REVISION OF THE HYRACHYIDAE

By HORACE ELMER WOOD, 2nd

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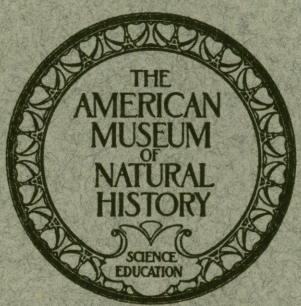

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Article V.—REVISION OF THE HYRACHYIDAE

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INTRODUCTION

The classic genus *Hyrachyus* Leidy (1871*a*) and its included specific and generic relatives represent an extinct group of primitive rhinoceros-like perissodactyls, which have been found only in the continental Lower to Upper Eocene of the western United States, in Wyoming, Montana, Utah and Colorado, running from the Lost Cabin (Wind River) Formation through the Bridger into the Uinta.

These lightly-built animals, ranging in size from a wolf-hound of the Russian plains to a mustang of the western plains of North America, were moderately cursorial, with no visible means of defense except flight. They were apparently browsing, plains border, savannah and forest forms. There are four digits on the manus and three on the pes. The group as a whole is hornless, but incipient, paired, nasal rugosities or hornlets appear twice in the family.

The dentition is primitive: there are small canine tusks; none of the premolars becomes molariform; the upper molars are very rhinoceros-like, when worn; and the lower molars resemble those of tapirs. The general appearance and proportions of the group are more suggestive of the tapirs than of any other living ungulates, but the body is more slender and the limbs are more graceful and cursorial than in any of the Tapiridae.

The phylogenetic relations of the Hyrachyidae are in two directions. On the one hand, the relationship to the Rhinocerotidae, Hyracodontidae, and Amynodontidae is one of approximate ancestry, although it is strongly probable that no known member of the *Hyrachyus* group is the actual common ancestor. Such an ancestor would probably be found lower down in the Lower Eocene section. On the other hand, there are clear relationships to other lines of Eocene perissodactyls, such as the Helaletidae (*Heptodon*, *Helaletes*, *Dilophodon*, and *Desmatotherium*), to the pseudo-tapir *Homogalax* (*"Systemodon"*), and even to the equine *Eohippus*. The special resemblances to primitive tapirs appear to be due partly to retention of primitive characters and partly to convergence, rather than to any specially close relationship.

It is this clear interrelationship of all the more primitive Eocene perissodactyls which made Cope and Matthew prefer to classify them all in a single, stem family, whereas Osborn (1898) divided them in his phylogenetic classification of the perissodactyls. In any case, judging from the small amount of actual, morphological diversification in the Lower and Middle Eocene, all the different lines of perissodactyls must

have arisen from a common stem form in the Paleocene, and, probably, in the Middle or Upper Paleocene.

This group was first made known through the pioneer work of Leidy, Marsh and Cope in the early eighteen-seventies. Additional forms were described, at long intervals, by Osborn, Scott and Speir, by Douglass, by Peterson and by Troxell. The group was tentatively revised by Leidy, later by Cope, and more recently, for the Bridger forms, by Troxell. There has, however, never been a complete taxonomic, morphologic, stratigraphic and phylogenetic revision of the entire group, based on all types and other important specimens (which are, fortunately, concentrated in a very limited number of collections). Nearly all the types, and numerous other important specimens, are either illustrated for the first time, or refigured, in this paper.

This paper is the result of a comparative study, made at intervals during the years 1925–31, of all the types of *Hyrachyus* and of related or possibly related species, in American and European museums, and of all important collections of *Hyrachyus* material—those in the American Museum, Carnegie Museum, National Museum, Philadelphia Academy of Natural Sciences, Princeton Museum and Yale Peabody Museum.

I am indebted to the New York Academy of Sciences for a grant to assist in making this comparative study of the collections enumerated, and to Dean James B. Munn of Washington Square College, New York University, for the opportunity, during the summer of 1928, to examine nearly all the formations and localities from which members of the Hyrachyidae have been obtained. The remaining *Hyrachyus* localities were visited later: the Sage Creek of Montana was visited in 1931, and the Huerfano in 1932. I wish to acknowledge my indebtedness, under one count or another, to the late Professor Charles Depéret, to the late Dr. J. W. Gidley, and to Dr. Walter Granger, Professor W. K. Gregory, M. André Laville, Professor R. S. Lull, Miss Jannette M. Lucas, to the late Dr. W. D. Matthew, and to Professer H. F. Osborn, Mr. O. A. Peterson, Professor W. B. Scott, Professor W. J. Sinclair, Dr. H. G. Stehlin, Dr. Witmer Stone, Dr. M. R. Thorpe and Professor E. L. Troxell. Finally, I wish to acknowledge my indebtedness to the long line of able field workers, without whom this study would have been impossible.

The type of *Hyrachyus "priscus"* Douglass in the Carnegie Museum was drawn by Mr. Sydney Prentice. All other drawings (except Fig. 50) are by Dr. Florence Dowden Wood, to whom I am greatly indebted for the time and effort thereby lost to her own work.

The standard molar cusp nomenclature is used for comparable elements in the premolars, as descriptive anatomical terms, without

necessary implications as to cusp homologies, although it might be preferable to substitute deuterocone (Scott) for protocone (Osborn) throughout the tooth series, as more accurately descriptive and less ambiguous. If the internal ridge of P^1 arises anterior to the apex of the parametacone, it is called the protoloph, as it has the essential topographic relations of that ridge. If its anterior end is opposite the apex of the parametacone, or farther to the rear, it has the essential character of a metaloph, and is so named. Both ridges appear to arise, originally, as cingula. The term parametacone (Wood, 1927*a* = amphicone, Simpson, 1929) is used for the upper premolar central cusp, when it is not subdivided into paracone and metacone.

The following names bear on the subject of this paper in one way or another. The forms preceded by asterisks belong to the Hyrachyidae; those preceded by interrogation-points are of uncertain affinities; those not marked belong to other families and hence have no bearing on this subject except from the standpoint of nomenclature.

**Lophiodon modestus* Leidy, 1870 (referred by him to *Hyrachyus* in 1872*a*, doubtfully referred to *Isectolophus* by Matthew in 1909).

**Hyrachyus agrestis* Leidy, 1871*a* (before June).

**Hyrachyus agrarius* Leidy, 1871*a* (before June).

**Lophiodon bairdianus* Marsh, July, 1871 (referred by Leidy to *Hyrachyus* in 1872).

**Lophiodon affinis* Marsh, July, 1871 (referred by Leidy to *Hyrachyus* in 1872, with doubt).

Lophiodon nanus Marsh, July, 1871 (referred by Leidy to *Hyrachyus* in 1872, with doubt).

Lophiodon pumilus Marsh, July, 1871 (referred by Leidy to *Hyrachyus* in 1872, with doubt).

**Hyrachyus eximius* Leidy, October, 1871*b*.

**Hyrachyus princeps* Marsh, July 22, 1872.

Helaletes boöps Marsh, 1872.

**Hyrachyus implicatus* Cope, March 8, 1873*a*.

**Colonoceras agrestis* Marsh, May, 1873.

Tapirus priscus Filhol, 1874 (homonym of *T. priscus* Kaup).

Hyrachyus singularis Cope, 1875 (referred by Cope to *Pachynolophus* in 1881, and by Matthew to *Heptodon* in 1899).

Protapirus priscus Filhol, 1877 (referred by Filhol to "*Hyrachius*" in 1885).

**Hyrachyus imperialis* Osborn, Scott and Speir, 1878.

?*Hyrachyus intermedius* Osborn, Scott and Speir, 1878.

**Hyrachyus crassidens* Osborn, Scott and Speir, 1878.

?*Hyrachyus paradoxus* Osborn, Scott and Speir, 1878.

Hyrachius Douvillei Filhol, 1885.

Hyrachius Zeilleri Filhol, 1885.

Hyrachius intermedius Filhol, 1885 (homonym).

Hyrachyus obliquidens Scott and Osborn, 1887.
**Hyrachyus priscus* Douglass, 1903 (homonym).
?*Hyrachyus* sp. Douglass, 1903.
Hyrachyus filholi Trouessart, 1904–1905 (to replace *H. intermedius* Filhol, 1885).
**Hyrachyus grande* Peterson, 1919.
**Metahyrachyus bicornutus* Troxell, 1922*a*.
**Hyrachyus affinis gracilis* Troxell, 1922*b*.

Tapirus priscus Filhol, 1874 (in Ann. Sci. Phys. Nat. Toulouse, fide Filhol, 1877) is a homonym of *Tapirus priscus* Kaup, 1832 or 1833, and therefore without standing. In 1877, Filhol redescribed the same specimen as *Protapirus priscus*, which name is valid, as of 1877. Gaudry, 1877 and 1878, referred *Tapirus priscus* Filhol to "*Hyrachius*," but, as he did not redescribe the species, his action has no effect. In 1885, Filhol redescribed this form as *Hyrachius priscus*, the context proving it to be a variant spelling of *Hyrachyus*. *Protapirus priscus* Filhol was justly reestablished by Zittel in 1893, was called *Hyrachyus intermedius* by Earle in 1898, and *Protapirus* once more by Depéret in 1904. As a result of Filhol's misidentification, *Hyrachyus priscus* Douglass, 1903, is a homonym, and must be replaced. Trouessart (1904–1905, p. 633) proposed *filholi* as a substitute for *Protapirus priscus* Filhol, on the basis of its being preoccupied by *Tapirus priscus* Kaup. Since, however, *Protapirus priscus* was validly redefined by Filhol, *filholi* Trouessart becomes its objective synonym.

Filhol's other names dating from 1885, *Hyrachius Douvillei*, *Zeilleri* and *intermedius*, have all been, correctly, removed from the Hyrachyidae. Depéret (1904) regarded *H. Zeilleri* and *H. intermedius* as belonging to *Paratapirus* Depéret, and apparently agreed with Gaudry, 1897, in associating *Douvillei* with *priscus* in *Protapirus*. It must be pointed out, however, that *Hyrachius intermedius* Filhol, 1885, is a homonym of *Hyrachyus intermedius* Osborn, Scott and Speir, 1878, and therefore without standing, nor can its reference to another genus save it. Trouessart (1904–1905, p. 623) proposes *Hyrachyus filholi* as a new name for *H. intermedius* Filhol (not Osborn, Scott and Speir). This name, of course, goes over to the tapirs, and must be used in place of *intermedius* Filhol. *Lophiodon nanus* Marsh, 1871, was referred by Leidy to *Hyrachyus* in 1872*b*, as was *L. pumilus* Marsh, 1871, with doubt. In 1872, Marsh founded *Helaletes boöps*, new genus and species, and considered *L. nanus* Marsh congeneric with it. In 1873*a*, Cope referred *Helaletes boöps* to *Hyrachyus*. These three species have since been placed, correctly, in *Helaletes*. *Hyrachyus singularis* Cope, 1875 (figured 1877 and 1884),

was somewhat doubtfully referred to *Heptodon* by Matthew. Examination of the type fully confirms this reference. *Hyrachyus obliquidens* Scott and Osborn, 1887, was correctly referred by them to *Prothyracodon* in 1889 (Wood, 1927*b*). The remaining forms are included in the scope of this paper. It should be noted that the words: *boöps, douvillei, filholi, intermedius, nanus, obliquidens, paradoxus, priscus, pumilus, singularis,* and *zeilleri,* and, of course, all the other names in the list above (except *bicornutus*) are permanently unavailable for application to any new species of *Hyrachyus* that may be found.

The following table summarizes the forms recognized in this paper.

Class MAMMALIA
Order PERISSODACTYLA
Superfamily Rhinocerotoidea
Family Hyrachyidae
Genus *Hyrachyus*

Sect. 1. *Hyrachyus modestus* (Leidy)
Hyrachyus eximius Leidy
Hyrachyus hypostylus, new species
Hyrachyus douglassi, new name for *H. priscus* Douglass
Sect. 2. *Hyrachyus princeps* Marsh
Hyrachyus grandis Peterson
Sect. 3. *Hyrachyus affinis* (Marsh)

Genus *Colonoceras*
Colonoceras agrestis Marsh
Genus *Metahyrachyus*
Metahyrachyus bicornutus Troxell
Metahyrachyus troxelli, new species
Genus *Ephyrachyus,* new genus
Ephyrachyus implicatus (Cope)
Ephyrachyus cristalophus, new species

A number of forms have been excluded from the scope of this paper and reserved for separate treatment, as study during the preparation of the paper has shown definitely that they are not members of the family Hyrachyidae. They are Heptodon *singularis, Desmatotherium guyotii, D. mongoliense, D. fissum,* and *Dilophodon minusculus,* which belong to the Helaletidae, and "*Hyrachyus*" *intermedius* Osborn, Scott and Speir,

1878. The position of the latter is obscure, but it is not a hyrachyid, nor does it fit into any other known genus. In order to give it a bibliographic pigeonhole, pending more extensive treatment later, I propose the genus **Chasmotheroides**, with the type *Hyrachyus intermedius* Osborn, Scott and Speir, 1878 (not Filhol, 1885). It may be assigned, very provisionally, to the family Helaletidae, the other alternative being to the Lophiodontidae (sensu strictu). As it has not previously been

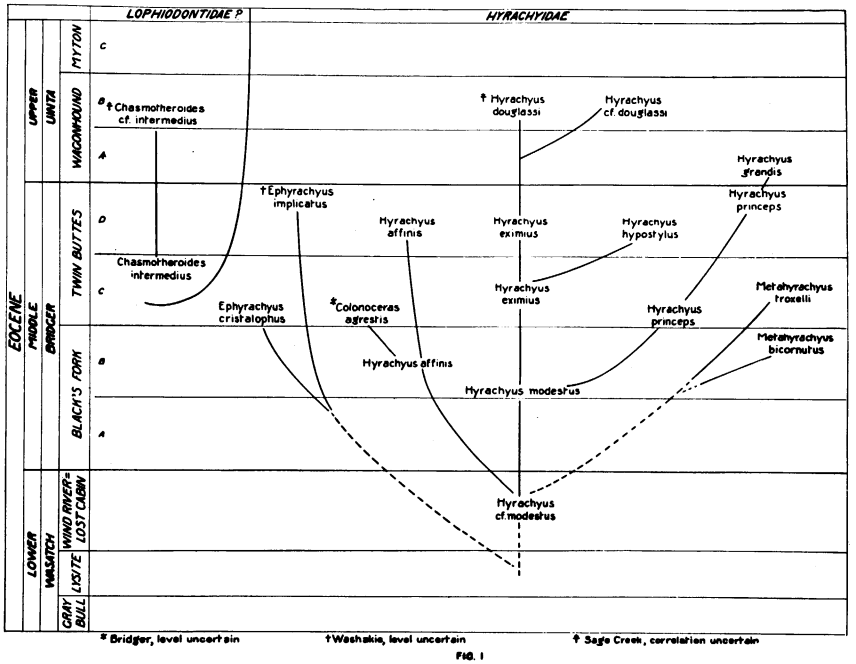


Fig. 1. Stratigraphic and phylogenetic chart of the Hyrachyidae.

figured, Fig. 48 is given to show the absence of any close resemblance to the Hyrachyidae.

Filhol proposed a number of species, on fragmentary material, which he referred to "*Hyrachius.*" Some other authors, European and American (e.g., Earle, 1898) have accepted this identification. In view of the fragmentary nature of the material, consisting of the less distinctive teeth, and of the general similarity of all Eocene perissodactyl teeth, and the existence of some parallelism, this confusion is entirely understandable. The present taxonomic status and accepted phylogenetic relationships of these species is discussed in the introduction. After

studying the types in the École des Mines, I am entirely in accord with Depéret and the other workers who have removed "*Hyrachius*" *Douvillei, filholi* (=*intermedius* of Filhol), *Zeilleri* and *priscus* from the Hyrachyidae. *Cesserassictis antiquus* Filhol apparently belongs among the tapirs; it is certainly unrelated to the Rhinocerotoidea.

A side branch of the European lophiodonts, *Chasmotherium*, strongly suggests *Hyrachyus*, provided one considers only properly mutilated specimens. The third lower molar has lost its hypoconulid, unlike all other lophiodonts, except *Atalonodon* Dal Piaz, 1929, giving a fictitious resemblance to other forms which have lost it, i.e., *Hyrachyus*, the true tapirs (e.g., *Protapirus*), and to *Dilophodon*, *Deperetella*, and *Teleolophus* among the helaletids. Filhol's paratype of "*Hyrachius intermedius*," M^3 right (figured in 1888, Pl. XIX, Fig. 8, and refigured here, Fig. 49, *Chasmotherium* cf. *cartieri*), is very suggestive of *Chasmotheroides intermedius*. Whether this resemblance signifies relationship or convergence must be left in doubt for the present. The Argenton *Chasmotherium* is a fifth larger than the Princeton specimen, and the hypocone interrupts the internal cingulum; they are otherwise indistinguishable. If found in the same region and horizon, they would certainly be referred to the same species. Stehlin (1903) figures some specimens of *Chasmotherium*, especially *Chasmotherium minimum*, Fig. 1, p. 55, M^{2-3}, and *Chasmotherium cartieri*, Pl. I, Fig. 9, which bear out this resemblance. It is only in the molars, of course, that any resemblance can be observed to the Hyrachyidae. It is now generally agreed that *Lophiaspis* and *Lophiodon*, at least, have no close relationship to any American perissodactyls, and that the so-called American lophiodonts are a distinct group, the Helaletidae.

SYSTEMATIC DESCRIPTION

HYRACHYIDAE

(=Hyrachyinae Osborn and Wortman, 1892; emended, Wood, 1927*b*).

GENOTYPE.—Hyrachyus Leidy, 1871*a*.

DIAGNOSIS.—Primitive, North American,[1] rhinoceros-like perissodactyls from the

[1]Zdansky recently described a right maxilla with P^4–M^1, and a left lower molar from another and larger individual, both from Honan, China, as Isectolophinæ?, gen. et sp. indet. (Zdansky, O. 1930. 'Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen.' Palaeont. Sinica, C, VI, 2, pp. 38–40, Pl. I, figs. 38–40). These fragments much more probably represent a hyrachyid; in fact, on the available data, they are inseparable from the genus *Hyrachyus*. Among the characters most suggestive of *Hyrachyus* are: the short and broad P^4, with a small, low and narrow metaloph, consisting of the metaconule only, which abuts against the metacone and protocone, enclosing a triangular medifossette, giving a generally triangular aspect to the tooth; the slightly buccally projecting metacone of P^4, which carries an external cingulum; the strong anterior and posterior cingula of P^4, separated for a brief interval, lingually, by the protocone; he pattern of wear on P^4 and M^1; and the internal cingulum across the outlet of the median valley of M^1. The slight development of the anterior limb of the talonid crescent of the lower molar is typical of hyrachyids, and the trigonid is within the range of variation in *Hyrachyus*, and can be duplicated in numerous individual teeth. The complete cingulum surrounding the lower molar, however, seems to be a distinctive character. The upper teeth indicate an animal rather smaller than *H. modestus*, and the lower tooth, one rather larger. The form might best be called *Hyrachyus?* sp., cf. *modestus*, until better material is found. This, then, would be the first hyrachyid (instead of the first isectolophid) found outside North America.

Lost Cabin, Bridger, Uinta and equivalents; size of Russian wolfhound to mustang; moderately cursorial, with tetradactyl manus and tridactyl pes; hornless or with incipient paired horns; nasals not shortened; nasal incision slight; posterior nares open opposite the middle of M^2; dental formula: $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}-\frac{4}{3}$, $M\frac{3}{3}$; I^{1-2}, transversely elongated chisels; I^3 broadly pointed at tip; I_1 is a transverse chisel-blade; I_2 intermediate between I_1 and I_3; I_3 small but nearly caniniform; small spaces between front teeth; small erect canine tusks, followed by moderate diastemas; permanent premolars never molariform except in some fourth lower premolars after prolonged wear; in the upper premolars, the protoloph usually overshadows the metaloph; paracones and metacones of the upper cheek teeth retain much of the character of free cusps; molar parastyles are prominent independent cusps rising from the anterior cingulum; cristae of upper molars usually retain their primitive prominence; posterior buttress of M^3 is always large; first lower premolar, when present, small and simple, without much cusp differentiation; second lower premolar with talonid demarked from trigonid; third and fourth lower premolars with nearly molariform trigonids combined with primitive talonids; external limbs of lower molar crescents are small; talonid crescents of lower molars never really overlap the trigonid in unworn teeth, as they do in all other rhinocerotoids; M_3 lacks the "extra lobe" or hypoconulid.

Hyrachyus Leidy, 1871*a*

Genotype, by original designation, *H. agrestis*, subjective synonym of *H. agrarius*, both subjective synonyms of *H. modestus*.

Diagnosis:—Hornless; protoloph of upper premolars much more prominent than the metaloph; no tendency for the metalophs of the upper premolars to touch the crista; attachments of upper premolar metalophs to ectolophs usually higher than corresponding attachments of the protolophs; upper cheek teeth subrhinocerine rather than rhinocerine, except after extreme wear.

The genotype of *Hyrachyus* has been a subject of dispute. Leidy described *Lophiodon modestus* in 1870 on the basis of a single tooth, which I interpret as the third left upper deciduous premolar (Fig. 8) of a species of *Hyrachyus* of moderate size. Leidy later (1871*a*) founded the genus *Hyrachyus*, saying, "An extinct genus, allied to *Hyracodon*, is founded on a fragment of a lower jaw of a young animal." This description clearly refers to the type of *H. agrestis*, which is therefore the genotype by original designation. Incidentally, Leidy describes *H. agrestis* on line 20, followed by *H. agrarius* on line 24. In 1872*a*, Leidy "suspected" *H. agrestis* was the same as *H. agrarius*. He also suggested that *H. agrarius* might be a synonym of *L. modestus*. In 1873, in revising the group, he made *H. agrestis* a synonym of *H. agrarius*. Leidy was followed by nearly all subsequent writers in substituting *agrarius* for *agrestis*, the only exceptions I have discovered being Pavlow (1888) and Troxell (1922*b*). Troxell considers that *H. agrestis* must be the genotype, but that the specimen is specifically indeterminable, and resurrects *H.*

bairdianus Marsh for the animal in question. All these early types are inadequate by modern standards, differing only slightly in degree, but I believe it is possible to show that *H. modestus, agrarius, agrestis* and *bairdianus* are all the same species, taking priority in that sequence. I submitted the question of the relative rank of *agrestis* and *agrarius* to Dr. C. W. Stiles, who stated, unofficially, on the basis of my data (letter dated Feb. 8, 1927): "It is best to have the citation read genus *Hyrachyus*, type by original designation *agrestis*, subjective synonym of *agrarius*."

Hyrachyus, sensu strictu, contains series of small, intermediate, and large forms, the two larger series being divisible into successive stratigraphic stages (Fig. 1). Such stages may be called species for convenience, without any implications as to whether they are larger or smaller taxonomic groups than living species. The most striking difference, at first glance, between these species, is that of size. The orders of magnitude are suggested by the following summary of the detailed tables of measurements of several species.

Range in Length of	P^{2-4}	M^{1-3}
H. affinis	26–30 mm.	43–46 mm.
H. modestus	33–36 mm.	49–57 mm.
H. eximius	36–39 mm.	60–67 mm.
H. princeps	40–45 mm.	66–72 mm.

The gaps between the extremes of specific range in size are so small (there are no gaps in some cases) as to suggest the query whether this may not be a continuous series. However, a continuous series should have the form of a simple curve with a single peak, whereas inspection of the full tables of measurements shows that four peaks occur, presumably indicating four distribution curves, of which the extremes may approach or even overlap. This is confirmed by the other morphologic or stratigraphic differences between these forms. Some of the species known from only one specimen, after extensive collecting, may, of course, be merely abnormal individuals, but as there is no way of determining whether this is the case, it is more convenient to treat them as real species.

The large number of individuals measured permits the determination of the size range of the common species. The measurements from both sides of the same individual give, at least, a minimum standard for size variation inside a species. The measurements are made as follows, as experience has shown that they are the most convenient units for rhinocerotoid teeth, and the least likely to be interfered with by breaking.

Upper Cheek Teeth:

A.P.—For P^1—the maximum distance perpendicular to the rear border of the tooth.

For P^2–M^3—the distance is measured across the middle of the tooth, median to the ectoloph, about above the base of the internal slope of the metacone.

Tr.—For P^1—the greatest distance perpendicular to the long axis.

P^{2-4}—one arm of the calipers is oriented parallel to and touching the base of the external border, i.e., the paracone and metacone, the other arm touching the most remote part of the internal border.

Tr.—For M^{1-3}—one arm of the calipers is oriented parallel to and touching the internal border, i.e., the protocone and hypocone; the other arm touches the most remote part of the external border, which would be the parastyle in the Hyrachyidae and the paracone in later rhinoceroses. The projecting parastyle of the Hyrachyidae makes this measurement not strictly comparable with the other rhinoceroses, as a somewhat greater reading is obtained for a tooth essentially comparable in size. This transverse measurement is essentially the width of the anterior half of the tooth.

Lower Cheek Teeth:

A.P.—For P_1–M_3, is measured at the middle of the tooth, in the longitudinal plane, over all, including the anterior and posterior cingula.

Tr.—For P_{1-4}, is measured for the greatest transverse width, perpendicular to the longitudinal axis, normally across the trigonid of premolariform teeth and across the talonid of molariform premolars.

Tr.—For M_{1-3}, is the greatest transverse width across the talonid, perpendicular to the long axis of the tooth.

Hyrachyus modestus (Leidy), 1870

Figures 4–8

LEIDY, 1873, Pl. II, Figs. 11–13, Pl. IV, Figs. 9–18; MARSH, 1884, Fig. 71; GREGORY, 1920, Fig. 169; TROXELL, 1922*b*, Figs. 1–2.

TAXONOMY:—*Lophiodon modestus* Leidy, 1870.
Hyrachyus agrestis Leidy, 1871*a*.
Hyrachyus agrarius Leidy, 1871*a*.
Lophiodon bairdianus Marsh, 1871.
Hyrachyus modestus (Leidy). Leidy, 1872*a*.
Hyrachyus bairdianus (Marsh). Leidy, 1872*b*.
Hyrachyus agrestis Leidy. Pavlow, 1888.
Hyrachyus agrarius Leidy. Osborn and Wortman, 1895.
Hyrachyus agrestis Leidy. Troxell, 1922*b*.

TYPE:—U. S. Nat. Mus. No. 661, a left dP^3, from the Lower Bridger Formation of Smith's Fork, Bridger Basin, Wyoming.

TOPHOMEOTYPE:—A. M. No. 12667, a skull and partial skeleton, from Bridger B, Millersville, Wyoming.

DIAGNOSIS:—P^2 triangular; P^{2-4}, 33 to 36 mm.; M^{1-3}, 49 to 57 mm.

P^2 either has no metaloph at all, or else the metaconule forms a wrinkle on the internal slope of the metacone, without connection with the protoloph. The general

aspect of the crown surface of P^2 is triangular, not quadrilateral, due partly to the actual contour of the tooth, partly to the absence or small size of the metaloph, and partly to the relative narrowness of the tooth, transversely, as compared with the length antero-posteriorly. There is little or no demarcation between the paracone and metacone of P^2; in other words, the ectoloph may be described as an undivided parametacone, in many specimens. The first lower premolar is almost always retained.

This species is abundant in the Lower Bridger (Horizons A and B), and appears in the Upper Huerfano. Two fragmentary specimens from the Lost Cabin, which are not, at present, separable from it, may represent its immediate ancestor. It is the smallest member of the most abundant line of hyrachyids—those of intermediate size.

The type, collected by Hayden in 1870, "from near Fort Bridger" (Leidy, 1870), is actually from Smith's Fork. It was described and figured by Leidy in 1873 (p. 67, Pl. II, Fig. 13). Leidy's figure gives an inaccurate impression. A new drawing, therefore, is furnished (Fig. 8). According to Matthew and Granger's valuable map (Matthew, 1909, Osborn, 1929, and Fig. 2), which permits the approximate determination of the geological horizon of a Bridger fossil of which only the geographic locality is known, this specimen comes from Horizon B of the Bridger. The affinities of this tooth have been misjudged in the past, as it has always been considered a molar. For example, Leidy (1873) called it M^1 or, more probably, M^2, and Osborn, Scott and Speir (1878) considered it an M^3. Among the anatomical features which establish its character as a dP^3 are the rough parallelism of the external and internal border, the marked slope to the rear of the protoloph and metaloph, the caudad slope of the anterior border of the tooth from the external to the median border, causing the parastyle to jut out, anteriorly, and the presence of a sharp mesostyle, and of a sharp cuspule at the outlet of the median valley. Allowing for the usual differences in size and shape between dP^3 and dP^4, Leidy's holotype (Fig. 8) is closely comparable with dP^4 of A. M. No. 12667, which consists of a skull and other fragments, including the left humerus, radius and ulna, of a young animal, collected by Sinclair in 1905, from Horizon B, Millersville, Bridger Basin (Figs. 4, 5, and 10). Millersville no longer exists, and is not shown on Matthew and Granger's map, but was located (fide Thomson, verbal communication) on the east bank of Smith's Fork, immediately below its confluence with Cottonwood Creek. A. M. No. 12667 becomes, therefore, the tophomeotype of *H. modestus*. This specimen is the key to the entire tangle of forms of intermediate size, as it furnishes the elements necessary for comparison with the various fragmentary types.

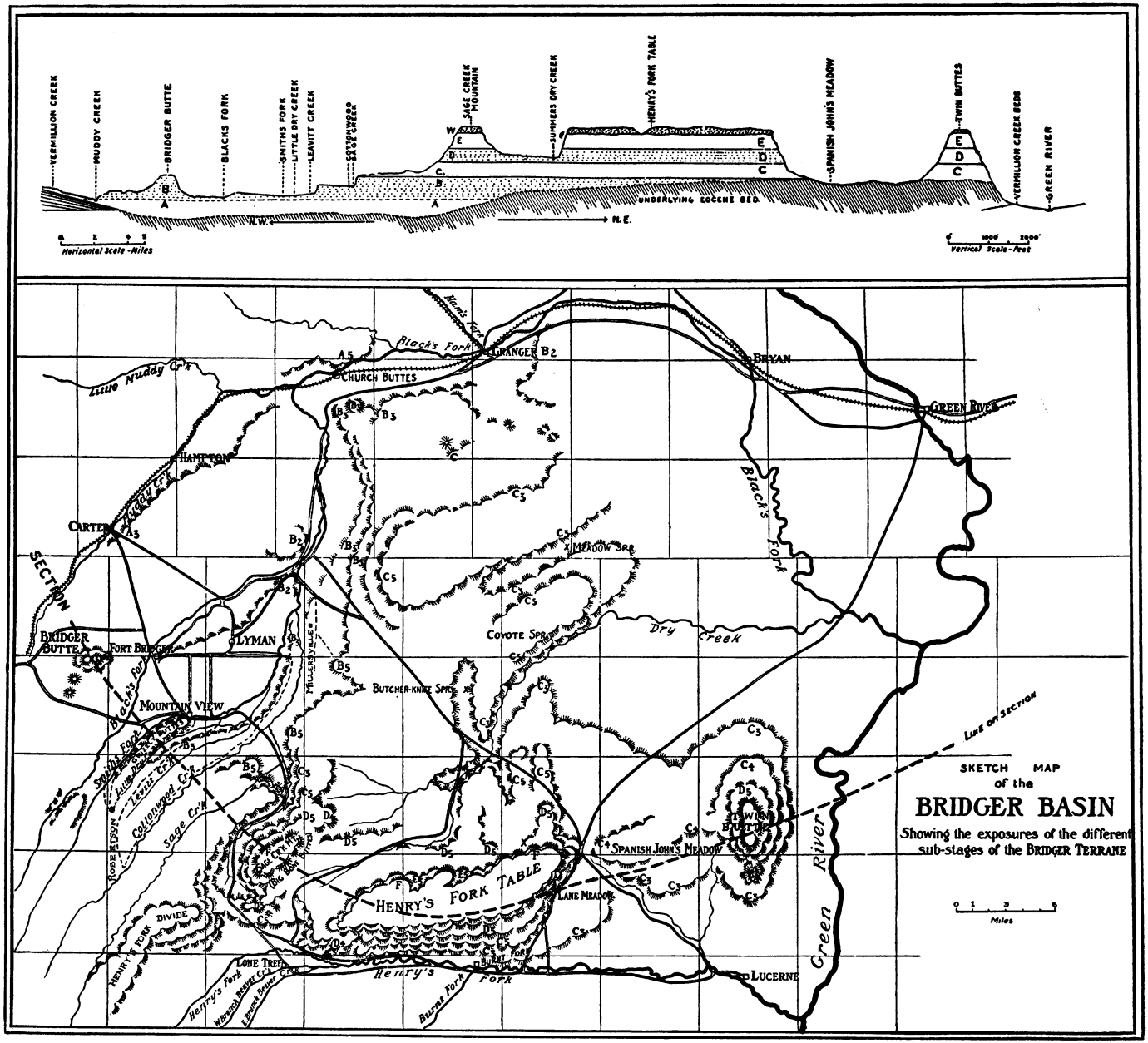


Fig. 2. Map of the Bridger Basin, southwestern Wyoming, slightly modified, after Matthew and Granger. Millersville is misplaced; it should be at the mouth of Smith's Fork.

This specimen is primitive, even for this species. In P^2 left, the parametacone is a continuous ridge with only one peak, and no demarcation whatever to show the future separation of the paracone from the metacone. In P^2 right there is a faint demarcation. There is no trace of a metaconule. It is noteworthy that this specimen is from B_1. It is definitely more primitive than the specimens of *H. modestus* from higher in horizon B, which show some advance toward *H. eximius*. A large number of the teeth, loose, appear to have dropped out of the skull, before fossilization. In the lower jaw, P_2 is exceedingly primitive, having hardly advanced beyond P_1. The protoconid is the dominant part of the tooth, the other cusps being hardly differentiated from it. In P_3 and P_4, the trigonids are approximately molariform, and the talonids are progressive for *Hyrachyus*. The supplementary "paralophid" sometimes found in dP_3 in rhinoceroses is present (Wood, 1927*b*, p. 28). M_1 has the characteristic *Hyrachyus* pattern.

Comparison of this specimen, A. M. No. 12667 (Fig. 5) with the type of *H. agrestis* Leidy, U. S. Nat. Mus. No. 660 (Fig. 6), collected by Hayden in 1870, from Black's Fork, Green River, Wyoming, and described (1871*a* and 1873) and figured by Leidy (1873, Pl. II, Fig. 12), abundantly justifies their reference to the same species. Matthew and Granger's map assigns the type of *H. agrestis* to Horizon B. It is a fragment of the left ramus of a young animal with P_1, the roots of dP_{2-3}, dP_4, and M_1 (not yet erupted). Leidy's figure shows the external aspect only. It was, therefore, necessary to expose M_1 as far as seemed safe, and to figure the specimen in crown view (Fig. 6). This permits comparison between the first lower molars of A. M. No. 12667 and the type of *H. agrestis* (Figs. 5 and 6 and table of measurements). They agree closely in both size and structure.

The type of *Hyrachyus agrarius* Leidy, U. S. Nat. Mus. No. 110, a left ramus from which the teeth are broken off, from Smith's Fork, Green River, Wyoming, collected by Hayden in 1870, was described (1871*a* and 1873) and figured (1873, Pl. II, Fig. 11) by Leidy. Roots of all four premolars and three molars are present; P_1 has two roots. It is a miserable specimen, but the geographic locality calls for Horizon B, the general character of the jaw justifies the reference to *Hyrachyus*, and the measurements permit the reference, among known species, only to *H. modestus*. This reference is confirmed by the assumed horizon, making it safe to drop *H. agrarius*, also, into synonymy with *H. modestus*.

