagre, New
Mexico.

TYPES OF SYNONYMS: *Orohippus cuspida-
tus:* U.S.N.M. No. 1077, fragment of maxilla
with DP^4-M^1 from the Almagre, New Mex-

ico. *Orotherium cristonense:* U.S.N.M. No. 1002, lower jaws, from the Almagre, New Mexico. *Orotherium loevii:* U.S.N.M. No. 1128, fragment of lower jaw with P_2–M_2, from the Almagre, New Mexico. *Systemodon etsagicus:* A.M.N.H. No. 4600, fragment of lower jaw with P_4–M_2, from the Gray Bull beds, Wyoming. *Hyracotherium cristatum:* A.M.N.H. No. 258b, fragment of lower jaw with P_2–M_2, from the Gray Bull beds, Wyoming. *Hyracotherium (Pliolophus) montanum:* A.M.N.H. No. 4593, fragments of right and left lower jaws with right P_4 and left M_{2-3}, from the Gray Bull beds, Wyoming. *Eohippus resartus:* A.M.N.H. No. 4657, fragment of left lower jaw with P_3–M_2 and in doubtful association fragments of upper jaws with left P^4–M^1 and right M^{2-3}, from the Gray Bull beds, Wyoming. *Eohippus borealis:* A.M.N.H. No. 214, fragments of right and left lower jaws with right P_2–M_3 and left P_3–M_3, from the Gray Bull beds, Wyoming.

HYPODIGM: The types, as above, and the samples listed under the subspecies.

KNOWN DISTRIBUTION: Almagre, New Mexico; Gray Bull beds, Wyoming; Sand Coulee beds, Wyoming; Powder River Basin (Sussex), Wyoming; and Indian Meadows, Wyoming.

DIAGNOSIS: Size medium to large; P^3 and P^4 triangular in shape with no apparent tendency towards molarization; heel of M_3 usually broad and short; diastema between P^1 and P^2 shorter than P^1; diastema between P_1 and P_2 shorter than P_1; femorotibial index about 110, reduced fifth metatarsal present.

There have been five species named from the Almagre member of the San Jose formation of New Mexico and five from the Gray Bull beds of the Willwood formation of Wyoming. The populations from these two areas differ significantly in the mean size of

FIG. 5. *Hyracotherium angustidens* (Cope), A.M.N.H. No. 48018 (part), P^4–P^4. Crown view. ×3.

the teeth, but there is extensive overlap in size variation between the two populations, and no other character distinguishes one population from the other. In morphological characters of the teeth there is great variation within each population, but no consistent differences between the two.

The Almagre and Gray Bull populations together with populations from the Sand Coulee beds of the Willwood formation and Powder River Basin can, however, be distinguished from populations from all later strata by the complete lack of molarization or tendency towards molarizations of P^3 and P^4. These teeth show great variation in size and shape, but in no case do they show any tendency to become quadrate. The heel of M_3 from these horizons and localities is usually short and broad, but this character shows considerable variation and cannot be considered as completely definitive. The diastema between P^1 and P^2 and between P_1 and P_2 is short in individuals of *H. angutidens*, but these teeth are found so seldom that the character is of little use in specific identification. The skeleton of *H. angustidens* is larger in all dimensions than that of *H. vasacciense*, and the two species differ somewhat in the proportions of some of the limb bones. No complete skeleton of *H. craspedotum* is known. In regard to size this species is apparently very close to *H. angustidens*.

Simpson (1948) has determined from an examination of the field records that nearly all of Cope's New Mexican Eocene specimens were collected in the Almagre rather than the Largo member of the San Jose formation. It is thus almost certain that Cope's four New Mexican hyracothere types are from the Almagre. In the case of three of the types, however, this could be certainly determined from the structure of the teeth, as they consist of lower teeth which are virtually identical in structure in *H. angustidens* and in *H. vasacciense* from the overlying Largo beds.

In the original description the type of *Orohippus angustidens* was compared with species of *Orohippus*. Subsequently (1877) Cope recognized the correct generic position of the type and separated it from other species on the basis of size. Granger (1908) further characterized this species by the slenderness of the lower molars and lower jaw. The type falls well within the observed
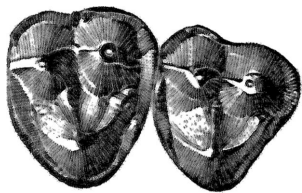
range of variation of the Almagre sample.

Orohippus cuspidatus was based on a first and second upper molar and was defined as the smallest species of the genus. Later (1877) Cope placed the species in *Hyracotherium*, characterizing it as the smallest species of this genus. The type is indeed near the lower limit of size for the genus, the M² falling as it does just within the observed size range of the Almagre sample. As additional specific characters the regularly quadrate form of the molars and the separation of the median tubercles from the interior were cited. The exact meaning of the latter distinction is unclear, but the type falls within the observed range of variation of the Almagre sample both in general shape of the upper molars and in the position and relationships of the protocone and the hypocone.

Baldwin's records indicate that he collected only west of the continental divide in the San Juan Basin and consequently only in the Largo member of the San Jose formation. The type of *H. validum*, however, resembles specimens from the Almagre member and is quite different from any specimen in the Largo sample. The type consists of a number of jaw and skeletal fragments of at least two individuals. In many of their dimensions the teeth are intermediate between the two distinct Largo species. Baldwin collected near Lindrith, New Mexico, and in this area there are beds lower than the typical Largo beds. The specimen in question may have come from these lower strata.

The type of *Orotherium cristonense* falls well within the range of variation of the Almagre sample in all characters. This species was separated from *Orotherium loevii* on the basis of the simplicity of the protoconule. Granger (1908), while admitting that the character was variable, cited the large, basin-shaped heel as distinctive of this species.

Orotherium loevii was distinguished on the basis of its small size and well-developed protoconulid. It falls within the known range of variation of the Almagre sample in every respect.

The type of *Systemodon etsagicus* was figured by Cope (1884) with no accompanying description. The specimen clearly is referable to *Hyracotherium* and was so referred by Granger (1908), who separated it from *H. cristonense* on the basis of the depth of the ramus, the absence of an entoconid on P₄, and the absence of a diastema. This type falls within, but rather close to, the lower limit of the observed size range of the Gray Bull sample.

Wortman (1896) stated that *Hyracotherium* (*Pliolophus*) *montanum* can be distinguished from *H. index* only by the presence of an entoconid on P₄. Wortman was fully aware of the great variability of this character and was apparently reluctant to recognize this character as of even specific importance. The type is clearly within the observed range of the Gray Bull sample in every respect.

Hyracotherium cristatum was defined principally on the basis of its very large size. The type specimen falls outside the ob-

TABLE 3

	P_2		P_3		P_4		M_1		M_2		M_3		M^1		M^2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Orohippus angustidens	—	—	—	—	—	—	—	—	7.2	5.0	10.3	5.1	—	—	—	—
Eohippus validus	—	—	—	—	5.7	5.3	7.1	5.4	8.2	6.3	12.4	6.2	—	—	—	—
Orotherium cristonense	5.8	3.2	6.0	4.1	6.5	4.9	7.0	5.2	7.8	6.0	11.8	6.0	—	—	—	—
Orotherium loevii	—	—	5.3	3.6	—	—	6.4	4.6	7.0	4.9	8.8	4.7	—	—	—	—
Systemodon etsagicus	—	—	—	—	6.3	4.4	7.6	5.2	8.2	5.5	—	—	—	—	—	—
Hyracotherium cristatum	—	—	7.1	4.0	8.0	5.3	9.6	6.5	10.6	7.2	—	—	—	—	—	—
Hyracotherium montanum	—	—	—	—	—	—	—	—	8.5	6.0	11.4	6.0	—	—	—	—
Eohippus resartus	—	—	7.2	4.5	7.9	5.4	9.5	6.4	11.2	7.3	—	—	—	—	—	—
Eohippus borealis	6.0	3.1	6.4	3.8	6.4	4.5	7.7	5.1	7.9	5.7	11.1	5.2	—	—	—	—
Orohippus cuspidatus	—	—	—	—	—	—	—	—	—	—	—	—	6.2	6.4	6.4	7.3

served size range of the Gray Bull sample in every dimension, but within the standard range. In view of the apparent tendency of many of the earlier workers to choose extreme variants as types, I believe that this type can be safely referred to *H. angustidens.* Of the four other specimens that Wortman refers to this species, three (A.M.N.H. Nos. 4653, 4655, and 4656) are almost certainly referable to *Homogalax,* and the fourth (A.M.N.H. No. 4650), a very weathered specimen, is considerably smaller than the type and falls within the observed range of the Gray Bull sample. In characters other than size the type is almost identical in structure with some of the larger specimens in the hypodigm.

Eohippus resartus is based on a large specimen so remarkably similar to the type of *Hyracotherium cristatum* that it is difficult to understand why they were ever considered distinct. This type also falls somewhat outside the observed range of size of the Gray Bull sample, but within the standard range.

Eohippus borealis is a species proposed by Granger (1908) to embrace the numerous medium-sized specimens from the Gray Bull.