Leidy's fine and well-known referred specimen of *H. agrarius* is also referable to *H. modestus*, and serves as the heautotype of *H. agrarius*

and as an important reference specimen of *H. modestus*. It was collected by Doctor Carter, "near Lodge-Pole Trail, 11 miles from Fort Bridger," and described and figured by Leidy in 1873 (pp. 59–66, Pl. IV, Figs. 9, 10, 13, 14, 15, 16, and 18). The "Lodge Pole Trail" ran from Fort Bridger to Henry's Fork, and presumably approximates the road still in use. If so, eleven miles from Fort Bridger, along the road, would place the specimen in Horizon B, but not far from exposures of Horizon C. The specimen consists of a well preserved series of right upper and lower cheek teeth. There are four premolars in each jaw. The size suggests the reference to *H. modestus*, and this is confirmed by the rudimentary character of the metaloph (metaconule) of P^2 and by the triangular shape and the slight degree of separation of the paracone and metacone of P^2. The internal cingulum is well developed on P^3-M^3. As Leidy pointed out, the metaconid is not demarked on P_3. P_4 has no entoconid; the hypoconid is an anteroposterior blade, sending out a low spur mediad. There are five mental foramina on one side, which must be close to a record. Of this specimen, only M_2 right, Phil. Acad. No. 10301, can now be located (Leidy, 1873, Pl. IV, Figs. 15–16). Leidy's figures are accurate, as far as they go. It is typical of *Hyrachyus* in general, and of *H. modestus* in particular, and confirms the allocation of this specimen. There is an external cingulum in the valley demarking the trigonid from the talonid, a moderate anterior cingulum, no internal cingulum, and a posterior cingulum rising to a peak in the middle.

Another of Leidy's figured specimens, Phil. Acad. No. 10302, P^4 left (Leidy, 1873, Pl. IV, Fig. 11), is, as Leidy said, clearly the same species. His figure is unsatisfactory. The specimen was collected by Doctor Carson from Grizzly Buttes, and can, therefore, be assigned to Horizon B of the Bridger. The cingulum is complete internally. A good-sized crista is present. The measurements are 12.8 mm. anteroposteriorly by 17.7 mm. transversely. This specimen is typical of *H. modestus* in all respects.

The next "species" to consider is *Hyrachyus bairdianus* (Marsh), 1871. Marsh based his description on a left maxilla with M^{1-3}, and a fragment of the left ramus with M_{1-3}, from "near Fort Bridger." The horizon is doubtful. If "near Fort Bridger" meant ten miles or less, the specimens come from Horizon B; but the early collectors were very loose in their geographic terms, and, judging from collectors' letters preserved at Yale, it may well mean nothing more definite than the Bridger Basin. Marsh did not figure the specimens, but Troxell has published very accurate figures of them (1922*b*, p. 41). Marsh and

Troxell regarded these two specimens as cotypes. They could not possibly belong to the same animal, as the upper molars are greatly worn, and the lower molars are almost unworn. In order to establish a definite basis of comparison, I hereby designate the upper molars, Y. M. No. 11035, as the lectotype, and the lower molars, Y. M. No. 11057, as the paratype, since the better condition of the lower molars is outweighed by the greater diagnostic value of the upper molars. M^1 and M^2 are badly broken and worn; M^3 is in good condition. In size, and in such characters as are present, these teeth agree well with A. M. No. 12667, with Leidy's referred specimen, and with the numerous other specimens in the American and Peabody museums which I refer to *H. modestus*. The lower teeth can be determined definitely as the molars, since, were they dP_4-M_2, the first tooth would be greatly worn. Another criterion is the rounded posterior border of M_3, as the posterior borders of the other molars are sharply truncated. These lower teeth show no very significant specific characters, except their size, in which they agree closely with the various specimens assigned to *H. modestus*. *H. bairdianus* was reduced to synonymy with *H. eximius* by Matthew in 1899, and revived by Troxell in 1922*b*, since he considered the earlier types as inadequate. I have followed the opposite course, accepting *H. modestus*, and referring the later forms to it, since all of these types are inadequate, and the use of any name other than *modestus* could be attacked at any time, on grounds of priority. In addition, the use of *modestus* settles the *agrestis* vs. *agrarius* difficulty. Comparison of the tables of measurements and of the figures of these various types, will show that they all, most probably, belong to the same species. Certainly it would be very difficult to make any sort of case for their belonging to different species.

To summarize, A. M. No. 12667 serves as a standard of reference, since its dP^4 is comparable with the type of *H. modestus*, dP^3; its second upper premolar is comparable with Leidy's referred specimen; its upper molars are comparable with the lectotype of *H. bairdianus* and with Leidy's referred specimen, and the first lower molar is comparable with the type of *H. agrestis*, the paratype of *H. bairdianus*, and with M_2 of Leidy's referred specimen.

A. M. No. 5067, a damaged skull with the cheek teeth and various miscellaneous fragments, was referred by Cope to *H. eximius* (1884). The teeth are not very distinctive in character, but the size and locality (Black's Fork) both indicate *H. modestus*.

A number of good specimens in the collections of the American and Yale museums which are referable to *H. modestus*, are listed below.

Most of them are also included in the tables of measurements. A. M. No. 11713, a skull without lower jaws, was collected in 1903 from B_2, Grizzly Buttes, Bridger Basin. P^2 has the characteristic triangular appearance of *H. modestus*, with paracone and metacone nearly connate, and the metaconule indicated by a wrinkle. The internal ends of the metaconules are bifurcated on both fourth upper premolars—a slight modification of the usual condition. Both infraorbital canals open above the anterior part of P^3. A. M. No. 11651, figured by Gregory (1920), consists of a skull in good condition and a mandible with damaged teeth, collected in 1903 from B_2, Grizzly Buttes, Bridger Basin. It is identical in size and character with Leidy's plesiotype of *H. agrarius*, and agrees very well with A. M. No. 12667, and with the types of *H. agrestis* and *H. agrarius*. The internal cingulum is virtually complete on P^3-M^3, marking about the extreme of variation in that direction. A. M. No. 11657 is a poor skull collected in 1903 from Grizzly Buttes East, presumably from B_2. Y. M. No. 11081, a good skull with lower jaws, was Troxell's apotype of *H. bairdianus* (1922*b*). It is from "near Fort Bridger"—that is, it was shipped from there. The upper premolars are without internal cingula, marking the limit of variation in the opposite direction from A. M. No. 11651. The other specimens represent all degrees of intergradation. Y. M. No. 11071, collected by Shoshone John from Church Buttes (and therefore, horizon A or B), was bought by Samuel Smith, May 10, 1876. It is a very typical specimen of the species. Y. M. No. 12527, a skull with other fragments, was collected at Millersville by R. E. Son, and came, therefore, from Horizon B. P^2 has no trace of a metaconule. A hypocone is incipiently defined from the protocone, by a groove, medially, in P^4. A. M. No. 19233, a right ramus with P_1-M_3, collected by Miller, in 1922, from Horizon B_3, Cottonwood Creek, Bridger Basin, has an unusually progressive P_4 for *Hyrachyus* (Fig. 11). A. M. No. 11650, collected by Osborn and Granger in 1903, from Church Buttes, Bridger Basin, at the base of the first bench (hence Horizon B), consists of a right ramus and symphysis with mixed deciduous and permanent dentition. It has a twinned metaconid on dP_3 (Fig. 9).

In addition to the numerous specimens known from the Lower Bridger, *H. modestus* also occurs in Huerfano B, in southern Colorado. A. M. No. 17436, a large part of the skeleton, without the skull, collected by Granger in 1918; A. M. No. 17014, right M^2 and M^3, and A. M. No. 17440, right P_3-M_3 (Fig. 12), collected by Olsen in 1918, two miles north of Gardner, and A. M. No. 17442, left P_2, M_1 and M_3, all seem to be referable to *H. modestus*, although they are too fragmentary for the reference

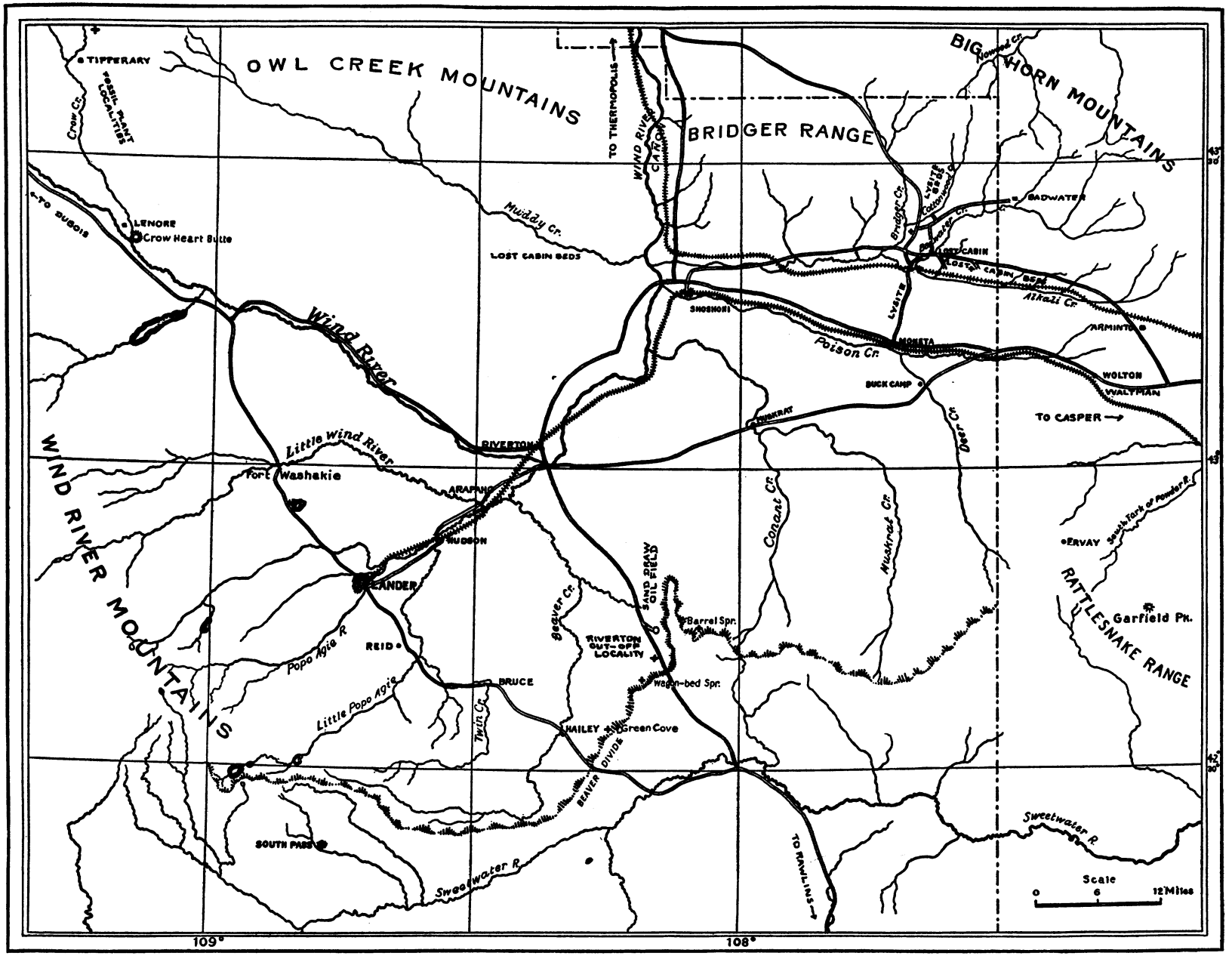


Fig. 3. Sketch map of the Wind River Basin, central Wyoming, modified from Granger, after N. H. Brown.

to be absolutely certain. This tends to agree with the accepted view that Huerfano B is at least a partial equivalent of the Lower Bridger.

Hyrachyus cf. **modestus**

From the Wind River (Lost Cabin)

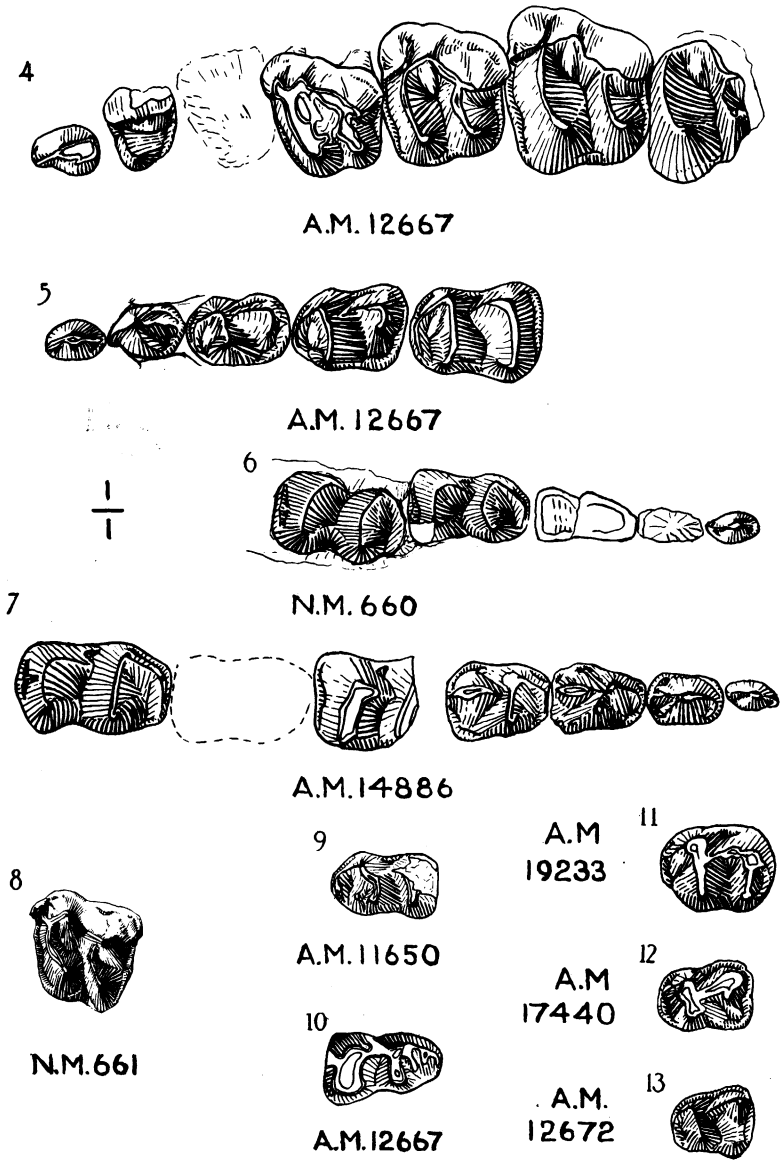
Figure 7

In spite of several published references (including Osborn, 1910, p. 135, and 1929, p. 72; Granger, 1910, p. 245, and 1914, p. 207), it still does not seem to be generally realized that *Hyrachyus* is now known from the uppermost Lower Eocene—from the Lost Cabin Formation (Lambdotherium Zone)—that is, the original "Wind River." I know of only two specimens, both consisting of lower teeth only, and both in the collections of the American Museum.

The more important specimen, A. M. No. 14886 (Fig. 7), is the one referred to in the literature. It was collected by George Olsen, August 27, 1909, from the Lost Cabin Formation, on Alkali Creek, Davis Ranch, Wind River Basin, Wyoming. It consists of loose teeth only—left P_{1-4}, talonid of M_1, trigonid of M_3, right P_1, P_4, M_1 (broken) and M_3, but as they are obviously *Hyrachyus*, contain no duplicate parts, agree in their character and extent of wear, and as left P_{2-4} fit together accurately, it seems reasonably certain that the teeth are parts of one specimen. The assumption is further strengthened by the extreme rarity of *Hyrachyus* in the collections from this formation. This specimen is closely comparable, in both size and character, with *H. modestus*. P_1 is small, single-rooted, and simple. P_2 is very similar to A. M. No. 12667; P_3 is a shade more primitive. As this specimen has never been figured or described, a drawing is appended (Fig. 7). As may be seen, so far as the animal is represented, it is absolutely indistinguishable from *H. modestus*.

The "typical" Lost Cabin area, north of Alkali Creek and the railroad, about six miles east of the town of Lost Cabin, can be reached by automobile as follows. From Lost Cabin, drive east on the old Arminto road (Old Yellowstone Highway to Casper) via crossing over Sand Draw (2.9 miles), Muddy Gap (6.4 miles), wooden bridge or crossing (7.1 miles), turning off along a dim trail, to the right, at 7.5 miles, to the top of the bluff above the exposures (8.2 miles). See map, Fig. 3, and Osborn, 1929, Pl. VIB.

The other specimen, A. M. No. 4887, was collected by Wortman, in 1880, in the Wind River Basin, Wyoming, presumably from the Lost Cabin, since no fossils were collected from the Lysite Formation until


4
A.M. 12667
5
A.M. 12667
1/1
6
N.M. 660
7
A.M. 14886
8
N.M. 661
9
A.M. 11650
10
A.M. 12667
A.M 19233
11
A.M 17440
12
A.M. 12672
13

Figs. 4–13

much later. It consists of a fragment of the right ramus containing P_{2-3} and the single-rooted alveolus for P_1, and of left P_2. The second lower premolars are closely comparable with the other specimen, A. M. No. 14886, except that they are more worn. P_3 is also similar, but its external cingulum is slightly better defined, and the postero-internal cingulum is more continuous. This specimen is doubtless the same species, and its chief interest is as a second individual. The presence of P_{2-3} in the jaw helps to confirm the similar association among the loose teeth of A. M. No. 14886.

It is, of course, quite likely that a better specimen would show specific differences from *H. modestus*. It seems safest, however, to await the discovery of such a specimen, rather than to saddle the literature with a new name on purely stratigraphic grounds, especially as it is perfectly possible that the separation might not be supported by further discovery. Neither of these specimens would make a satisfactory type specimen.

Hyrachyus eximius Leidy, 1871

Figures: 14–17 and 50

LEIDY, 1873, Pl. IV, Figs. 19–20; COPE, 1884, Pl. XXIII*a*, Fig. 1; Pl. LIII, Figs. 2 and 2*a*; Pls. LIV and LV; Pl. LV*a*, Figs. 1–5; Pl. LVIII*a*, Figs. 5 and 6; ZITTEL, 1893, Figs. 224 (after Leidy) and 225 (after Cope); OSBORN AND WORTMAN, 1894, Pl. II, H; 1895, Figs. 9–11; OSBORN, 1898, Figs. 1, 5, 6, 8 and 33A, and Pl. XII*a* (include the figures from Osborn and Wortman, 1894 and 1895); OSBORN, 1907, Figs. 177, 178 and 180 (from Osborn and Wortman, 1895).

TAXONOMY:—*Hyrachyus eximius* Leidy, 1871*b*.
Hyrachyus agrarius Leidy. Osborn and Wortman, 1895.
Hyrachyus eximius Leidy. Matthew, 1899.
Hyrachyus cf. *princeps* Marsh. Troxell, 1922*b*.
Hyrachyus eximius Leidy. Wood, 1927*b* (Table VII).

Fig. 4. *Hyrachyus modestus*, tophomeotype, A. M. No. 12667, Bridger B, P^1-M^3 left, ×1.

Fig. 5. *Hyrachyus modestus*, tophomeotype, A. M. No. 12667, Bridger B, P_1-M_1 right, ×1.

Fig. 6. *Hyrachyus agrestis*, type [=*Hyrachyus modestus*], U. S. N. M. No. 660, Bridger B, dP_{1-4}, M_1 left, ×1.

Fig. 7. *Hyrachyus* cf. *modestus*, A. M. No. 14886, Lost Cabin, P_{1-4} left, M_1, M_3, ×1.

Fig. 8. *Hyrachyus modestus*, type, U. S. N. M. No. 661, Bridger B, dP^3, left, ×1.

Fig. 9. *Hyrachyus modestus*, A. M. No. 11650, Bridger B, dP_3 right, ×1.

Fig. 10. *Hyrachyus modestus*, tophomeotype, A. M. No. 12667, Bridger B, dP_3 left, ×1.

Fig. 11. *Hyrachyus modestus*, A. M. No. 19233, Bridger B, P_4 right, ×1.

Fig. 12. *Hyrachyus modestus*, A. M. No. 17440, Huerfano B, P_4 right, ×1.

Fig. 13. *Ephyrachyus*? A. M. No. 12672, Bridger D, P_4 right, ×1.

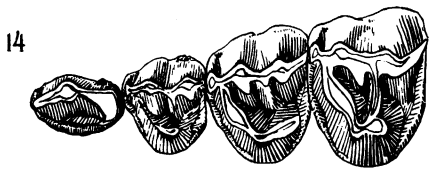
TYPE:—Phil. Acad. No. 10320, a fragment of the right ramus containing P_4 and most of M_1, from the Upper Bridger Formation of Henry's Fork, Wyoming.

NEOTYPE:—A. M. No. 1645, a skull and lower jaws, from the Upper Bridger Formation of Twin Buttes, Wyoming.

DIAGNOSIS:—P^2 quadrilateral with metaconule forming a metaloph; P^{2-4}, 36 to 39 mm.; M^{1-3}, 60-67 mm.

The type of this species, Philadelphia Academy No. 10320 (Fig. 16), consists of a fragment of the right ramus containing P_4 and most of M_1, collected by Doctor Carter from Henry's Fork, hence from Horizon C or D of the Bridger. Leidy described it in 1871*b*, and figured it, quite accurately, in 1873 (Pl. IV, Figs. 19 and 20). This species is abundant in the Upper Bridger (C and D). It is closely related to *H. modestus*, presumably by direct descent, but is definitely larger and more progressive. Matthew (1909) showed that few species pass from the Lower to the Upper Bridger, and this line is no exception. In fact, Leidy recognized this difference almost from the start, without the advantage of knowing the stratigraphic separation of the two forms. Since his time, however, *H. eximius* has usually either been ignored or else confused with its predecessor. The antero-posterior length of P^{2-4} ranges from 36 to 39 millimeters, of M^{1-3} from 60 to 67. P^{2-4} are wider transversely, even in proportion to their greater length, than in *H. modestus*. (See tables of measurements.) P^2 is quadrilateral, instead of triangular as in *H. modestus*, and its metaconule is developed into a distinct metaloph, which abuts against the protocone, forming a shallow, inclosed medifossette, and the paracone and metacone are fairly distinct. P_1 is sometimes lost. These differences from *H. modestus*, stated in words, do not seem very striking, and there is occasional overlapping in the extremes of variation of one or another of these differences. Nevertheless, when adequate specimens are compared, the general impressions as to size and advancement seem to be uniformly associated with the difference in horizon. The only doubtful cases are either very fragmentary specimens, or a few consisting of lower jaws and teeth only.

The type, Phil. Acad. No. 10320 (Fig. 16), was kindly sent to me, for study, by Dr. Witmer Stone. It is, of course, an unsatisfactory type, but furnishes sufficient data to establish the species. It is a fourth larger than *H. modestus*, as well as later in time. The hypolophid of P_4 was still a nearly simple, antero-posterior blade, without trace of an entoconid or of a postero-internal cingulum. Both teeth, in fact, are devoid of internal cingula. M_1 has a slight external cingulum at the base of the valley between the metalophid and hypolophid. A discontinuous cingulum runs along the greater part of the external border of P_4 (Fig. 16). The



A.M. 1645

A.M. 1645

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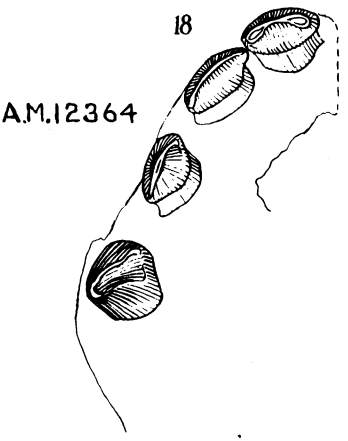
Phil. Acad. 10320



A.M. 1645

Fig. 14. *Hyrachyus eximius*, neotype, A. M. No. 1645, Upper Bridger, P^{1-4} left, ×1.

Fig. 15. *Hyrachyus eximius*, neotype, A. M. No. 1645, Upper Bridger, P_{1-4} left, ×1.

Fig. 16. *Hyrachyus eximius*, type, Phil. Acad. No. 10320, Upper Bridger, P_4-M_1 right, ×1.

Fig. 17. *Hyrachyus eximius*, neotype, A. M. No. 1645, Upper Bridger, I_1-C_1 left (I_{1-2} reversed from opposite side), ×1.

Fig. 18. *Hyrachyus princeps*, A. M. No. 12364, Bridger D, I^1-C^1 right, ×1.

measurements compare closely with those of the other specimens assigned to this species. P_4 is 15.4 mm. long by 11.2 mm. wide. The ramus is 37.8 mm. deep below P_4 and 41.2 below M_1, comparing closely with A. M. No. 1645.

Leidy, in 1873 (Pl. XXVI, Figs. 9 and 10), figured a left second lower molar, from Dry Creek (hence C or D), which he regarded as a second specimen of *H. eximius*. According to Leidy it was one inch long, which agrees in size with *H. princeps* rather than *H. eximius*. The coarseness of the tooth also favors this reference. Cope made this correction in 1884. The tooth is now smashed, but examination of the fragments confirms this reference.

The next specimen to be referred to this species was the famous skeleton fully described and measured by Cope (1873*b*, *c*, and 1884, pp. 662–675, Pls. XXIII*a*, Fig. 1, LIV, LV, and LV*a*, Figs. 1–5), now mounted in the American Museum (A. M. No. 5065), which may be regarded as the plesiotype of the species (Fig. 50). Unfortunately, all but the occiput of the skull is missing. In these publications, Cope also described A. M. No. 5066, a lower jaw (1884, Pl. LIII, Figs. 2 and 2*a*, Pl. LVIII*a*, Figs. 5 and 6), which seems referable to *H. eximius*, and a palate, A. M. No. 5067, which should be referred to *H. modestus*.

The most important reference specimen is a fine skull, A. M. No. 1645 (Figs. 14, 15 and 17), collected by the Expedition of 1893 at Twin Buttes, Bridger Basin (hence Bridger C or D), and described and figured by Osborn and Wortman (1894, p. 214, Pl. II, H; 1895, p. 367, Figs. 9–11) and Osborn (1898, Pl. XII*a*). Figures of this specimen, especially of the upper premolars, have frequently been republished, so that this skull is probably the most widely known specimen of *Hyrachyus*, and is generally used as a standard of reference. It is, therefore, unfortunate that it was assigned to the wrong species. A. M. No. 1645 may be considered the neotype of *H. eximius*, in view of the inadequacy of the type specimen, with which it agrees closely in size, horizon and other characters. It possesses all the specific characters listed above for *H. eximius*. Its horizon is above that of *H. modestus;* it is larger (tables of measurements) and more progressive. P^1 has no metaloph, the protoloph running antero-posteriorly. P^2 is more quadrate than in *H. modestus*, has the usual type of protoloph, and a low but distinct metaloph, formed from the metaconule. This metaconule is distinctly more prominent than in *H. modestus*, and the paracone and metacone are more distinct from each other. P^{2-4} are broader for their length than in *H. modestus*. The internal cingulum is broadly interrupted by the protoloph

on P^{1-4}, and by both lophs on the upper molars. P_1 is more progressive and differentiated than in *H. modestus*, as is P_3, which has a minute entoconid on the left side (absent on the right). In the lower molars, the rib on the anterior face of the metaconid seems slightly less pronounced. In the comparable teeth, P_4-M_1, the agreement is exact between Leidy's holotype of *H. eximius* and A. M. No. 1645. Although these are, in general, anything but distinctive teeth in the Hyrachyidae, it seems legitimate, in view of the agreement in horizon, size, and morphology, to regard them as conspecific, in which case an already well-known, fine specimen has the best claim to be regarded as the neotype.

Other characteristic specimens of *H. eximius* are: A. M. No. 11660, collected by the Expedition of 1903 from Horizon C_3, Henry's Fork, consisting of a good skull and lower jaw; A. M. No. 12366, collected by Granger in 1904 from horizon C_4, Lone Tree, Henry's Fork, a poor palate with front and cheek teeth; A. M. No. 12355, collected by the Expedition of 1904 from Horizon D_3, Cat-tail Spring, Bridger Basin, consisting of the lower jaws; A. M. No. 12670, collected by Granger in 1905 from Horizon D, Sage Creek Mountain, a pair of lower jaws with the deciduous premolars and M_{1-2}; A. M. No. 12223, collected by the Expedition of 1904 from Horizon C_4, Cottonwood Creek, consisting of P^3-M^2 left, and notable for the fragmented metaconule of P^4; A. M. No. 12360, collected by Granger in 1904 from Twin Buttes (hence C or D), consisting of the upper cheek teeth; A. M. No. 5063 from the Bridger Basin, described and figured by Cope, 1885, p. 661, and referred by him to *H. imperialis*, consisting of the right ramus of the lower jaw; A. M. No. 5066, from the Bridger Basin, referred by Cope to *H. eximius* (1873*b*, p. 213; 1884, p. 662, Pl. LIII, Fig. 2, and LVIII*a*, Figs. 6 and 7), including the left ramus of the lower jaw and the atlas; Y. M. No. 12533, collected Sept. 23, 1871, by G. M. Keasbey, west of Henry's Fork Divide (hence presumably from Horizon C or D), consisting of P^4-M^3 left and other fragments; Y. M. No. 12535, collected Sept. 12, 1871, by C. Harger, "N. Henry's Fork Divide, near road and Divide" (hence presumably C or D), consisting of a damaged skull with upper teeth; Y. M. No. 12524, collected June 19, 1874, by J. Heisey, from Lone Tree, Henry's Fork (C or D), consisting of C^1 left, P^3-M^2 left and other fragments.

Other specimens, with features of interest, probably referable to *H. eximius*, include: A. M. No. 12137, collected by Granger in September, 1904, from Henry's Fork Hill, Bridger C_4, including dP^2-M^1 right in the maxillary, part of dP^1 left, and dP^{3-4} left, dP^2 having the metaconule

confluent with the protoloph, but much lower at the point of junction (Fig. 39); A. M. No. 1646, collected by the Expedition of 1893 from Twin Buttes (Bridger C or D) mixed with A. M. No. 1645, including right $dP^{1-2, 4}$, M^1, and various limb bones (Fig. 38); A. M. No. 12668, collected by Granger in 1905, from Horizon C_4, Lone Tree, Henry's Fork, including both rami of the mandible with the milk premolars; and Y. M. No. 12537, from Henry's Fork (Bridger C or D), consisting of dP_{1-4}, M_{1-2}. In this last specimen, dP_1 is a conical tooth, with anterior and posterior ridges incipiently demarked into protoconid and metaconid, and an antero-posterior ridge, the hypoconid, swinging around to merge with the metaconid. This tooth seems to furnish additional evidence of the lack of any succession in regard to $dP_1 \rightarrow P_1$ in the Hyrachyidae, a situation long recognized in the true rhinoceroses. The protoloph of dP_2 has about reached the stage of P_3; the posterior crescent, though very low, is complete, with a large external cingulum. The disproportionate length of dP_3 is characteristic of rhinoceroses and numerous other perissodactyls, as are its nearly molariform structure and its antero-external hump. The completely molariform dP_4 is of interest, in view of the failure of P_4 to be completely metamorphosed in any member of the genus.

Transition to *Hyrachyus douglassi* is suggested by two specimens, Y. M. No. 12529 and Y. M. No. 12553, which are probably best left in *H. eximius*. Y. M. No. 12553 consists of a mass of fragments of skull, jaws and teeth, from Henry's Fork, Bridger Basin, Wyoming (hence C or D). The brain cast of this specimen was figured by Marsh, 1884, Fig. 71. A fragment of the right premaxillary with I^2 and I^3 shows that the third incisor is nearly caniniform, as in other members of the Hyrachyidae. Right P^4 is the most interesting tooth. It is 14.9 mm. in length (antero-posteriorly). There is a short posterior cingulum and none internally. The metaconule does not reach the protoloph. The hypocone is beginning to be constricted off from the protocone, thereby suggesting P^3 of Y. M. No. 12553 and P^2 of *H. douglassi*. Y. M. No. 12553 consists of P^3-M^2 right, P^1 left, P^4 left, P_2-M_3 right, P_2-M_1 left, M_3 left, from "South Twin Buttes," Wyoming—presumably C or D. In P^1 left, the cingulum surrounds three sides of the tooth, and nearly surrounds the buccal side. A small groove externally suggests a division of the parametacone into paracone and metacone. The antero-posterior protoloph has a hypocone incipiently divided off by an internal groove. There is no trace of a metaloph. P^3 right has the hypocone incipiently separated from the protocone by an internal groove.

This incipient hypocone is already connected, basally, with the metaconule. P^3 left, however, is of the normal *H. eximius* type. In P_{2-4}, the functional parts of the talonids are the high longitudinal hypoconid blades. However, the posterior cingula sweep down and around from them, as low, but well defined, continuous crescents, cutting off the posterior valleys, and abutting against the metaconids. These crescents are probably not homologous with true entoconids. The posterior cingulum of M_3 rises into a cuspule in the median axis. The other teeth are fairly typical of *H. eximius*, as are the measurements.

Hyrachyus hypostylus, new species

Figures 19–22

TYPE:—A. M. No. 12666, a skull with lower jaws, and the atlas.

HORIZON AND LOCALITY:—Bridger D at Sage Creek Spring, Bridger Basin, Wyoming.

DIAGNOSIS:—Hypostyles on upper premolars; slightly larger than *H. eximius*.

The type is A. M. No. 12666, collected by Granger from Horizon D of the Bridger at Sage Creek Spring (Figs. 19–21). The name suggests the chief peculiarity, a tendency for hypostyles to appear on the upper premolars. This species may well have been derived from *H. eximius*, or, less probably, from *H. princeps*. It is a shade larger than the average of *H. eximius*. Conceivably, it might be merely an aberrant individual; but it possesses a degree of individuality that necessitates discussion, and, therefore, a name.