Wortman (1896) synonymized *H. index,* *H. vasacciense, H. cuspidatum, H. venticolum, H. angustidens,* and *H. cuspidatum.* The first two are here regarded as synonyms as are the latter four. To synonymize the first two and the latter four, however, while permitted by morphological similarity of the known parts, is improbable on the grounds of their stratigraphic positions. The types of *H. vasacciense* and *H. index* are from the Knight formation near Evanston, Wyoming. No upper premolars are known from this horizon and locality, but because this formation is generally agreed to be of Lysite age (Wood *et al.,* 1941), I believe that it is safe to assume that the hyracotheres from this formation belong to an upper rather than to the lower Wasatchian species. The species from the Knight agree quite as well with Lysite specimens as they do with specimens from the Almagre or Gray Bull.

It should be noted that Cope (1884) stated that *H. angustidens* was abundant in the "Wind River bad lands," a conclusion that I consider doubtful for the reasons given above.

Granger (1908) synonymized *H. angustidens* with *H. cuspidatus,* and *H. loevii* with *H. cristonense.*

Hyracotherium angustidens angustidens (Cope)

Orohippus angustidens COPE, 1875, pp. 20, 22.
Hyracotherium angustidens COPE, 1877, p. 265.
Eohippus angustidens (Cope) Marsh, KING, 1878, p. 377.
Orohippus cuspidatus COPE, 1875, pp. 20, 22.
Hyracotherium cuspidatum COPE, 1877, p. 267.
Eohippus cuspidatus (Cope) Marsh, KING, 1878, p. 377.
Eohippus validus MARSH, 1876, p. 401.
Orotherium cristonense COPE, 1877, p. 254.
Pliolophus cristonense COPE, 1884, p. 651.
Hyracotherium (Pliolophus) cristonense Cope, WORTMAN, 1896, p. 102, figs. 11, 12.
Pliolophus cristonensis Cope, HAY, 1902, p. 610.
Eohippus cristonensis (Cope), GRANGER, 1908, p. 237, fig. 5.
Orotherium loevii COPE, 1877, p. 257.
Pliolophus loevii COPE, 1884, p. 651.

TYPE: Type of the species.

HYPODIGM: Types of synonyms and a large number of jaw fragments and isolated teeth from the Almagre member of the San Jose formation.

KNOWN DISTRIBUTION: Almagre, New Mexico, and Powder River Basin (Sussex), Wyoming.

DIAGNOSIS: Size small, length of M_3 (all specimens), mode 8.5–9.5.

The Almagre sample consists of a large number of jaw fragments and isolated teeth (A.M.N.H. Nos. 48007–48080) collected by the American Museum expeditions of 1946, 1947, and 1948.

It is highly probable this sample is heterogeneous, that is, that it contains individuals from more than a single population. This may be inferred from the fact that the observed range and coefficient of variation for the linear dimensions of the teeth are much greater than might reasonably be expected if a single population were represented. The coefficient of variation has, of course, no intrinsic biological significance. It has been found, however, that the coefficient of variation for tooth dimensions in single species of recent mammals almost never exceeds 10 and rarely exceeds 8. In the case of the present sample the coefficient of variation was over 14 for some dimensions. The dis-

tributions of these dimensions are strongly skewed to the right. The distributions are, however, unimodal. The time factor may be eliminated in the consideration of this sample, because the relative level at which each specimen was found was carefully recorded, and analysis shows that there is no correlation between level and size or morphological character of the teeth.

If the hypothesis that two populations are present in this sample is correct, then it is clear that there are fewer individuals in the sample from the population of higher mean tooth size. The disparity could be the result of selective deposition and preservation from slightly different ecological or geographic niches. It is of course possible that the predominance of one form in the sample reflects a difference in population

TABLE 4

STATISTICAL DATA ON THE TEETH OF *Hyracotherium angustidens angustidens* AND *Hyracotherium angustidens etsagicum* FROM THE ALMAGRE MEMBER OF THE SAN JOSE FORMATION

	N	OR
M^1		
L	3	7.0– 7.5
W	3	8.0– 9.9
M^2		
L	11	6.4– 8.8
W	11	7.8–10.9
M^3		
L	21	6.8– 9.6
W	21	7.2–11.2
P_4		
L	11	5.3– 7.5
W	11	3.9– 5.2
M_1		
L	16	5.7– 7.6
W	16	3.8– 5.6
M_2		
L	21	6.3–10.2
W	21	4.4– 7.7
M_3		
L	29	8.0–12.7
W	29	4.3– 6.9

TABLE 5

STATISTICAL DATA ON THE TEETH OF *Hyracotherium angustidens angustidens* FROM THE POWDER RIVER BASIN LOCAL FAUNA

	N	OR	M
P^4			
L	1	—	5. 6
W	1	—	6. 6
M^1			
L	2	6.7– 7.6	7.15
W	2	7.2– 8.6	7.90
M^2			
L	2	7.1– 8.3	7.70
W	2	8.4– 9.5	8.95
M^3			
L	1	—	8. 0
W	1	—	8. 2
M_1			
L	1	—	7. 1
W	1	—	4. 7
M_3			
L	2	10.1–10.4	10.25
W	2	5.1– 5.5	5.30

size, but if this is true the two populations occurred in the same ecological and geographic niche or in niches from which deposition and preservation were equally likely. I consider the possibility that the two populations were completely sympatric unlikely in view of the apparent extensive overlap in size ranges and absence of morphological distinctiveness.

The question of whether the two populations here represented should be regarded as specifically or only subspecifically distinct is a difficult one. There are no P^3's or P^4's that are particularly large and clearly belong to the population of larger individuals. In the absence of positive evidence to the contrary and in view of the distinct possibility of ecological and geographic separation between the population, they are here regarded as subspecifically distinct.

The mode of the distribution of lengths of M_3 falls into the next to smallest, 0.5-mm., class. It is probable that if the two popula-

tions contained in the sample could be separated, the distribution of the population with the smaller mean tooth size would still be skewed to the right, a situation that might be expected in a population under selection for small size. It is possible that during this time selection against individuals morphologically intermediate between the two populations and consequently in competition with individuals of the other population was under way.

Because it is not possible to separate the populations contained in the sample, no valid statistical treatment is possible. *Hyracotherium a. angustidens* can be defined only on the basis of the modes of the distributions and the lower limit of the observed range.

Of the five types from the Almagre, three fall near the mode of the size distribution and are almost certainly referable to *H. a. angustidens*. The types of *Orohippus cristonense* and *Eohippus validus* are, however, larger, and their subspecific position is uncertain. They have been tentatively referred to *H. a. angustidens*.

A number of jaw fragments and isolated teeth (field nos. 51-4, 51-6, 51-10, 52-13, and 52-25) collected in the Powder River basin by H. E. Wood have been tentatively referred to this subspecies. The upper teeth in this collection are rather small (see table 5) to be included in *H. a. grangeri*. The upper premolars in this sample are simple and triangular.

Numerical data on *H. a. angustidens* are given in tables 4 and 5.

Hyracotherium angustidens etsagicum (Cope)

Systemodon etsagicus COPE, 1884, pl. 56, fig. 5.
Eohippus etsagicus Cope, GRANGER, 1908, p. 239.
Hyracotherium cristatum WORTMAN, 1896, p. 96, fig. 6.
Hyracotherium (Eohippus) cristatum Wortman, MATTHEW, 1899, p. 33.
Eohippus cristatus Wortman, HAY, 1902, p. 609.
Hyracotherium index (in part) Cope, WORTMAN, 1896, p. 99, figs. 9, 10.
Hyracotherium (Eohippus) index (in part) Cope, TROUESSART, 1898, p. 771.
Hyracotherium (Pliolophus) montanum WORTMAN, 1896, p. 103.

Pliolophus montanus Wortman, HAY, 1902, p. 610.
Eohippus montanus Wortman, GRANGER, 1908, p. 239.
Eohippus resartus GRANGER, 1908, p. 240.
Eohippus borealis GRANGER, 1908, p. 242, fig. 4, pl. 15, fig. 3.

TYPE: A.M.N.H. No. 4600, fragment of lower jaw with P_4–M_2.

HYPODIGM: Types of synonyms and a large sample of jaw fragments and isolated teeth from the Gray Bull beds of the Willwood formation.

KNOWN DISTRIBUTION: Gray Bull beds, Wyoming; Almagre, New Mexico; Indian Meadows, Wyoming.

DIAGNOSIS: Size large, length of M_3 (33 specimens), mode 11.4–12.0, mean 11.90.

The Gray Bull beds consist of a great thickness of sediments that were apparently deposited during a considerable period of time. The detailed stratigraphy within these beds of the Willwood formation is not completely clear, and it is not always possible to conclude from available collecting data whether a particular level and locality is relatively high or low in the section.

The sample chosen for analysis consists of a great number of jaw fragments and isolated teeth collected from a relatively restricted area south of Elk Creek by the American Museum expedition of 1916 (A.M.N.H. Nos. 16904a–16904qqq). This locality, as far as can be determined, is near the middle of the Gray Bull section. Samples from the Museum of Comparative Zoölogy, the United States National Museum, and Princeton University, which were collected over a wide area and at diverse levels in these beds, contain specimens of teeth that are somewhat larger than the largest specimens in the Elk Creek sample and specimens that are considerably smaller than the smallest specimens in this sample. All these samples, however, resemble one another closely in that the modes of the size distributions are equal or nearly equal. Regarding the specimens in their care Jepsen and Gazin have stated (personal communication) that the smallest specimens could be from levels low in the section.

Because the smallest specimens in the

TABLE 6

STATISTICAL DATA ON THE TEETH OF *Hyracotherium angustidens etsagicum* FROM THE GRAY BULL
BEDS OF THE WILLWOOD FORMATION

	N	OR	SR	M	σ	V
M^1						
L	7	6.9– 8.5	3.63	7.81±0.18	0.56±0.15	7.17±1.92
W	7	8.5– 9.9	3.18	9.18±0.18	0.49±0.13	5.34±1.43
M^2						
L	14	7.8–10.8	5.12	8.77±0.21	0.79±0.15	9.01±1.70
W	14	9.5–12.0	4.73	10.39±0.19	0.73±0.14	7.03±1.33
M^3						
L	11	7.4–10.3	5.25	8.81±0.24	0.81±0.17	9.19±1.96
W	11	8.8–12.9	8.62	10.49±0.40	1.33±0.28	12.69±2.70
P_4						
L	7	6.4– 7.8	2.66	7.07±0.15	0.41±0.11	5.78±1.54
W	7	4.3– 5.1	1.94	4.61±0.11	0.30±0.08	6.51±1.74
M_1						
L	13	7.3– 8.8	3.30	7.99±0.14	0.51±0.10	6.40±1.25
W	13	5.0– 5.9	1.94	5.46±0.08	0.30±0.06	5.50±1.08
M_2						
L	12	8.2–10.1	4.02	9.25±0.18	0.62±0.13	6.70±1.37
W	12	6.0– 7.1	2.40	6.46±0.11	0.37±0.08	5.73±1.17
M_3						
L	32	10.4–13.6	5.05	11.90±0.13	0.78±0.10	6.55±0.81
W	32	5.4– 7.0	2.66	6.20±0.07	0.41±0.05	6.61±0.81

samples examined are quite possibly from levels low in the section, and because these specimens are within the observed range of size of the Sand Coulee population, it is probable that there was gradual increase in mean size of the hyracothere population in this area during the time of deposition of the Sand Coulee and Gray Bull beds.

In no sample examined is there any indication that more than a single population of hyracotheres was present at any time. All size distributions for teeth approach the normal curve depending more or less on the number of individuals represented (see fig. 6). The value for the coefficient of variation (*V*) for the hypodigm is consistently high, but not remarkably so when one considers that the specimens, even in a sample such

TABLE 7

STATISTICAL DATA ON THE TEETH OF *Hyracotherium angustidens etsagicum* FROM THE
INDIAN MEADOWS FORMATION

	N	M
M_1		
L	1	7.8
W	1	5.9
M_2		
L	1	8.7
W	1	8.8
M_3		
L	1	11.4
W	1	6.4

as this one collected in a restricted area, are the remains of animals which lived during a considerable span of time.

In tooth characters other than size there is great variation, the extremes in each case being very different, but always with a more or less complete series of intergrades.

A single specimen from the Indian Meadows formation (M.C.Z. No. 3401), consisting of three associated lower molars, has been tentatively assigned to this subspecies, as it agrees closely in size and form with specimens from the Gray Bull.

Numerical data on *H. a. etsagicum* are given in tables 6 and 7.

Hyracotherium angustidens grangeri,
new subspecies

TYPE: A.M.N.H. No. 16134, fragment of maxilla with P³–M³.

HYPODIGM: A sample of jaw fragments and isolated teeth from the Sand Coulee beds of the Willwood formation of Wyoming.

KNOWN DISTRIBUTION: Sand Coulee beds, Wyoming.

DIAGNOSIS: Size small, but larger than *H. a. angustidens*, length of M₃ (14 specimens), mode 10.0–10.5, mean 10.02.

The Sand Coulee sample (A.M.N.H. Nos. 16134, 16135, 16137, 16897a–16897c, 16898a–16898k, and 16899a–16899s) resembles that

TABLE 8

STATISTICAL DATA ON THE TEETH OF *Hyracotherium angustidens grangeri* FROM THE SAND COULEE LOCAL FAUNA OF THE WILLWOOD FORMATION

|	N	OR	SR	M	σ	V
P⁴						
L	4	6.0– 6.5	—	6.27	—	—
W	4	6.5– 7.9	—	7.25	—	—
M¹						
L	7	7.2– 7.6	0.91	7.40±0.05	0.14±0.04	1.91±0.51
W	7	8.1– 8.8	1.56	8.43±0.09	0.24±0.06	2.89±0.77
M²						
L	7	7.7– 8.6	1.68	8.23±0.10	0.26±0.07	3.21±0.86
W	7	9.0– 9.9	1.68	9.47±0.10	0.26±0.07	2.78±0.74
M³						
L	6	7.0– 8.2	—	7.62	—	—
W	6	9.1– 9.5	—	9.35	—	—
P₄						
L	4	5.6– 6.7	—	6.07	—	—
W	4	3.9– 5.0	—	4.22	—	—
M₁						
L	8	6.6– 8.0	2.79	7.17±0.16	0.44±0.11	6.07±0.52
W	8	4.7– 5.5	1.68	5.00±0.09	0.26±0.07	5.28±0.32
M₂						
L	8	7.4– 8.6	2.33	8.01±0.13	0.36±0.09	4.49±0.12
W	8	5.1– 6.3	2.07	5.59±0.11	0.32±0.08	5.65±0.41
M₃						
L	14	9.2–10.8	2.66	10.02±0.11	0.41±0.08	4.11±0.78
W	14	4.8– 5.7	1.43	5.28±0.06	0.22±0.04	4.24±0.80
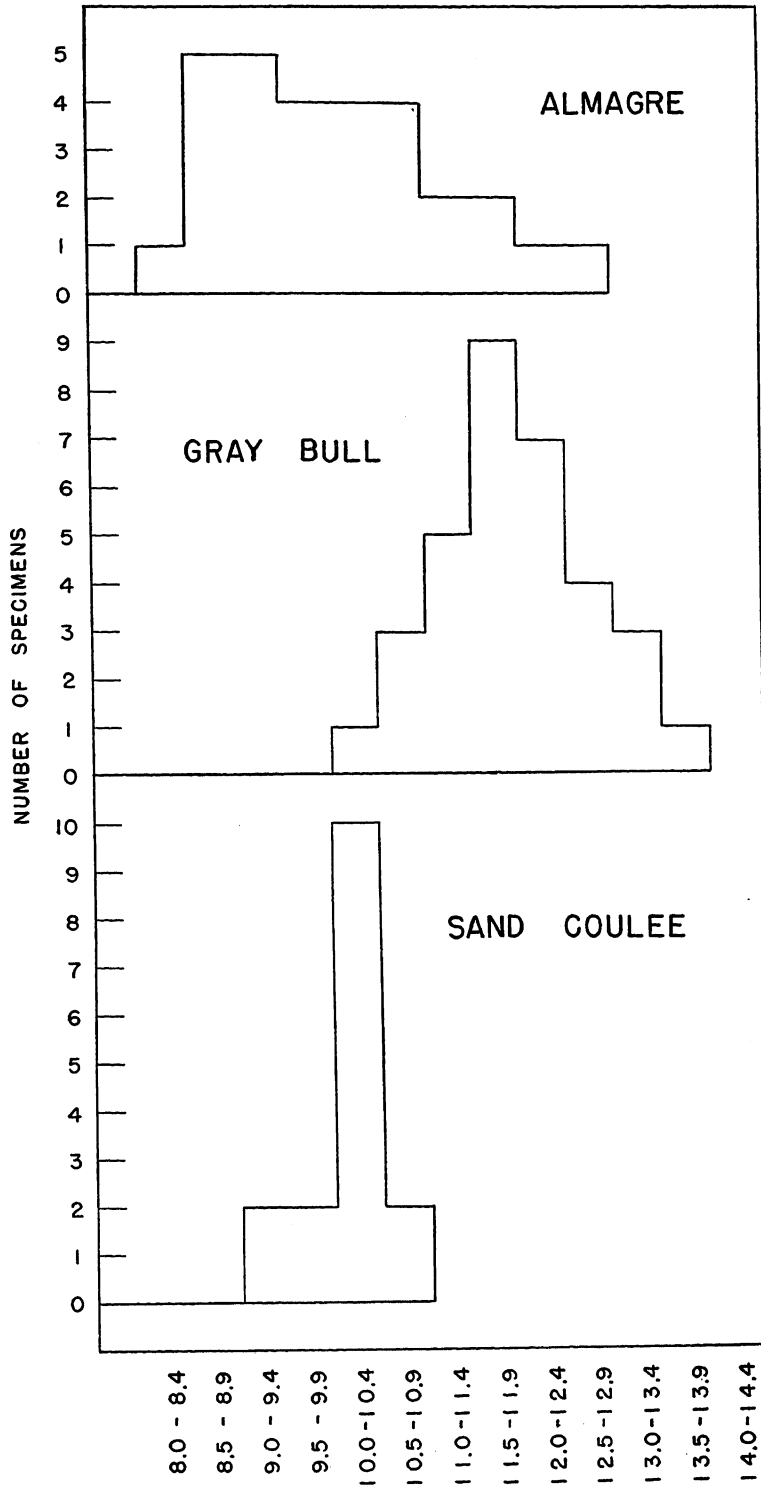
FIG. 6. Histograms of length of M$_3$ in populations of *H. angustidens* from three localities. See text for discussion.

from the Gray Bull in every respect except for the significantly lower mean tooth size. The lower values of V for this sample suggest that it is more homogeneous than the Gray Bull sample.