The specimen includes a crushed skull with most of the cheek teeth, lower jaws, and the atlas. $I\frac{?}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. The first upper premolars have a minute metaconule on the postero-internal slope of the parametacone. The protoloph is longitudinal and continues at the rear as the postero-internal cingulum. The hypocone, P^2 left, is nearly divided off from the protocone, but has not yet coalesced with the metaconule. As usual, the protoloph is barely connected with the ectoloph. There is no trace of a separate hypocone in P^3 right. The fourth upper premolars have the hypocone incipiently demarked from the protocone by an internal groove. A small, worn hypostyle is present on P^3 right, a large one on P^4 right and a trace on P^4 left. The other premolars are damaged, so that they give no information as to its presence or absence. The protoconule interrupts the anterior cingulum on P^3 and P^4. The molar cristae are small. The lower canines are large, as compared with the incisors. The talonid basin of P_2 is enclosed. The hypoconid is the only cusp on the talonid of P_3 and P_4, forming, as usual, a longitudinal blade. M_{2-3} right and left have no external or internal cingula, but have

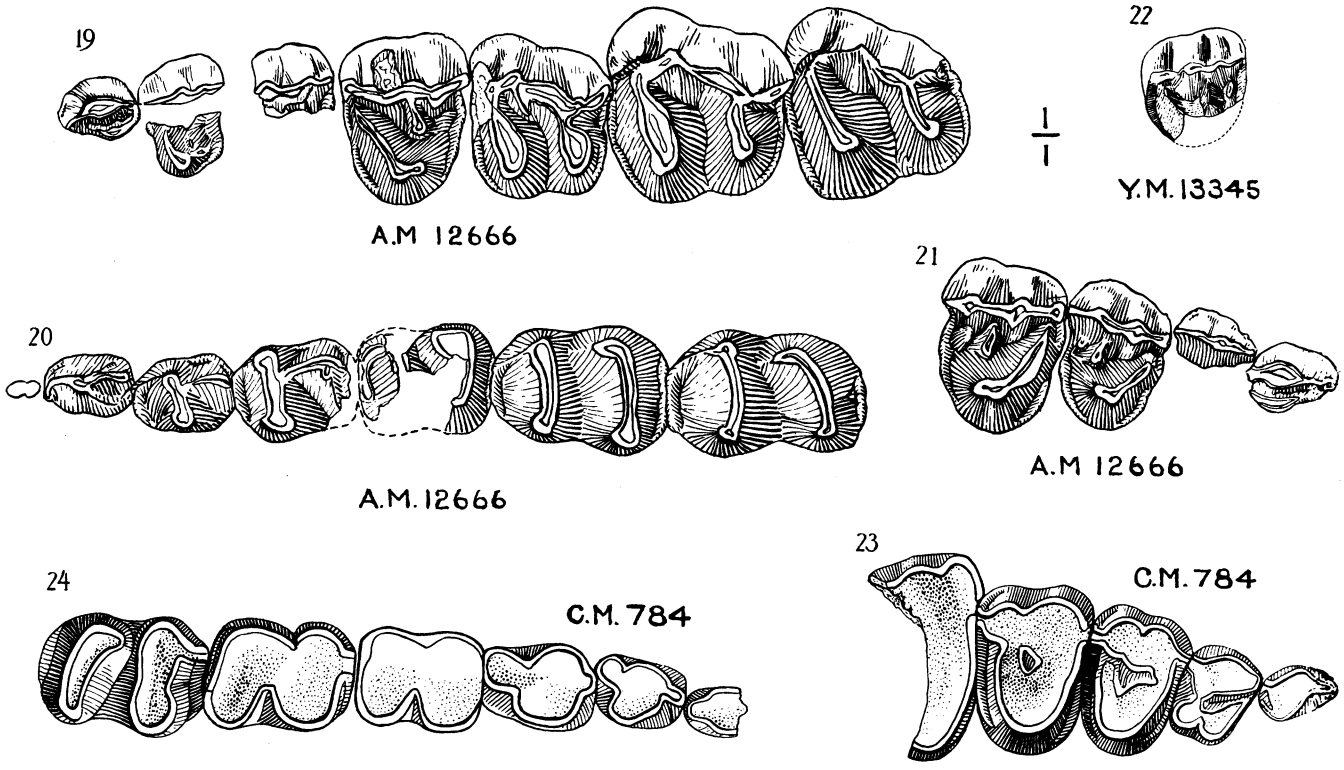


Fig. 19. *Hyrachyus hypostylus*, type, A. M. No. 12666, Bridger D, P^1-M^3 left, ×1.
Fig. 20. *Hyrachyus hypostylus*, type, A. M. No. 12666, Bridger D, P_2-M_3 right, ×1.
Fig. 21. *Hyrachyus hypostylus*, type, A. M. No. 12666, Bridger D, P^{1-4} right, ×1.
Fig. 22. *Hyrachyus hypostylus*, Y. M. No. 13345, Upper Bridger, P^3 left, ×1.
Fig. 23. *Hyrachyus douglassi*, type, C. M. No. 784, Sage Creek Beds, Montana, P^1-M^1 right, ×1.
Fig. 24. *Hyrachyus douglassi*, type, C. M. No. 784, Sage Creek Beds, Montana, P_2-M_3 left, ×1.

the usual anterior and posterior cingula. Full measurements appear in the tables.

A second specimen appears to be represented by Y. M. No. 13345, a broken P^3 left (or possibly P^2 left), with a good-sized hypostyle (Fig. 22), collected by Sam Smith at Lone Tree, Henry's Fork, June 21, 1874. This specimen, also, is evidently of Upper Bridger age.

"**Hyrachyus paradoxus** Osborn, Scott and Speir, 1878"

TAXONOMY:—*Hyrachyus* ———? Osborn, Scott and Speir, 1878, p. 53.
Hyrachyus paradoxus Osborn, Scott and Speir, 1878, p. 135.

The original description is as follows: "There are three premolars of the upper jaw which we cannot refer to any known species; but they are too imperfect to justify the formation of a new species for their reception. What appears to be a first premolar is inserted by a single broad fang: it is too much worn to show the characteristic enamel folding, and is peculiarly broad and short. The second premolar shows the usual foldings of *Hyrachyus*, save that a distinct valley enters the tooth from the posterior edge, running forward to the transverse crest, and inclosed by the curving backwards of the internal cone. The crown is nearly square; the basal ridge is scarcely marked at all." Measurements (fide Osborn, Scott and Speir):

	P^1	P^2
Length	11 mm.	12 mm.
Breadth	16 mm.	14 mm.

No locality or horizon in the Bridger is given; Matthew (in Osborn, 1909) refers *H. paradoxus* to the Lower Bridger, on what basis I do not know; Matthew (1909) leaves the horizon blank. No figure is given, and it is obvious that the original description does not furnish an adequate basis for recognition. It seems unfortunate that the authors did not keep to their original intention of giving no specific name, as indicated in the text (see above) and heading "Hyrachyus ———?"), but the catalog at the end lists "*Hyrachyus paradoxus*" (not otherwise mentioned), and refers to page 53, on which this description occurs. It might be possible, on this basis, to construct a plausible argument that *H. paradoxus* is a nomen nudum; but, in any case, the question is settled in a different manner. In a letter dated October 29, 1926, Professor W. B. Scott informed me that "Unfortunately no type can be identified for *Hyrachyus paradoxus*, as great confusion obtained in the collection of vertebrate fossils after the death of Dr. Hill and before the appointment of Mr. Hatcher as his successor."

Considering all these elements of uncertainty, the only reasonable disposition for *H. paradoxus* is to discard it as an indeterminate form, so that its sole remaining effect is to make the adjective "paradoxus" unavailable for any future species of *Hyrachyus*. If it is necessary to speculate as to what the type actually was, I should, as a wild guess, suggest a badly worn dP^2, followed by P^3 and P^4 of *H. modestus*. Any one of several other suggestions would be about equally plausible—and equally unverifiable.

Hyrachyus douglassi, new name

for **Hyrachyus priscus** Douglass, 1903 (not Filhol, 1885)

Figures 23 and 24, and Douglass, 1903, Figure 2

TYPE:—Carnegie Mus. No. 784, a snout with the lower jaws and atlas.

HORIZON AND LOCALITY:—Sage Creek Eocene, near Lima, Beaverhead Co., Montana.

DIAGNOSIS:—Metaloph of P^2 formed from metaconule and hypocone.

Hyrachyus douglassi is here proposed as a new specific name, based on Carnegie Museum No. 784, described by Douglass (1903) as *Hyrachyus ? priscus* from the Sage Creek Beds (Eocene, Upper Bridger or Lower Uinta) of southwestern Montana, near Dell. The probable correlation of the Sage Creek with the standard continental section is discussed in the section on stratigraphic correlation and nomenclature. *H. priscus* Douglass is obviously a homonym of *H. priscus* Filhol, even though Filhol's form is not a hyrachyid at all. Dr. C. W. Stiles (letter dated February 8, 1927) concurs in this, on the basis of the data presented in my letter to him. I communicated the facts to Mr. Douglass, to give him the opportunity to propose a substitute name, and he suggested (letter dated April 1, 1927) that I rename the species in connection with my revision of the group. I take the opportunity to retain his name in connection with this form.

This form is certainly a member of the genus *Hyrachyus*, and is more progressive than *H. eximius* (to which it is closely related, probably by direct descent), in having a hypocone on P^2, which, with the metaconule, forms a metaloph which is fairly separate from the protoloph, differing from any other species of *Hyrachyus*. This difference, together with the presumably later horizon, justifies at least provisional retention of specific rank, with the expectation that additional differences will appear in more complete specimens.

TYPE, C. M. No. 784.—$I\frac{3}{?}$, $C\frac{1}{1}$, $P\frac{4}{4\text{-}3}$ $M\frac{?}{3}$. Douglass' figure of the skull, in side view, is accurate, but as the crowns of the teeth are not figured, drawings are included in this paper (Figs. 23 and 24), P_2 being reversed, and P_4 and M_2 completed, from the

opposite side. The diastema is rather long. The hypocone of P^2 is separate from the protocone, and joins the metaconule to form a real metaloph. P^3 and P^4 and the front of M^1 (which is all that is preserved) are characteristically hyrachyid, and are not separable from *H. eximius*. The lower canines, judging from the roots, were probably of full size. P_1 had apparently been reduced to a small nubbin or lost altogether. In P_{2-4}, the hypoconids are longitudinal blades, and there are no entoconids nor internal cingula. M_3 is typically hyrachyid in the emphasis on the cross crests and the reduction of the posterior cingulum to a nubbin. The nasal incision is more marked, and the nasals are a shade less prominent, than is usual in *Hyrachyus*. The atlas has the typical *Hyrachyus* pattern.

The following middle-sized specimens of *Hyrachyus* from the Uinta of Utah may be grouped, provisionally, under this name, since they are about the same size, and perhaps are of similar age. A. M. No. 1929 (Fig. 37), consisting of dP^{2-4} and M^1 left, was collected by the expedition of 1894 from Uinta B, the Telmatotherium Beds, of White River, Utah, and interpreted by Osborn and Wortman (1895) and Osborn (1898), as P^4–M^3 of *Helaletes guyotii* Scott. This is the only basis for references to *Desmatotherium guyotii* from the Uinta. The three deciduous premolars are completely molariform in cusp structure; only the relative proportions reveal the situation. If this is really the deciduous dentition of *H. douglassi*, as the size suggests, it establishes another specific difference from *H. eximius*, that is, dP^2 is molariform, with the median valley opening lingually, as the protoloph and metaloph are complete and separate. The measurements (in millimeters) are as follows:

	dP^{2-4}	dP^2	dP^3	dP^4	M^1 (crushed)
A. P.	43.7	12.7	15.0	16.4	16+
Tr.		e14.7	18.0	21.6	24—

Carnegie Museum No. 3112, described by Peterson in 1919, pp. 129–130, from Horizon B, southeast of Kennedy's Hole, Uinta Basin, Utah, may also belong to this species. P_4 is more advanced than *H. eximius* in the "proportionately greater development of the metaconid, and a slight basal elevation indicating the tetartoconid." Peterson's measurements compare well with the type of *H. douglassi*, P_4 being 15× 11 mm. and M_1, 22×14 mm.

Princeton Mus. No. 11289 is a lower jaw collected by Hatcher from the gray clays (upper *T. cornutum* beds, Uinta B) of Kennedy's Hole, White River, Utah. P_3 is larger than the type, and the measurements are those of a slightly larger animal; but the resemblance is close throughout. P_3 and P_4 have postero-internal cingula on the talonid.

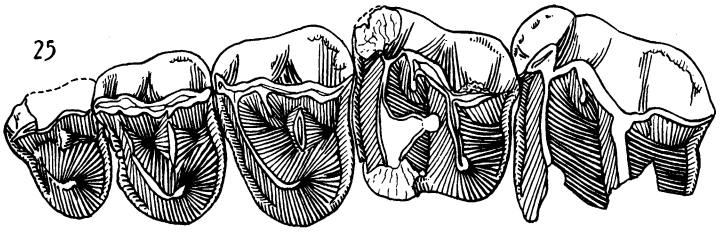
Yale Mus. No. 10259, a hyrachyid lower jaw from the Uinta, may belong in this species, as may Y. M. No. 10260, a hind foot collected by R. E. Son, also from the Uinta.

Hyrachyus princeps Marsh, 1872

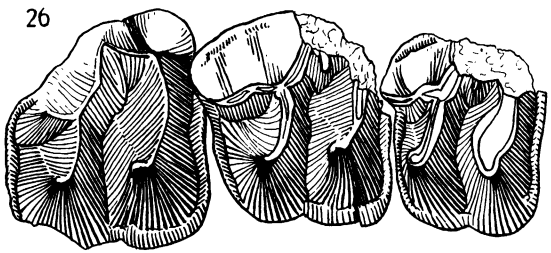
Figures 18 and 25–28; Plates XX–XXIII

LEIDY, 1873, Pl. XXVI, Figs. 9–10; COPE, 1884, Pl. LII, Fig. 4; PETERSON, 1919, Fig. 19; and TROXELL, 1922*b*, Fig. 5.

TAXONOMY:—*Hyrachyus princeps* Marsh, 1872.
Hyrachyus eximius Leidy, 1873, Pl. XXVI, Figs. 9–10.
Hyrachyus imperialis Osborn, Scott and Speir, 1878.

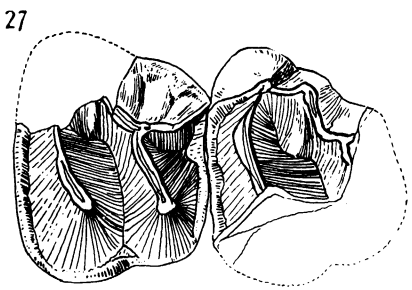


Y.M. 11157



Y.M. 11157

P.M. 10789



P.M 10789

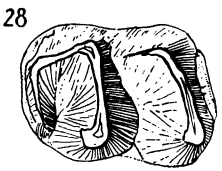


Fig. 25. *Hyrachyus princeps*, type, Y. M. No. 11157, Upper Bridger?, P^2-M^2 left, ×1.

Fig. 26. *Hyrachyus princeps*, type, Y. M. No. 11157, Upper Bridger ?, M^{1-3} right, ×1.

Fig. 27. *Hyrachyus imperialis*, type [=*Hyrachyus princeps*], P. M. No. 10789, Upper Bridger, M^{2-3} left, ×1.

Fig. 28. *Hyrachyus imperialis*, type [=*Hyrachyus princeps*], P. M. No. 10789, Upper Bridger, M_2 right, ×1.

TYPE:—Yale Mus. 11157, P^2-M^2 left, M^{1-3} right and M_3 left.

HORIZON AND LOCALITY:—Bridger Formation (probably Upper Bridger), Bridger Basin, Wyoming.

DIAGNOSIS:—Largest Bridger species; P^{2-4}, 40–45 mm.; M^{1-3}, 66–72 mm.; teeth coarsely modeled; parastyles very prominent.

Yale Mus. No. 11157 is the type. Its level in the Bridger is not beyond question, as the label with the specimen (followed by Troxell) gives "Fort Bridger, Wyoming," whereas the Y. M. catalogue gives "near Henry's Fork, Wyoming." Henry's Fork, if correct, would make the specimen Upper Bridger (C or D), agreeing with all referred specimens. On the other hand, "Fort Bridger," if correct, and to be taken as a limited, rather than a broad locality, would assign the holotype to the Lower Bridger (presumably B), in which horizon this species would be otherwise unrepresented. However, in view of the contradiction between the catalogue and the label and, particularly, of the loose application of locality terms by the early collectors, it seems justifiable to accept Henry's Fork, a relatively exact locality term, in preference to Fort Bridger, on which the expedition was based—the nearest "town," only twenty miles away. (Often the nearest town was cited as the locality, no matter how distant or inappropriate. For example, the original labels with some oreodons in the Columbia University Geology Department, obviously from the turtle-oreodon zone of the Big Badlands Oligocene, give "Deadwood, Dakota." If correct, this would represent an unprecedentedly early appearance of the oreodons!). This suggestion of Upper Bridger age is greatly strengthened by the fact that of six characteristic specimens of *H. princeps* in the American Museum, the five with their levels recorded are all from the Upper Bridger, four from Bridger C and one from the top of D. Both Princeton specimens are also from the Upper Bridger. In sum, *Hyrachyus princeps* appears, so far, to be confined to the Upper Bridger, and to be sufficiently characteristic and frequent to be considered an index fossil for that horizon. The most striking specific characters are the coarse modeling of the teeth, the large size for a Bridger hyrachyid, running definitely larger in almost every dimension and specimen than in *H. eximius* or *H. hypostylus*, the next larger forms. The dentition is apparently unreduced. The premolar metalophs are formed from the metaconule only. P^2 is broad transversely, but with only a small metaconule. The upper premolars are a shade more advanced than in *H. modestus*, a shade more primitive than in *H. eximius*. In the upper molars, the tapir-like parastyles are especially prominent, projecting appreciably above the

adjoining portion of the lophs in M^3. In spite, then, of the large size, this line seems rather unprogressive. It may well have been derived from *H. modestus* of the Lower Bridger, and rather probably gave rise to *H. grandis* of the Lower Uinta. No side lines are known.

The type, Y. M. No. 11157, consisting of P^2-M^2 left, M^{1-3} right, and M_3 left, was described briefly by Marsh (1872), without figures. Peterson (1919, Fig. 19) figured M_3 left accurately, and Troxell (1922*b*) published the first figure of the upper dentition, an accurate composite from the two sides. For the sake of completeness, figures 25 and 26 show the upper cheek teeth as they are. The upper premolars have no internal cingulum. P^2, like P^3 and P^4, is wide transversely. The median valley opens anteriorly, the protoloph failing to reach the ectoloph. The protoloph greatly overshadows the metaconule, which is almost separate from it. A suggestion of a groove on the inner side of the protocone hints at the future demarcation between protocone and hypocone. In P^3 and P^4, the metaconule is a rather distinct but very low cusp. In P^3, the outer attachment of the protoloph to the ectoloph is much lower than that of the metaconule, and barely closes the median valley, but, lingually, the protoloph rises higher, and the metaconule laps up on its flank. In this way, the valley is an enclosed pit. The condition is similar in P^4, except that the outer attachments of the protoloph and metaconule are at about the same level. There is a prominent external cingulum on the metacone of P^3-M^2. The cristae of P^4-M^2 are very prominent, but nearly absent on the other teeth. The molar parastyles seem more prominent and recurved than in other species of *Hyrachyus*, so that the eye centers on the parastyle to the neglect of the paracone. In M^1, the internal cingulum is interrupted by both lophs; it continues around the protolophs of M^2 and M^3, being interrupted by their metalophs only. As usual, M^1 is squarish, and M^2 is the largest tooth. Slight ridges run postero-externally from the protocones and metacones of M^2 and M^3. The anterior and internal borders of M^3 form nearly a right angle to each other. The metacone is prominent absolutely but not relatively. The posterior cingulum laps around onto the outside of the metacone. The M_3 left of the holotype, figured by Peterson, is 28.3 mm. long, 17.3 mm. across the trigonid and 16.8 across the talonid. Its morphological characters are unexciting. The talonids of M_3 right and M_2 right are also present, and measure, respectively, 16.4 and 17.3 mm. transversely.

Phil. Acad. No. 10321, the M_2 left figured by Leidy in 1873, Pl. XXVI, Figs. 9–10, as a referred specimen of *H. eximius*, was correctly transferred by Cope (1884) to *H. princeps*. It was collected by Doctor Carter from buttes near Dry Creek, hence from C or D. Since then it has been broken to pieces, only the part of the trigonid surrounding the basin being intact. This alone, however, justifies the reference to *H. princeps*, as the width across the surviving part of the trigonid is 15.2 mm., which, without allowance for the missing portion, would put it inside the specific limits of *H. princeps*. Leidy gave the length as one inch (25+ mm.), which agrees closely with other specimens. The coarseness of the tooth helps to confirm the reference. The chief significance of this correction is in leaving the status of *H. eximius* dependent solely upon the holotype.

In 1884, Cope figured a right M^3 of *H. princeps* (Pl. LII, Fig. 4) from the Washakie of South Bitter Creek. This specimen is now A. M. No. 5060. The locality suggests the Lower Washakie, and as the specimen is undoubtedly *H. princeps*, it gives some additional confirmation to the generally accepted correlation of the Lower Washakie with the Upper Bridger.

Hyrachyus imperialis Osborn, Scott and Speir, 1878, was based on P. M. No. 10789, consisting originally of "the second and third molars of each upper jaw, and three premolars, and one lower molar, portions of the skull and vertebrae," not all of which are still extant. It was collected by the Princeton Expedition of 1877, at Henry's Fork Divide, Bridger Basin, Wyoming—hence Bridger C or D. Marsh had published no figures of *H. princeps*, and his verbal description was misleading in several particulars, so that it is not surprising that this specimen was described (again, unfortunately, without figures) as a new species. In fact, Troxell figured the type of *H. princeps* for the first time in 1922, and "*H. imperialis*" is figured, for the first time, in this paper (Figs. 27–28). Osborn, Scott, and Speir recognized the resemblance of their form to *H. princeps*, but drew the following distinctions (wording modified): it differs from *H. princeps* in the greater proportionate length of the molars, in their larger size, compared with the bulk of the animal (how was the bulk of *H. princeps* determined!), and in less separation of the parastyle from the paracone, which is regarded as the chief diagnostic character. All the other anatomical characters listed are merely typical of *Hyrachyus* in general. According to Osborn, Scott and Speir, P^4 measured 18×24.5 mm. It is sufficient to say that these supposed differences are mistaken throughout, and that the closeness of the resemblance both in morphology and in measurements (see tables of measurements) between the Yale type of *H. princeps* and the Princeton type of *H. imperialis* is as close as is usually to be found between the two sides of the same jaw (Figs. 25–27). Troxell's suggestion (1922*b*) that "*H. imperialis* is either a synonym or at most only a subspecies of *H. princeps*" is amply justified. In sum, then, it is possible to relegate *H. imperialis* definitely to synonymy with *H. princeps*, with certainty that there will never be either occasion or excuse to resurrect it.

Certain referred specimens of *H. princeps* deserve mention. A. M. No. 12669, collected by Olsen, in 1905, from Henry's Fork Hill, C_5, consisting of upper and lower dentitions, is a typical specimen, except that P^2 shows a faint beginning of the internal groove incipiently demarking the hypocone from the protocone. A. M. No. 12371, a good skull collected by Granger in 1904, from Summer's Dry Creek, C_4, retains part of the deciduous dentition. The protoloph and metaloph of dP^2 are separate, but the tooth has still preserved its triangular shape, with the apex pointing forward. The fourth upper premolars have the hypocone incipiently demarked from the protocone. There is no trace of horn rugosities on the dorsal surface of the skull, such as are found in *Colonoceras* or *Metahyrachyus*.

P. U. No. 10339, collected by the expedition of 1885 from Twin Buttes, Bridger Basin, Wyoming, hence C or D, consists of a palate with P^4-M^3 left, P^2-M^3 right and P_3-M_3 left. P^3 has more of a metaloph than usual, as does P^4. The slightly accentu-

ated eversion of the posterior buttress of M^3 gives a suggestion of *Amynodon*. The internal cingula are slightly better developed than is usual in the genus.

A specimen of considerable interest, in its suggestion of evolutionary progress within the species, is A. M. No. 12364 (Fig. 18 and Plates I-IV), collected by Matthew, in 1904, from Henry's Fork, opposite the mouth of Beaver Creek, thirty feet above the upper white stratum. This skull with lower jaws and parts of the skeleton, from Bridger D_5, is the most recent representative of the species, running appreciably larger in almost all measurements than the other specimens, most (if not all) of which come from Bridger C. Except for the increase in size, suggesting progress toward *H. grandis*, there is no change which could justify the erection of a new species or variety. I^3, C^1, $P\frac{4}{4}$, $M\frac{3}{3}$. The upper front teeth are unusually well preserved, and deserve illustration (Fig. 18), together with a brief discussion. The chisel-blade of I^1 is transversely elongated, that of I^2 is elongated longitudinally, I^3 is pointed, but longer than it is wide. The upper and lower premolars show no morphological advance over the type. The roof of the skull is complete and without any trace of horn rugosities. The nasals are asymmetrically bifurcated anteriorly, on the top and side of the skull. The post-glenoid and mastoid processes do not touch. The paroccipital process is rather long. The dimensions, as well as those of other good specimens of *H. princeps*, are given in the table of measurements.

It is not certain from what species *H. princeps* arose; but, among known forms, *H. modestus* of the Lower Bridger seems the most likely claimant. This is based on the following lines of reasoning: the ancestor of the Upper Bridger *H. princeps* should be looked for in the Lower Bridger; *H. modestus*, though much smaller than *H. princeps*, is the largest Lower Bridger form, other than *Metahyrachyus*, which is obviously on a side line; morphologically, the two forms are much alike, *H. princeps* being slightly more advanced. It seems probable that *H. princeps*, the largest Bridger *Hyrachyus*, gave rise to the still larger *H. grandis* of the Uinta.

Hyrachyus grandis Peterson, 1919

TAXONOMY:—*Hyrachyus grande* Peterson, 1919, pp. 129–130, Figs. 18–19.
Hyrachyus grandis Peterson. Hay, 1930.

TYPE:—Carnegie Mus. No. 2908, a lower jaw.

HORIZON AND LOCALITY:—Uinta A, near White River, Uinta Basin, Utah.

DIAGNOSIS:—Largest species of genus, a third larger than *H. princeps*.

The type and only specimen is Carnegie Mus. No. 2908, a lower jaw collected from Horizon A of the Uinta Formation, near White River, Uinta Basin, Utah. This jaw indicates the largest known member of the Hyrachyidae, a third larger than *H. princeps*, the next largest species. As would be expected, this lower jaw is almost devoid of distinctive characteristics, other than its large size; but it seems reasonable to derive it from *H. princeps*, since *H. princeps* is the next largest species and comes from the next lower formation (the Upper Bridger), especially

as A. M. No. 12364 (*H. princeps*) from Bridger D_5 shows an increase in size over any specimen from Bridger C, which suggests that it is tending toward *H. grandis*. Finally, there is no evidence in favor of any other species being ancestral to *H. grandis*. The form of the specific name was changed by Hay to agree with the gender of the generic name, derived from ὗς, which can be masculine or feminine, but not neuter.

There are no clear specific distinctions from *H. princeps* (or, for that matter, from other members of the genus), except the large size. In P_1, the postero-internal cingulum is smaller than would appear from Peterson's Fig. 19; the external cingulum of P_4 is complete, instead of interrupted as shown in his Fig. 18. In M_3, the anterior cingulum is continuous with the anterior crescent instead of cut off from it. Aside from these details, Peterson's figures are both complete and accurate, making it unnecessary to refigure the species in this paper. Detailed measurements are given in the table.

Most of the systematic revision up to this point, as well as the evolutionary and stratigraphic implications drawn therefrom, seem strongly probable. Further discoveries should extend them, but there is no reason to anticipate any great reversals. However, the situation in regard to the line of small Bridger hyrachyids is by no means so clear-cut. Any attempt to clean up the mess is liable to attack on the basis of other methods of handling taxonomic problems, or of differences of judgment; and the whole proposed basis may be upset at any time by future discoveries. The provisional solution which I propose is perhaps the least unlikely, and has, at least, the negative merit of not making the taxonomic situation any more complicated than it is now, in case future discoveries prove it incorrect. The names involved in considering these small hyrachyids are:

Hyrachyus affinis (Marsh), 1871.
Colonoceras agrestis Marsh, 1873.
Hyrachyus crassidens Osborn, Scott and Speir, 1878.
Hyrachyus affinis gracilis Troxell, 1922*b*.

"*Hyrachyus*" *implicatus* and "*Hyrachyus*" *intermedius* can be segregated from the tangle, as these species do not belong in the genus. The evidence for this will be given later.

Hyrachyus affinis (Marsh), 1871

Figures 29, 30 and 32–36

TROXELL, 1922*b*, Figs. 3 and 4 and Pl. I.

TAXONOMY:—*Lophiodon affinis* Marsh, 1871.
Hyrachyus (?) *affinis* (Marsh). Leidy, 1872*a*.
Hyrachyus crassidens Osborn, Scott and Speir, 1878.
Hyrachyus (*?*) *affinis* (Marsh). Hay, 1902.
Hyrachyus affinis affinis (Marsh). Troxell, 1922*b*.
Hyrachyus affinis gracilis Troxell, 1922*b*.

TYPE:—Yale Mus. No. 12530, P^4-M^3 right.

HORIZON AND LOCALITY:—Lower Bridger, near Grizzly Buttes, one mile from Marsh's Fork, Bridger Basin, Wyoming.

DIAGNOSIS:—Smallest species of genus; M^{1-3}, 43 to 46 mm.

The type (Fig. 29) was collected "near Grizzly Buttes, one mile from Marsh's Fork," Bridger Basin, Wyoming. Marsh (1871) states that H. D. Ziegler collected the principal specimens near Marsh's Fork. The data clearly indicate Bridger B, with a presumption in favor of B_2. The collector's label seems to settle the doubt expressed by Granger (1908, p. 247) as to the whereabouts of Marsh's Fork, confirming the belief which he expressed that its probable location was in the "Grizzly Buttes" area. This individual belonged to the group of the smallest members of the genus *Hyrachyus*, all of which are smaller than *H. modestus* in every dimension. The range of this species extends throughout the Bridger. I hoped, during the earlier part of this investigation, to be able to distinguish distinct though related forms characterizing the Upper and Lower Bridger (as had turned out to be the case with *H. modestus* and *H. eximius*), and to be able to restrict certain of the extant names to evolutionary stages characterizing the particular horizons. Matthew, in his general analysis of the Bridger fauna (1909), points out that few species persist unchanged from the Lower to the Upper Bridger, so that, given sufficient material, a specific difference might well be expected, a priori. However, it developed that the combinations of characters that I had provisionally thought of as *H. a. affinis* and *H. a. gracilis* both run through the entire Bridger, and, further, that they appear to be only the extreme variants in a completely intergrading series, which appears to represent a normal curve of variation, and that no evolutionary changes or trends can be recognized. *H. crassidens*, as will be argued later, is a hopeless type, which should be discarded.

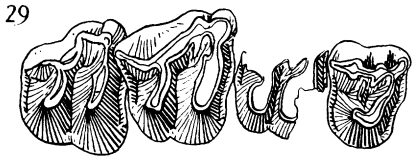
The principal specific characters of *H. affinis* would be as follows (composite description): range—throughout the Bridger; slenderer than the larger forms, and smaller than *H. modestus* in every dimension, the length of M^{1-3} ranging from 43 to 46 mm.; premolars more primitive than in *Colonoceras* or *Ephyrachyus;* internal cingu-

lum on upper cheek teeth highly variable, ranging from strong to very weak, but always stronger than in *Colonoceras;* P^2 more triangular than in *Colonoceras;* paracone and metacone of P^2 already distinct cusps—not connate as in *H. modestus;* hardly any metaconule on P^2, so that the median valley is fully open to the rear between the ectoloph and protoloph; P^{3-4} have low metalophs, with the protolophs curving around to the rear and enclosing the inner ends of the metaconules.

The type of *Hyrachyus affinis*, Y. M. No. 12530, from Horizon B, consists of P^4-M^3 right (Fig. 29). The protoloph of P^4 is less firmly attached to the ectoloph than in *Colonoceras*, and swings around, due to a developing, but still confluent, hypocone, to form a right angle. The metaloph consists solely of the transversely elongated metaconule, which is much lower than the protoloph and not closely connected with the incipient hypocone. In other words, the median valley escapes to the rear through a "wind-gap" between the metaconule and hypocone. The cingulum on P^4 is interrupted internally, although a faint suggestion of it can be traced all the way around from the anterior to the posterior cingulum. M^1 was worn in life and badly broken before collection, so that little remains to be seen. The posterior cingulum is very short. The internal cingula in M^{1-3} are represented only by small shelves across the median valley. M^2 is not especially distinctive. The crista is prominent, with sharp notches setting it off both anteriorly and posteriorly. The parastyles of M^2 and M^3 have the typical hyrachyid prominence and independence. The posterior buttress of M^3 is large and distinct in relation to the size of the tooth.

The type of *Hyrachyus affinis* is somewhat inadequate, considered purely by itself. Y. M. No. 12572D is morphologically identical with the holotype, and may be regarded as the plesiotype (Fig. 30). The exact locality is not recorded, although, since 12572E is from H. F. (Henry's Fork?), it seems likely that it was collected at the same locality. It consists of P^2-M^3 right. The ectolophs of all three molars and the protocone of M^3 are broken off. There are two other maxillae associated with it under the same catalogue number, and closely resembling it; but, obviously, not all can have belonged to the same individual. This specimen shows that *H. affinis* is exceedingly like Troxell's *H. affinis gracilis* (Fig. 32) and that it also resembles Marsh's *Colonoceras agrestis* (Fig. 31) very closely. P^2 has retained more of the primitive triangular shape than in *Colonoceras*. There is a deep prefossette. The metaconule is almost absent, represented only by a faint trace on the anterior slope of the metacone. The metaloph (metaconule only) of P^3 is considerably lower than in *C. agrestis*, and the protoloph is scarcely attached to the ectoloph. The metaloph of P^4 is very low as in the type of *H. affinis*, differing from the condition in *Colonoceras*. Traces of the internal cingula of M^{1-2} are retained in the form of slight shelves across the outlets of the median valleys. The comparative dimensions are given in the tables.

The question has already been raised, whether *H. affinis affinis* is the Lower Bridger representative of the line of small hyrachyids, and,



29

Y.M. 12530

32

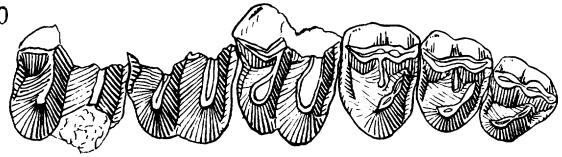
Y.M.11170

33

A.M.19242

34

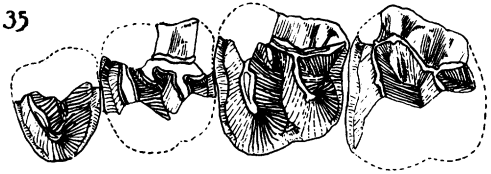
P.M.10138



30

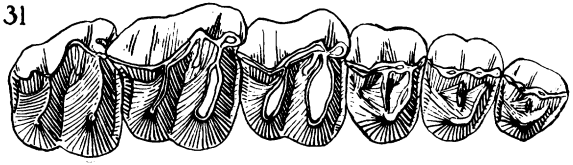
Y.M. 12572 D

1/1



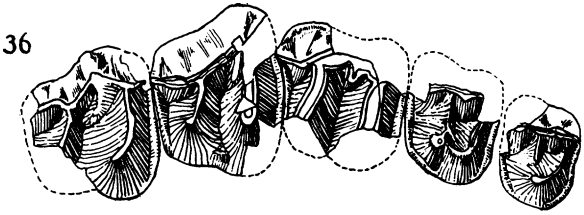
35

A.M.5072



31

Y.M. 11082



36

A.M.5072

Figs. 29–36

if so, whether the Upper Bridger representative is taxonomically different, as in most other cases. These small hyrachyids are about equally well represented in the two levels. *H. affinis gracilis* Troxell (1922*b*) comes from the Upper Bridger, and, of all available specimens, seems the least like the holotype. The morphological basis for separation is insufficient, however, as the other specimens form a nearly perfect intergrading series. Any possible stratigraphic presumption that these two forms are different will not hold, as Y. M. No. 12572E and A. M. No. 12166 from the Upper Bridger agree closely with the type of *H. agrestis* from the Lower Bridger, and A. M. No. 12664 from the Lower Bridger agrees most nearly with Troxell's *H. affinis gracilis* from the Upper Bridger. On the basis of all the data now available, then, it seems necessary to consider this a single, rather variable species, running throughout the Bridger.