Hyracotherium vasacciense (Cope)

Lophiotherium vasacciense COPE, 1872a, p. 2.
Notharctus vasacciensis COPE, 1872b, p. 3.
Notharctus vasachiensis COPE, 1872c, p. 473.
Orotherium vasacciense COPE, 1873a, p. 606.
Orohippus vasacciensis COPE, 1875, p. 21.
Hyracotherium vasacciense COPE, 1884, p. 634, pl. 24, fig. 24.
Hyracotherium (Eohippus) vasacciense Cope, TROUESSART, 1898, p. 771.
Eohippus vasacciensis (Cope), HAY, 1902, p. 610.
Orotherium index COPE, 1873b, p. 4.
Orohippus index COPE, 1875, p. 20.
Hyracotherium index COPE, 1884, p. 630.
Hyracotherium (Eohippus) index (in part) Cope, TROUESSART, 1898, p. 771.
Eohippus index (Cope), HAY, 1902, p. 609.
Eohippus pernix MARSH, 1876, p. 402.
Hyracotherium venticolum COPE, 1881, p. 198.
Protorohippus venticolus (Cope), WORTMAN, 1896, p. 105, fig. 14, pl. 2, fig. D.
Eohippus venticolus (Cope), GRANGER, 1908, p. 245, figs. 3, 4, 5.

TYPE: A.M.N.H. No. 4658, a lower molar, probably the second, from the Knight, Wyoming.

TYPES OF SYNONYMS: *Orotherium index*: A.M.N.H. No. 4680, fragment of lower jaw with P$_4$–M$_3$, from the Knight, Wyoming. *Eohippus pernix*: Y.P.M. Nos. 11307 and 11308, various skeletal fragments and teeth of several individuals from near Bitter Creek, Wyoming. *Hyracotherium venticolum*: A.M.N.H. No. 4832, skull, jaws and large part of skeleton from the Lost Cabin, Wyoming.

HYPODIGM: The type of the synonyms and the samples listed under the subspecies.

KNOWN DISTRIBUTION: Knight, Wyoming; Largo, New Mexico; Lysite, Wyoming; Lysite equivalent of Willwood, Wyoming; La Barge, Wyoming; Hiawatha, Wyoming; Huerfano (A), Colorado; De Beque, Colorado; Big Bend, Texas; Lost Cabin, Wyoming.

DIAGNOSIS: Size medium to small; P^3 with paraconule large and anteriorly located; P^4 simple and triangular; heel of M$_3$ usually long and narrow. Diastema between P^1 and P^2 longer than P^1. Diastema between P$_1$

and P$_2$ longer than P$_1$. Femorotibial index about 100. Fifth metatarsal possibly absent.

The late Wasatchian populations included in this species can be distinguished from other populations of early Eocene hyracotheres on the basis of the molarization of the P^3. The protoconule is large and located well anterior to a line drawn between the protocone and the paracone. The crown of the
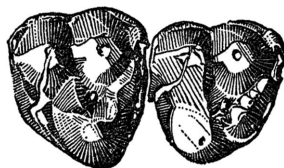

FIG. 7. *Hyracotherium vasacciense* (Cope), A.M.N.H. No. 48017 (part), P^3–P^4. Crown view. ×3.

tooth is shaped like a right triangle, with the right angle posteroventral, rather than like a triangle with the base internal as in *H. angustidens*. The P^4 is unmodified and cannot be distinguished from that of *H. angustidens*. The heel of the M$_3$ in *H. vasacciense* is usually narrower and longer than in the other species, but there is great variation in this character, and it is by no means definitive. This species differs from *H. angustidens* in having a long diastema between P^1 and P^2 and between P$_1$ and P$_2$. In other characters of the teeth there is great variability, with no consistent differences from other species.

The type of *Lophiotherium vasacciense* has had a complicated history, having been referred successively to *Lophiotherium* (Cope, 1872a), *Notharctus* (Cope, 1872b), *Orotherium* (Cope, 1873a), *Orohippus* (Cope, 1875), and finally to *Hyracotherium* (Cope, 1884). As this badly weathered single tooth was the first specimen referable to *Hyracotherium* to be found in North America, the confusion is understandable. Granger (1908) considered this type indeterminate. It is unfortunate that no upper premolars are known from the Knight formation, but, as stated above, I believe that the stratigraphic position of this type makes it probable that it belongs to a Lysite species. Cope (1884) referred specimens from the Almagre and Gray Bull to this species. The type is, I believe, an M$_2$ and falls close to the mean of the Lysite population in size.

TABLE 9

DIMENSIONS OF THE TYPE OF *Hyracotherium vasacciense* AND OF THE TYPES OF ITS SYNONYMS

	Lophiotherium vasacciense	*Orotherium index*	*Eohippus pernix*	*Hyracotherium venticolum*
P₃				
L	—	—	—	7.1
W	—	—	—	4.6
P₄				
L	—	5.2	—	7.0
W	—	3.7	—	5.6
M₁				
L	—	6.1	7.8	7.9
W	—	4.3	6.9	6.1
M₂				
L	8.3	7.0	8.0, 8.7	8.1
W	6.0	5.0	5.2, 7.3	6.5
M₃				
L	—	9.5	—	12.1
W	—	4.9	—	6.7

The type of *Orotherium index* is from the Knight formation near Evanston, Wyoming. It was considered specifically distinct because of its small size. The M₃ falls within the range of size variation of the Lysite sample. The other teeth are below the lower limit of size variation of this sample, but within the standard range. The specimen is badly weathered, and it is evident that all the teeth were somewhat larger in life.

The type of *Eohippus pernix* is from near Bitter Creek, Wyoming. It was distinguished on the basis of its small size. It falls within the observed size range of all populations of this species.

The type of *H. venticolum* from the Lost Cabin member of the Wind River formation was separated from *H. vasacciense* because of the slenderness of the lower jaw. The type consists of the skull, lower jaw, and greater part of the postcranial skeleton. Cope apparently never recognized the distinctive character of P³, probably because the teeth are quite worn. P³ of this specimen is as molariform as any I have examined. The fifth digit of the hind foot is lacking in this specimen, but I do not consider this certain evidence of its absence in life. The type falls well within the observed range of variation of the Lost Cabin sample in every respect.

The dimensions of the upper teeth of *Hyracotherium venticolum* are as follows:

P¹	
L	5.1
W	2.8

P²	
L	6.3
W	5.1

P³	
L	6.7
W	7.6

P⁴	
L	6.9
W	8.6

M¹	
L	8.0
W	10.3

M²	
L	8.1
W	10.9

M³	
L	8.3
W	10.4

Wortman (1896) synonymyzed *H. vasacciense* and *H. index* with the early Wasatchian species *H. angustidens* and *H. cuspidatum*. As stated in the discussion of *H. angustidens*, I consider it probable on stratigraphic grounds that *H. vasacciense* and *H. index* are referable to early Wasatchian species. Wortman placed *H. venticolum* in the genus *Protorohippus*. This is discussed under the generic synonymy.

Granger (1908) considered the types of *H. vasacciense* and *H. pernix* to be indeterminate, but tentatively referred them to *E. borealis* from the Gray Bull and to *H. index*, respectively.

Hyracotherium vasacciense vasacciense (Cope)

Lophiotherium vasacciense COPE, 1872a, p. 2.
Notharctus vasacciensis COPE, 1872b, p. 3.
Notharctus vasachiensis COPE, 1872c, p. 473.
Orotherium vasacciense COPE, 1873a, p. 606.
Orohippus vasacciensis COPE, 1875, p. 21.
Hyracotherium vasacciense COPE, 1884, p. 634.
Hyracotherium (Eohippus) vasacciense Cope, TROUESSART, 1898, p. 771.
Eohippus vasacciensis (Cope), HAY, 1902, p. 610.
Orotherium index COPE, 1873b, p. 4.
Orohippus index COPE, 1875, p. 20.
Hyracotherium index COPE, 1884, p. 630.
Hyracotherium (Eohippus) index (in part) Cope, TROUESSART, 1898, p. 771.
Eohippus index (Cope), HAY, 1902, p. 609.
Eohippus pernix MARSH, 1876, p. 402.

TYPE: Type of the species.

HYPODIGM: Types of the synonyms and a large number of jaw fragments and isolated teeth from Lysite, Wyoming; Lysite equivalent of the Willwood, Wyoming; Largo, New Mexico; La Barge, Wyoming; Huerfano (A), Colorado; and Hiawatha, Wyoming.

KNOWN DISTRIBUTION: Lysite, Wyoming; Lysite equivalent of the Willwood, Wyoming; Largo, New Mexico; La Barge, Wyoming; Huerfano (A), Colorado; Hiawatha, Wyoming; and De Beque, Colorado.

DIAGNOSIS: Size somewhat smaller than *H. v. venticolum*, length of M_1 Lysite (11 specimens), mean 10.49, mode 11.0–11.5. Protoconule of P^3 less anterior and internal than in *H. v. venticolum*.

The hyracotheres from the Largo member of the San Jose formation collected by the American Museum of Natural History expeditions of 1912, 1913, 1946, 1947, and 1948 fall into two quite distinct size groups. In almost all linear dimensions of the teeth the distributions are at least strongly bimodal. It is probable that the two groups, which consist of approximately equal numbers of individuals, represent the remains of two distinct sympatric species. They have consequently been treated separately statistically. A P^3 (A.M.N.H. No. 48017) associated with P^4–M^3 which fall clearly into the smaller size group (A.M.N.H. Nos. 16285, 16766, and 48084–48092) shows the degree of molarization typical of this subspecies. The specimens that fall within the group exhibiting smaller mean size have consequently been referred to *H. v. vasacciense*. The population of large individuals contained within this sample have been referred to *H. craspedotum* (discussed in the next section).

A sample of jaw fragments and isolated teeth from the lower part of the Huerfano formation (Huerfano A) collected by the American Museum expeditions of 1918 and 1952 is very similar to the sample from the Largo. Most of the specimens in this sample (A.M.N.H. Nos. 17516, 17448, 17447, 17511, 17512, 17514, 17515, 17517, 17518, 17520, and 55101–55105) fall into the group of smaller mean tooth size and have been referred to *H. v. vasacciense*. A P^3 associated with teeth falling within the limits of the small size group shows a degree of molarization about equal to the Largo P^3 mentioned above.

The mean tooth size of *H. vasacciense* specimens from the Huerfano is consistently higher than that of specimens of the same species from the Largo. It should be noted that in the Huerfano sample, *H. craspedotum* is represented by fewer specimens than in the Largo sample. If this condition reflects a true ecological condition, that is, if *H. craspedotum* was actually present in fewer numbers in the Huerfano, then competition between the two species would have been less severe than in the Largo area. When two species are completely sympatric, selection will operate to eliminate individuals intermediate in character between the two species and in this way reduce competition. In the present case such selection could have oper-

TABLE 10

STATISTICAL DATA ON THE TEETH OF *Hyracotherium vasacciense vasacciense*
FROM THE LARGO MEMBER OF THE SAN JOSE FORMATION

	N	OR	SR	M	σ	V
P⁴						
L	3	6.0–6.7	—	6.37	—	—
W	3	5.2–7.3	—	6.50	—	—
M¹						
L	4	6.5–7.0	—	7.02	—	—
W	4	7.9–8.5	—	8.30	—	—
M²						
L	4	6.3–7.6	—	6.82	—	—
W	4	7.9–9.2	—	8.72	—	—
M³						
L	3	7.1–7.2	—	7.13	—	—
W	3	8.2–9.0	—	8.60	—	—
P₄						
L	5	5.4–6.1	—	5.84	—	—
W	5	3.6–4.0	—	3.86	—	—
M₁						
L	7	6.4–7.2	1.75	6.79±0.10	0.27±0.07	3.98±1.06
W	7	4.2–5.0	1.42	4.57±0.08	0.22±0.06	4.73±1.26
M₂						
L	5	7.2–7.9	—	7.54	—	—
W	5	4.7–5.5	—	5.04	—	—
M₃						
L	6	9.7–10.3	—	9.97	—	—
W	6	5.0–4.5	—	5.20	—	—

ated against large individuals of *H. v. vasacciense.*

A sample of hyracothere teeth collected by Patterson at the "High Schindler Hill" locality in the Rifle member of the De Beque formation is similar in the distributions of the tooth dimensions to the sample from the Largo. A P⁴ of rather small size which is included in this sample is simple and triangular. Individuals from this sample which fall within the limits of the group of smaller mean tooth size have been referred to *H. v. vasacciense.*

A large sample of jaw fragments and isolated teeth (A.M.N.H. Nos. 15657–15659, 16900a–16900nnn, 16901, 16902a–16902o) from the Lysite equivalent of the Willwood formation was obtained by the American Museum expedition of 1911 in the vicinity of Fifteen Mile Creek. The sample is almost certainly heterogeneous. As in the Almagre sample the distributions for the linear dimensions of the teeth are skewed strongly to the right, and, when the sample is treated as a unit statistically, the coefficient of variation is 10 or above for most tooth dimensions. Three P³'s associated with molars of which the dimensions fall just above or below the mode of the sample show the structure typical of *H. v. vasacciense.* Unfortunately the sample includes no P³'s or P⁴'s of notably large size.

The ranges of the tooth dimension distributions of the Willwood Lysite sample closely

TABLE 11

STATISTICAL DATA ON THE TEETH OF *Hyracotherium vasacciense vasacciense*
FROM THE HUERFANO FORMATION

	N	OR	SR	M	σ	V
P₃						
L	8	5.9– 6.9	2.01	6.44±0.11	0.31±0.08	4.83±1.21
W	8	3.7– 4.8	2.46	4.11±0.13	0.38±0.10	9.29±2.32
P₄						
L	10	5.7– 7.1	3.05	6.51±0.15	0.47±0.11	7.27±1.62
W	10	4.1– 5.9	3.50	4.76±0.17	0.54±0.12	11.32±2.53
M₁						
L	10	6.5– 8.1	3.56	7.35±0.17	0.55±0.12	7.55±1.69
W	10	4.8– 6.0	2.20	5.32±0.11	0.34±0.08	6.35±2.20
M₂						
L	11	7.2– 8.3	2.85	7.52±0.13	0.44±0.09	5.88±1.25
W	11	5.2– 6.5	2.66	5.73±0.12	0.41±0.09	7.22±1.54
M₃						
L	11	9.5–11.0	3.11	10.37±0.15	0.48±0.10	4.62±0.98
W	11	4.9– 6.0	2.59	5.44±0.12	0.40±0.09	7.43±1.58

approximate the ranges of the combined *H. vasacciense* and *H. craspedotum* sample from the Largo. Even in the absence of clear morphological data, I believe that it is reasonable to assign the larger specimens in the Willwood Lysite sample to *H. craspedotum*. The two populations within the sample cannot be defined statistically because of their overlapping distributions. *Hyracotherium vasacciense* in this sample can be defined only on the basis of the modes and lower limits of the ranges for the various tooth dimension distributions. The modes of most of the tooth dimension distributions are remarkably similar to those of the Huerfano sample and consequently greater than those of the Largo sample. This fact is consistent with the suggestion that the Largo sample of *H. vasacciense* was of smaller mean size than the Huerfano sample of *H. vasacciense* because of more severe competition with *H. craspedotum* in the former area, as the great disparity between numbers of specimens referable to *H. vasacciense* and to *H. craspedotum* could hardly be spurious in the present case when the sample is so large.

A sample of isolated teeth and jaw fragments (A.M.N.H. Nos. 12796, 12798, 12800–12804, 12806, 12809, 12811, 12814, 12816,

14826, 14828, 14835, and 14836) from the Lysite member of the Wind River formation collected in the vicinity of Cotton Wood Creek by the American Museum expeditions of 1905 and 1909 is very similar to the sample from the Lysite equivalent of the Willwood formation, but it contains no specimens which are clearly referable to *H. craspedotum*. No P³'s are contained in this sample, but all P⁴'s are simple and triangular. The absence of *H. craspedotum* may well be spurious, as the sample is small, and even in the very large Willwood sample *H. craspedotum* is rare.

A sample of Lysite hyracotheres in the collections of Amherst College is nearly identical in its dimensions to the sample described above, and most of the specimens contained in it have been assigned to *H. v. vasacciense*. The sample contains, however, a few large molars and a number of P⁴'s which are referable to *H. craspedotum*. Kelly and Wood (1954) have concluded that two species are present in this sample.

A large sample of jaw fragments and isolated teeth (U.S.N.M. Nos. 19698–19701, 19703, 19706, 19708–19716, 19718–19724, 19726, 19730–19731, 19733–19736, 19738) collected by Gazin (see Gazin, 1952) near

TABLE 12

STATISTICAL DATA ON THE TEETH OF *Hyracotherium vasacciense vasacciense* AND *Hyracotherium craspedotum* FROM THE LYSITE EQUIVALENT OF THE WILLWOOD FORMATION

	N	OR
M^1		
L	3	6.2– 6.9
W	3	6.9– 8.2
M^2		
L	7	7.0– 8.3
W	7	8.2–10.0
M^3		
L	10	7.0– 8.8
W	10	8.0–11.3
P$_3$		
L	6	6.0– 7.5
W	6	3.7– 4.6
P$_4$		
L	11	5.7– 8.6
W	11	4.1– 6.0
M$_1$		
L	23	6.9– 8.7
W	23	4.4– 5.9
M$_2$		
L	28	7.3– 9.6
W	28	4.7– 6.8
M$_3$		
L	46	9.3–13.9
W	46	4.5– 7.1

La Barge, Wyoming, in the Knight formation is rather difficult to interpret. Three large specimens in the sample are apparently referable to *H. craspedotum*. In addition to these the sample contains a large number of specimens which are strongly bimodal in most of their tooth dimension distributions. When these specimens are treated as a unit statistically, the coefficients of variation run rather high. Most of these specimens are probably referable to *H. vasacciense*, although in the absence of P^3's this is by no means certain. Some of the specimens are very small, in fact smaller than any other specimens from the Lysite or Lost Cabin equivalents. Gazin recognizes three species in this group of specimens, and I am inclined to agree with him in this, although the systematic position of the very small specimens in the sample is difficult to determine. They resemble most closely the smallest specimens from the Almagre sample. It is possible that *H. angustidens* survived in restricted areas until Lysite time.