Troxell's subspecies *Hyrachyus affinis gracilis* was based on Y. M. No. 11170 from Henry's Fork, Wyoming (hence Bridger C or D). (See Fig. 32 and Troxell, 1922*b*, Fig. 4 and Plate I, the latter being reprinted in Schuchert, 1924.) There are four toes on the manus and three on the pes, as in all other known skeletons belonging to *Hyrachyus*. As Troxell's photograph shows, the animal was rather slender-limbed and graceful—appreciably more so, even in proportion, than the well-known *H. eximius* skeleton (Fig. 50). The cheek teeth are worn, so that many characters are obscured (Fig. 32), and the front teeth are not preserved. The strongly developed cingula are the most distinctive features of Troxell's type. The internal cingula are complete on P^4 and M^3, nearly complete on P^3, and quite prominent across the valleys of M^1 and M^2. The external cingula are also well developed on the metacones of P^3-M^2,

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Fig. 29. *Hyrachyus affinis*, type, Y. M. No. 12530, Bridger B, P^4-M^3 right, ×1.

Fig. 30. *Hyrachyus affinis*, plesiotype, Y. M. No. 12572D, Bridger Basin, P^2-M^3 right, ×1.

Fig. 31. *Colonoceras agrestis*, type, Y. M. No. 11082, Bridger Basin, P^2-M^3 left, ×1.

Fig. 32. *Hyrachyus affinis gracilis*, type [=*Hyrachyus affinis*], Y. M. No. 11170, Upper Bridger, P^{1-4} right, ×1.

Fig. 33. *Hyrachyus affinis*, A. M. No. 19242, Bridger B, M^3 left, ×1.

Fig. 34. *Hyrachyus crassidens*, type [*Hyrachyus affinis* ?], P. M. No. 10138, Upper Bridger, M_1 left, ×1.

Fig. 35. *Hyrachyus implicatus*, type 1 [=*Hyrachyus affinis*], A. M. No. 5072, Bridger Basin, P^4-M^3 left, ×1.

Fig. 36. *Hyrachyus implicatus*, type 1 [=*Hyrachyus affinis*], A. M. No. 5072, Bridger Basin, P^3-M^3 right, ×1.

that of M^2 being almost an accessory cuspule. P^2 is nearly or quite devoid of any metaloph, and the protoloph curves around to the rear, so that the median valley is fully open to the rear. This condition agrees with the plesiotype of *H. affinis*, and with no other known member of this line. In P^3 and P^4, the protoloph curves around the metaloph (composed of the metaconule alone), quite as usual, so that, at this fairly advanced stage of wear, the median valley forms an isolated medifossette. The cristae or internal slopes of the paracones of P^3 and P^4 are prominent. The molar parastyles are sharply separate from the paracones. M^3 has a strong crista. Its posterior buttress is weaker than in the holotypes of *H. affinis* or of *Colonoceras*. P_2 is more advanced than Troxell's figure shows, the metaconid being partly separated from the protoconid. Ridges run posteriorly from these two cusps and coalesce, surrounding a small talonid basin. P_3-M_3 have anterior cingula and small external cingula in the valleys between the two crescents. The hypoconid of P_3 has a real crescentic shape, extended internally; it is bordered by cingula both externally and internally. P_4 has an incipient entoconid, slightly connected with the hypoconid. P_4-M_3 have posterior cingula of the usual pattern. The anterior opening of the infraorbital canal is single, above P^3. Other foramina preserved include: the lachrymal duct, the sphenopalatine and a single posterior opening of the left posterior palatine, and numerous vascular foramina on the parietals and squamosals. The postglenoid and post-tympanic processes are wide apart, not coming within eight millimeters of each other. Part of the hyoid apparatus is preserved.

The anatomical character in which this specimen differs most from the typical *H. affinis* is the presence of heavy internal and external cingula. However, other specimens form an intergrading series, and both extremes, as well as intermediate stages, of the series are found in both the Lower and Upper Bridger. The same kind of variation in the degree of development of the internal cingula, although not as great in degree, is found inside *H. modestus*, and, to a lesser degree, in *H. eximius* and *H. princeps*. Troxell's four stated differences from *H. affinis* do not seem very impressive. The suggestion that P^3 and especially P^4 are nearly molariform is exaggerated; they are typical of the genus *Hyrachyus*. The confluence of the protoloph and metaloph of P^4 is solely a function of the greater degree of wear. As he says, the posterior buttress and the external groove between the paracone and metacone are less prominent in M^3 than in the type of *H. affinis;* these may easily be purely individual differences. In sum, then, no valid taxonomic distinction can be drawn, on our present information, either horizontally or vertically, inside the *Hyrachyus affinis* line.

The following individuals are most like the type, Y. M. No. 12530: A. M. No. 12166, consisting of upper and lower jaws, badly crushed and distorted, collected by Miller in 1904, from Bridger D_4, Henry's Fork, near the B. F. P. O. (presumably the Burnt Fork Post Office); Y. M. No. 12572E, from P. M. Ranch, H. F. (presumably Henry's Fork, and hence C or D), Wyoming, consisting of the right maxilla with M^{1-3}, and the right ramus with M_2 and parts of the other teeth, with the upper molars almost devoid of internal cingula; Phil. Acad. No. 10300, an M^2 left, figured by Leidy (1873, Pl. IV, Fig. 11), collected by Doctor Carter from Henry's Fork (hence C or D), with no trace of an internal cingulum. There are other, but more fragmentary, specimens, from the Lower Bridger.

A. M. No. 12664, a fine skull and skeleton, which deserves monographic treatment, is somewhat intermediate, but on the whole more like the type of *H. affinis gracilis*. It comes from the middle course of Cottonwood Creek, Bridger B_3. Under the name of *H. affinis gracilis*, its skeletal measurements are given in Table VII, Wood, 1927*b*. The roof of the skull is completely preserved, and shows that there could not have been a trace of horn rugosities, as contrasted with *Colonoceras*. The nasal incision seems rather less marked than in the larger forms.

The following specimens are very like Troxell's type of *H. affinis gracilis*: P. M. No. 11395, collected by the 1877 Expedition in the Bridger Basin, consisting of P^4-M^3 left, P^3-M^3 right, and P_3–M_3 of both sides; Y. M. No. 13334, collected by La Mothe and Chew, August, 1874, at Little Spring, Wyoming, with P^{3-4} right of this kind; A. M. No. 12367, both rami of the lower jaw, collected by Granger in 1904 from Bridger C_4, Henry's Fork, almost exactly comparable with A. M. No. 12664 from B_3, except that it is slightly larger, and that P_4 has an incipient entoconid; Y. M. No. 12549, from the east side of Henry's Fork Divide (hence C or D), with a progressive P^3 with a high metaloph and an incipient division of the hypocone from the protocone. (A manuscript note by "O. C. M." considers it a "new genus, first [lower] premolar only one fang." This character is, of course, to be expected).

A. M. No. 19242, consisting of P^4-M^3 left and the left ramus with the roots of P_2-M_3, while otherwise closely resembling the type of *H. affinis*, has a peculiar M^3, the median valley being blocked by a mure (Fig. 33). As it is entirely characteristic of *H. affinis* in all other respects, it does not seem to deserve taxonomic separation on the basis of this character alone, particularly as no other similar specimens are known. It was collected by George Olsen, in 1922, at Grizzly Buttes, Bridger Basin (B_2). This blocking of the median valleys by mures occurred independently in various species and individuals, e.g., *Subhyracodon gidleyi* and *Caenopus dakotensis*.

Several specimens show the deciduous teeth. Y. M. No. 12526, collected by R. E. Son in 1874 at Millersville (hence Bridger B), consists of the fragmentary skull of a young animal, with dP^2-M^1 right and left (Fig. 41). The second upper molars have formed but have not yet erupted. The internal cingula are weak as in the type of *H. affinis*. The hypocone of dP^2 is almost completely separated off from the protocone, but is oriented in the same direction, i.e., longitudinally. The protoloph is parallel to, and separate from, the ectoloph. The metaconule is a small nubbin. Both dP^3 and dP^4 are completely molariform, and can be distinguished from molars only by their proportions. There are slight shelves across the median valleys and slight external cingula on the metacones of dP^3-M^1. A. M. No. 12693, collected by Granger in 1905, five miles southwest of the town of Granger (hence Lower Bridger), consists of the right maxillary with dP^{2-4} and the right mandible with dP_{2-4} and M_1. It is

of interest on account of the primitive character of dP^2 (Fig. 40). Y. M. No. 12528 consists of dP^{2-4} left. These deciduous teeth are quite characteristic, that is, dP^2 may be recognized as such at first glance, with the diagonal protoloph partly separated from the transverse metaconule, but dP^3 and dP^4 are morphologically like M^1, differing only in proportions. The keystone shape of dP^3, tapering internally, is always unmistakable; but it requires careful comparison and, often, measurement, to show that dP^4 also tapers internally, as compared with M^1. The external cingulum on the metacone of dP^3 rises into what might be called a mesostyle.

Incertae sedis: **Hyrachyus crassidens** Osborn, Scott and Speir, 1878

Figure 34

TAXONOMY:—*Hyrachyus crassidens* Osborn, Scott and Speir, 1878.
Hyrachyus crassidens Osborn, Scott and Speir—invalid. Matthew, 1899.
Hyrachyus implicatus Cope. Trouessart, 1904–1905.

Hyrachyus crassidens Osborn, Scott and Speir, 1878, is based on P. M. No. 10138, collected by the Expedition of 1877 from Henry's Fork, Bridger Basin, Wyoming, hence from Bridger C or D. The holotype and only assigned specimen consists of the left ramus of the lower jaw, with a part of the right ramus. The teeth, except M_1 left, are broken off at the roots. The specimen has never been illustrated until now (Fig. 34). There are four mental foramina, beneath the diastema and the anterior roots of P_2, P_3 and P_4, respectively. The multiplication of openings of the mental foramen appears to happen sporadically in many unrelated forms, may differ greatly on the two rami of one individual, and seems to be purely an individual anomaly, giving separate outlets for some or all of the different mental branches of the inferior alveolar nerve and of the inferior alveolar artery. The diastema is very short—10.5 mm. P_1 must have been quite small. M_1 is, as might be expected, a very nondescript tooth. The anterior cingulum circles around onto the protoconid; an external cingulum runs from the protoconid to the hypoconid; the posterior cingulum is of the usual character, and there is no internal cingulum. The creation of this species was very unfortunate, as its indeterminate character makes it difficult to assign it definitely to any particular known form, while its early date leaves room for possible priority over any later name for a small hyrachyid, whether yet discovered or not. The morphology of the molar permits fairly definite assignment to the Family Hyrachyidae, and the size limits it to the smaller forms. The occlusal relations of M_1 would agree with the type of *H. affinis*. The jaw in general, and M_1 in particular, agree closely with Y. M. No. 11170, the type of *H. affinis gracilis*, also from the Upper Bridger, and with A. M. No. 12664 from the Lower Bridger. The very

short diastema is a feature of all four of these specimens. The diastema is almost as short, however, in the type of *Colonoceras agrestis*. *Ephyrachyus* (described below), which is of about the same size, may fairly be excluded from consideration, as the diastema is considerably longer. The only other basis for dealing with *H. crassidens* is its Upper Bridger age. If *H. crassidens* is synonymous with *H. agrestis* (type from the Lower Bridger), *H. agrestis* has priority; if it is synonymous with *Colonoceras* (probably Upper Bridger), it may also be discarded. If it could be proved to be identical with *H. affinis gracilis*, and if there should ever be evidence to split the latter off as the Upper Bridger representative of the *H. affinis* line, *H. crassidens* would take precedence. Some disposition of *H. crassidens* seems to be called for. So far as I know, no other specimens which could be regarded as defining it more exactly, have been referred to this species. It is specifically, and, perhaps, generically, indeterminate. For practical convenience, it is perhaps best to consider it as a probable synonym of *H. affinis* and to allow it to rest in peace.

Colonoceras Marsh, 1873

TYPE SPECIES:—*Colonoceras agrestis* Marsh, 1873.

DIAGNOSIS:—Upper premolars more progressive than in *H. affinis;* paired rugosities on nasals.

The generic characters are discussed below, in connection with the genotype and only known species.

Colonoceras agrestis Marsh, 1873

Figure 31

MARSH, 1884, Fig. 70; 1897, Fig. 2; and TROXELL, 1922*a*, Figs. 1–3.

TYPE:—Yale Mus. No. 11082, a skull without lower jaws.

HORIZON AND LOCALITY:—Bridger Formation, Bridger Basin, Wyoming.

DIAGNOSIS:—Upper premolars more advanced than in *H. affinis;* paired rugosities on nasals.

The type and only known specimen is Y. M. No. 11082, collected by B. D. Smith in 1872, "near Fort Bridger," according to the Yale catalogue, from the "Dinoceras Beds." The generic name, from κόλος stunted, and κέρας horn, is very appropriate. No questions of priority or taxonomy are involved with this species as long as it is recognized as a distinct genus, closely related to, and derived from, *Hyrachyus*. If, however, it were to be regarded as a species of the genus *Hyrachyus*, the species *C. agrestis* Marsh, 1873, would then become a homonym of *H. agrestis* Leidy, 1871*a*, and the form represented by Y. M. No. 11082 would require a different specific, as well as generic, name. Unless,

then, this change were clearly necessitated, it would seem preferable to keep the old name and status. The most striking characters are the presence of paired horn rugosities on the nasals, toward their lateral borders, and about half-way from front to back (about above the second upper premolars), and, in the teeth, the presence of a metaconule in P^2, the somewhat greater size and progressiveness of the metaconule in P^3 than in *H. agrestis*, and the well developed metaloph (metaconule only) of P^4, which is nearly as high as the protoloph, and nearly confluent with it. This specimen certainly came from the Bridger, but the level is very doubtful. Matthew, in Osborn (1909), refers it to the Lower Bridger, presumably on the basis of "near Fort Bridger"; Matthew (1909) does not assign it to either horizon. There are only three possible clues to its horizon in the Bridger. The first is strictly morphological; that *C. agrestis* is closely related to *H. affinis* and presumably derived from it, and therefore, other things being equal, would be a shade more likely to be from the Upper than from the Lower Bridger. In the second place, the question arises how many miles away could still have been called "near Fort Bridger" in 1872. If it was found within ten miles by air, the locality would be Lower Bridger; if more, it would probably be Upper Bridger. The former loose locality usage has been discussed in connection with *H. princeps*. It is also possible that the label "near Fort Bridger" was affixed at Yale, as the point from which the fossils were shipped. The third line of evidence is the Yale catalogue entry as "Dinoceras Beds," which, if accurate, would mean Upper Bridger. Dr. W. D. Matthew was of the opinion (verbal discussion, 1929) that Marsh's collectors already recognized two geographic facies, so that "Dinoceras Beds," if based on Smith's determination, probably meant Upper Bridger, if on Marsh's entry in New Haven, merely Bridger. It is plain that the evidence is anything but conclusive, but there is perhaps a very slight balance of probability in favor of Upper Bridger age.

Colonoceras agrestis is more like *Hyrachyus affinis* (particularly the holotype and plesiotype) than any other form, both in size and morphology. The upper canines, four premolars and three molars were originally present, the canines and first premolars having dropped out of the skull, leaving their alveoli only. The diastema was short, slightly longer than in *H. affinis*. P^1 had two roots. There is no trace of an internal cingulum on P^2-M^3, thereby somewhat exceeding the limits of the broad range of *H. affinis*. Even the holotype and plesiotype of *H. affinis* have shelves at the outlets of the median valleys of the molars. There are no external cingula, except on the metacone of P^4, which is

also beyond the extreme range of *H. affinis*. P^2-M^3 have well-marked anterior and posterior cingula. P^2 is more quadrilateral than is usual in *Hyrachyus*. The paracone and metacone of P^2 are fairly distinct—definitely more so than in *H. affinis*. The protoloph of P^2 is slightly attached to the ectoloph, and a small metaloph, consisting of the metaconule only, is transversely elongated, and forms a low dam in the median valley. Even this characteristic hyrachyid stage, however, is more advanced than *H. affinis*. The protolophs of P^2-^{4} curve around the end of the metaconules, internally, but show no tendency whatever for the hypocones to bud off. In P^3, the protoloph is attached well up on the ectoloph, contrasting with the lower attachment of *H. affinis*. The external attachment of the metaconule is still higher, and, medially, it rises definitely higher than in *H. affinis*, so that it is less distinctly set off from the protoloph. The protoloph and metaloph of P^4 are nearly confluent, forming a V with sides of equal height, the only separation being a slight groove running postero-externally. This is decidedly more progressive than *H. affinis*, or any other species of *Hyrachyus*. The molars are very like those of *H. affinis*, except for the complete loss of external and internal cingula. The molar parastyles have not advanced beyond the usual hyrachyid condition. The molars have well-defined cristae.

The nasal rugosities are situated on the lateral borders of the nasals, about midway from front to back (not posterior as in *Metahyrachyus*). The horns were apparently everted. The radiating lines of the rugosities center at the lateral borders of the nasals, and run forward, backward, and mediad—the latter being most prominent. The various cranial foramina are clearly indicated, and warrant brief mention. The infraorbital canals open above the posterior roots of the second premolars, and are double on the left and single on the right side. The lachrymal canal has two openings on each side. The sphenopalatine and posterior palatine are present, the latter with double anterior openings on the palate. There is an ethmoidal foramen on the left side. The optic foramen, foramen lacerum anterius, foramen rotundum, foramen ovale, postglenoid foramen, supraglenoid foramen, jugular foramen and hypoglossal canal are present on both sides. There are two lateral foramina in each squamosal and parietal, which probably include Cope's postparietal and postsquamosal. The lateral flange of the pterygoid and alisphenoid, between the origins of the two pterygoid muscles, is very prominent. The postglenoid and posttympanic processes are wide apart—7.8 mm. A median keel runs along the basioccipital. Detailed measurements are given in the tables.

If I were describing this form, de novo, I doubt if I should separate it generically from *Hyrachyus*. Troxell (1922*a*) justly considers the generic separation from *H. affinis* as tenuous. On the other hand, as has been pointed out, merging it with *Hyrachyus* would necessitate the

change, not only of the generic, but also the specific name, of a form that has enjoyed over sixty years without nomenclatural vicissitudes. On this basis, I suggest that hornlessness and a primitive P^4 be regarded as essential characters of *Hyrachyus*, and that *Colonoceras agrestis* be maintained as a separate genus for convenience. If it were once merged with *Hyrachyus*, it is doubtful whether the specific name could ever, properly, be restored. On this basis, *Colonoceras agrestis* would be defined generically (as opposed to *Hyrachyus* and *Metahyrachyus*) by horn rugosities about the middle of the nasals, by a P^2 of normal type, and by the protoloph and metaloph of P^4 forming a V, with the two limbs of equal height. The specific characters distinguishing it from *H. affinis* in particular would be the fairly well-developed metaconule of P^2, the more progressive P^3, and the greater reduction of external and internal cingula on the cheek teeth. There is, perhaps, some balance of probability for Upper rather than Lower Bridger age. All available evidence points toward *H. affinis* as the ancestor of *Colonoceras*.

Metahyrachyus Troxell, 1922*a*

TYPE SPECIES:—*Metahyrachyus bicornutus* Troxell, 1922*a*.

DIAGNOSIS:—Protocone and metaconule of P^2 form a hybrid loph.

The most surprising generic character is that the protocone of P^2 is attached to the ectoloph by way of the enlarged metaconule, the protoconule being reduced (*M. troxelli*) or virtually lost (*M. bicornutus*). The protocone and metaconule form a single hybrid cross-crest, which, if an applicable and undeceptive name is called for, might be christened an "amphiloph." This is closely comparable with the evolutionary history of P^3 in the Eocene horses, as worked out by Granger (1908). When the lower dentition is discovered, there should be some associated peculiarity in the talonid of P_2. It might be molariform, or it might consist of a transverse ridge. The specimens are not sufficiently worn to offer any clue. The paracone and metacone of P^2 are connate as in *H. modestus*, not distinct as in *H. eximius*. P^3 and P^4 are more progressive than is usual in *Hyrachyus*. The internal cingula of the cheek teeth are weak. There may have been paired horns on the posterior parts of the nasals. The genus is closely comparable in size with *H. eximius*, but it would seem reasonable to derive it, not from *H. eximius*, but from its forebear, *H. modestus*. I agree with Troxell that the degree of difference from *Hyrachyus* amply justifies the creation of a new but related genus, fitting comfortably into the family Hyrachyidae.

Metahyrachyus bicornutus Troxell, 1922*a*

Figure 42, and Troxell, 1922*a*, Figures 4 and 5

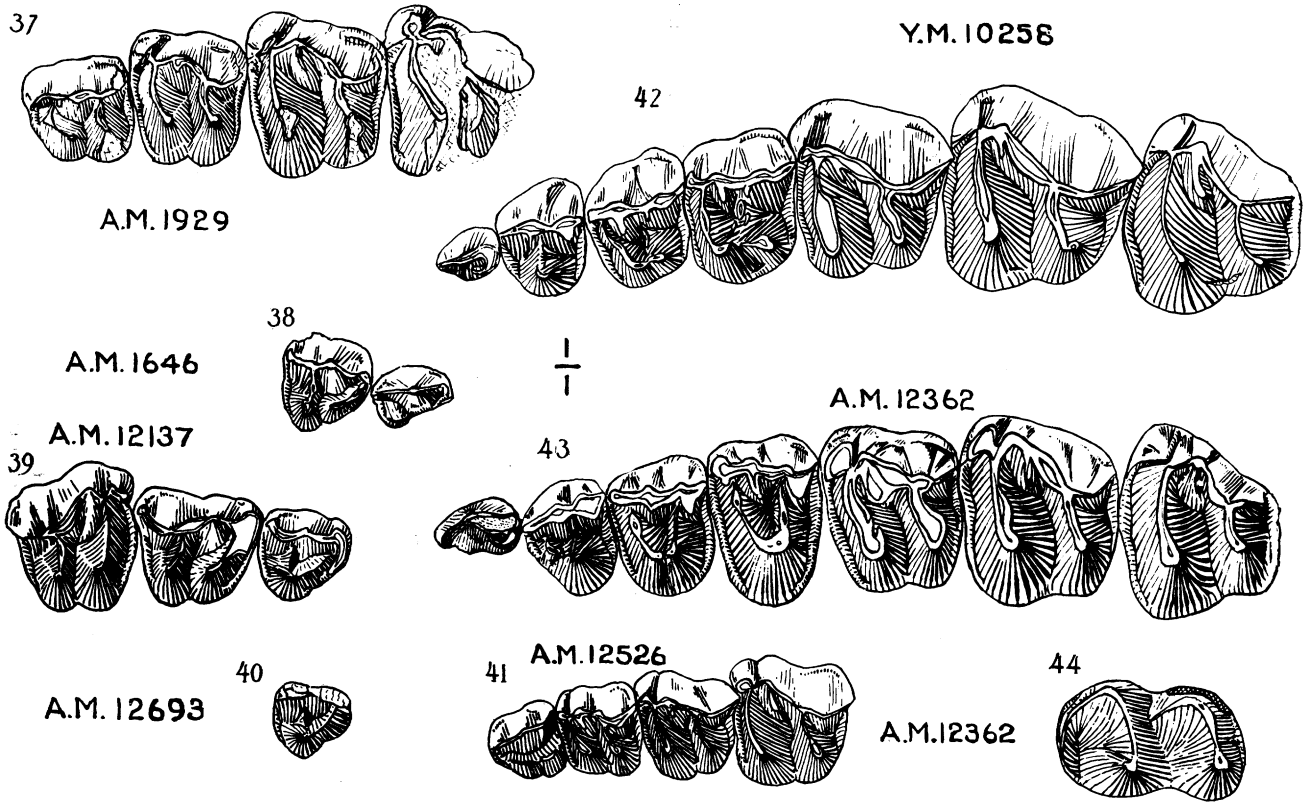
TYPE:—Yale Mus. No. 10258, a skull without the lower jaws.

HORIZON AND LOCALITY:—Lower Bridger, Millersville, Bridger Basin, Wyoming.

DIAGNOSIS:—P^2 without protoconule; hypocones budding off from protocones in P^{3-4}.

The type is Y. M. No. 10258, collected by R. E. Son in 1873 at Millersville, therefore Bridger B. The premolars show the most distinctive characters. In P^2, there is no transverse crest or element except the "amphiloph" (and, of course, the anterior and posterior cingula). P^3 and P^4 are notable in that hypocones are budding off from the protocones. There are slight "horn" rugosities on the posterior ends of the nasals. Millersville is no longer in existence, but, according to Dr. Granger (verbal communication), it was at the junction of Black's Fork and Smith's Fork. (It is incorrectly placed on Fig. 2). The following A. M. specimens from "Millersville" are from these levels: No. 11647, B_2; No. 11666, B_2; No. 12667, B_1. Nothing but Bridger B is exposed for miles. It seems reasonably certain, then, that Y. M. No. 10258 is from B, unless an entirely wrong locality was given. The only basis for suggesting this as a faint possibility is the progressiveness of this species, and the presence of another, and, in some respects, less advanced species, in the Upper Bridger. *M. bicornutus* is probably derived from the line of middle-sized hyrachyids, from a form not later in time than *H. modestus*, and, conceivably, from a still earlier form.

The detailed characters of the type, Y. M. No. 10258, follow: I^3, C^1, P^4, M^3. I^1 is small, showing no tendency to enlarge, and, therefore, no hint of the ancestral relationship to the true rhinoceroses suggested by Troxell. I^2 is smaller than I^3. In other words, the incisive region is characteristic of the Hyrachyidae, not of the Rhinocerotidae. The upper canine is of the hyrachyid type, without special features. P^1 is a simple cusp except for the antero-internal cingulum and the protoloph arising from the parametacone and swinging directly to the rear. P^2 is at once primitive and highly aberrant. The parametacone is only incipiently separated by an external groove into a large paracone and a smaller metacone. The single, strong cross-crest, the "amphiloph," is composed of protocone and metaconule, and runs from the inner side of the tooth to the posterior part of the paracone. Its position is much more analogous to that of a metaloph than of a protoloph. Minor ridges descend toward each other from the posterior sides of the metaconule and protocone, respectively. Anterior and posterior cingula are present, but no trace of external or internal cingula. The paracones and metacones of P^3 and P^4 are separated by unusually deep grooves, both externally and internally. The external attachment of the protoloph of P^3 is high and unusually far forward, between the paracone and parastyle. The hypocone is slightly elongated antero-posteriorly and is as high as the protocone, from which it has budded off. It is demarked from the protocone, medially, by a groove, and


37
A.M. 1929
Y.M. 10256
42
38
A.M. 1646
1/1
A.M. 12362
A.M. 12137
39
43
A.M. 12526
41
44
40
A.M. 12693
A.M. 12362

Figs. 37–44

buccally, by another groove, on P^3 right, but not on P^3 left. The low metaconule abuts against the postero-external part of the protocone, so that the median valley is completely dammed, with the lowest divide to the rear. P^3 has anterior and posterior, but no internal, cingula. The protoloph of P^4 is quite prominent, and attached well up on the anterior slope of the paracone, as in hyrachyid molars in general. The hypocone of P^4 is lower than the protocone, and abuts against its posterior flank. Although relatively lower than in P^3, it is larger in area, and more separated from the protocone. It is rounded posteriorly, the pointed anterior end overlapping the protocone. The metaconule appears to be fragmented into several cuspules, the largest of which occupies the normal position of a low premolar metaconule. It is attached to the anterior slope of the metacone, but fails to reach the protocone internally, so that the median valley is partially open to the rear. The internal cingula are represented by shelves across the median valleys of the fourth upper premolars. The molars have the typical hyrachyid pattern. Their parastyles are of the same relative size as in the small and medium-sized species of *Hyrachyus*. The posterior buttress of M^3 is rather more prominent than in some species of *Hyrachyus*, and rather less prominent than in others. It shows no evidence of any tendency toward reduction. Traces of an external cingulum are present on the metacones of P^3-M^2 right and P^3 and M^1 left, but are absent on P^2, P^4 and M^2 left. The internal cingulum of M^1 is represented by a shelf in the middle of the valley (almost absent in M^1 left). In M^2, it is apparently represented by a cuspule on the posterior slope of the protocone. M^3 has a well-defined internal cingulum across the valley. Full measurements are included in the table.

The nasal rugosities are not sharply defined, but certainly suggest the bases for some kind of horn. The premaxillaries are broadly in contact with the nasals. The posterior opening of the left infraorbital canal is double. The spheno-palatine and posterior palatine foramina are visible on both sides, and subequal in size.

The most aberrant character is the "amphiloph" of P^2, rather than the nasal rugosities. The well developed hypocones and the high outer attachments of the protolophs of P^3 and P^4 are definitely progressive features. All these features, as well as some others, mark a line of evolution, distinct from the main stem of hyrachyid development. As this species is more primitive in some respects and more advanced in others than *M. troxelli*, it seems unlikely that either form is directly ancestral

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Fig. 37. *Hyrachyus ? douglassi*, A. M. No. 1929 (so-called *Helaletes guyotii*), Uinta B, dP^{2-4}, M^1, left, ×1.

Fig. 38. *Hyrachyus eximius*, A. M. No. 1646, Upper Bridger, dP^{1-2} right, ×1.

Fig. 39. *Hyrachyus eximius*, A. M. No. 12137, Bridger C, dP^{2-4} right, ×1.

Fig. 40. *Hyrachyus affinis*, A. M. No. 12693, Lower Bridger, dP^2 right, ×1.

Fig. 41. *Hyrachyus affinis*, Y. M. No. 12526, Bridger B, dP^{2-4} left, M^1, ×1.

Fig. 42. *Metahyrachyus bicornutus*, type, Y. M. No. 10258, Bridger B, P^1-M^3 left, ×1.

Fig. 43. *Metahyrachyus troxelli*, type, A. M. No. 12362, Bridger C, P^1-M^3 left, ×1.

Fig. 44. *Metahyrachyus troxelli*, type, A. M. No. 12362, Bridger C, M_3 right, ×1

to the other. Neither *Colonoceras* nor either branch of *Metahyrachyus* can be ancestral to any known later form, including, of course, any true rhinoceroses, such as the diceratheres (Wood, 1927*b*). The six or seven independent acquisitions of paired horns in the Rhinocerotoidea have been listed elsewhere (Wood, 1929*a*).

A. M. No. 1611, collected by the expedition of 1893 from the Bridger, including various upper teeth, and P. U. No. 11201, consisting of M^1 and M^3 right, may belong in this genus. The specimens are too fragmentary for certain determination.

Metahyrachyus troxelli, new species

Figures 43 and 44

TYPE:—A. M. No. 12362, both maxillae with P^1-M^3, and M_3 right.

HORIZON AND LOCALITY:—Bridger C_3, Henry's Fork, Bridger Basin, Wyoming.

DIAGNOSIS:—Protoconule of P^2 present; metalophs of P^{3-4} well developed and only incipiently separated from protolophs.

The type was collected by Miller, July 21, 1904, opposite the mouth of Burnt Fork, Henry's Fork, "middle level," Bridger C_3. The specific name is given in recognition of Professor Troxell's work on *Hyrachyus* and its horned relatives. The general hyrachyid affinities of this species are unmistakable. In spite of definite differences, especially in P^{3-4}, the closest resemblance is with *Metahyrachyus bicornutus*, in the amphiloph of P^2, in size (see tables of measurements) and general character. As the nasal region is not preserved, no information is available as to the presence or absence of nasal rugosities.

All measurements compare strikingly with the type of *M. bicornutus*. The cristae of P^3-M^3 are fairly prominent. The cheek teeth are almost completely devoid of any trace of internal cingula. P^2-M^3 bear traces of external cingula on the metacones, which become fairly prominent on M^{1-2}. P^1 consists mainly of the undivided parametacone. An anterior ridge, which may fairly be homologized with the parastyle, swings around internally, delimiting a small basin. The single accessory loph, which has the character of a metaloph, turns posteriorly and merges with the posterior cingulum, enclosing a small basin, which would seem to be a postfossette. P^2 is similar in principle to that of *M. bicornutus*, but is less aberrant and shows the mode of evolution from the primitive type. The protocone is high, and connects with the metaconule to form an amphiloph as the main transverse element. The outer attachment of the amphiloph to the ectoloph, however, is definitely lower than in *M. bicornutus*, so that the loph descends buccally from the protocone. Another more primitive feature is the retention of the protoconule, in its normal position, but much lower than the protocone, or, even, than

the metaconule, and sharply defined from the protocone. (The protoconule is entirely absent in *M. bicornutus.*) Anterior and posterior cingula are present, but there is no internal cingulum. This tooth strongly suggests the following mode of evolution for *M. bicornutus:* the protocone lost its connection with the protoconule, became firmly connected, by way of the metaconule, with the ectoloph, and the protoconule finally disappeared entirely. The possible concomitant changes in the talonid of P_2 have already been suggested. P^3 and P^4 of *M. troxelli* are somewhat more progressive than in *M. bicornutus,* but along a different line, that is, instead of the development of the hypocone as a partly independent cusp budding off from the protoloph, the metaloph is developed as a whole, without sharp differentiation into cusps or separation from the protoloph, so as completely to enclose the median valley. The cross lophs of P^3 are subequal, converging, and incipiently separated. The protoloph is of normal type, its external connection with the ectoloph being of the normal hyrachyid type, considerably lower than in *M. bicornutus.* The protoloph is demarked from the metaloph by external and internal grooves; in the unworn tooth, there is a slight notch between the protocone and the hypocone. However, the median valley is completely enclosed, forming a medifossette, with the lowest point in the divide between the ectoloph and the protoloph. The metaloph is a unified ridge, with only a shallow groove, posteriorly, marking the division between the hypocone and the metaconule. The outer attachment of the metaloph is high up on the anterior flank of the metacone. Altogether, the cross lophs of P^3 are in almost the same stage of development as in *Subhyracodon trigonodus.* It will be observed that this mode of premolar metamorphosis (Wood, 1927*b*, p. 238, 3*b*) is opposed to that pursued by *M. bicornutus,* that is, the metaconule unites with the hypocone to form an enclosed basin before the latter has separated from the protocone. P^4 represents a modification in degree of the normal hyrachyid pattern, based on a considerable enlargement of the metaconule, and would represent the stage through which P^3 had presumably passed. The lophs are triangular in shape, instead of quadrilateral as in *M. bicornutus.* The protoloph of P^4 is of the normal type, with a low external attachment to the ectoloph, then swinging around to the rear, enclosing the metaconule. There is virtually no suggestion of demarcation of the hypocone. The metaconule is, as usual, a transverse blade, but is considerably higher than usual in *Hyrachyus,* and is attached well up on the ectoloph and protoloph, so that it is lowest in the middle. The median valley is completely dammed. There are two

outlets over the divides of nearly equal height, anteriorly, between the ectoloph and the protoloph, and posteriorly, the somewhat higher outlet over the middle of the metaconule. The upper molars resemble *M. bicornutus* closely, except that they are completely devoid of internal cingula. M_3 shows the usual hyrachyid pattern, with no trace of the hypoconulid. The posterior cingulum rises to a peak, in the center of the tooth, as is frequently the case. The tooth measures about 24×15 mm.