Apparently all three of the species described from the La Barge sample are present in a small sample collected by William J. Morris in the Hiawatha member of the Wasatch group.

An excellent collection of hyracothere teeth collected by Patterson and his associates from the Rifle member of the De Beque formation consists of a number of small samples from several localities. Three of these localities, "Hyracotherium Slide," "Four Points Hill," and "Deardorff Hill,"

TABLE 13

STATISTICAL DATA ON THE TEETH OF *Hyracotherium vasacciense vasacciense* FROM THE LYSITE MEMBER OF THE WIND RIVER FORMATION

	N	OR	SR	M	σ	V
M$_1$						
L	7	6.9– 7.6	1.75	7.18±0.10	0.27±0.07	3.76±1.01
W	7	4.5– 5.3	1.56	4.97±0.09	0.24±0.06	4.83±1.29
M$_2$						
L	7	7.4– 8.3	1.68	7.88±0.10	0.26±0.07	3.30±0.88
W	7	5.0– 5.6	1.23	5.37±0.07	0.19±0.05	3.54±0.95
M$_3$						
L	11	9.9–11.5	3.30	10.49±0.15	0.51±0.11	4.86±1.04
W	11	5.0– 5.9	1.56	5.34±0.07	0.24±0.05	4.49±0.96

TABLE 14

STATISTICAL DATA ON THE TEETH OF *Hyracotherium vasacciense vasacciense*
FROM THE LA BARGE LOCAL FAUNA

	N	OR	SR	M	σ	V
M¹						
L	5	6.0– 7.5	—	6.90	—	—
W	5	6.5– 9.1	—	8.14	—	—
M²						
L	3	6.2– 7.5	—	6.73	—	—
W	3	7.3– 9.7	—	8.33	—	—
M³						
L	4	7.1– 7.7	—	7.40	—	—
W	4	7.5– 9.1	—	8.42	—	—
P₂						
L	3	5.0– 5.3	—	5.10	—	—
W	3	2.5– 3.1	—	2.90	—	—
P₃						
L	7	5.1– 6.3	2.59	5.64±0.15	0.40±0.11	2.02±0.54
W	7	3.4– 4.0	1.10	3.73±0.06	0.17±0.04	4.64±1.24
P₄						
L	20	5.4– 7.3	3.56	6.25±0.12	0.55±0.09	8.75±1.39
W	20	4.0– 5.1	1.94	4.55±0.07	0.30±0.05	6.59±1.04
M₁						
L	17	5.8– 8.1	4.21	7.05±0.16	0.65±0.11	9.18±1.58
W	17	4.2– 6.3	3.43	5.13±0.13	0.53±0.09	10.32±1.77
M₂						
L	18	6.2– 8.3	3.69	7.48±0.13	0.57±0.09	7.67±1.28
W	18	4.5– 6.4	3.63	5.49±0.13	0.56±0.09	10.13±1.69
M₃						
L	20	8.3–10.7	4.47	9.68±0.15	0.69±0.11	7.13±1.13
W	20	4.2– 5.8	2.72	5.15±0.09	0.42±0.07	8.23±1.30

have yielded samples of Willwood Lysite aspect. Two P³'s from "Four Points Hill" are referable to *H. v. vasacciense*. Specimens from two other localities, "Meniscotherium Hollow" and "High Schindler Hill," are of Largo aspect. I believe that the small individuals in all these samples are referable to *H. v. vasacciense*.

Hyracotherium vasacciense venticolum (Cope)

Hyracotherium venticolum COPE, 1881, p. 198.
Protorohippus venticolus (Cope), WORTMAN, 1896, p. 105.
Eohippus venticolus (Cope), GRANGER, 1908, p. 245.

TYPE: A.M.N.H. No. 4832, skull, jaws, and large part of skeleton.

HYPODIGM: Large series of jaw fragments and isolated teeth from the Lost Cabin member of the Wind River formation.

KNOWN DISTRIBUTION: Lost Cabin, Wyoming; De Beque, Colorado.

DIAGNOSIS: P³ with protoconule more anterior and internal than in *H. v. vasacciense*. Length of M₃ (28 specimens), mode 11.0–11.5.

The Lost Cabin sample consists of a large number of jaw fragments (A.M.N.H. Nos. 14811, 14815, 14817–14819, 14822, 14823,

14825, 14829, 14834, 14838, 14843, 14844, 14846, 14851, 14853, 14858, 14859a–14859m) collected in the vicinity of Alkali Creek in the Wind River Basin by the American

formity than specimens of *H. v. vasacciense.* This is also true of a specimen from the Lost Cabin in the collection of Princeton University (P.U. No. 1931) and a single P³ collected
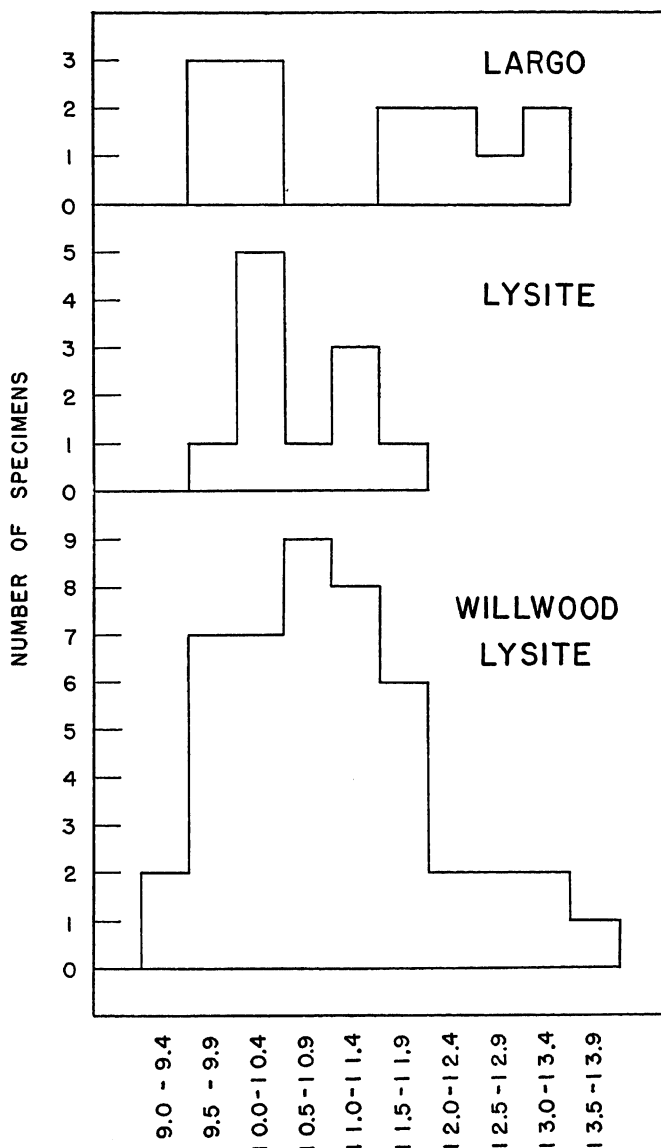

FIG. 8. Histograms of length of M_3 in populations of *H. vasacciense* and *H. craspedotum* from three localities. See text, under the respective species, for discussion.

Museum expedition of 1909. The distributions of the linear dimensions of all the teeth are strongly skewed to the right. The type specimen and several isolated P³'s in the sample exhibit a greater degree of molari-

by Patterson from the "Nipple Hollow" locality in the Rifle member of the De Beque formation. The very large teeth and several isolated P⁴'s indicate that *H. craspedotum* is present in the Lost Cabin sample in small
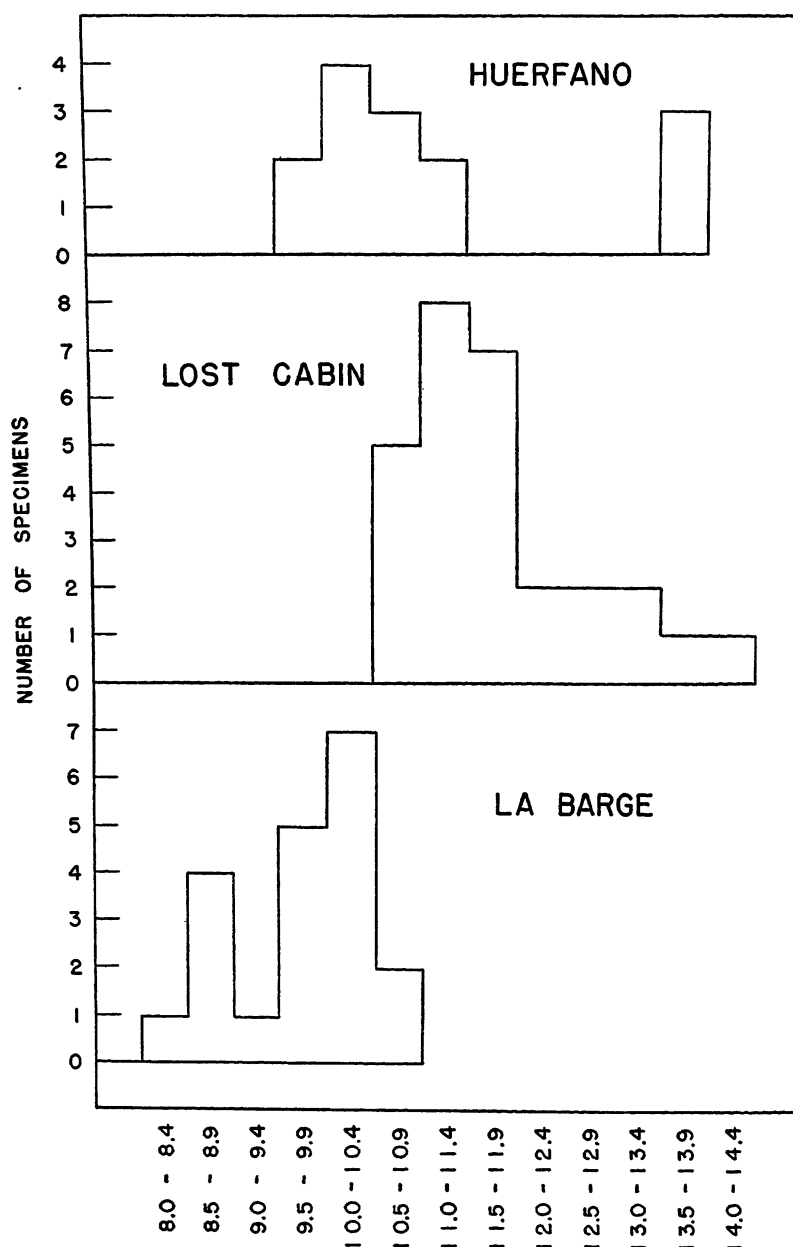
FIG. 9. Histograms of length of M_3 in populations of *H. vasacciense* and *H. craspedotum* from three localities. See text, under respective species, for discussion.