It seems almost certain that neither of the two known species of *Metahyrachyus* is ancestral to the other, but that they represent divergent lines of specialization. P^2 of *M. troxelli* shows the ancestral condition of *M. bicornutus*. The original stage in this line of development should show about the condition of the cross lophs of P^2 in *Protapirus simplex*—not, of course, implying anything but parallelism. P^3 and P^4 are on divergent lines of specialization in the two species; none of these teeth would be plausible morphological ancestors for the corresponding teeth in the other species. There seems, however, no reason to doubt their relationship. Finally, *M. bicornutus*, the more progressive species, is apparently earlier in time.

Ephyrachyus, new genus

TYPE SPECIES:—*Hyrachyus implicatus* Cope, as represented by A. M. No. 5078.

DIAGNOSIS:—More progressive than *Hyrachyus*, suggesting later rhinoceroses; upper cheek teeth with paracones and metacones more fully merged to form ectolophs; metaconules of P^{3-4} very high for a hyrachyid.

The genus is based upon *Hyrachyus implicatus* Cope, as represented by A. M. No. 5078. The genotype is given in this form to fix the status of the genus, in case the specific name *implicatus* should be held to be unavailable. This genus of small hyrachyids is marked by the progressive external surfaces of the ectolophs of the cheek teeth, representing an appreciable advance from the sub-rhinocerotid stage represented by *Hyrachyus* toward the rhinocerotid grade, in that the paracone and metacone are nearly merged into the general external slope of the ectoloph, instead of standing out as if modeled in bas-relief, as in *Hyrachyus*. The paracone and metacone of P^2 are as separate as in P^3 and P^4. The anterior cingulum of P^2 is unusually small; the posterior cingulum is larger than usual and swings well around onto the median surface. The outer attachment of the protoloph of P^2, although low, is rather higher than in *Hyrachyus*. The metalophs (metaconules only) of P^{3-4} are definitely higher and more progressive than in *Hyrachyus*. The metaconule of P^4, in addition to its normal attachment to the anterior end of the metacone, is also fused with the crista (internal slope of the para-

cone), thereby cutting off a very small basin from the medifossette. This is a morphological stage to be expected in the ancestor of *Caenolophus obliquus* Matthew and Granger of the Shara Murun, but is much more probably parallelism than an actual ancestral stage. The parastyles of M^{1-3}, although independent as compared with the true rhinoceroses, seem rather less emphasized than in other hyrachyids. Beyond anything that can be stated in words, there is a definitely progressive "feel" to the teeth, as opposed to the almost static, early Eocene character of *Hyrachyus* (from some early member of which *Ephyrachyus* is probably derived). The generic name suggests this progressive character, the iota being omitted before an aspirated vowel. There are two species: *E. implicatus* and *E. cristalophus.*

Ephyrachyus implicatus (Cope), 1873*a*

Figures 45 and 46

COPE, 1884, Pl. LVIII, Figs. 6, 6*a*, and 7.

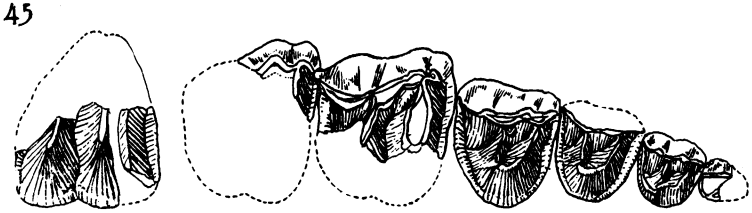
TAXONOMY:—*Hyrachyus implicatus* Cope, 1873*a* (republished 1873*c*).
Hyrachyus implicatus Cope, 1884.
Hyrachyus agrarius Leidy. Trouessart, 1904–1905.
Hyrachyus implicatus Cope. Matthew, 1909.
Hyrachyus, not *implicatus* Cope. Troxell, 1922*b*.

LECTOHOLOTYPE:—A. M. No. 5078, a partial skull and lower jaws.

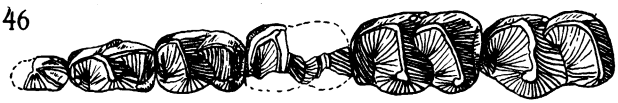
HORIZON AND LOCALITY:—Washakie Formation, near South Bitter Creek, Washakie Basin, Wyoming.

DIAGNOSIS:—P^2 subquadrate, with protoloph making sharp elbow. and metaconule a high, transverse blade.

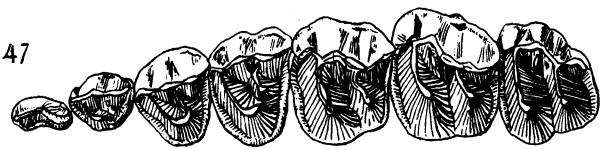
The determination of the lectoholotype of *Hyrachyus implicatus* Cope presents certain difficulties. Cope described the species (1873*a*) "represented, first, by both maxillary bones with most of the molars complete, from Cottonwood Creek, Wyoming [now A. M. No. 5072]; then by the side of the face with molars of both jaws complete, with symphysis and portions of all the incisors, from South Bitter Creek" [now A. M. No. 5078]. In revising the genus, in 1884, Cope referred his first type, A. M. No. 5072, to *H. agrarius* [=*H. modestus*], specifically selecting his second type, A. M. No. 5078, as the lectoholotype. Troxell, 1922*b*, states: "It is the opinion of the writer that the species must stand on the merits of its first type, and that, in order to make the second specimen a valid type, it must be renamed." I submitted the question, unofficially, to Dr. C. W. Stiles, and he answered (letter dated Feb. 8, 1927), on the basis of the data in my letter, "A. The expression 'first . . . then' sounds rather ambiguous to me as a definite type designation,



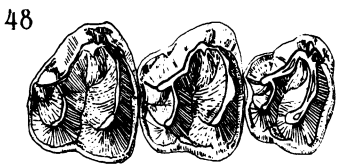
A.M. 5078



A.M. 5078



A.M. 12359



P.M. 10095

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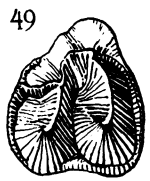

Fig. 45. *Ephyrachyus implicatus*, lectoholotype, A. M. No. 5078, Washakie. P^1-M^3 right, ×1.

Fig. 46. *Ephyrachyus implicatus*, lectoholotype, A. M. No. 5078, Washakie, P_1-M_3 right, ×1.

Fig. 47. *Ephyrachyus cristalophus*, type, Bridger C, A. M. No. 12359, P^1-M^3 left, ×1.

Fig. 48. *Chasmotheroides intermedius*, type (*"Hyrachyus" intermedius*), Bridger C?, P. M. No. 10095, M^1-^{3} right, ×1.

Fig. 49. *Chasmotherium* cf. *cartieri* (Paratype of *"Hyrachius intermedius* Filhol"), Argenton, France, École des Mines, M^3 right, ×1.

and I would personally be inclined to follow B. Cope, 1884, as the reviser of the species." It might also be argued that Cope, 1884, is the best judge as to whether Cope, in 1873*a*, meant "first . . . then" to fix the first specimen as the holotype and the second as the paratype, or whether he was describing them as cotypes. In this paper, Cope, 1884, will be considered to have fixed A. M. No. 5078 as the lectoholotype.

The lectoholotype, A. M. No. 5078, was collected by Cope, in 1872, "near South Bitter Creek, Washakie Basin"—that is, in the northwest part of the Washakie formation, according to his printed description. This might be either Upper or Lower Washakie, that is, Upper Bridger or Lower Uinta, with a definite decision possible only through an exhaustive microscopic study of the matrix in comparison with the lithology of the various levels in the Washakie. However, the exposures of the Washakie nearest Bitter Creek are all Lower Washakie; and this hint is strengthened by the presence of a related species, *E. cristalophus*, in the Upper Bridger. On the other hand, Cope's manuscript label, with the specimen, gives Mamm. Buttes (=Mammoth Buttes=Haystack Mountain). A specimen found well above the base of Haystack Mountain would be Upper Washakie; one found near the base, or a short distance away, would probably be Lower Washakie. It would seem less likely that a specimen found well up the slopes of Haystack Mountain should be called "near South Bitter Creek" than that one found at the base should be called both "near South Bitter Creek" and "Mamm. Buttes." There seems, then, a balance of probability in favor of regarding the specimen, provisionally, as from the Lower Washakie = Upper Bridger.

$I\frac{?}{3}$, $C\frac{?}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. P^{2-4} have high metalophs, composed of the metaconules only, barely separated from the protolophs by notches. The median valleys are partially open to the rear, except in P^4. P_3 and, especially, P_4 have progressive talonids, in association with the progressive upper teeth (Fig. 45). There can be no possible question as to the association of the lower and upper jaw, as the symphyseal region of the lower jaw is attached to the upper jaw by the matrix and fits onto the separate portion of the lower jaw. The stumps of I_1-C_1 right and I_1 left are present. The incisors are subequal in size, but increase slightly in size from front to rear. The canine is considerably larger than I_3, but not as much so as in *Hyrachyus*. Except for this, no definitely rhinocerotine specializations appear in the front teeth.

P^1 is broken and badly worn. It evidently had been in use much longer than the other premolars, suggesting the non-replacement which is frequently observed for this tooth. P^2 is subquadrate, and has a very distinctive pattern. The protoloph has a moderately low attachment to the ectoloph, runs inward and a little to the rear as a ridge of uniform height, bends about eighty degrees to the rear, and, opposite the metaconule, descends sharply toward the crown level, and continues internally and posteriorly as a well-developed cingulum. The metaconule is a high transverse blade,

very narrow from front to back. It reaches only to the bottom of the slope of the protoloph, so that the median valley is almost completely open to the rear, around the inner end of the metaconule. The paracone and metacone are more distinct from each other than in P^2 of any member of *Hyrachyus* or *Metahyrachyus*. There is no external cingulum. P^3 and P^4 are still more progressive, along the same general lines of specialization. The protolophs swing around to the rear, more sharply in P^4 than in P^3, until opposite the ends of the metaconules, which are higher and longer than in P^2. The protolophs are separated from the metaconules by a notch, only, so that the median valleys are enclosed medifossettes. This notch is well marked in P^3, but nearly obliterated in P^4. There are well-developed anterior and posterior cingula. The internal cingula of P^{2-4} are suggested in outline, though not present in relief. The metaconule of P^4, in addition to its normal attachment to the front of the metacone, is also fused with the crista, enclosing a small basin. The molars, at the present time, are badly smashed, but, judging from Cope's figure (1884), they seem to have had a slightly progressive version of the hyrachyid pattern. Such parts as are still preserved agree with this. There is no external cingulum on the metacone of M^1. The roots of the lower incisors and canines are of the primitive type, that is, C_1 is the largest, not I_2 as in the true rhinoceroses. P_1 is indicated by a portion of the alveolus. P_2 is small and primitive, the talonid consisting of a low ridge, the hypoconid, descending from the outer side of the rear of the protoconid. A ridge indicating the site of the metaconid descends the inner slope of the protoconid and swings around to the rear, as the postero-internal cingulum, to join the hypoconid and enclose a shallow basin. The front half of the tooth is broken off. P_3 is rather progressive. The trigonid is a well-developed crescent, consisting of protoconid, metaconid, and a low but rather distinct paraconid, which is constricted off from the rest of the crescent to an unusual extent. The trigonid basin is well developed. The hypoconid, although merely an antero-posterior blade, is well developed, with a postero-internal cingulum running to the metaconid. P_4 is more progressive (Fig. 46), with a slightly curved hypoconid, surrounded internally and to the rear by a cingulum rising to a cuspule opposite the posterior end of the hypoconid, which may fairly be called an entoconid. A small twin cusp is budded off from the posterior end of the hypoconid. The pattern of the molars is not distinctive, but the anterior limbs of the talonid crescents seem rather better developed than in other hyrachyids, and hence more rhinocerotine. M_3 has no hypoconulid. An external cingulum is present between the trigonids and talonids of P_{3-4} and is represented by small cuspules in M_2 (double) and M_3. P_{3-4} have internal cingula on the talonids, continuous with the posterior cingula. Their metaconids are devoid of internal cingula, as are M_{2-3}, in their entirety. M_1 had an anterior cingulum; the rest of the tooth is too broken to give any information.

A. M. No. 12672, an axis and lower jaw, collected by W. J. Sinclair, July 6, 1905, from Bridger D_1, Lone Tree, Bridger Basin, Wyoming, may belong in or near this species. P_1 is missing, P_{2-3} have distinct, low entoconids. The entoconid is incipient in P_4 (Fig. 13).

E. implicatus (A. M. No. 5078) could have been derived from a form very close to *E. cristalophus*.

Hyrachyus affinis (*"Hyrachyus implicatus"*), A. M. No. 5072

Figures 35 and 36

TAXONOMY of specimen:—

Hyrachyus implicatus Cope, 1873*a*.
Hyrachyus agrarius Leidy. Cope, 1884.
Hyrachyus affinis implicatus Cope. Troxell, 1922*b*.

Although it does not belong here systematically, this is the most convenient place to discuss and describe Cope's type No. 1, A. M. No. 5072, which has not been previously figured. Its claim to be regarded as the lectoholotype of *H. implicatus* has been discussed above. The essential references to the literature are the same as for *Ephyrachyus implicatus*. This specimen was collected by Cope, July 28, 1872, near Cottonwood Creek, Bridger Basin, Wyoming. This is probably Bridger B, but Bridger C is exposed along the upper course of Cottonwood Creek, so that the level is not certainly determinable.

It consists of portions of both maxillae, containing respectively, P^3-M^3 right and P^4-M^3 left, all damaged. It is intermediate in size between *H. modestus* and *H. affinis*, but is closer to the latter, to which it has the strongest general resemblances. There is nothing about P^4-M^3 left which would not fit comfortably into this species (Fig. 35); the same thing is true about P^3 right and M^{1-3}; P^4 right, however, is aberrant in several respects (Fig. 36). Were it not for the fact that the wear is exactly equivalent on the corresponding teeth of the two sides, there might be room for speculation as to whether the right maxilla might not belong to a different and otherwise unknown species. As it is, it seems best to interpret this as simply an abnormal P^4 right, in which the hypocone is well developed, attached to both metaconule and protocone, and enclosing with them a small pit, distinct from the main medifossette. P^3 right has a low metaloph, composed of the metaconule only, not completely damming the median valley, but allowing it to escape to the rear, over a low divide between the metaconule and the protocone. There is no trace of a hypocone. The outer attachment of the protoloph is low. The cingulum is widely interrupted, internally. The same description would apply to the inner part of P^4 left, which is all that is preserved, except that the external attachment of the protoloph is somewhat higher, and that the posterior slope of the protocone is a definite ridge, suggesting the future site of the hypocone. The premolar metaconules are rather higher than in typical specimens of *H. affinis*, but not as high as in *Colonoceras* or *Ephyrachyus*. The hypocone of P^4 right is a conical cusp, attached, in front, both to the recurved hook of the protoloph and to the metaconule. The metaconule, in turn, laps well up on the inner flank of the recurved protoloph. This leaves a pit (to which it does not seem necessary to give a special name), cut off from the median valley, since it is surrounded by the protoloph, hypocone, and metaconule. Similar but less aberrant conditions are observed on P^4 left of *Desmatotherium guyotii* and P^4 right of *Trigonias osborni secundus* Gregory and Cook. Such teeth, when greatly worn, would give the aberrant pattern sometimes seen in rhinoceroses, with the hypocone forming a bulbous posterior swelling of the metaloph. The molars have sharp cristae. M^1 has a strong external cingulum on the metacone. The internal cingulum of M^2 is represented by a definite

shelf across the median valley. M^3 has a large posterior buttress. Except for P^4 right, A. M. No. 5072 would fit without any difficulty into *H. affinis*. Even considering the peculiar features of this tooth, the same disposition is warranted, on the basis of the evidence now known.

Ephyrachyus cristalophus, new species

Figure 47

TYPE:—A. M. No. 12359, the palate and teeth.

HORIZON AND LOCALITY:—Bridger C_3, Twin Buttes, Bridger Basin, Wyoming.

DIAGNOSIS:—P^2 very primitive, protoloph nearly longitudinal, metaconule virtually absent; crista and metaconule of P^4 fused, enclosing a small pit.

The holotype of this species is A. M. No. 12359, collected by Granger, July 15, 1904, from the red stratum, Bridger C_3, at Twin Buttes, Bridger Basin, Wyoming. The specific name is given to suggest the junction of the crista with the metaloph of P^4 and to recall the similar condition in *Caenolophus obliquus* of Mongolia. I^3, C^1, P^4, M^3. The most striking characters are the long, primitive, triangular P^2, narrow transversely and almost devoid of metaconule, the progressive P^3, and the progressive and aberrant P^4, with the crista joined to the metaconule, enclosing a small pit, and the inner end of the metaconule bifurcating, with the posterior section turned posteriorly, suggesting *Caenolophus obliquus*. This form seems to be near, but not exactly on, the ancestral line of *E. implicatus*.

The specimen consists of the palate of a young individual, with P^1-M^3 left, and P^1 and M^{1-3} right, with the left incisors and canine indicated by the alveoli, and with the third upper molars just cutting the gums. The canine is larger than any of the incisors. The almost unworn P^1 suggests either replacement or else very late eruption of a non-replacing tooth. It consists of a single cusp, elongated anteroposteriorly, with an internal cingulum indicating the future site of the protoloph. It is essentially comparable with the condition in *Eohippus* and *Homogalax*, and is far more primitive than in any other hyrachyid. P^2 is triangular, with the longitudinal axis markedly longer than the transverse, and the protoloph running more posteriorly than medially. These unusual features of P^2 are its most striking characteristics, and are reminiscent of *Homogalax*. It is more primitive in these respects than any other hyrachyid, although the ectoloph is more progressive than in the otherwise more primitive forms (e.g., *H. modestus*). The protoloph is fairly well developed, but swings to the rear and forms a forty-five-degree angle with the ectoloph, giving proportions more typical of a hyrachyid first upper premolar than of a second. The outer attachment of the protoloph to the ectoloph is fairly low, but, for P^2 of a hyrachyid, it is definitely high. The metaconule is virtually unrepresented, the only trace consisting of two small nubbins on the inner slope of the metacone, which do not touch the protoloph. The anterior cingulum is unusually small. The posterior cingulum is unusually large and abuts against the rear of the protoloph. Except for the inner end of the posterior cingulum, there is no internal cingulum. There is a small external cingulum between the paracone and the metacone, and on the metacone. It is to be

noted that P^2 is much more primitive than in *E. implicatus*, and is definitely more primitive than in any species of *Hyrachyus*. P^3 is progressive, bearing a close resemblance to the corresponding tooth of *E. implicatus*. The protoloph is attached well up on the ectoloph, and curves around to the rear, until it is shaped like a fish-hook, with the barb directed externally, and with no demarcation between protocone and hypocone. It encloses, and is almost continuous with, the metaconule, which is high and attached externally to the anterior face of the metacone (the primitive condition) and slightly bowed to the rear. There is a slight gap between, or rather, an incomplete fusion of, the metaconule and the protoloph, so that the median valley escapes to the rear, over a divide; a moderate amount of wear would convert the valley into a medifossette, making the metaconule entirely confluent with the protoloph. P^3 and P^4 have unusually strong anterior and posterior cingula, not fully confluent internally, although a connecting internal cingulum is outlined nearly across the gap; their metacones carry external cingula. The protoloph of P^4 has a high external attachment to the ectoloph, as in P^3, but is less recurved, so that the internal end is directed posteriorly. The metaconule is attached to the anterior face of the metacone, runs internally and slightly anteriorly until it meets and fuses with a sharp ridge, the crista, enclosing, with it, a small pit, and then turning, at an oblique angle, and running medially and posteriorly. The internal end of the metaconule is forked, one end pointing internally, the other to the rear. The median valley opens to the rear, between the protoloph and the metaconule. The molar parastyles and cusps are closer to the *Hyrachyus* pattern than to that of the later forms, but the metacones form smaller external ribs on the outer slopes of the ectolophs than in *Hyrachyus*, marking an advance toward the rhinocerotine grade of organization. M^1 is nearer M^2 in size than in *Hyrachyus*, suggesting the later forms in that respect. M^{1-3} have fairly prominent cristae. The molars have no internal cingula, but M^{1-2} have external cingula on their metacones. The posterior cingulum of M^3 is confluent with the posterior buttress. On the left side, the anterior opening of the infraorbital canal is over the front end of P^3.

The fusion of the crista and metaconule of P^4 in *Ephyrachyus implicatus* and *cristalophus* may explain the course of evolution of the peculiar metalophs of P^3 and P^4 of *Caenolophus obliquus* Matthew and Granger (1925*a*), in which the metalophs are connected externally with the paracone and have lost their universal primitive attachment to the metacones. It should be observed that Matthew and Granger (1925*a*) described four species: *Caenolophus promissus, C. obliquus, C. progressus,* and *C.* (?) *minimus*, without definitely selecting a genotype, but later (1925*b*) selected *C. promissus* as the genotype, in addition to describing *C. proficiens*. *C. obliquus*, at least, is in all probability generically distinct from the genotype, *C. promissus;* some of the other species, also, may later prove to require separation. No definite suggestion of ancestral relationship of *Ephyrachyus* to *C. obliquus* is intended; parallelism is a much more probable explanation.

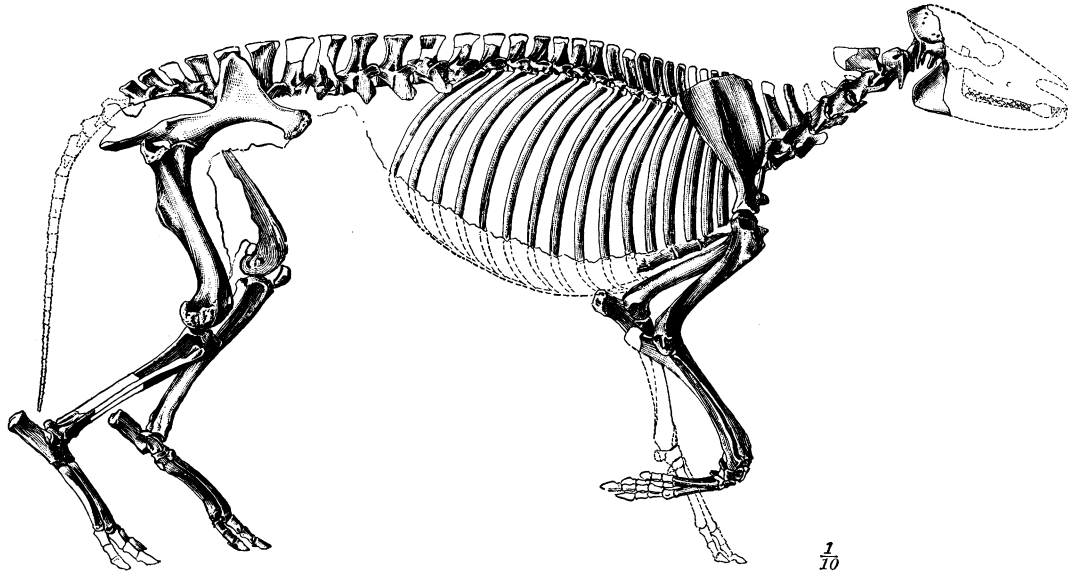

Fig. 50. *Hyrachyus eximius*, A. M. No. 5065, skeleton as originally mounted (from Osborn, 1898, Fig. 1).

STRATIGRAPHIC CORRELATION AND NOMENCLATURE

Eocene Nomenclature

The preparation of the phylogenetic chart (Fig. 1) raised the question as to what terminology to use for the various horizons. Uniformity and convenience suggest the desirability of introducing certain new names, for reasons explained below, as well as of determining the exact significance which should be attached to various names now in use.

The type locality of the "Wasatch" contains mammalian fossils of Lysite age only. Usage, however, has broadened the term Wasatch to be equivalent to "Lower Eocene" in the continental section, to which meaning it would be most convenient to confine it. The original "Wind River" included only beds of what are now often called Lost Cabin age; it was later stretched to include the present Lysite also. The discovery that the original Wasatch [=Knight] contains fossils of Lysite age should automatically restrict the term Wind River to the section above the Lysite, that is, to its original usage, in which sense it is exactly synonymous with "Lost Cabin." Wind River is a much older term, but as it is subject to varying interpretations, it may be desirable, for the present, to use both names, Wind River (=Lost Cabin), since Lost Cabin is not subject to misunderstanding. After the confusion is thoroughly straightened out, however, it may be safe to use the older term alone. See Granger (1914) for Lower Eocene correlation. It should be observed that the Gray Bull Formation of Granger (1914) essentially preoccupies Hewett and Lupton's Greybull member of the Cloverly Formation (1917). Hewett and Lupton recognize this essential preoccupation in the same paper in which they propose their term. In spite of this fact, Knappen and Moulton (1930) follow the unfortunate usage of Hewett and Lupton.

By the present somewhat unwieldy terminology, Bridger A+B, Bridger C+D, Uinta A+B, and Uinta C are each, essentially, members, each containing distinctive fossil mammals. They deserve equal rank with such commonly recognized units as the Lysite, Lost Cabin (=Wind River, sensu strictu) and, almost, the Chadron, but are not, at present, named or fully treated as such. I accordingly propose the term **Black's Fork Member** for the lower half of the Bridger, A+B of Matthew (1909), the name being taken from Black's Fork of Green River, which flows past most of the best known exposures (Fig. 2). The most famous and typical locality is "Grizzly Buttes" on Smith's Fork, starting half a mile south of the town of Mountain View, and ending a mile and a half southwest of the town. I propose the name **Twin Buttes**

Member for the upper half of the Bridger, C+D of Matthew, the name being taken from Twin Buttes, west of the Green River and east of Henry's Fork Table. Bridger C and D are both exposed on the slopes of Twin Buttes (Fig. 2). Various other possible geographic names, perhaps intrinsically more desirable, are, unfortunately, preoccupied. The type locality would be Henry's Fork Table and Twin Buttes. I propose the name **Wagonhound Member** for the lower Uinta, A+B of Peterson, the name being taken from Wagonhound Canyon, which opens into the White River, Utah. Typical and fossiliferous exposures of A and B occur in and near this canyon. I propose the term **Myton Member** for the Upper Uinta, C of Peterson, the "true Uinta" of various authors, from the town of Myton, Utah. Typical exposures occur east, north, northwest of the town at the mouth of Lake Fork, and at other points in almost all directions from the town. The Lower and Upper Bridger, as well as the Lower and Upper Uinta, are rather distinct from each other geographically as well as faunistically, so that they fully deserve to rank as separate units. The Black's Fork occupies the northwestern part of the Bridger Basin, and the Twin Buttes is confined to the southeastern portion. The Wagonhound is exposed in the southern part of the Uinta Basin, the Myton being confined to the more northern portion.

There seems to be considerable lack of agreement in the literature as to whether the term "Uinta" is properly applicable to the quartzite which forms the core of the Uinta Mountains, or to the Tertiary sediments in the Uinta Basin. The facts appear to be as follows. Comstock, in January, 1875, in his chart (opposite page 103), lists the "Uinta Basin Beds" as "Upper Eocene," equivalent to the upper part of the Bridger. He refers to these beds at sufficient length to identify them on pages 126–127, although not by name. King and Emmons, November 15, 1875, sent twelve copies (fide Emmons, 1907) of Map II to prominent American geologists, in advance of the publication of the entire atlas (1878), on which the "Uinta" is listed as Upper Eocene, and appears in essentially its correct geographic location. Powell, about September, 1876, published the names "Uinta Sandstone" and "Uinta Group" for the quartzite forming the main mass of the Uinta Mountains, giving the name "Brown's Park" to the various sediments in the Uinta Basin above the Green River Formation. There is no question that Comstock, Peale (quoting Comstock), King and Emmons, and Powell, would take precedence in that order, except for doubts whether Comstock identified the beds with sufficient definiteness, or whether the King and Emmons map was validly published. There is no bar to the validity of Powell's name.

Comstock's discussion (pp. 126–127) seems sufficiently explicit to identify and fix the term "Uinta Basin Beds" used on his chart. That this is not reading a strained, ex post facto interpretation into his words, is shown by the fact that Peale, (1876) an exact contemporary, had no hesitancy in reaching the same interpretation of his meaning. Map II, by King and Emmons, although later than Comstock, would still take precedence over Powell, if it is a valid publication. There is no authoritative decision as to the number of copies required to constitute publication, particularly for works issued as far back as 1875. Twelve copies would hardly constitute publication at the present time, even if sent, as this appears to have been, to the leading authorities in the field concerned. On the other hand, contemporary opinion, on the whole, seems to have regarded it as a valid separate publication, rather than merely "authors' proofs," which of course, have no standing. "Map number II . . . has been issued as authors' proofs, dated Nov. 15th, 1875 . . . . . It is the first of the series issued, and will be noticed more fully when the other parts are issued." (Am. Journ. Sci., (3) XI, p. 161, Feb., 1876). "The atlas has all been engraved, printed, and prepared, and is ready to be issued as soon as the volumes can be printed" (report to the Chief of Engineers, from Clarence King, dated Aug. 29, 1876). "One of the maps of this atlas has already been noticed in this Journal in volume XI (page 161). The completed atlas has recently been issued." (Am. Journ. Sci., (3) XV, pp. 396–397, May, 1878). "A few copies of Mr. King's map have been distributed to different persons and institutions in advance of a geological report. . . . A large proportion of the names of the different groups of strata which are used in this report are, by the custom of priority in such cases, adopted from Mr. King's map, which is regarded as having been published in November, 1875 . . . . I therefore adopt Mr. King's name 'Uinta Group' instead of Professor Powell's name 'Brown's Park Group'." (White, 1878). Was this map actually considered as published in 1875? "A few copies" and "authors' proofs" suggest a negative answer. King's letter to the Chief of Engineers, however, and Emmons (1907) show that these were not proofs, but copies of the map itself, agreeing with White and the later Am. Jour. Sci. reference. The 1876 notice in the Am. Jour. Sci. does not regard the pre-issue as a publication; the later notice probably, and White, explicitly, regard it as actually published. On the other hand, Emmons himself, later (1907) considered that Map II was not really published, and, therefore, that Powell's use had priority, as do Berkey (1905), Weeks (1907) and Doug-

lass (1914). All of these authors, however, apparently failed to consider Comstock. If King and Emmons (1875) is ruled out, we should then have the unfortunate situation that the correct name for the Tertiary beds would be "Uinta Basin Beds" and for the quartzite "Uinta Quartzite," unless these names be regarded as sufficiently similar so that Powell's name was substantially preoccupied by Comstock's. Weeks (1907), although disagreeing with it, cites an unpublished decision in 1907, by the Committee on Geologic Formation Names of the U. S. Geological Survey, to retain the name Uinta for the Tertiary, on the basis of priority and usage.

To summarize, the name "Uinta" should be restricted to the Tertiary beds. The term should be credited to Comstock, as of January, 1875 (see appendix of revised report for original date of publication), as emended by King and Emmons. Even if Comstock's explicitness were attacked, King and Emmons, Map II, still precedes Powell, if it is regarded as published. Powell's use could be established only by proving that Comstock is too vague to understand, in spite of the fact that Peale, a contemporary, understood him perfectly, and, in addition, that Map II was not actually published, White to the contrary, or else by retaining both "Uinta Basin Beds" and "Uinta Quartzite" for formations in the same region. It is certainly clearer, and probably more proper, to consider Powell's name, "Uinta Quartzite," as a homonym to be discarded, since it is essentially preoccupied by the "Uinta Basin Beds" of Comstock and perhaps by the "Uinta" of King and Emmons. A similar case is the preoccupation of the "Wasatch Limestone" of King by Hayden's term. The use of such invalid terms should be discontinued as improper and possibly misleading. Certainly, less difficulty will be created by this course than if a name in use in the standard Eocene continental section had to be abandoned, since the quartzite, although covering a considerable area, is, essentially, of local significance.

Apparently, no substitute name has ever been proposed for the "Uinta Quartzite" of Powell, except that attempts have been made to correlate it with the Weber Quartzite of the Wasatch Mountains. This interpretation is now regarded as incorrect, but even if the correlation were correct, the quartzite deserves a local name of its own. I, therefore, propose the name **Emmons Peak Quartzite**, from the peak of that name, which is an appropriate term geographically and geologically, since it is a high peak carved in that formation, as well as sentimentally, since it bears the name of an original student of the formation.

Powell's "Brown's Park" originally included both the Uinta and the overlying Miocene beds. Irving (1896) was apparently the first

definitely to restrict the term Brown's Park to the beds above Uinta C, and this usage has usually been followed since, particularly in Peterson's monograph (1928), the most recent and most extensive treatment of this formation. The explicit restriction by Irving conformed to the previous implicit usage of King (1878), who restricted the Uinta to the post-Bridger, Eocene deposits. The use of Brown's Park, then, for the Miocene beds above and exclusive of the Myton (Uinta C) and the Eocene-Oligocene transition beds, is in conformity with the rules of priority, with usage, and with common sense.

Age of the "So-Called Bridger" of the Wind River Basin

Deposits of Bridger age are known in the Bridger and Washakie Basins of Wyoming, the Huerfano Basin in Colorado, and, possibly, in the Sage Creek area in Montana. The existence of a Bridger equivalent in the Wind River Basin of Wyoming has been suggested. Granger and Sinclair found evidence indicating continuous subaërial sedimentation in central Wyoming throughout the greater part of the Eocene, from the Lost Cabin Formation through the Uinta. Their section was based on exposures near Green Cove, Wagonbed Spring and Barrel Spring, along Beaver Divide, on the southern margin of the Wind River Basin (Fig. 3). Small but characteristic faunas of Lost Cabin and Uinta age were collected. The following excerpts summarize their evidence and interpretation as to the age of the intervening beds. "No break in sedimentation was detected in the Eocene series, yet a careful examination by a competent stratigrapher might bring it to light. The Bridger formation in the Bridger Basin has a maximum thickness of 1,800 feet, and the only beds in this section which might be assigned to that formation are the 200 or 250 feet of unfossiliferous strata between the Lower Eocene banded beds and the layers lying immediately below the unconformity, which are unquestionably Upper Eocene." (Granger, 1910, p. 239.) "About 375 feet of sandstone, shale and tuff lying between the red banded clays of the Wind River and the Uinta shales have been referred doubtfully by Granger to the Bridger. Although repeatedly examined during two seasons, no fossils have been found in these beds, the age determination depending entirely on stratigraphic relationships. So far as has been determined, this so-called Bridger is conformable with the underlying Wind River. There may be an erosional unconformity with the Uinta. . . . " (Sinclair and Granger, 1911, p. 95.) "In the Wind River Basin, sedimentation was continuous from the later Lower Eocene to the Lower Oligocene, with the exception of an interval of erosion at

the close of the Upper Eocene." (Sinclair and Granger, 1911, p. 85.) Since, as will be shown, there is doubt about the exact correlation of these beds, and since "so-called Bridger" is an unwieldy term, the geographical name **Green Cove Beds** is suggested provisionally, from the section at Green Cove, east of Hailey (Fig. 3).