numbers. As there is overlap of the tooth dimension distributions of the two species, *H. v. venticolum* can be defined, as far as size is concerned, only in terms of the lower limit of the ranges and the modes for the size distributions of the various teeth.

Hyracotherium craspedotum Cope

Hyracotherium craspedotum COPE, 1880, p. 747.
Hyracotherium (Eohippus) craspedotum Cope, TROUESSART, 1898, p. 771.
Eohippus craspedotus (Cope), HAY, 1902, p. 609.

TYPE: A.M.N.H. No. 4830, fragments of

TABLE 15

STATISTICAL DATA ON THE TEETH OF *Hyracotherium vasacciense venticolum* FROM THE LOST CABIN MEMBER OF THE WIND RIVER FORMATION

	N	OR
M_3		
L	3	7.5– 9.6
W	3	9.2–12.2
P_2		
L	3	6.3– 7.7
W	3	3.5– 4.6
P_3		
L	5	6.5– 7.2
W	5	4.1– 5.1
P_4		
L	8	6.6– 8.4
W	8	4.9– 6.2
M_1		
L	9	7.3– 9.2
W	9	5.6– 7.2
M_2		
L	11	7.8– 9.9
W	11	5.8– 7.3
M_3		
L	28	10.5–14.0
W	28	5.1– 7.8

both rami with right M_1–M_3 and left P_4–M_1.

HYPODIGM: A large sample of jaw fragments and isolated teeth from the Lost Cabin, Willwood Lysite, Largo (A.M.N.H. Nos. 16275–16277, 16294, 16759, and 48093–48101) and Huerfano (A.M.N.H. Nos. 17509, 17510, 17513, 17519, and 55100).

KNOWN DISTRIBUTION: Lost Cabin, Wyoming; Largo, New Mexico; Huerfano (A), Colorado; La Barge, Wyoming; Knight, Wyoming; Hiawatha, Wyoming; New Fork, Wyoming; Fossil, Wyoming, and De Beque, Colorado.

DIAGNOSIS: Size large; P^3 triangular; P^4 with protocone produced posteriorly and with flat shelf at postero-internal angle.

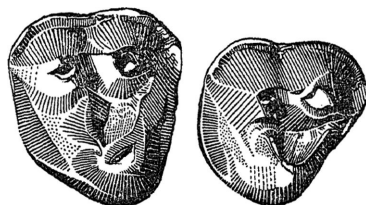*Hyracotherium craspedotum* can readily be distinguished from *H. vasacciense* in late

FIG. 10. *Hyracotherium craspedotum* Cope, A.M.N.H. No. 55100 (part), P^3–P^4. Crown view. ×3.

Wasatchian deposits by the large size of the teeth. In the Largo and Huerfano populations, and in populations from the "Meniscotherium Hollow" and "High Schindler Hill" localities of the Rifle member of the De Beque formation the species fall into non-overlapping groups on the basis of the linear dimensions of the teeth. In the Lost Cabin and Willwood Lysite populations, and in populations from the "Hyracotherium Slide," "Four Points Hill," and "Deardorff Hill" localities in the De Beque formation, *H. craspedotum* is rare and there is overlap in the tooth size distributions of the two species.

Hyracotherium craspedotum does not differ significantly in any of the linear dimensions of the teeth from *H. angustidens etsagicus*. In the Largo sample, however, a P^4 (A.M.N.H. No. 48016) associated with molars that fall beyond the upper limit of the size range of any population of *H. vasacciense* shows the posterior attenuation of the protocone and the postero-internal shelf. An upper dentition from the Huerfano (A.M.N.H. No. 55100) and another from the Lost Cabin (A.M.N.H. No. 4831), both with very large molars, show P^3 simple and triangular, and P^4 with the structure described above. A large P^4 from near Fossil, Wyoming, in the collection of Princeton University also shows this structure.

TABLE 16

DIMENSIONS OF THE TYPE OF
Hyracotherium craspedotum

	P_4	M_1	M_2	M_3
L	8.0	8.6	10.2	13.5
W	6.4	7.0	8.0	7.4

TABLE 17

STATISTICAL DATA ON THE TEETH OF *Hyracotherium craspedotum* FROM THE LARGO MEMBER
OF THE SAN JOSE FORMATION

	N	OR	SR	M	σ	V
P_3						
L	4	7.0– 8.2		7.35	—	—
W	4	4.0– 5.1		4.55	—	—
P_4						
L	7	6.9– 8.3	3.56	7.47±0.21	0.55±0.15	7.38±1.97
W	7	4.8– 6.2	3.24	5.37±0.19	0.50±0.13	9.37±2.50
M_1						
L	8	7.7– 9.0	2.66	8.45±0.15	0.41±0.10	4.89±1.20
W	8	5.3– 6.4	2.14	5.91±0.12	0.33±0.08	5.67±1.42
M_2						
L	9	8.9–10.5	3.37	9.63±0.17	0.52±0.12	5.44±1.28
W	9	6.3– 7.3	2.07	6.71±0.11	0.32±0.07	4.74±1.12
M_3						
L	7	11.5–13.4	2.72	12.37±0.16	0.42±0.11	3.37±0.90
W	7	6.9– 6.8	1.81	6.46±0.11	0.28±0.07	4.32±1.15

The type of *H. craspedotum* from the Lost Cabin falls within, but close to the upper limit of, the size range of the Lost Cabin sample in all linear dimensions of the teeth, and almost certainly outside the size range of the specimens of *H. vasacciense* present in this sample. The type was distinguished from *H. tapirum*, here considered as indeterminate, because it lacked cross crests on the lower molars. The type is within the observed range of variation of the Lost Cabin sample for this character.

Hyracotherium OF UNCERTAIN SPECIES

A small sample of hyracothere teeth collected by John A. Wilson in the Big Bend region of Texas is clearly referable to *Hyracotherium*. No P_3 or P_4 is included in the sample, and consequently no specific determination has been made. The specimens are probably referable to *H. angustidens* or *H. vasacciense*, because they are rather small.

TABLE 18

STATISTICAL DATA ON THE TEETH OF *Hyracotherium craspedotum* FROM THE HUERFANO FORMATION

	N	OR	M
M_1			
L	2	8.9– 9.8	9.35
W	2	5.3– 6.9	6.10
M_2			
L	4	9.4–10.5	10.10
W	4	6.2– 7.3	6.97
M_3			
L	3	13.5–13.7	13.60
W	3	7.1– 7.3	7.20

EVOLUTION

The Order Condylarthra, as defined by Simpson (1945), consists of three rather distinct groups at the time of its first appearance in the early Paleocene. These groups, generally given family rank, are the Hyopsodontidae, Periptychidae, and Phenacodontidae. The early Paleocene members of the order, particularly the phenacodontids, are very like primitive creodonts.

It is within the Order Condylarthra that the ancestry of the later ungulate orders almost certainly lies. The hyopsodontids, for example, closely resemble the earliest artiodactyls, while the phenacodontids, particularly in the morphology of the teeth, are similar to the first perissodactyls. Most of the phenacodontids are, however, in at least one respect, more specialized than the earliest known perissodactyls, *Hyracotherium* and *Homogalax*, in that they possess a mesostyle on the upper molars. Only *Desmatoclaenus*, the earliest known phenacodontid, is without a mesostyle. A serial arrangement of the carpus is apparently a specialization peculiar to *Phenacodus*, as it is not found in the middle Paleocene *Tetraclaenodon*, the probable ancestor of *Phenacodus*, and presumably was not present in *Desmatoclaenus*.