An automobile reconnaissance party, consisting of Dr. Florence D. Wood, Mr. Albert E. Wood and myself, spent two days (July 10–11, 1928) at a part of Beaver Divide escarpment which had not been readily accessible to Granger and Sinclair, but has since been opened up by a new road, the Riverton-Rawlins cut-off. We found no fossils in the Green Cove, but just west of where this road starts to climb the steep escarpment of Beaver Divide (about 23 miles south-southeast of Riverton by road), we found, in the ravine of an intermittent stream, three exposures of the contact between the red-banded Lost Cabin and the overlying yellow-brown arkose, two of which offer clearcut evidence as to the character of the contact. All three are corresponding undercut bluffs of successive small meanders, in rough alignment with each other along a total extent of, perhaps, a hundred yards. This contact is definitely a disconformity. The alignment of the three exposures might suggest the possibility of a modern stream exposing the valley of a "fossil" stream which might once have been diverted suddenly into this course, rather than representing any appreciable time interval. However, as may be seen (Pl. XXIV), the contact is corrugated, so that this explanation seems improbable. High and low points in the unconformity are marked by the pick and hammer, respectively. The vertical difference between the highest and the lowest points is at least four feet in a horizontal distance of not more than eight feet. There is some cross-bedding immediately above the contact.

Another good exposure of the disconformity, of about the same vertical magnitude, occurs around the next bend to the north, perhaps a hundred feet down the present stream-bed, also on the right bank. An iron film along the contact marks the old surface. The horizontally stratified shale (locally gray) of the Lost Cabin is followed, immediately above, by a thin layer of white sandstone, of irregular thickness, and, in turn, by the locally cross-bedded, yellow-brown, arkosic Green Cove, which, at this point, dips about 25° to the east. The arkose contains several small, normal faults with throws of two to four inches, often filled with calcite. The dip of the Green Cove is about 2° toward the south as compared with the 1° 15′ dip obtained for the Lost Cabin by Sinclair and Granger, suggesting the possibility of slight tilting during the interval

represented by the disconformity, although the case would be more convincing if the figures were reversed, or if the discrepancy were larger.

Some confirmatory evidence as to the nature of the disconformity at the Riverton cut-off locality was obtained in a second visit, in 1931. An additional exposure of the disconformity was found in the same region, northeast of the other exposures, and out of alignment with them, decreasing the likelihood of contemporaneous channeling as the interpretation. Also, in the same region, the contact was seen in the distance, in two long stretches, and appeared to be a nonconformity. As is often the case, the character was more apparent at a distance than on closer approach.

In a preliminary study of a sample of the matrix of the soft chocolate shale of the Green Cove from this locality, Mr. Arthur D. Howard finds numerous volcanic shards scattered through the fine-grained clay, some partly devitrified. Their frequent sharp edges indicate the absence of reworking. As far as it goes, the presence of volcanic shards is evidence against Lost Cabin age, and tends to associate these shales with the tuffs, above, as well as with the middle or upper Eocene beds elsewhere, but is inconclusive as between Bridger and Uinta age (Johannsen, 1914, and Sinclair and Granger, 1911).

It is unsafe to guess at the length of time required for this erosion interval. It might have been developed in only a few months or years, like the channeling within the Lost Cabin, described and figured by Sinclair and Granger (1911, pp. 92–93, and Pl. VII). On the other hand, this interval may be equivalent to most or all of the Bridger, which formation may be entirely unrepresented in the Wind River Basin. This latter interpretation, as Granger pointed out, would explain the lack of sufficiently thick deposits to correspond with those in the Bridger Basin.

Berry (1925 and 1930) discusses the correlation of the "so-called Bridger" (=Green Cove) of the Wind River Basin, on the basis of a fairly extensive flora from Crow Heart Butte, Lenore and Tipperary (Fig. 3). He considers it approximately equivalent to the Green River, and that both are about equivalent to the Claiborne and Auversian. The earlier paper seems more confident of the exactness of this correlation than does the later paper. Exact correlation of the Green Cove with the Green River, or of the Green River with the Auversian, is difficult to reconcile with other available data. He also states: "Although Osborn, as already remarked, correlated the Wind River with the upper Wasatch of the Big Horn Basin and the lower Huerfano of Colorado, I believe all three are somewhat younger than the position usually assigned to them by vertebrate paleontologists."

Sears and Bradley (1924) have shown that the Green River interfingers with the upper part of the Wasatch, which would make it reasonable to regard the great mass of the Green River as about of Lost Cabin age. This approximate correlation is supported by Berry's description of a Lysite flora (1932). It is also a well-known and easily verifiable fact that the Green River underlies the Black's Fork (Lower Bridger), which would also agree with its being about equivalent to the Lost Cabin, or to the Lysite and Lost Cabin together. Unless vertebrate correlations are completely negligible, the Gray Bull is about equivalent to the Lower Ypresian, and the Chadron to the Sannoisian. On that basis, the Lysite should be about Upper Ypresian, the Lost Cabin about equivalent to the Lutetian, the Bridger approximately equivalent to the Auversian, and the Uinta to the Ludian. It is difficult to see how these correlations can be very seriously inaccurate. The Huerfano bridges any possible gap between the Lower Eocene and the Bridger, Huerfano B being equivalent to at least part of the Lower Bridger, and Huerfano A to the Lost Cabin, so that there is no room to intercalate the Green River as a separate time interval between the Lost Cabin and the Bridger. The Green Cove, then, might equal part or all of the Auversian, but the Green River[1] would have to be about of Lutetian age. Since the Green River interfingers with the upper part of the type Wasatch, which contains fossil mammals of Lysite age, it would seem that the Green Cove, which overlies the Lost Cabin, must be younger than the Lost Cabin, and, hence, than the Green River.

If Berry's view is correct, that the Green River is Auversian, and that the Upper Wasatch, Wind River and Huerfano A should be pushed up the column, the rest of the Wasatch, i.e., Gray Bull and Sand Coulee, would presumably have to be moved up also, leaving no North American continental formations to be correlated with the Ypresian (unless, perhaps, the Paleocene!). In view of the close resemblance between the mammals of the Sparnacian and the Gray Bull, these correlations are not likely to be accepted by vertebrate palaeontologists. If the most specialized and most rapidly evolving organisms permit the most exact correlation, the evidence for difference in age, from mammals and stratigraphy, should take precedence over that from plants indicating similarity in age. The most reasonable interpretation of the real resemblance between the Green River and Green Cove floras would seem to be that discrimination between the floras of two successive formations in the same geographic region may not always be possible, even though the mammalian faunas can be distinguished successfully. (The disagree-

[1]The Green River of the Uinta Basin may well extend into Bridger time.

ment in regard to the age of the Lance illustrates the same principle.) Indeed, it seems entirely reasonable that the Green Cove flora should resemble that of the Green River more than any other well-known flora—certainly than any other of the floras with which Berry compares it—since it occurs in the same geographic region and is of the same general age, while the others are widely removed, geographically.

To summarize, the presence of a basal disconformity or nonconformity and the lithology tend to push the Green Cove up toward the Upper Bridger or the Uinta, although without offering any satisfactory evidence as to whether the time interval is long or very short; the resemblance in flora tends to pull it down toward the Green River, and, hence, toward the Lost Cabin. Its thinness in comparison with the standard Bridger section raises strong doubts as to its being equivalent to the whole Bridger. At present, it does not seem possible to settle its age more definitely than as rather probably equivalent to some part of the Bridger or Lower Uinta.

Stratigraphy of the Sage Creek Beds of Montana

Douglass discovered two small exposures in Beaverhead County, Montana, north of Sage Creek, in 1897, which he considered, tentatively, as of Eocene age, from the presence of four recognizable fossil mammals. Apparently he revisited this region twice, the last time in 1905. Until 1931, no other vertebrate palaeontologist is known to have worked these beds. Douglass (1902, 1903 and 1909) described the locality as about seven miles northeast (actually about north) of Lima, north of Sage Creek where it flows "eastward" (actually westward) toward Red Rock Creek. Such a position would appear to be in the "Big Bend" of Sage Creek, or immediately north of it. This general position is confirmed by Douglass' map (1902). He describes the fossiliferous beds where "*Heptodon*" and "*Hyrachyus*" were found as a hill composed of sands and clays, distinctly banded and stratified, with calcified logs and twigs, geodes, and vertical tubes lined with calcite and quartz. The other two fossils were found about half a mile away.

Douglass found the following fossils: the damaged front of the skull of a *Hyrachyus*, with the lower jaws and atlas, C. M. No. 784, which he named *H. priscus*, and which is emended, above, to *Hyrachyus douglassi* (Figs. 23–24, and Douglass, 1903, Fig. 2); a left M^3, C. M. No. 718, which Douglass (1903, Fig. 3) correctly compared to *Hyrachyus intermedius* (Fig. 48), which should, therefore, be called *Chasmotheroides* cf. *intermedius;* C. M. No. 717, a left maxillary, with P^4-M^3 (Douglass,

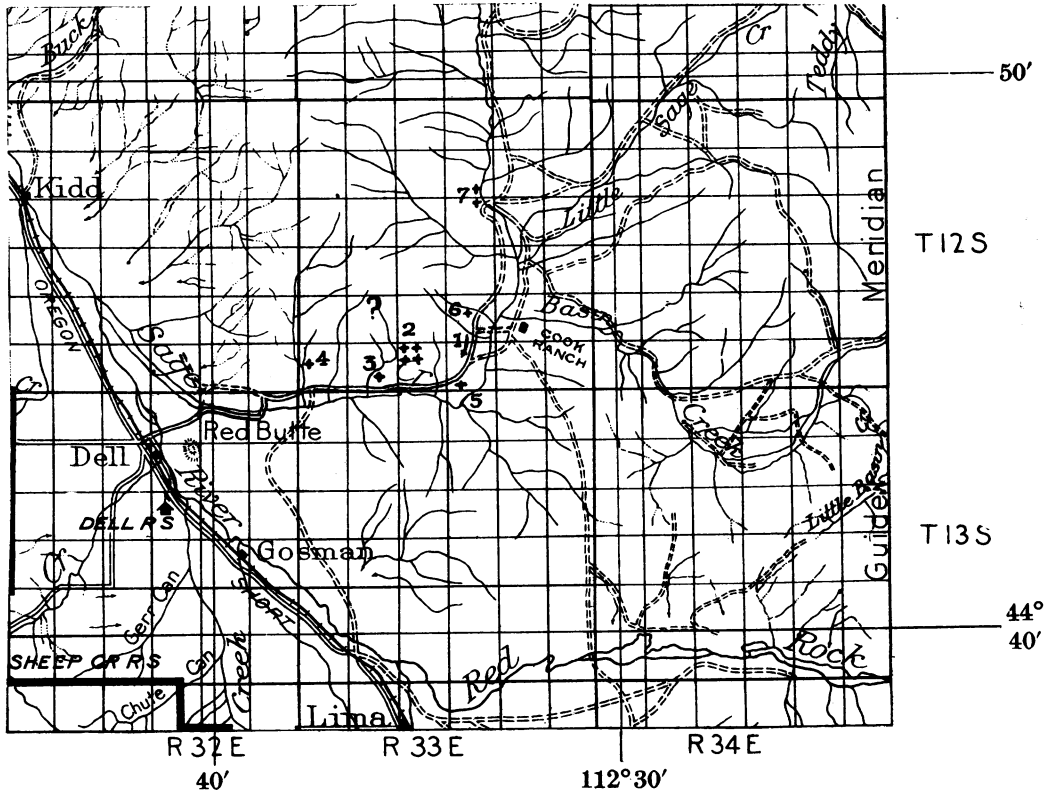

Fig. 51. Map of Sage Creek Region, Beaverhead County, Montana, modified from U. S. Forest Service Map of Beaverhead National Forest.

1903, Fig. 1), which Douglass called *Heptodon?*, and which Matthew (Osborn, 1909, pp. 99) emended to *?Helaletes;* and C. M. No. 734, the right ramus of the jaw of a small amynodont, which Douglass called *Metamynodon* sp., and which Matthew (Osborn, 1909, p. 99) emended to *?Amynodon.* Unfortunately, the matrix has been almost completely removed from these fossils. The mode of preservation is fairly uniform, and is more suggestive of, say, Chadron fossils than of the Eocene as known in Wyoming and Utah. Douglass' determinations (*Heptodon, Hyrachyus* and *Metamynodon*) suggest, respectively, Lower Eocene, Middle Eocene, and Oligocene age, which is a rather large discrepancy. I hoped by a visit to the Sage Creek Beds to obtain additional fossils or stratigraphic evidence that might help to settle the age of these beds.

Seven patches of exposures (numbered 1–7, see map, Fig. 51) were found in the area. Number 1 can be eliminated, as it contains the Oligocene fauna described below. Fragmentary, unidentifiable fossil bones were found at numbers 2, 3, 6 and 7, the mode of preservation and the matrix being similar to that of Douglass' fossils, except the amynodont, which retains patches of matrix composed of small quartz sand grains. The matrix of Douglass' fossils clearly eliminates number 4 from consideration. Douglass' map can hardly apply to number 7. Number 2 agrees fairly well with Douglass' description of his first locality, as there is a hill with quartz and calcite geodes and fossil roots (indicated by the southeastern cross at 2 on Fig. 51). His other fossil locality might be any of various exposures close by, or even number 3 or 5. Douglass' map appears to indicate either 2, 3, or immediately north of them, not farther than the interrogation point (Fig. 51). All things considered, Douglass' locality is probably not far from locality 2, although, unfortunately, no definite proof of this inference was obtained. If this is not his locality, it is difficult to imagine where it can be.

Although no identifiable Eocene fossils were found, the discovery of a fairly extensive Oligocene fauna in this region raises the question whether Douglass' collection might not be a mixed fauna, the amynodont having been secondarily derived from a higher level. Mr. Peterson kindly sent me all four specimens for study. Matthew suggested that C. M. No. 717 might be *Helaletes* rather than *Heptodon.* This seems likely on a stratigraphic basis, and the morphology fully confirms this assumption. It is not at all like any *Heptodon* except *H. singularis,* and is clearly distinct from it. It is smaller than *Heptodon* and larger than *Dilophodon,* but it agrees exactly in size and character with *Helaletes* in general, and is not separable from *H. boöps* of the Lower Bridger in

particular, although it is probably not specifically determinable. It must, however, be referred to the genus *Helaletes* (sensu strictu), which is known, so far, only from the Middle Eocene (Bridger and equivalents). Douglass' figure is thoroughly representative.

The protoloph and metaloph of P^2 of *Hyrachyus douglassi*, C. M. No. 784, form definite lophs, a distinct advance over all other species of *Hyrachyus*. The presence of a *Hyrachyus* generally similar to *H. eximius* might seem to indicate Upper Bridger age, but the progressive second upper premolar suggests that this form might well be of Uinta age.

The type of *Chasmotheroides intermedius* is from Bridger B, C or D, with a fair balance of probability in favor of Bridger C as the horizon. The referred tooth, C. M. No. 718, is very similar to the type, and no verbal differences can be stated, except that it is about 2 mm. less in breadth. Douglass' figure is very accurate, except that it does not show the region of the posterior cingulum, which is broken off in the specimen. The affinities of *Chasmotheroides* are uncertain: it may be related to the European lophiodonts, or to the helaletids. It suggests Bridger age.[1]

The amynodont, C. M. No. 734, was found below *Chasmotheroides* cf. *intermedius* and seems, even according to Douglass' description, to be inside the limits of the genus *Amynodon*, as Matthew suggested, rather than of *Metamynodon*, although it is, possibly, a distinct species. It is somewhat advanced over *Amynodon antiquus*, but is comparable in size with *Amynodon intermedius* from the Myton, and is more advanced, in the loss of one incisor (I_3?), in the reduction in size of the remaining median incisor (I_1?), in the slightly larger canine and in the loss or extreme reduction of P_2. It is somewhat smaller and more primitive than, but otherwise rather close to, Stock's form from the Sespe Formation of Ventura County, California. Comparison is desirable with Peterson's form from the Eocene-Oligocene transition beds of the Uinta Basin. It is much smaller than *Paramynodon cotteri* from Burma, though perhaps comparable to it in evolutionary grade, and is still less comparable with *Metamynodon*, either in size or character. The advances over described species of *Amynodon* are: it is larger than usual, only two lower incisors were present, the median being reduced; the lower canine is somewhat larger than in *A. intermedius*, and P_2 has been either lost or extremely reduced. The size of the lower canine and the loss of the first premolar would not separate it from *Amynodon*, as Douglass apparently believed.

[1] A left m^3, inseparable from *Chasmotheroides intermedius*, has just been described from a Uinta level in Saskatchewan by I. S. Russell and R. T. D. Wickenden. 'An Upper Eocene Vertebrate Fauna from Saskatchewan,' Trans. Roy. Soc. Canada, (3) Sect. IV, XXVII, p. 62, and Pl. 1, fig. 6, Nov., 1933. The *Chasmotheroides* in the Sage Creek, then, suggests either Uinta or Bridger age.

The most distinctive feature is the apparent loss of one incisor, which is possibly a valid specific character, but it is hardly of generic value.

The *Helaletes* (suggesting Bridger age) and *Hyrachyus douglassi* (suggesting Uinta age) were found close together, *Helaletes* being a few feet the higher. These two specimens together suggest Bridger or Uinta age, with the balance of evidence favoring the Upper Bridger. *Chasmotheroides* cf. *intermedius* (suggesting Bridger age), and *Amynodon*, advanced species (suggesting Uinta C or a little higher), were found close together, about a half-mile from the other pair.

Obviously, there are three possibilities:

1, The two localities where Douglass collected might be of two different ages, in which case the probabilities would be, respectively, Upper Bridger and Uinta age.

2, If Douglass was correct in associating these two localities, the total evidence would favor Lower Uinta, as Matthew suggested (Osborn, 1909).

3, The amynodont might have been washed down from a higher horizon, in which case the other three fossils would suggest Upper Bridger age. The reasons for suggesting this third alternative are: the distinct, sandy matrix of *Amynodon*, the fact that the advanced amynodont can fit with the other three forms only with difficulty, and the presence of a hitherto undiscovered Middle Oligocene fauna close by, which suggests the possibility that beds of intermediate age might be present from which the amynodont could conceivably have been derived. In any case, the emended identifications of Douglass' fossils reduce the uncertainty from any period between Lower Eocene and Middle Oligocene to between Middle and Upper Eocene, and, probably, to Upper Bridger or Lower Uinta, that is, to equivalence to some part of the Washakie. It is highly desirable that more fossils should be collected from Sage Creek, to furnish additional information about the only Eocene in Montana.

The only hint of a later horizon at Sage Creek was furnished by Douglass (1909, pp. 256 and 281) who says that the Sage Creek beds, judged from fragmentary fossils, are partly of Middle Eocene with overlying Lower Oligocene, and partly of Miocene age. A field party consisting of A. E. Wood, F. D. Wood, H. E. Wood, and Rolena Dowden, spent August 23–25, 1931, in the Sage Creek region. The most important discovery was a fairly abundant fauna, largely a micro-fauna, at locality number 1 (see map, Fig. 51). This is the badlands west of the Cook Sheep Company Home Ranch, directly across Sage Creek and the road.

The fauna was determined as follows (rodents and lagomorphs by A. E. Wood, other forms by H. E. Wood):

Leptomeryx evansi, left ramus of mandible with P_4-M_2 and fragments of other teeth.

Hyracodon, fragment of ectoloph of upper cheek tooth.

Peratherium, right lower molar.

Paleolagus haydeni, parts of lower jaws and numerous upper and lower teeth.

Heliscomys, new species, more advanced than *H. vetus*, left maxilla with P^4-M^3.

Sciuromorph P^3?.

Eumys, new species, five lower jaws.

Turtle fragments.

All the genera are Oligocene, and the fauna as a whole is clearly Middle Oligocene. The absence of such common forms as *Oreodon* and *Mesohippus*[1] is a striking feature and may be due to a difference in facies between an intermontane valley and the open plains, but the striking resemblances rule out any other interpretation than Middle Oligocene age. The new species of *Heliscomys* and *Eumys* will be described elsewhere by A. E. Wood[2]. As this fauna clearly has nothing to do with Douglass' Sage Creek, which term must be restricted to the Eocene beds, a different geographic name for the Oligocene level becomes necessary. The only appropriate name available, Cook Ranch, is used locally in, at least, a quasi-geographic sense, and appears on some road maps. The name **Cook Ranch** is hereby proposed for the Middle Oligocene beds of this region, the type locality being the prominent badlands west of the southward-flowing reach of Sage Creek, north of the westward-flowing portion, 8.1 miles by road from Dell Railroad Station, in Township 12 South, Range 33 East, Sections 27 and 34, opposite (west of) the buildings of the Cook Sheep Company Home Ranch, between the two approach roads to the Cook Ranch and immediately west of the main road. These badlands erode into patterns much like the Brule of the Big Badlands. The dip is 10°, S. 10° E. The beds consist of buff clays, not very different from the putative Eocene at locality number 2, with interbedded sandstone lenses of the "*Metamynodon* Sandstone" type. The thickness exposed is estimated at 125 feet. This bluff is the most prominent exposure in the region, and is quite unmistakable. The fossils were found in three pockets, at almost the same level, just above the bulk of the sandstone lenses.

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[1] An additional collection was secured by F. D. Wood in 1933, about thirty feet below the level of the 1931 collection, including:

Leptomeryx evansi, left maxilla with P^3-M^3.

Mesohippus sp., dP^2 left.

Cynodictis cf. *gregarius*, left ramus with P_{3-4} and roots of C_1-P_2.

Lizard jaw, teeth worn down to bone.

Fish vertebra.

[2] The new *Heliscomys* was described as *H. gregoryi*, Journ. Mammalogy, XIV, 2, pp. 134–141, May, 1933.

The main unsettled question is whether there are two or three vertebrate levels in the Sage Creek region. If there are two, they are Middle Oligocene, and, probably, Lower Uinta; if three are present, they are Middle Oligocene, probably Upper Bridger, and possibly Upper Uinta, or even Uinta-Chadron transitional beds, resembling the Duchesne Formation, of the Uinta Basin. This possibility is suggested to take care of the advanced *Amynodon*. Finally, it is still uncertain exactly where Douglass collected his specimens.[1]

DISCUSSION

Stratigraphic Distribution and Phylogeny of the Hyrachyidae

In arriving at the conclusions as to the phylogeny of the Hyrachyidae shown in figure 1, I first arranged the specimens and species morphologically, and then evaluated these tentative conclusions on the basis of the horizons of the various species and specimens. Unfortunately, the precise horizon had not been recorded for most of the types and other early specimens. The exact locality, however, was often stated, which

[1]The type locality of the Sage Creek Formation was finally located by F. D. and H. E. Wood, June 30–July 5, 1933, northwest of locality No. 3 on figure 51 about at the boundary between sections 29 and 30. This locality (our No. 8) is eight miles north by west of Lima, instead of seven miles northeast, but agrees perfectly, otherwise, with Douglass' description, and is the only locality in the region that does. This is unmistakably the hill described by Douglass (really the north rim of a badland pocket) with abundant quartz and calcite geodes and calcified twigs, where he found *Helaletes* and *Hyrachyus douglassi*. It is visible only from the higher hills around, and was first seen from one of them through field glasses. What is presumably his other locality, about half a mile away (our No. 9), is in the northern part of section 32. Locality No. 9 can be reached by car, by driving .6 mile north on a trail which turns north off the Cook Ranch road, 2.8 miles, by road, east of the bridge over Sage Creek. Locality No. 8 can best be reached by walking about half a mile north up a dry gulley from .2 mile north of No. 9. Not a scrap of bone was found at No. 8, and only unidentifiable fragments at No. 9. As Douglass found his four fossils in 1897 and nothing on his later visits, it seems likely that his specimens were the debris from a long period of slow weathering. At locality No. 3, which also turns out to be the Sage Creek Formation, was found a good-sized pelvis, with other fragments, not yet developed and studied.

The Sage Creek is a unit formation, and there is no reason to believe that it covers any large passage of time. It consists of regularly bedded, fine-grained, greenish-gray sandstones, with interspersed, coarser, cross-bedded, channel sandstones, ranging into conglomerates in some places. The Sage Creek dips northeasterly, and is separated from the underlying salmon-colored beds by a marked erosional unconformity. The upper surface of the Sage Creek had been strongly eroded, having formed a northwardly-facing cliff at No. 8, with a considerable accumulation of talus, which was later cemented with, and buried by, the Cook Ranch Formation. This relationship suggests the Snake Creek—Sheep Creek contact in Nebraska, but is even more striking. The Cook Ranch, which has a generally southerly dip, overlies the Sage Creek at its type locality, No. 8, and also at No. 6, just north of No. 1 (the type locality of the Cook Ranch), so that there is certainly no intervening formation. The sandy matrix of Douglass' amynodont agrees with the more finely-grained of the Sage Creek channel beds. As far as the field relationships are concerned, the amynodont could have come from the Cook Ranch Beds and yet from topographically below exposures of the Sage Creek; but as, on morphological grounds, the amynodont is certainly not of Middle Oligocene age, it must have come from the Sage Creek. Restudy indicates reference to *Amynodon advenus*, of the Lower Uinta. Therefore, on the basis of the entire assemblage of fossils, the Sage Creek should be considered as of Lower Uinta age, and is the only known Uinta between central Wyoming and southern Saskatchewan.

The local succession may be summarized as follows:

Miocene?—Basalt, above Cook Ranch Formation, south of the bend of Sage Creek.

Contact covered.

Upper Oligocene? or Miocene?—Pebble beds, degree of consolidation varies; no fossils.

Angular unconformity.

Middle Oligocene—Cook Ranch Formation, grayish buff clays with *Metamynodon*-type channel sandstone lenses; fossils moderately abundant in limited pockets.

Angular and marked erosional unconformity.

Upper Eocene (Lower Uinta)—Sage Creek Formation, greenish gray, regularly bedded sandstones. Marked erosional unconformity, with coarser channel lenses; sparingly fossiliferous.

Lower Eocene?—Salmon-colored beds, varying from conglomerate, through argillaceous conglomerate, to pebbly shale; no fossils.

usually permitted the horizon to be deduced with a fair degree of confidence. The map by Matthew and Granger (Matthew, 1909, Osborn, 1929, this paper, Fig. 2) is invaluable in determining the stratigraphic levels of the Bridger specimens. The recorded levels of the extensive later collections in the American Museum afford an additional check, and make it possible to define specific ranges, with varying degrees of accuracy, but with a close approach to exactness in the case of the better-documented species. The levels predicted from a phylogenetic viewpoint usually agree almost exactly with the horizons recorded or indicated.

It is interesting to observe that the family Hyrachyidae, although represented by numerous individuals, is known only from the Eocene (Lost Cabin to Uinta, inclusive), and only from the States of Wyoming, Utah, Colorado and Montana. *Hyrachyus* has the greatest time range of any American Eocene ungulate genus, and has an unusually long generic range, for a placental mammal, due to its conservatism, that is, to its slow rate of evolution.

Such an overwhelming proportion of the known specimens has come from the Bridger that it is justifiable to consider the genus *Hyrachyus* as one of the most characteristic index fossils for that age, in spite of its occasional presence in older and younger formations. *H. modestus* is now established as an index fossil for the Black's Fork, and *H. eximius* and *H. princeps* for the Twin Buttes. The presence of *H. modestus* in Huerfano B helps to confirm its approximate correlation with the Lower Bridger. I am unable to subdivide *H. affinis* into earlier and later stages. The other species (as well as the other genera of the family) are not known from enough individuals to prove whether they are index fossils or not. Their rarity, so far, would suggest that they would not be of any great use, as such, in any case.

The family Hyrachyidae was rather unprogressive during its known career, and, when the various aberrant offshoots are left out of account, the stability of the genus *Hyrachyus* during the long period of time for which its history is known, is its most striking character. It is interesting, then, that the best-marked specific changes occur, not where they might be expected, that is, at the transition from the Lower to the Middle, or from the Middle to the Upper Eocene, but in the middle of the Bridger, that is, between the Black's Fork and the Twin Buttes. If it were legitimate to assume a uniformly slow rate of evolution for the stolid Hyrachyidae, which, of course, it is not, this change, which seems to be the result of evolution in place rather than migration, would demand a hiatus nearly equivalent, in length, to the Black's Fork! The

close resemblance of the Lost Cabin to the Black's Fork hyrachyids, and of the Wagonhound to the Twin Buttes forms, fits with the established fact that the Huerfano and Washakie lap over these gaps, being roughly equivalent, respectively, to the Lost Cabin+Black's Fork, and to the Twin Buttes+Wagonhound. Neither Huerfano A+B nor the Washakie is sufficiently thick to suggest any marked hiatus either below or above the Bridger. In any case, it is worth emphasizing that the data regarding *Hyrachyus* agree with Matthew's conclusions from other groups (1909) as to the relatively sharp distinction between the faunas of the Lower and Upper Bridger.

Three main series (or phyla) can be recognized. The best known consists of the forms of medium size, commencing with *H.* cf. *modestus* in the Lost Cabin, continuing through *H. modestus* of the Black's Fork, *H. eximius* of the Twin Buttes, and apparently culminating in *H. douglassi* of the Sage Creek Eocene (Uinta?) of Montana and doubtfully referred specimens from the Wagonhound of Utah. *Metahyrachyus* and *H. hypostylus* appear to be offshoots of this line. The line of large forms, consisting of *H. princeps* of the Twin Buttes and *H. grandis* of the Wagonhound, may well be derived from the same line. The series of small forms is represented by the rather variable *H. affinis* throughout the Bridger. *Colonoceras*, certainly, and *Ephyrachyus*, probably, are offshoots of this line, although *Ephyrachyus* may have branched off much earlier. *Chasmotheroides* ["*Hyrachyus*"] *intermedius* is of uncertain affinities, but can hardly be a hyrachyid.

Evolution of the Premolars and Molars

From a mechanical point of view, the upper cheek teeth of a primitive perissodactyl may be considered as a series of mortars, and the lower teeth as the pestles. The mortars are, alternately, the interdental spaces (bounded by the metaloph, metacone, parastyle and protoloph, with the posterior and anterior cingula forming the floor), and the median valley, bounded by the protoloph, paracone and metaloph. The trigonids and talonids are the pestles, occupying their primitive occlusal positions, respectively, in the interdental spaces in front of, and in the median valleys of, the corresponding upper teeth. The ectolophs act as stops to delimit the possibilities of the lateral swing of the lower teeth. This is the general arrangement in nearly all Eocene and Oligocene perissodactyls (including, of course, the Hyrachyidae), as well as in some later ones; in the more highly specialized horses and rhinoceroses, it is modified into a grinding mill at essentially a uniform level, utilizing the differential hardness of enamel, dentine and, often, cement.

The condition described above is found in both the premolars and molars of most Oligocene rhinoceroses, but in the Hyrachyidae, as in most Eocene perissodactyls, it is fully developed only in the molars. The chief feature in the dental evolution of the hyrachyids consists in the various starts made by the premolars toward attaining this molariform condition. The generalized primitive premolar arrangement consists in a trigonid, having the same occlusal relations as in the molars (although it may be only a single cusp, instead of a transverse ridge), and a low talonid consisting of the longitudinal hypoconid blade only, which bites into the usually acute angle between the ectoloph and the protoloph, the metaloph being small or absent. This condition still preserves, essentially, the up and down, chopping movement of the carnivorous or insectivorous ancestors. As soon as the hypoconid approaches respectable size the confinement of the hypoconid between the ectoloph and the protoloph would markedly restrict any lateral swing of the jaws, which would be, and is, obviously, efficient in grinding up plant food. If lateral movement is to be employed, and if the premolar median valleys and talonids (i.e., half the available surfaces) are to be utilized, the metamorphosis of the premolars is necessary. The greater survival value, due to more efficient mastication, obtained in this way, probably explains the independent molarization of the premolars in so many different lines of perissodactyls. The simplest way to secure this result is the one usually followed, that is, the protoloph swings around from an acute angle with the ectoloph, nearly to a right angle, the talonid changes from an antero-posterior to a transverse ridge, and the metaloph grows up so that it occludes behind the talonid of the corresponding tooth, and in front of the trigonid of the next tooth to the rear. It is possible for this general result to be obtained in a number of ways; and such different ways are followed by various perissodactyls, even by different members of the same family.

It is a permissible speculation that if a grazing tooth of the *Equus* or *Elasmotherium* type had been developed directly from a primitive perissodactyl tooth, molarization of the premolars would have been unnecessary and would probably have been omitted, the necessary grinding area being obtained by elaboration of the primitive pattern. According to this concept, it is only because the great development of grassy plains occurred late enough in time for a fully efficient browsing pattern already to have been developed, that the premolars of the specialized later forms are molariform. It would seem possible to have evolved efficient grazing patterns directly from the unmetamorphosed premolars,

if the environmental limiting conditions (the development of grassy plains at the expense of the forests) had taken place earlier. With a grinding surface at one level, the premolar protoloph would not act as an internal stop to lateral movement by imprisoning the hypoconid between itself and the ectoloph, so that there would be no advantage in completely discarding the primitive pattern.

The development of the initial stages of such a process as this premolar metamorphosis, previous to the acquisition of functional utility, has often been interpreted, on the one hand, as due to the inheritance of acquired characters, and, on the other hand, to orthogenesis. As neither of these alleged, and rather mutually contradictory, causes has ever been demonstrated, explanations based on either of them leave something to be desired. It is known that any gene in the embryo may affect many parts of the body during ontogeny. Therefore, it seems more plausible that the initial stages in such an evolutionary line are produced as a by-product of a series of mutations in a gene or genes, which mutations give the individuals carrying them a positive survival value, due to some effect produced elsewhere (quite probably on the soft anatomy or physiology of the organism). Only after a tooth or skeletal character has "accidentally" been carried to a point where it can be utilized, does it also become a factor in natural selection. If any evolutionary line is markedly more efficient than any genetically possible side branches, such incipient side branches would promptly be eliminated by selection before they would have time to make much impression on the palaeontological record. Such a line could seem to a palaeontologist, in retrospect, to show orthogenetic evolution. In this case, however, "orthogenesis" would not be a cause, but a summary of the observed effect. Unless orthogenesis can be proved to have some more significant meaning than this, it is not a particularly helpful or significant concept. If orthogenesis is interpreted to mean that possible immediate lines of evolution are finite in number at any given stage of any form, that is, that only such mutations as are chemically possible can take place in such genes as are present, it is undoubtedly true, but does not seem to be a particularly useful term. Naturally, the number of such changes which would be improvements, and, hence, which might become established, would be only a minute fraction of the total number possible.

In determining the evolutionary advance represented by the hyrachyid dentition, it is necessary to start from the primitive perissodactyl dentition. Matthew has frequently pointed out that *Eohippus* is a close approach to such a stem form. If *Eohippus* and *Homogalax* are

considered together, it is possible to visualize their probable common ancestor still more closely. The perissodactyls as a whole show a very definite and early evolutionary dichotomy, into the horse-palaeotherе-titanothere-chalicothere complex, on the one side, for which the subordinal name Solidungula Blumenbach, 1779, would be most appropriately revived, and the rhinoceros-lophiodont-tapir complex, on the other, for which the subordinal name Tridactyla Latreille, 1825, would be in order, unless *Trichena* Gray, 1821 (London Medical Repository), is preferred, despite its unfortunate similarity to *Trichinia* and *Trichina*. Since *Eohippus* and *Homogalax*, although anatomically quite similar, are already on different sides of this dividing line, the common ancestor should be approximately inferred by omitting all specializations found in only one of the two.

The most useful differences in trend between the two suborders are listed in the following table:

Solidungula	Tridactyla
The lower molars, starting with trigonid and talonid crescents whose limbs are slightly asymmetrical, with the hypoconid attached to the trigonid between the protoconid and metaconid,	
a) become progressively more symmetrical, with the hypoconid attached to the metaconid.	a′) become (and remain) asymmetrical, with the hypoconid attached to, or pointing toward, the protoconid.
The premolars, when metamorphosed, conform to their respective molar patterns.	
b) The hypoconulid of M_3 is retained.	b′) The hypoconulid of M_3 is usually lost.

There is no reason to assume that these differences in dental structure have any great selective value, per se; they are, however, very useful as indicators which seem to be more constant than other characters and less subject to exceptions. It is, of course, possible that they are controlled by genes which have other and more far-reaching effects. Since these tendencies appear very uniformly in the later members of each suborder, it is a legitimate working hypothesis that the relatively few mutations which had separated the very similar earlier members of the two suborders (e.g., *Eohippus* and *Homogalax*) nevertheless restricted future possible mutations so as to produce the observed clean-cut differences in their evolutionary trends.

Leidy and others have considered *Hyrachyus* as intermediate between the rhinoceroses and tapirs. As a structural description, this is true, since the tapirs have remained more primitive than the later rhinoceroses, and the hyrachyids are rather primitive members of the Tridactyla. However, the one specifically tapir-like feature of the Hyra-

chyidae is the reduction of the anterior limb of the crescents in the lower molars, so that the teeth are functionally bilophodont as in tapirs. In all other respects, the Hyrachyidae are primitive rhinoceroses. Since neither the most primitive Perissodactyla in general, nor Tridactyla in particular, have this character, and since no trace of it occurs in any true rhinoceros, hyracodont or amynodont, it seems reasonable to regard it as a specialization of all known hyrachyids away from the rhinocerotoid stock. The other lines would presumably be derived from an early (and still unknown) hyrachyid which had not yet acquired bilophodont lower molars. This form would, in turn, be descended from an undiscovered lower Eocene genus somewhat more like *Homogalax* than like *Eohippus*, and, eventually, from a common stock with them. The bilophodont condition of the lower molars in the Hyrachyidae, then, represents parallelism with the tapirs, rather than ancestral relationship to them, since the tapir ancestry apparently runs well back into the Eocene of Europe, and hence excludes any possibility of a contemporary, but very different, American ancestry.

Matthew, in various papers, has considered primitive, undiscovered amynodonts as ancestral to the true rhinoceroses, a view with which I have disagreed. This is, perhaps, partly a matter of definition, provided that the true rhinoceroses and amynodonts have an immediate common and exclusive ancestor. This is by no means certain, however; it seems fully as likely that hyracodonts, amynodonts and true rhinoceroses are independently derived from an early, and undiscovered, hyrachyid. Even if such an implied phylogeny were proved, it would be undesirable and confusing to call the common ancestor an amynodont, as the known amynodonts, even in the Uinta, are much more specialized than any other contemporary members of the Tridactyla, especially in such features as reduction in the size of the premolars. If they are considered primitive due to the possession of a complete dentition, it is a character which they share with nearly all other Eocene Tridactyla. Even the Oligocene genus *Trigonias* is only moderately more specialized than the Eocene genus *Amynodon* as to the front teeth; and its premolars are considerably more primitive. Matthew's arrangement, then, whether technically defensible or not, would be likely to cause confusion in regard to the true evolutionary history of the rhinocerotoids. Even by definition, such a hypothetical stage would not be more specifically amynodont than hyracodont; and its being non-rhinocerotid is purely a matter of arbitrary definition, which could equally well be made to exclude *Trigonias*, *Allacerops* and *Epiaceratherium* from the family Rhinocerotidae.

The generic description of *Hyrachyus* covers the general characters of the incisors and canines. A good set of the upper front teeth is figured for *H. princeps* (Fig. 18 and Pl. XXII), and a good lower set for *H. eximius* (Fig. 17). Sufficient data are not yet available to show whether an evolutionary story can be traced for the front teeth, but, if so, the changes inside the family Hyrachyidae are probably small. It is interesting to note that I_2 of A. M. No. 1645 (Fig. 17) shows the wear from an upper tooth (presumably I^2) such as would be made by an obliquely set blade with a nearly even crown, such as I^2 of *H. princeps* (Fig. 18), suggesting that this same type of upper dentition also occurs in *H. eximius*, and, probably, throughout the genus.

In the upper cheek teeth of the Hyrachyidae, the paracone and metacone still show clear evidence of their former condition, when they were independent cusps. In the later rhinoceroses they are almost completely merged into the ectoloph. In the hyrachyid lower premolars, also, the cusps are not yet fully merged into lophs. This is best seen in P_{3-4}, which are moderately progressive, rather than in P_{1-2}, which are hardly yet subdivided into cusps. After a hyrachyid upper or lower premolar or molar is thoroughly worn down, it approximates closely the pattern of a correspondingly worn primitive true rhinoceros or hyracodont tooth. As an example, A. M. No. 11675 is quite similar to *Subhyracodon*. This is not surprising in view of the real relationship of the Hyrachyidae to the later rhinoceroses.

It seems never to have been clearly pointed out that the crista is merely the remaining, internal, conical slope of the old paracone cusp. The closest approach to an explicit statement occurs in Osborn (1907). As a result, surprising misconceptions sometimes occur. Osborn (1898, p. 107) regards the crista as analogous with the mesostyle, which occurs on the opposite side of the ectoloph. Abel (1910, pp. 44–45) considers the presence of a crista in the upper molars of *Hyrachyus* as a specialized character. In the same way, the external "ribs" on the paracones and metacones are merely the external remains of their original slopes as conical cusps.

In the most primitive perissodactyls, P^1 consists essentially of a single cusp, the parametacone, which is somewhat elongated anteroposteriorly. Among the Hyrachyidae, this condition is found only in *Ephyrachyus cristalophus*, slightly modified in P^1 left by the presence of a minute internal cingulum, which is larger in P^1 right and suggests the basis for a protoloph. In all other hyrachyids, different species and even different individuals of the same species, vary as to whether a protoloph

only is developed, as in *H. hypostylus* (Figs. 19 and 21), a metaloph only, *H. modestus* (Fig. 4), *H. douglassi* (Fig. 23), *Metahyrachyus troxelli* and *bicornutus* (Figs. 42 and 43), *H. affinis*, and *H. princeps*, or whether both are indicated (*H. eximius*, Fig. 14). Whichever loph is developed, it is derived from the internal cingulum; if both are present, they represent two successively appearing cingula. Similar variation is found also in the Eocene and Oligocene Rhinocerotidae and Hyracodontidae, showing extremely wide variation, even among members of one limited species. The metaloph appears to have arisen from a postero-internal cingulum, and the protoloph from an antero-internal cingulum. When both lophs are present, the protoloph is usually lower (closer to the gum) and appears to have arisen as a later cingulum than the metaloph. It seems legitimate to correlate the usually greater development of the metaloph of P^1 with the fact that it opposes the trigonid of P_2, which is good-sized from the start and increases in size. On the other hand, the front part of P^1, including the protoloph, can work only against P_1, a small and functionally unimportant tooth, which disappears, entirely, early in rhinocerotoid evolution. This explanation applies with equal or greater force to the usual greater development of the metaloph of P^1 in Oligocene hyracodonts and true rhinoceroses, explaining the type of premolar evolution observed in P^1, which is distinctly exceptional as compared with the other upper premolars. So far as is known, as in other rhinocerotoids, there is no replacement of P^1 in the Hyrachyidae. It is not certain whether it belongs to the deciduous or permanent series. It is occasionally lost before death.

The primitive perissodactyl pattern of P^2 seems to be found in *Hyracotherium*, and is approximated in *Homogalax* [=*Systemodon*] *primaevus* and several species of *Eohippus*. The ectoloph is a single cusp (*Hyracotherium*) or partially divided into two connate cusps in the American forms, with the internal part of the tooth consisting of an internal cingulum which can not yet be regarded as more than incipiently demarked into cusps. The resemblance in evolutionary grade to that found in P^1 of *Hyrachyus* is striking. The most primitive P^2 among the Hyrachyidae is found in *Ephyrachyus cristalophus*, with an elongate ectoloph consisting of the connate paracone and metacone, and the protoloph forming a 45° angle with it (Fig. 47), so that it suggests that it arose as an internal cingulum. *Hyrachyus modestus* and *Metahyrachyus* are a shade more primitive in having the two outer cusps even less separated; they are more progressive in having a shorter ectoloph. In *H. modestus*, the protoloph is also at a greater angle with the ectoloph.

(The internal part of P^2 of *Metahyrachyus* is, of course, both progressive and aberrant). The fact that *E. cristalophus* is the most primitive of the Hyrachyidae as to P^2, and, with *E. implicatus*, among the most progressive, elsewhere, suggests that perhaps the immediate common ancestor of *Hyrachyus* and *Ephyrachyus* is still to be discovered. The paracone and metacone become more distinct in the more progressive forms, specifically, in *E. implicatus* (change not great), *H. eximius*, *H. hypostylus*, *H. douglassi*, *H. princeps*, *H. affinis* and *Colonoceras*. Except in *Ephyrachyus cristalophus* and *Metahyrachyus*, the position and height of the protoloph are very similar throughout the family. Its angle with the ectoloph is most acute in *E. cristalophus* and *H. affinis* (about 45°), whereas, in the other forms, it runs from 75° to 90°. In the more primitive forms, there is no trace of a hypocone, as such, that is, the protoloph is continuous and straight or nearly so (*H. modestus*, *H. eximius*, *H. princeps*, *H. affinis*, *Colonoceras* and *E. cristalophus*). A small hypocone appears, partially budded off from the protocone, but not yet fully joined to the metaconule to form a metaloph, in *H. hypostylus*, *H. douglassi*, and *E. implicatus*. Even in these three forms, the median valley still escapes to the rear, over a low "wind-gap." The development of the metaconule is quite variable. It is virtually absent in *E. cristalophus*, absent or very small in *H. modestus* and *H. affinis*, larger in *H. eximius*, *H. princeps* and *Colonoceras*, no larger, but more or less attached to the hypocone in *H. hypostylus* and *H. douglassi*, and largest and most progressive in *E. implicatus*, in which it forms a blade. The internal part of P^2 of *Metahyrachyus* is aberrant (Figs. 42 and 43). The main cross loph (amphiloph) is formed from the protocone and metaconule. The metaconule is low in *M. troxelli*, high in *M. bicornutus*. The protoconule is small and not closely attached to the protocone in *M. troxelli*, and lost altogether in *M. bicornutus*. So far as P^2 goes, *M. troxelli* represents the stage through which *M. bicornutus* must have gone; but their horizons and the characters of P^{3-4} indicate that it is not a real ancestral relationship. This peculiar condition recalls the condition in horses, in which Granger (1908) has shown that the "metaloph" of P^3 is composed of the protocone and metaconule, the protoloph consisting of the protoconule only. It may be of interest to consider what peculiar associated conditions might be expected in the lower premolars. The left cheek teeth of *M. troxelli* occlude perfectly with *H. eximius*, A. M. No. 1645, suggesting that, as is so often the case, the lower teeth may have preserved their primitive character in spite of the aberration of the upper teeth. The large amphiloph suggests that the trigonid of P_3, in front of which it bites, was

already fully molariform. The hypoconid of P_2 must have been quite short, antero-posteriorly, but might have been higher than usual, in view of the low or absent protoconule.

The primitive perissodactyl P^3 is probably to be found in *Eohippus*. The tooth is triangular, with the apex pointing inward. The paracone and metacone are well defined from each other, and, with the parastyle, form the ectoloph. The only internal cusps are the protocone and protoconule, which are partly separate, but form a protoloph of sorts. *Homogalax* is similar, except that the protocone and protoconule are definitely united into a protoloph. The primitive hyrachyid pattern shows surprisingly little advance over *Homogalax*. The tooth is broader (buccolingually), the ectoloph is strikingly similar, the protoloph is somewhat higher. The only outstanding difference is the appearance of a metaconule. This tooth is rather conservative in most members of the family, i.e., *H. modestus*, *H. eximius*, *H. douglassi*, *H. princeps*, *H. affinis* and *Colonoceras agrestis*. Such modifications as appear are described below. A hypostyle appears in P^3 of *H. hypostylus*. In *M. bicornutus*, the hypocone has largely budded off from the protocone. In *M. troxelli*, the metaconule and hypocone are fully united to form a progressive metaloph, which, however, is only incipiently separated from the protoloph. P_3, therefore, could not have had a molariform talonid, nor could the hypoconid have been much better developed than in *H. eximius*. In *Ephyrachyus implicatus* and *cristalophus*, both cross lophs are high, the protoloph still including the site of the hypocone, the metaloph composed of the metaconule only, with the median valley partly open to the rear. P_3 of *E. implicatus* is, as would be predicted, still definitely premolariform.

If the primitive perissodactyl P^4 is found in *Eohippus*, the tooth is triangular, with the apex pointed internally; the ectoloph consists of parastyle, paracone, and metacone, well defined from each other; and the internal cusps are only the protoconule and protocone, partly united to form a protoloph, and the distinct metaconule. The three internal cusps are distinctly cuspidate. In *Homogalax*, the protoconule and protocone form a unified protoloph, and the metaconule is elongated transversely, abutting against the ectoloph and the protocone. A similar stage, intermediate between these two, with a somewhat lower metaconule, is primitive for the Hyrachyidae. It occurs in *H. modestus*, *H. eximius*, *H. douglassi*, *H. princeps*, and *H. affinis*. *Colonoceras agrestis* and *Metahyrachyus troxelli* have a progressive modification of the same essential pattern, with higher metaconules. *H. hypostylus* has

a hypostyle superimposed on the primitive hyrachyid groundplan, behind the metaconule and separate from the posterior cingulum, as in many horses (e.g., *Mesohippus* and *Miohippus*), *Trigonias hypostylus* and its probable descendant, *Trigonias wellsi*. These three independent occurrences are clearly parallelism. In *M. bicornutus*, the hypocone has nearly separated from the protocone, but shows no tendency to unite with the metaconule. In association with this, the talonid of P_4 may have been well on the road toward becoming molariform. The metaconule is twinned, as in A. M. No. 12223 (*H. modestus*), perhaps to be explained as parallel mutations. P^4 of *Ephyrachyus* is generally similar to P^3, except for the junction of the crista and metaconule. An approach to this condition is found in P^4 of the type of *Eotrigonias petersoni*, A. M. No. 2341. This condition here and in *Caenolophus obliquus* is presumably parallelism. In *E. implicatus*, the posterior outlet of the median valley is virtually closed; in *E. cristalophus*, it is more open, and the internal end of the metaconule is forked.

The hyrachyid upper molars are an elaboration of the primitive perissodactyl pattern, with the internal cones and conules entirely fused into the protolophs and metalophs, and the external cusps partly fused to form the ectolophs. The principal advance made by the earlier true rhinoceroses and hyracodonts over the hyrachyids consists in the complete fusion of the outer cusps to form fully developed ectolophs. In the Hyrachyidae, as in the Rhinocerotidae and Hyracodontidae, M^2 is larger than either M^1 or M^3, as opposed to the Tapiridae and Helaletidae, in which the molars increase regularly in size from M^1 to M^3. M^1 is a squarish tooth, M^2 tapers to the rear. In M^{1-3}, the internal cusps are fully merged into the cross lophs; on the other hand, the parastyle is quite independent, and the paracone and metacone are by no means fully merged into the ectoloph. The hyrachyid molars are exceedingly uniform through the group, differing chiefly in size, except in *Ephyrachyus*, in which the ectolophs of the cheek teeth are slightly more advanced toward a rhinocerotid condition. M^3 is the most interesting of the molars. The tooth is more tapering than M^2, due to the fusion of the ectoloph and metaloph at a wide obtuse angle, so that the crest pattern is essentially a V, pointing externally. This involves the reduction in size of the metastyle and posterior half of the metacone (the "posterior buttress"). Early in the history of the Rhinocerotidae this is lost altogether. This loss is fully discussed elsewhere (Wood, 1927*b*). In the most primitive perissodactyls, the hypoconulid of M_3 is a good-sized cusp, occluding between the metaloph and posterior buttress of M^3.

In such lines of perissodactyls as retain the hypoconulid, one would expect the posterior buttress to be retained, and such is the case (e.g., the horses). The earliest known hyrachyids, amynodonts, hyracodonts, and rhinocerotids have lost the hypoconulid of M_3 (or, rather, reduced it to a posterior cingulum); as would be expected, the posterior buttress is more or less reduced in all these forms, and is obviously on the road toward total loss. A similar result might have been expected in such other lines of closely related perissodactyls as lost the hypoconulid, had they not become extinct shortly after (i.e., the *Teleolophus-Cristidentinus-Deperetella* line, *Dilophodon*, *Atalonodon* and *Chasmotherium*). In the chalicotheres, on the other hand, a similar effect is obtained in a different way. After the loss of the hypoconulid of M_3, the metaloph and posterior buttress of M^3 are squeezed together into what is almost a single loph, functionally. The tapirs retain the posterior buttress of M^3, in spite of its loss of function.

Subhyracodon gidleyi (Wood, 1927*b*) has been described as an unusually early appearance of a mure. In *Hyrachyus* cf. *affinis*, A. M. No. 19242 (Fig. 33), collected by Olsen in 1922 at Grizzly Buttes, hence Bridger B, the valley of M^3 is completely blocked by a mure, which can be considered a crochet. This is quite certainly to be interpreted as a parallel mutation, rather than as actual ancestry to any other known form. Such scattering, new characters, which appear constantly in teeth, fit far better with the idea of random mutations followed by selection of the most efficient "new models," than with an orthogenetic interpretation. It is only when the short, sterile, side branches are ignored that there is a fictitious appearance of orthogenetic evolution.

For the premolar hypolophid to develop into a full-sized, transverse crest, the hypocone must be completely separated from the protocone, giving an internal opening for the median valley. If the cingula of two adjoining upper cheek teeth block the interdental space at about the level of the median valley, the talonid should be about as high as the trigonid; and any difference of level should approximate the difference in the occluding jaw. It is, therefore, possible to predict an unknown rhinocerotoid lower dentition with fair accuracy from the upper dentition. The greater uniformity of the lower dentition is, of course, a help in this. The reverse is less true.

P_1 is a small tooth, apparently not functionally important. There is no evidence that it is replaced. It is uncertain whether it belongs to the deciduous or permanent series. It is sometimes absent, especially among the later hyrachyids, and still oftener in the later rhinocerotoids.

The tooth consists of a blade, expanded antero-posteriorly, with the protoconid the main cusp, but with the paraconid, metaconid, and hypoconid incipiently expressed by radiating ridges.

P_2 is similar, but is larger, with the hypoconulid definitely expressed as a short, antero-posterior blade. The paraconid may be more or less distinct from the protoconid; the metaconid is not yet a real cusp. In other words, in the Hyrachyidae, P_2 is more like P_1 than like P_3; in the Rhinocerotidae and Hyracodontidae, the reverse is the case.

The primitive perissodactyl P_3 resembles P_4 more than P_2 in size and in the relative proportions of the various cusps and incipient cusps. On the other hand, the incipient paraconid and metaconid form a nearly straight line with the protoconid and hypoconid, whereas in P_4 the paraconid, protoconid and metaconid are already crescentic, so that the trigonid is essentially molariform. The hypoconids of P_3 and P_4 are of the same general premolariform type, that is, antero-posterior blades. The talonid crescent, then, has not yet been established. Hyrachyids in general have not advanced far beyond this pattern. P_3 is more rectangular than P_2, less so than P_4. The metaconid is a small cuspule, which has not reached full size nor fully fused with the protoconid to form the metalophid. It is, however, definitely postero-internal to the protoconid. There is usually no entoconid. Except for the more rectangular outline and the molariform trigonid, P_4 is usually much like P_3. In *Ephyrachyus implicatus* (Fig. 46) and in occasional random individuals of the various species of *Hyrachyus*, one or more of the lower premolars may show some tendency for the rear end of the hypoconid to give off an internal hook, which, however, does not form a real loph (*H. modestus*, A. M. No. 12667, Fig. 5, and A. M. No. 19233, Fig. 11). Again, in various individuals, an entoconid appears on P_4 (*Ephyrachyus implicatus*, Fig. 46, *H. modestus*, A. M. No. 17440, Fig. 12, A. M. No. 12354, A. M. No. 12365) and on P_3 as well (*H. modestus*, A. M. No. 12672, Fig. 13, A. M. No. 12663, and A. M. No. 19233, Fig. 11). To judge from the hyrachyids, the rhinocerotoid premolar entoconid arose originally as a postero-internal cingulum, developed into a cuspule, and fused with the hypoconid to form the hypolophid. Apparently (cf. *Protapirus*) the tapirs followed the same course, as did the helaletids (cf. *Dilophodon*)

The lower molars are uniform and uninteresting throughout the family. Their only progressive character is the over-reduction of the anterior limb of the posterior crescent (i.e., of the longitudinal portion of the hypoconid). This tapir-like specialization, which is not found in any

of the most primitive Perissodactyla, would seem to rule all known hyrachyids out of the line of ancestry to the true rhinoceroses, hyracodonts, and amynodonts. Leidy, probably on this basis, considered *Hyrachyus* intermediate between the rhinoceroses and tapirs; but the lack of any tendency toward a proboscis, together with the presence of Eocene tapirs in Europe, indicates that this is probably a parallel specialization of the Hyrachyidae. If this interpretation is correct, it is the only family specialization which takes them off from the immediate line of ancestry of the later rhinoceroses. This tapir-like reduction of the longitudinal blade of the hypoconid increases from M_1 to M_3. The lower molar cingula are of very uniform pattern. Strong anterior and posterior cingula are present. No internal cingula appear, but a small external cingulum may, or may not, appear across the groove between the trigonid and talonid. The only other variable feature is the posterior cingulum of M_3, which is usually slighter here than on the other molars, and may rise to a peak in the central axis of the tooth, suggestive of a cuspule. This is probably a survival of the ancestral condition, before the hypoconulid was reduced from an independent cusp to the posterior cingulum; at least, the Helaletidae furnish an analogous case in which this transition can be followed step by step, in the series *Helaletes-Dilophodon*.

Evolution of the Deciduous Premolars

An adequate basis for discussing the evolution of the deciduous incisors and canines does not exist. There is no evidence against the natural assumption that each member of the permanent series had a smaller deciduous predecessor. The few worn deciduous incisors which I have seen do not indicate anything more elaborate than simple, peg-like teeth (e.g., dI_2 right of *H. modestus*, A. M. No. 11650).

The apparent non-replacement of the first upper and lower premolars has already been discussed. It is reasonably certain that there is no replacement in the Rhinocerotidae. Probably the same holds good for the Hyracodontidae and the Hyrachyidae, but the evidence is less complete. In this case, the question is whether to call the first premolars $dP\frac{1}{1}$, $P\frac{1}{1}$, or sometimes one and sometimes the other. They erupt after $dP\frac{2\text{-}4}{2\text{-}4}$, almost always before $P\frac{2\text{-}4}{2\text{-}4}$, and about coincidentally with $M\frac{1}{1}$ or $M\frac{2}{2}$, but before $M\frac{3}{3}$. As they may be present up to extreme old age, it seems most reasonable to call them permanent teeth, although they are often lost in late maturity.

In contrast to the permanent dentition, it is not yet possible to trace the actual phylogenetic evolution of the deciduous premolars.

The series to be discussed below are morphological series only. However, it does not seem likely that further evidence will introduce any material changes, other than additions. The second upper deciduous premolar is always a wedge-shaped or triangular tooth and is always widest across the posterior part of the tooth. The most primitive hyrachyid dP^2 which I have seen is Y. M. No. 12526, *Hyrachyus affinis*, from Bridger B (Fig. 41, see above under *H. affinis*). The ectoloph consists of a parametacone, not yet subdivided. The inner part of the tooth is still more primitive. The protoloph is a longitudinal rather than a transverse crest, being almost parallel to the ectoloph. The hypocone is partly budded off, but it lies in the same longitudinal line as the protoloph so as virtually to continue it. The median valley is fully open both to front and rear. A stage more advanced, in most respects, is represented by A. M. No. 12693, *H.* cf. *affinis*, from Bridger B (Fig. 40), in which the protoloph swings obliquely to the rear, and the low metaloph, consisting of the metaconule, partially dams the median valley, which opens to the rear, only. In this tooth, however, the hypocone has not yet appeared. The internal portion of this tooth is comparable to P^4 of *H. eximius*. The next stage is shown by A. M. No. 12137, *H. eximius*, from Bridger C_4 (Fig. 39). The parametacone is still undivided, and the general arrangement is similar to that of A. M. No. 12693, except that the hypocone has begun to bud off from the protocone, and that a small anterior cingulum has appeared. The tooth is a shade more advanced in shape, and in the degree of development of various characters, although hardly enough to describe in words. A marked advance appears in A. M. No. 1646, *H. eximius*, from the Twin Buttes Member (Fig. 38). The ectoloph consists of parastyle, paracone, and metacone, rather than parametacone only. The protoloph is still oblique. The median valley opens internally, as the metaloph is here completely separate from the protoloph. The metaconule and hypocone are fully confluent, and, as the metaloph runs transversely, as compared to the oblique protoloph, dP^2 continues to be wider across the rear than across the front. A similar stage occurs in *H. princeps*, A. M. No. 12371, also from the Twin Buttes Member. The most advanced stage occurs in A. M. No. 1929, *H.* cf. *douglassi* from the Wagonhound (Fig. 37). The protoloph is less oblique than in A. M. No. 1646, so that the tooth is more nearly rectangular. It is more molariform throughout, and has reached a stage as advanced as dP^2 of the Hyracodontidae and Oligocene Rhinocerotidae. It is interesting to notice that dP^2 of the Hyrachyidae seems to follow the same course in metamorphosis as that which occurs most frequently in the metamorphosis of the rhinocerotoid permanent premolars.

The two posterior upper deciduous premolars serve the function of molars, and are fully molariform. The outline varies from keystone-shaped (e.g., A. M. No. 12137, Fig. 39), to a shape almost indistinguishable from M^1. It is always smaller than M^1, of course, and less rectangular, as it always tapers slightly, lingually. These two teeth may have a small conical cuspule at the internal outlet of the median valley. It may be impossible to distinguish dP^4 from M^1, except by its size, position and the fact that it always tapers slightly more, lingually, than does M^1, although less than dP^3. As is always the case, the posterior deciduous premolars are more molariform than their replacing teeth. They are sometimes said, therefore, to foreshadow the future course of evolution of the permanent premolars. However, $dP^{3\text{-}4}_{3\text{-}4}$ are more molariform than $P^{3\text{-}4}_{3\text{-}4}$, whether they belong to a series in which the permanent premolars are undergoing metamorphosis or not. A more accurate form of expression would be that the deciduous series must fulfil the functions of the entire series of cheek teeth in the adult; hence the posterior deciduous premolars must serve the purpose of molars, and, accordingly, are essentially molariform. It is, of course, obvious that the young individual is as much, if not more, subject to natural selection than the adult, so that the result observed is exactly what would be anticipated.

As in the permanent series, although the lower deciduous premolars do not necessarily evolve exactly pari passu with the upper deciduous series, there is a limit to the extent to which one can advance without necessitating changes in the other. The second lower deciduous premolar is very like its permanent successor. The differences are that it is narrower than P_2, the postero-internal cingulum is better developed, and the metaconid, which forms a ridge down the postero-internal flank of the protoconid, is usually better developed than in P_2, from which, in fact, it may be altogether absent. The external cingulum is likely to be heavier on the permanent tooth. The protoconid, incipient paraconid, and small, longitudinal hypoconid are very similar in dP_2 and P_2. Good examples of dP_2 are *H.* cf. *affinis*, A. M. No. 12693, and *H. modestus*, A. M. No. 11650.

The third lower deciduous premolar is a very interesting tooth throughout the rhinocerotoids. It is always unusually long, and often has the paraconid developed into a third transverse crest, which may appropriately be named the protolophid, anterior to the other crests. This crest may, even in the Rhinocerotidae and Hyracodontidae, develop an anterior hook, and become an asymmetrical crescent, smaller than, but otherwise exactly comparable with, the regular trigonid and talonid

crescents (Wood, 1927*b*, Figs. 12–13). This end stage is never fully reached in the Hyrachyidae, but it is approximated (e.g., *H.* cf. *affinis*, A. M. No. 12693, *H.* cf. *modestus*, A. M. No. 11650, Fig. 9, and *H. modestus*, A. M. No. 12667, Fig. 10). This transverse crest (or protolophid) of dP_3 occludes in front of the metaloph of dP^2, and assumes the function which the transverse crest of the talonid crescent of dP_2 would take, if it were present. The hypolophid-like shape of the protolophid of dP_3 is to be expected, since it has exactly the function and occlusal relations of a hypolophid on dP_2. The fact, then, that dP_3 bites into the median valley of dP^2, the interdental space between dP^2 and dP^3 and the median valley of dP^3, accounts for its unusual length, as it occludes with half a tooth more than its proper quota. Since the protolophid bites in front of the metaconule of dP^2, it would be expected to be small when the protoloph blocks the median valley internally, as in A. M. No. 12693 (Fig. 40), as is actually the case. Therefore, a protolophid which is wide transversely, on dP_3, calls definitely for a dP^2 with the median valley fully open, lingually, or proper occlusion would be impossible. The metaconid of dP_3 usually has a lower "twin" anterior to it (Figs. 9 and 10). This twinned metaconid has nothing in common, except verbally, with the horses, in which the two cuspules are subequal and apparently derived by a subequal division of the original metaconid, in which the posterior element is, perhaps, more nearly a "new" cusp. In dP_3 of the Hyrachyidae, the anterior element is a definitely new structure, which is arising in situ, on the anterior flank of the metaconid. This anterior metaconid "twin" occludes behind the metaloph of dP^2 and thereby increases the efficiency of the bite. Except for the presence of the additional structures described above, the trigonid of dP_3 is essentially molariform, and has the primitive occlusal position, that is, it bites into the interdental embrasure between dP^2 and dP^3. The talonid of dP_3 is fully molariform, as would be expected, since it bites into the molariform median valley of dP^3.

The fourth lower deciduous premolar is fully molariform, and is even more like the first lower molar than the fourth upper deciduous premolar is like the first upper molar. It is smaller than M_1, tapers a little more, anteriorly, and, of course, occupies a different position in the jaw and begins to show wear sooner, but it is not always easily identifiable.

Evolution of the Brain

The brain of *Triconodon* (Simpson, 1927) with its enormous olfactory lobes and its smooth cerebrum, triangular as seen from above, may be taken as the starting-point for the mammalian brain. The primitive protungulate stage is represented by the endocranial cast of the condylarthran *Pleuraspidotherium* (Gaudry, 1896, Fig. 120, after Lemoine) which is at about the evolutionary level of the modern *Didelphis* brain. The olfactory lobes, although relatively reduced in size, compared with *Triconodon*, are large and still lie entirely in front of the small, smooth cerebral hemispheres. The cerebral hemispheres are short, anteroposteriorly, and do not meet in the mid-line, posteriorly, so that they entirely fail to overlap the corpora quadrigemina, to say nothing of the cerebellum. In other words, the parts of the brain still follow each other in the primitive, linear sequence, and the brain is definitely of the olfactory type. The brain of *Phenacodus* (A. M. No. 4369, figured by Cope, 1884, Pl. LVII*b*, Figs. 2, 2*a*, 2*b*, 2*c* and 2*d*) is considerably more advanced than *Pleuraspidotherium*, and is comparable with *Dasyurus* in evolutionary grade. The cerebral hemispheres are larger, relatively, as well as absolutely, and partly overlap the corpora quadrigemina (instead of being entirely in front of them), but still fail to meet in the mid-line, posteriorly.

The most primitive described perissodacyl brains show rather more advance over *Pleuraspidotherium* than the latter does over *Triconodon*. The advance beyond *Phenacodus* is by no means so striking. This primitive perissodactyl stage is known from the endocranial casts of *Hyrachyus*, *Colonoceras* and *Mesohippus*, and is suggested by the living tapirs. (The brains of *Eohippus* or *Homogalax*, when described, should furnish a more primitive stage.) As would be expected, the endocranial cast of *Colonoceras agrestis* (Marsh, 1884, Fig. 70) is very similar to *Hyrachyus modestus* (Marsh, 1884, Fig. 71). The olfactory lobes are still largely anterior to the cerebrum. The cerebral hemispheres meet in the mid-line, cover the corpora quadrigemina, and reach, but fail to overlap, the cerebellum. The arcuate gyri and sulci are nearly, but not quite, longitudinal, spreading laterally a little from front to rear. *Mesohippus* (Scott and Osborn, 1890*b*, pp. 87–88) is closely similar in general pattern, except that the gyri and sulci are almost exactly longitudinal. The transition to the modern horse involves chiefly the partial overlap of the cerebrum over the cerebellum, and more elaborate cerebral convolutions, together with a marked increase in width across the frontal lobe. These changes recall the similar but greater advances in the evolu-

tion of the human brain, and are presumably also associated with increasing intelligence. Modern tapir brains (e.g., Eudes-Deslongchamps, 1842, Pl. III) recall *Mesohippus*, and, more closely, the hyrachyid brain, which is about half-way intermediate between the other two. The arcuate gyri and sulci spread laterally, in the tapir, from front to rear, more than in the hyrachyids, so that they are definitely oblique in position, although not so much so as in the true rhinoceroses. The hyrachyid cerebrum does not overlap the cerebellum at all; in the tapir, there is a slight overlap. The tapir cerebrum is, of course, much more convoluted than the endocranial casts of *Mesohippus* and *Colonoceras*. However, when the difference between the brain and the over-simplified endocranial cast is allowed for, it seems legitimate to consider all three as essentially comparable in evolutionary grade. *Amynodon* (Marsh, 1884, Fig. 72) parallels the true rhinoceroses in the shortening of the cerebral hemispheres, with marked widening across the temporal region. The failure of the cerebrum to overlap the cerebellum is a retention of the primitive character. It is only in rough outline that the brain of *Amynodon* suggests the true rhinoceroses; in all other respects, it has not advanced beyond the hyrachyid brain. A similar combination occurs in *Palaeosyops* (Earle, 1892, Pl. XI). Perhaps both are associated with the shortening of the cranial region.

The various known true rhinoceros brains all represent an advance over the hyrachyid brain, on an essentially uniform plan, with the cerebral hemispheres relatively shorter than in the hyrachyids, and wider across the temporal lobes. The cerebrum overlaps the cerebellum and is more convoluted than in the less advanced forms. *Diceratherium* (*armatum*, not "*advenum*" as stated, which belongs in *Amynodon*—Marsh, 1897, Fig. 3) seems to have reached almost the level of the living rhinoceroses, except that the olfactory lobes are still anterior to the cerebral hemispheres and more distinct from them. The shape of the brain, and the overlap of the cerebrum over the cerebellum, recall modern rhinoceroses. The living Indian and Sumatran rhinoceros brains are very similar to each other, except that the Sumatran is more richly convoluted and the Indian more expanded across the frontal lobes (Owen, 1862, Pl. XIX, and Garrod, 1879, Pl. LXX). The most advanced rhinoceros brain known is that of *Teleoceras* (Scott and Osborn, 1890, pp. 93–94), which is proportionately much larger than the brain of the Sumatran rhinoceros, and shows a marked expansion across the frontal lobes, so that the endocranial cast, in top view, is more advanced than the Indian rhinoceros, and rather suggests *Pliohippus*. The lateral

aspect of the brain is closely comparable with the Sumatran and Indian rhinoceroses. The brain of *Elasmotherium* (Gaudry and Boule, 1888, Pl. XVI, Fig. 3) seems fairly comparable with the Indian rhinoceros, except that it is proportionately a little narrower across the temporal region. It is actually larger in size, being about seven inches long, as compared with six for *R. unicornis*. This greater size, however, would be expected, in view of the larger size of the animal, and does not, in itself, indicate a more advanced condition.