The perissodactyls were probably derived from a phenacodontid very like *Desmatoclaenus* at a time no later than early Paleocene. Because forms intermediate in structure between *Desmatoclaenus* and *Hyracotherium* have been found in the relatively extensive and fossiliferous North American Paleocene deposits, it is probable that the transition occurred elsewhere, undoubtedly in Eurasia. The sudden appearance of *Hyracotherium* in North America at the beginning of the Eocene would then be accounted for by migration from Eurasia.

It is quite clear that the primitive perissodactyl which was ancestral to all the later members of the order was somewhat, but not greatly, more primitive than *Hyracotherium*. The teeth of *Hyracotherium* are characteristically hippomorph, while those of the contemporary genus *Homogalax* show ceratomorph characters, indicating specialization along two separate lines. Furthermore, the astragalus and calcaneum are more specialized, that is, less condylarth-like, in *Hyracotherium* than in other Eocene perissodactyls. The inferred characters of the stem perissodactyl have been discussed at some length by Gregory (1910).

Hyracotherium angustidens from the early Wasatchian deposits is the most primitive species of the genus and was almost certainly ancestral to both of the late Wasatchian subspecies.

Hyracotherium a. grangeri from the Sand Coulee beds and *H. a. etsagicum* from directly overlying Gray Bull beds are very similar to each other, differing only in their mean tooth size. Some teeth from the lower part of the Gray Bull section are as small as teeth from the Sand Coulee. It is probable that *H. a. grangeri* was ancestral to *H. a. etsagicum*, and the two forms are consequently, in their relationship to each other, temporal subspecies. *Hyracotherium a. angustidens* of the Almagre member of the San Jose formation closely resembles *H. a. grangeri*. It is a somewhat smaller form, however, a fact that may possibly be explained by the presence of a large form from the same locality and horizon that has been provisionally referred to *H. a. etsagicum*.

There is no direct evidence bearing on the question of which of the early Wasatchian subspecies gave rise to which of the late Wasatchian species. In tooth size *H. a. angustidens* is very close to *H. vasacciense*, while in this character *H. a. etsagicum* is very close to *H. craspedotum*. These facts are perhaps suggestive of relationship between the former two and between the latter two, but are by no means proof of a direct ancestral descendent relationship.

A more important item of evidence bearing indirectly on the problem of the origin of *H. vasacciense* and *H. craspedotum* is the fact that in the Almagre there were apparently present two subspecies of *H. angustidens*, isolated ecologically or geographically to some extent and possibly in competition with each other. It is possible that during

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the time of deposition of the Almagre sediments speciation was actually in progress. I am fully aware that any statement concerning the exact evolutionary state of a particular extinct population of animals must be highly speculative owing to many variable biological and geological factors affecting fossil samples which necessarily go undetected.

One of the most striking facts about *H. vasacciense* and *H. craspedotum* is that the character of the populations of the two species varies from locality to locality and from horizon to horizon. The sample from the Largo member of the San Jose formation apparently reflects a situation in which the two species were fully sympatric. They fall into two distinct groups which are non-overlapping in the distributions of the linear tooth dimensions, and the range of variation for each of the species is rather low. The two species were apparently present in about equal numbers. The sample from the Lysite equivalent, on the other hand, apparently reflects a situation in which the two species were nearly, or even fully, allopatric. There is overlap between the tooth dimension distributions of the two species; *H. vasacciense* is more variable than in the Largo and *H. craspedotum* is rare in the sample.

If the foregoing interpretation is correct then it is not surprising that *H. vasacciense* in the Largo should have been composed of individuals of somewhat smaller mean size and less variability than was the same species in the Willwood Lysite. Where two species are sympatric, avoidance of competition will be of advantage to both, and consequently individuals of one species that approach individuals of the other species in their morphology will tend to be selectively eliminated. Thus two species will be more distinct in areas where their ranges overlap than in areas where the ranges do not overlap. This phenomenon is well known in recent mammals (see, for example, Hall, 1951).

The Largo and Lysite deposits are thought to be about equivalent in age (see Simpson, 1948). It is possible that the faunal differences between the two deposits are the result of a facies difference. The Largo deposits are predominantly reddish in color, while the Willwood deposits are pale and varie-

gated. Van Houten (1945) has suggested that the red layers within the variegated beds accumulated in a savanna or open flood plain, while the gray beds accumulated in swampy lowlands. If this interpretation is correct, the variegated beds reflect fluctuating conditions between savanna and swampy lowland during the early Eocene in this area. In the area of the San Juan basin, on the other hand, a savanna was apparently present throughout the time of deposition of the Largo beds (Simpson, 1948, has already suggested on the basis of Van Houten's suggestion, that the Largo beds were deposited in a predominantly savanna environment).

A striking faunal difference between the Largo and Willwood Lysite is the abundance of *Meniscotherium* in the former deposits and its absence in the latter. Although there is some uncertainty concerning the exact temporal distribution of *Meniscotherium*, it had apparently been present in North America since late Paleocene time. For a discussion of the occurrence of *Meniscotherium*, see Van Houten (1945).

In the environment in which the reddish beds accumulated, probably a savanna, *H. vasacciense* and *H. craspedotum* occurred sympatrically and *Meniscotherium* was abundant. In the environment in which the gray beds were deposited, probably a swampy lowland, *H. v. vasacciense* was abundant and *H. craspedotum* and *Meniscotherium*, being more restricted in their ecological requirements, were rare or absent. The few specimens from the gray beds referable to *H. craspedotum* and *Meniscotherium* may represent stragglers or even specimens which have been redeposited from older red beds.

The other samples of hyracotheres from Eocene deposits of Lost Cabin or Lysite age conform more or less to either the Largo or the Willwood Lysite pattern. The La Barge sample is of particular interest, as it contains some very small hyracotheres. *Meniscotherium* was found in great abundance by Gazin in this area, but the lithology is not predominantly red as it is in the Largo deposits. Perhaps the La Barge sediments were deposited under conditions differing from those under which both the Largo and Willwood Lysite were deposited.

It is very difficult to evaluate the relative

importance of environment as opposed to time in producing the differences between various hyracothere populations discussed above, particularly as geographic isolation must be added as a third factor. Because, however, evidence for facies differences is so clear, it is probably safe to conclude that they are at least partially responsible for the marked differences between the populations of *H. vasacciense* and *H. craspedotum* from different localities.

Hyracotherium v. venticolum differs from *H. v. vasacciense* both in being somewhat larger and in having a more molariform P³. As one might expect, this advanced subspecies developed in a restricted area, as it occurs in the Lost Cabin and De Beque but not in the contemporaneous Huerfano and La Barge. The subspecies apparently evolved in an area where *H. craspedotum* was rare. It is unlikely that the character of larger size could have developed in an area where competition from a closely related large form was possible.

P³ of *H. v. venticolum* is almost indistinguishable from the P³ of primitive species of *Orohippus*. In *Orohippus* P⁴ apparently became molariform by a postero-internal migration of the posterior intermediate cusp and thus bears little resemblance to P⁴ of *H. craspedotum*. It is very probable that *H. v. venticolum* was ancestral to the genus *Orohippus* of the middle Eocene.

SUMMARY

THE TEETH OF *Hyracotherium* are in most respects quite primitive. They do, however, possess well-developed lophs and lophids, and in one species there is a definite tendency towards the molarization of P³. Although the teeth of *Hyracotherium* are in most respects more primitive than those of the phenacodontids, the possession of a mesostyle excludes all phenacodontid genera except *Desmatoclaenus* from the ancestry of *Hyracotherium*.

The skull of *Hyracotherium* is not strikingly similar to the skulls of later horses. The orbit is relatively more posteriorly located than it is in any of the condylarths, and in the arrangement and relationship of the skull bones *Hyracotherium* closely resembles *Mesohippus*.

The lumbar neural spines are almost vertical, indicating a relative unimportance of the longissimus muscle. Some of the lumbar zygopophyses were apparently embracing. In these characters *Hyracotherium* resembles the later horses. It is probable that the lumbar series was relatively inflexible.

The scapula and fore limb are remarkably primitive, while the pelvis and hind limb exhibit most of the fundamental equid specializations. The feet, although strongly mesodactyl, were digitigrade.

In view of the structure of the vertebral column, pelvis, and hind limb it is probable that *Hyracotherium* ran more or less in the typical ungulate manner, gaining most of the propulsive force from the action of the hind limb relative to the pelvis rather than from an alternate flexing and straightening of the back.

All the lower Eocene perissodactyls are very similar in general structure, and it is only in the structure of the teeth and the astragalus and calcaneum that *Hyracotherium* is more horse-like than its closely related contemporaries.

A study of large samples of teeth has shown that most of the specific characters cited by earlier authors show great variation within single populations. On the basis of the structure of P³ and P⁴ three species have been recognized, one from the Gray Bull and equivalents, and two from the Lost Cabin and Lysite and equivalents. Subspecies have been defined on the basis of significant mean tooth size differences.

It is possible that two subspecies found in the Almagre member of the San Jose formation, *H. a. etsagicum* and *H. a. angustidens*, which were partially isolated but apparently in competition, gave rise to the two late Wasatchian species *H. vasacciense* and *H. craspedotum*.

Hyracotherium v. venticolum from the Lost Cabin member of the Wind River formation is clearly the most advanced form of the genus and is undoubtedly ancestral to the genus *Orohippus*.

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