The titanothere brain undergoes a similar longitudinal contraction combined with lateral expansion across the temporal lobes, but always remains proportionately smaller and more primitive than in the true rhinoceroses.

In addition to Marsh's summary of the tendencies in brain evolution, it is interesting to notice the frequent change, in unrelated lines, from an elongated oval to a triangular cerebrum, and, less often, from the triangular to a shorter oval (all dorsal view). This is presumably due, in part, to the development, starting from an olfactory brain, of a more auditory and visual type, followed, in the most successful lines, by a development of more elaborate intercoördination and of the frontal lobes which largely control such "higher thought." The cerebellum remains very stable throughout all these changes; the real advances are in the relative size and complexity of the cerebrum, and are indicated by the extent to which it overlaps the cerebellum. Analysis of the comparative anatomy of the brains and endocranial casts agrees with the somewhat over-simplified generalization that the tapirs remain at an Oligocene evolutionary level, the Asiatic rhinoceroses at a Miocene level, and the African rhinoceroses at a Pliocene level. Only the horses, among living perissodactyls, can be considered as "modern" forms, in contrast to the other perissodactyls, which are fairly considered as "living fossils." It is an interesting subject of speculation whether this is not the principal reason for the gradual replacement of perissodactyls by artiodactyls, during the Tertiary.

Skeletal Evolution

The known skeletons of the hyrachyids (*H. affinis*, *H. modestus* and *H. eximius*) are exceedingly homogeneous. No evolutionary trends appear, except differences in size and proportions. *H. affinis* is more slender than the *modestus-eximius* line, as well as smaller. No tendency is visible toward the loss of the fifth digit of the manus. The transition to the Hyracodontidae rather probably coincided with this loss of

the fifth digit, although this has not been proved definitely. This loss was entirely independent from that in the Rhinocerotidae and it probably took place independently in several different lines of the true rhinoceroses. It never occurred at all in the Amynodontidae. For measurements and skeletal proportions, see Wood, 1927*b*, Table VII.

SUMMARY

1. The Perissodactyla show a very early and very fundamental dichotomy into two suborders, for which the names Solidungula and Tridactyla could be appropriately revived. The family Hyrachyidae is a very primitive group of the Rhinocerotoidea, and still closely resembles the other Eocene families of the suborder Tridactyla. The family is known from the Eocene (Lost Cabin to Uinta, inclusive) of Wyoming, Utah, Colorado and Montana. It includes four genera, of which *Hyrachyus* is by far the best known. *Hyrachyus* has the greatest time range of any American Eocene ungulate genus, and has an unusually long range for a placental mammal. The taxonomy, stratigraphic distribution and probable phylogeny are summarized in figure 1.

2. The genus *Hyrachyus* apparently includes three contemporary main series (consisting of small, medium-sized and large forms, two of which series have side branches, of which a few are rather aberrant in one or more characters). Each series contains successive grades of organization which are best treated as species. It is significant that, when known from sufficiently numerous specimens, the individual measurements of the representatives of each species form normal curves of distribution, with relatively slight, or no, overlapping with other contemporary forms, or with earlier or later forms. Certain of these forms are now sufficiently well documented to deserve rank as index fossils for their respective horizons. *H. modestus* is an index fossil for the Lower Bridger, *H. eximius* and *H. princeps* for the Upper Bridger, and the genus *Hyrachyus* is very characteristic of the Bridger in general, although not confined to it.

3. Paired horns appear independently in the second and third genera of the family, *Colonoceras* and *Metahyrachyus*. *Colonoceras* is close to *H. affinis*. *Metahyrachyus* is a rather aberrant form, particularly as to P^2, in which the peculiar "amphiloph" parallels the similar development in P^3 of the horses.

4. The fourth genus, *Ephyrachyus*, not previously separated from *Hyrachyus*, is the most advanced member of the family, and shows progress toward a rhinocerine grade of organization. It could hardly be

ancestral to any of the American or European true rhinoceroses, but might conceivably lead to *Caenolophus* of Mongolia, especially to *C. obliquus*. I doubt Matthew's view that *Caenolophus* might be ancestral to the true rhinoceroses, since it is rather too late in time, nor can I accept his alternative hypothesis that primitive amynodonts were the ancestors of the true rhinoceroses. On the contrary, this study confirms the traditional view that the Hyrachyidae are approximate, morphological ancestors of the other rhinocerotoids, although the actual common ancestor has probably not yet been discovered, and should be found in the early Lower Eocene, in view of the presence of a true rhinoceros, *Prohyracodon*, in the Auversian of Transylvania (Wood, 1929*b*).

5. The Hyrachyidae agree with other lines (Matthew, 1909) in suggesting a hiatus between the Lower and Upper Bridger. The following new stratigraphic names are proposed, to represent units which are already rather widely, although tacitly, accepted: Black's Fork, Twin Buttes, Wagonhound, and Myton. Emmons Peak is proposed as a substitute for "Uinta" Quartzite, and Green Cove for "so-called Bridger." The Sage Creek Beds are apparently of either Lower Uinta or Upper Bridger age. Cook Ranch is proposed for new Middle Oligocene Beds in the Sage Creek region of Montana.

6. Study of the brain casts of the hyrachyids, as compared with more primitive and more progressive forms, illustrates the same tendencies seen in other lines.

7. It is possible to follow the evolution of the permanent premolars, deciduous premolars, and molars. In some of the lines, the metamorphosis of the upper premolars may be followed step by step, from one horizon and its species to the next. It is not possible to do this for the lower premolars and deciduous premolars, but general trends may be recognized. Although the molars are usually notable for their conservatism, some changes may be observed. Evolution of the upper and lower teeth usually moves pari passu, as would be predicted, thereby safeguarding the occlusal relations, or if aberrant changes do occur, they are of such a character as not to interfere with the occlusion. All phases of the evolution of the cheek teeth conform to mechanical principles, but there is no evidence favoring orthogenetic or neo-Lamarckian interpretations of this accordance. On the contrary, the data may best be explained on the strictly neo-Darwinian basis of natural selection from among random mutations.

COMPARATIVE MEASUREMENTS—TABLE I

(Measurements in Millimeters)	*H. modestus* type U. S. N. M. No. 661	*H. modestus* A. M. No. 12667		*H. bairdianus* cotype Y. M. No. 11035	*Hyrachyus bairdianus*, apotype Y. M. No. 11081		*H. modestus* A. M. No. 11651	
	L.	R.	L.	L.	R.	L.	R.	L.
Across zygomas							e122.9	
Pmx. to condyle							e268.5	e265.5
Nasal to occipital crest							e270.8	e272.8
Occiput above condyle							70.1	71.0
Bet. P^2s					25.7		30.6	
Bet. M^2s							e41.4	
P^1-M^3			e96.9		93.5	97.3	93.7	
P^2-M^3			e86.0		85.6	87.4	83.3	82.7
P^{1-4}			46.4		42.0	44.5	43.6	
P^{2-4}			36.3		33.2	33.6	33.0	32.8
M^{1-3}		e50.0	e49.6	51.6	53.6	53.3	51.4	51.1
Diastema			28.6				25.6	
Length P^1			8.8		8.5		9.6	
Width P^1			6.2		6.0		6.6	
Length P^2			9.1		9.6	8.6	9.9	9.7
Width P^2			11.1		11.0		11.1	11.3
Length P^3	d13.4				10.7	11.0	11.0	11.5
Width P^3	d14.1				15.3	15.0	15.0	15.9
Length P^4		d14.3	d14.4		12.4	12.4	12.6	12.3
Width P^4		d16.4	d16.8		18.0	18.0	17.2	17.1
Length M^1		16.9	16.6	15.1	16.0	16.7	15.3	15.2
Width M^1		19.9	19.0		19.8		18.5	18.9
Length M^2		19.4	19.0	18.4	18.9	18.8	18.6	17.8
Width M^2		21.8	21.7		21.4	21.0	21.4	20.9
Length M^3				18.5	18.7	18.9	18.0	18.2
Width M^3				21.7	22.0	21.3	21.1	20.9

H. modestus A. M. No. 11713		*Hyrachyus* cf. *modestus* Huerfano A. M. No. 17014	*H. eximius* neotype A. M. No. 1645		*H. eximius* A. M. No. 12366		*H. eximius* Y. M. No. 12533	*H. eximius* A. M. No. 11660 (teeth shoved together by crushing)		*Hyrachyus eximius* Y. M. No. 12535		*Hyrachyus eximius* Y. M. No. 12553 (tending toward *H. douglassi*)	
R.	L.	R.	R.	L.	R.	L.	L.	R.	L.	R.	L.	R.	L.
				e140.0				161.0					
e259.0			e291.0	e290.0									
			74.0	74.0									
33.6													
e45.0								52.3					
101.1			109.8	111.5	106.6								
93.0	e91.3		100.0	101.0	98.1			96.9					
44.6			50.5	50.6	45.8								
35.4	e34.4		39.4	39.6	36.1			36.3					
57.2	57.2		60.5	61.4	61.3	61.0	62.2	61.2	64.9		67.3		
20.6	21.3		27.5	27.5		e34.2							
8.6			10.4	10.8		10.0							
6.3			7.7	7.8		7.6							
9.9	e9.9		11.5	11.4	8.7			10.1					11.5
12.3	12.0		13.8	13.7	13.6			12.4					11.4
11.9	11.8		13.2	13.3	11.9	11.9		12.2	12.1			13.7	
16.5	16.4		16.8	17.0		17.2		17.8	17.6			18.4	
13.1	13.1		14.8	15.2	14.7	14.0	16.6	14.0	14.9		14.8	16.7	16.2
17.9	18.1		19.2	19.4	e21.5	20.8	20.3	21.1	21.0		21.1	22.3	22.2
17.6	17.6		18.6	19.0	17.5	17.9	e19	18.1	17.5			21.2	
20.0	20.2			22.2	22.4	22.9	21.7		23.0		25.4	24.0	
20.0	20.1	17.3	21.6	22.2	20.0	21.0	22.6	21.0	21.6	24.0	24.0	22.9	
23.0		19.2	24.4	24.3	25.7		26.4	25.0				25.6	
19.8	19.6	16.5	20.4	20.6	22.1	21.9	22.3	23.0	23.6		25.4		
24.0		18.0	22.6	23.9	24.8	25.7	25.4		26.6		28.6		

d—deciduous.
e—estimated.

COMPARATIVE MEASUREMENTS—TABLE II

(Measurements in Millimeters)	*H. hypostylus*, holotype A. M. No. 12666		*Hyrachyus douglassi*, holotype C. M. No. 784	*Hyrachyus princeps*, holotype Y. M. No. 11157		*H. imperialis*, holotype P. U. No. 10789	
	R.	L.	R.	R.	L.	R.	L.
Across zygomas							
Pmx. to condyle							
Nasals to occipital crest							
Height occiput above condyle							
Width between P^2s							
Width between M^2s							
P^1-M^3							
P^2-M^3							
P^{1-4}	48.2		46.7				
P^{2-4}	e38.2		35.0		45.6		
M^{1-3}		65.4		e72			
Diastema							
Length P^1	10.3	10.8	10.0				
Width P^1	8.8	8.5	6.4				
Length P^2		10.0	8.7		13.		
Width P^2			11.5		e17.		
Length P^3	12.8		12.0		15.2		
Width P^3	19.1		e18.0		21.7		
Length P^4	15.9	16.2	14.5		18.0		
Width P^4	21.7	22.0	e22.0		25.5		
Length M^1	18.1	19.2		20.6	21.6		
Width M^1	22.5	22.7	25.0	e24	26.3		
Length M^2	23.8	23.2		24.5	25.5	24.1	24.4
Width M^2	27.9	26.7			e29	30.0	30.2
Length M^3	24.5	23.7		26.7			
Width M^3	26.8	26.2		30.8			

H. princeps A. M. No. 12371 (not fully adult)		*H. princeps* A. M. No. 12669	*Hyrachyus princeps* A. M. No. 12364		*Metahyrachyus bicornutus*, holotype Y. M. No. 10258		*Metahyrachyus troxelli*, holotype A. M. No. 12362	
R.	L.	L.	R.	L.	R.	L.	R.	L.
136.4			179.5					
	317.5		346.0	346.0				
			339.0	339.0				
			77.8	74.6				
33.7					e37			
42.5			e58.0		43			
116.3	116.6		126.2			112	110.0	109.5
108.3	107.1	108.6	114.0	115.9		102.3	100.3	101.0
51.5	51.4		55.3			50.0	48.6	48.0
42.2		40.8	43.5	44.6		39.6	38.8	38.4
65.6	66.4	68.1	70.8	71.4	63.9	63.5	61.0	61.7
28.0	29.0		39.3	35.4	24.7			
10.1	10.2		11.6	12.4	10.5	10.5	10.0	9.9
7.1	7.1		9.8	9.7	7.6	8.0	7.4	7.1
		11.1	11.7	11.9		11.2	10.7	10.5
		14.3	16.3	16.2		13.0		14.6
		13.4	14.4	15.0	13.3	13.3	12.5	12.8
		e21.0	22.5	23.2	17.9	18.3	18.4	18.4
16.4	16.5	15.9	16.8	16.8	15.9	16.0	15.1	15.6
23.0	22.6	23.8	24.7	26.4	20.9	21.0	21.4	21.5
21.0	20.8	20.6	20.0	21.0	19.4	19.2	19.0	18.5
26.1	25.7		27.2		24.4	e23.5	22.2	22.7
24.0	24.0	24.0	24.5	24.4	22.8	22.8	22.6	21.9
28.8	28.7		30.0	29.4	26.8	e25	25.0	
22.4	21.9	23.3	27.3	26.8	22.3	22.5	21.8	22.0
26.8	26.4	26.5	30.7	30.8	26.7	e25.2	25.8	25.5

e—estimated.

COMPARATIVE MEASUREMENTS—TABLE III

(Measurements in Millimeters)	*Hyrachyus affinis*, holotype Y. M. No. 12530	*H. affinis*, plesiotype Y. M. No. 12572	*H. affinis* Y. M. No. 12572*D*	*H. affinis* A. M. No. 12664		*Hyrachyus affinis gracilis*, holotype Y. M. No. 11170	
	R.	R.	R.	R.	L.	R.	L.
Across zygomas							
Pmx. to condyle				e221.5			
Occiput above condyle				64.1	63.3	63.5	64.2
Bet. P^2s						e20	
Bet. M^2s						22+	
P^1-M^3				84.0		74.8	74.2
P^2-M^3		71.0	72.2	75.2	76.3	70.7	69.0
P^{1-4}				39.4		32.	32.6
P^{2-4}		28.1	28.8	30.0	31.0	26.7	26.7
M^{1-3}	43.4	43.3	43.8	45.3	46.0	43.7	43.1
Diastema				9.9	11.2		
Length P^1				9.4			7.3
Width P^1				5.0			6.4
Length P^2		8.4	9.3	9.1	9.4	7.2	7.5
Width P^2		10.4	10.5	10.0	9.3		8.9
Length P^3		9.0	9.3	9.9	10.0	9.5	9.2
Width P^3		12.6	12.6	12.5	12.6		12.2
Length P^4	11	10.7	10.8	10.9	10.8	10.1	10.3
Width P^4	14	14.3	14.3	14.3	14.4	15.–	14.7
Length M^1	13.4	13.4	13.9	13.9	13.7	14.0	13.2
Width M^1				17.0	17.6	16.9	16.3
Length M^2	15.7	14.7	15.8	15.4	16.5	14.9	15.0
Width M^2	17.0			19.2	19.0	18.0	e18
Length M^3	15.1	15.1	15.8	15.8	16.0	15.0	15.0
Width M^3	17.1			18.0	18.0	17.5	

H. affinis (*H. "implicatus,"* type I) A. M. No. 5072		*Colonoceras agrestis*, holotype Y. M. No. 11082		*Ephyrachyus implicatus*, type II. A. M. No. 5078	*Ephyrachyus cristalophus*, holotype A. M. No. 12359		*H. "paradoxus"* type lost (measurements fide O. S. S.)
R.	L.	R.	L.	R.	R.	L.	
		83+					
		e69.5	e68.4				
		16.5					
		22.2					
				e82		78.0	
		71.1	71.3	e79		71.0	
		36.2	37	e37.5		37.4	
		28.4	28.6	31.0		30.2	
e48	e48	44.2	43.6	e45		41.0	
		14.4	15.0				
					8.4	8.4	11
				5.6	4.7	4.2	16
		8.3	8.8	8.7		7.8	12
		10.2	9.8	9.6		7.5	14
e10.8		9.9	9.6	10.0		9.6	
e13.5		12.8	12.5			11.4	
11.6	11.5	10.5	10.6	12.2	11.4	11.4	
		13.7	14.2	15.0	13.9	13.7	
15.0	e15	13.7	13.7	15.0	13.3	13.6	
		16.1	16.2	17.3	15.6	15.8	
17.0	17.0	15.1	15.4		14.6	14.7	
	e20	17.6	18.0	e18	16.4	16.5	
	e16.2	15.4	15.6			e14.0	
e19.5		17.0	e17.1			e14.5	

e—estimated.

COMPARATIVE MEASUREMENTS—TABLE IV

(Measurements in Millimeters)	*Hyrachyus agrarius*, holotype U. S. N. M. No. 110 (roots only)	*Hyrachyus bairdianus*, apotype Y. M. No. 11081		*Hyrachyus agrestis*, holotype U. S. N. M. No. 660	*Hyrachyus* cf. *modestus* Huerfano A. M. No. 17442	*Hyrachyus* cf. *modestus* Huerfano A. M. No. 17440
	L.	R.	L.	L.	L.	R.
A–P I_3		e7	7.1			
A–P C_1		7.8	8.0			
Diastema		31.4				
Symphysis, length		63.0				
Length P_1-M_3	93.2					
Length P_2-M_3	84.5	86.7	87.0			
Length P_{1-4}	40.6			d45.2		
Length P_{2-4}	32.0	34.6	34.6	d38.8		
Length M_{1-3}	52.4	53.7	53.8			49.9
Ramus, below P_2			33.6			
Ramus, below M_2	39.0					
Length P_1	7.6			6.7		
Width P_1				3.9		
Length P_2	8.0	9.7	9.6	d9.3 roots	8.5	
Width P_2		5.7			6.4	
Length P_3	10.5	12.7	12.8	d13.2 roots		11.0
Width P_3		8.2	8.2			8.2
Length P_4	11.6	12.8	12.6	d15.7		12.1
Width P_4		9.5		d9.2		9.0
Length M_1	15.0	15.7	15.6	e17.3	14.5	14.5
Width M_1		10.8	11.0	e11	10.0	
Length M_2	16.6	18.4	18.3			17.0
Width M_2		12.1	12.0			11.4
Length M_3	17.6	19.7	19.5		17.3	18.0
Width M_3		11.2	11.7		10.5	10.2

H. modestus A. M. No. 12667		*H. bairdianus* Y. M. No. 11057 Cotype	*Hyrachyus modestus* Phil. Acad. No. 10301	*H. modestus* A. M. No. 11651	*H.* cf. *modestus* A. M. No. 14886 Lost Cabin		*H.* cf. *modestus* A. M. No. 4887 Lost Cabin	
R.	L.	L.	R.	L.	R.	L.	R.	L.
7.5				8.7				
				25.5				
48.9				55.6+				
				96.6				
				87.6				
				44.0		43.1		
				35.1		35.6		
		51.8		53.0				
				31.7				
				38.6				
				8.9	7.4	7.2		
				4.1	4.0	3.9		
	10.4					10.2	10.6	10.1
	6.6					6.7	6.1	6.2
12.9	13.0					12.1	12.3	
8.4	8.5					8.7	8.1	
14.4					14.1	13.8		
10.5					10.0	10.0		
17.7		16.9		15.5				
11.9		10.2		10.4		11.1		
		17.7	18.3	18.6				
			12.1	12.1				
		19.1		20.4	20.0			
		10.8		11.0	11.2			

d—deciduous.
e—estimated.

COMPARATIVE MEASUREMENTS—TABLE V

(Measurements in Millimeters)	*Hyrachyus eximius*, holotype Phil. Acad. No. 10320	*H. eximius*, neotype A. M. No. 1645		*H. eximius* A. M. No. 11660	
	R.	R.	L.	R.	L.
A–P I_3			7.1		
A–P C_1		10.7	10.5		
Diastema			30.8	37.9	37.0
Symphysis			60.5		e68.0
P_1-M_3			111.4	111.4	107.7
P_2-M_3		102.8	101.8	104.3	100.9
P_{1-4}			49.7	46.2	44.7
P_{2-4}		40.5	39.8	38.5	37.6
M_{1-3}		63.3	63.7	66.0	63.4
Depth ramus below P_2		34.6	35.6	37.1	37.6
Depth ramus below M_2		43.1	44.5	41.9	43.0
Length P_1			10.3	8.1	8.1
Width P_1			5.1	4.0	4.0
Length P_2		11.7	11.6	11.1	10.7
Width P_2		6.8	6.6	6.0	6.0
Length P_3		14.8	15.1	12.6	12.6
Width P_3		9.1	9.3	8.8	8.8
Length P_4	15.4		16.0	15.0	14.7
Width P_4	11.2		11.1	11.8	11.8
Length M_1		19.6	19.3	17.4	17.6
Width M_1	13.1	12.9	13.0	12.6	12.8
Length M_2		21.8	21.0	21.1	21.3
Width M_2		13.9	14.0	e14.2	
Length M_3		22.1	22.3	25.7	24.5
Width M_3		12.8	12.8	13.9	14.1

H. eximius Y. M. No. 12553 (tending toward *H. douglassi*)		*H. hypostylus*, type A. M. No. 12666		*Hyrachyus douglassi*, holotype C. M. No. 784		*H.* cf. *douglassi* Y. M. No. 10259	
R.	L.	R.	L.	R.	L.	R.	L.
111.0							
43.0	43.5		40.1				
48.7				57.8	57.8	52.8	53.0
38.4				40.0	38.4		
						33.0	33.4
12.2	12.2	11.9	11.3				
7.6	7.5	7.5	7.3	6.8			
15.0	14.2	14.2	13.3	12.0	12.2	12.0	11.6
10.4	10.4		10.0	10.0		7.4	7.9
16.7	17.5		15.5		14.3	12.9	13.7
13.5	12.8			11.0		9.1	9.2
21.1	21.6			16.1	16.0	17.0	17.0
13.8	14.0			12.3	12.3	11.4	11.3
22.8		23.5	23.7	20.4	20.0	18.8	18.5
15.8		16.6	16.2			11.7	11.5
25.2	25.4	25.3	25.7	22.0	21.0	19.4	19.0
14.0	14.8	15.0	14.9	13.5	13.3	10.5	10.5

e—estimated.

COMPARATIVE MEASUREMENTS—TABLE VI

(Measurements in Millimeters)	*H. princeps*, holotype Y. M. No. 11157		*H. princeps* A. M. No. 12669	*H. imperialis*, holotype P. U. No. 10789	*H. princeps* A. M. No. 12364	
	R.	L.	R.	R.	R.	L.
A–P I_3						
A–P C_1						
Diastema						
Symphysis, length						
Length P_1-M_3					124.4	125.2
Length P_2-M_3					116.0	114.9
Length P_{1-4}					52.9	54.1
Length P_{2-4}					44.8	45.4
Length M_{1-3}					72.6	72.0
Ramus below P_2					45.8	45.5
Ramus below M_2					52.8	48.8
Length P_1					8.7	9.1
Width P_1					5.8	6.0
Length P_2					12.6	12.6
Width P_2					8.6	8.6
Length P_3					14.9	15.3
Width P_3					11.2	11.8
Length P_4					17.8	16.9
Width P_4					13.3	13.8
Length M_1					21.7	21.8
Width M_1					14.7	15.1
Length M_2				25.0	25.0	24.5
Width M_2	17.3			18.0	16.3	16.3
Length M_3		28.3	27.0		27.4	28.0
Width M_3	16.4	16.8	15.7		17.9	16.9

Hyrachyus grandis, holotype C. M. No. 2908		*Hyrachyus affinis gracilis*, holotype Y. M. No. 11170		*H. affinis* A. M. No. 12664		*H. crassidens*, holotype P. U. No. 10138	*Metahyrachyus troxelli*, holotype A. M. No. 12362	*Ephyrachyus implicatus* (lectoholotype) A. M. No. 5078
R.	L.	R.	L.	R.	L.	L.	R.	R.
				6.1	6.0			
11.5	11.5				7.3	7.3		
20.2	30.4				12.8	10 5		18.5
86.5				e46.0				e38
	161.0				84.2	e81		
146.0	148.0	74.2	72.1	77.8	77.8	e78.5		e77
	70.6				38.2	r31.7		
58.0	57.7	29.0	27.4	32.0	31.5	r29.0		30.3
88.8	90.5	44.7	45.0	47.3	47.3			e47.5
48.0	46.2	24.6	23.2	29.0	27.9	21.8		23.0
	52.0	29.0		32.3	31.5	24.6		
10.0	13.6				7.3			
7.0	8.0				3.8			
18.0	16.7	9.0	8.1	9.6	9.1			
11.5	10.9	4.4	4.4	5.4				4.5
19.7	20.6	10.5	10.5	11.2	10.5	9.4		11.0
13.2	13.7		6.3	7.5	7.3			7.0
20.7	21.4	11.2	11.0	11.4	11.9	10.2		12.1
15.5	15.0		8.0	8.5	8.4			7.8
24.6	23.4	14.0	13.7	14.0	14.0	14.0		14.8
19.1	19.1		9.8	9.6	9.7	9.0		
31.5	31.5	15.9	16.3	16.0	15.6	r15.2		17.4
22.1			10.3	10.8	10.8			10.5
35.0	36.3	17.5	17+	16.9	17.0		24.1	e17.0
21.9		10.1		10.8	10.2		14.0	e10.0

e—estimated.
d—deciduous.
r—across roots.

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Plate XX. *Hyrachyus princeps*, A. M. No. 12364, lateral view of skull, $\times\frac{1}{2}$.


A.M. 12364
1/2

Plate XXI. *Hyrachyus princeps*, A. M. No. 12364, skull roof, $\times\frac{1}{2}$.


A.M. 12364
1/2

Plate XXII. *Hyrachyus princeps*, A. M. No. 12364, palate, $\times\frac{3}{4}$.

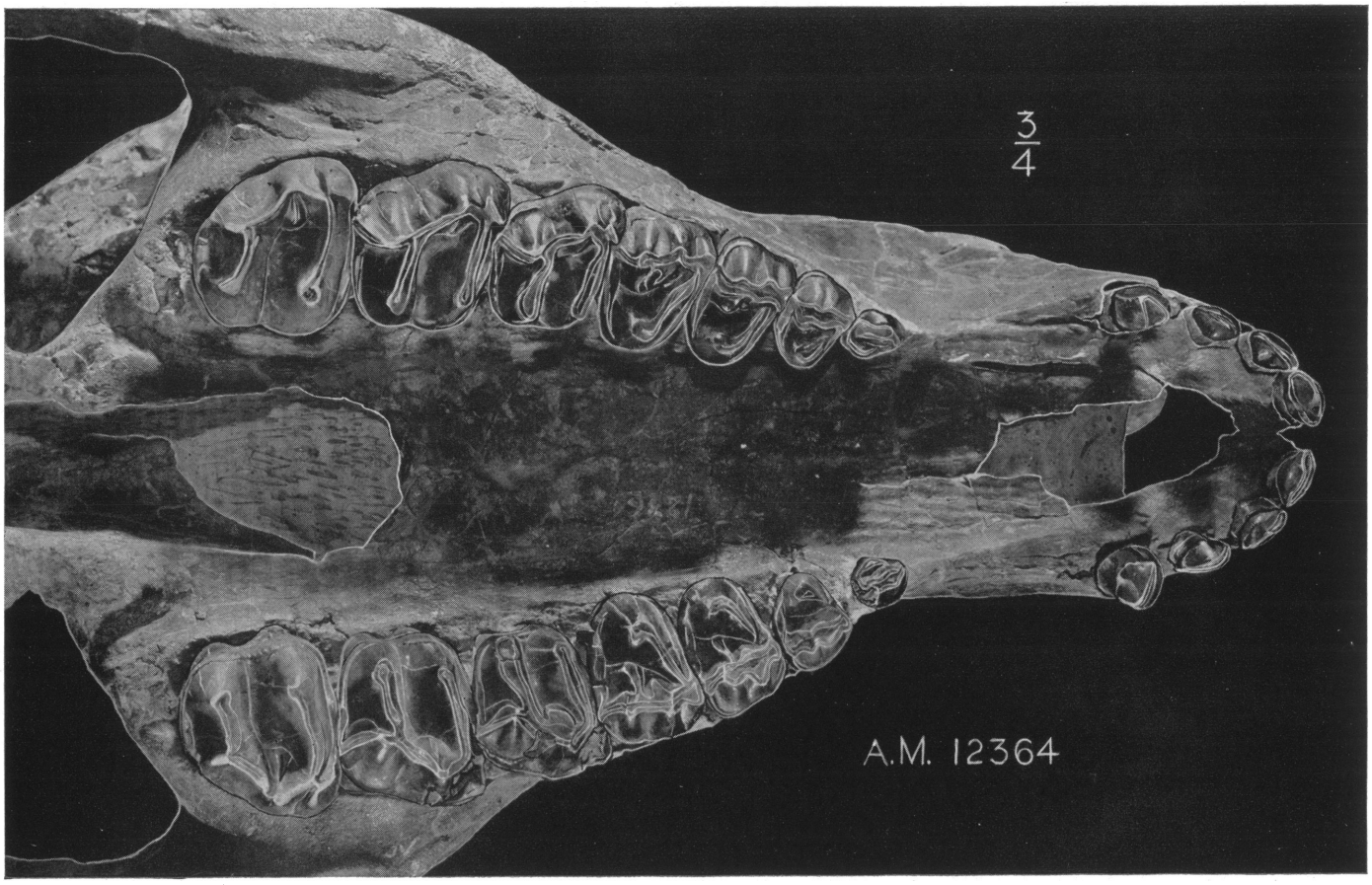

3/4
A.M. 12364

Plate XXIII. *Hyrachyus princeps*, A. M. No. 12364, lower jaws, $\times\frac{3}{4}$.

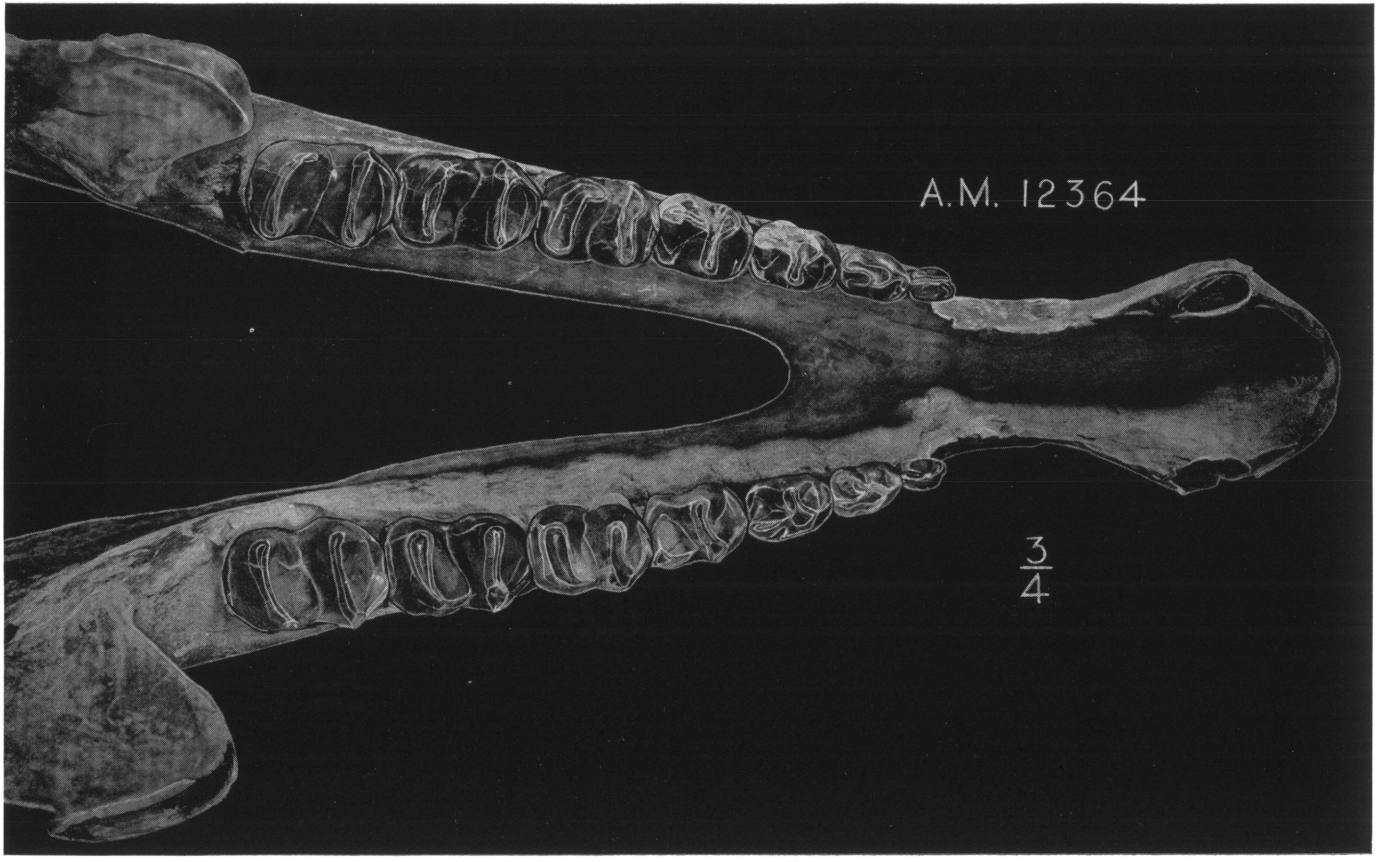
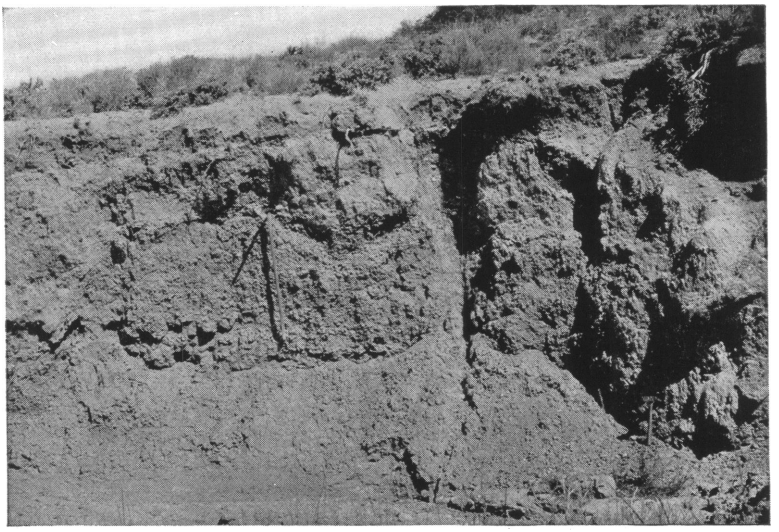

A.M. 12364
3/4

Plate XXIV*a*. Disconformity between the Lost Cabin Formation and the yellow-brown arkose ("so-called Bridger"), Riverton cut-off locality (Fig. 3), Wind River Basin, Wyoming, looking north. The contact is emphasized by a broken line.

Plate XXIV*b*. Closer view of part of the exposure shown in Plate XXIV*a*.

a



b