In Prothero, [illegible], *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge.

29. Hyracodontidae

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ABSTRACT

The taxonomy of *Hyracodon* has long been confused by the variability of the cusps and crests on the upper premolars. Some authors have oversplit the genus into as many as 11 species, while others recognized only a single species. Based on much larger collections now available, I recognize five valid species of *Hyracodon*: *H. primus* from the Duchesnean; *H. petersoni* from the early Chadronian; *H. priscidens* from the early and middle Chadronian; the highly variable type species, *H. nebraskensis*, from the late Chadronian to early Arikareean; and the larger *H. leidyanus* from the Whitneyan and early Arikareean. Both *H. nebraskensis* and *H. leidyanus* last appear in the lower Sharps Formation, and their extinction coincides with the early Arikareean faunal reorganization.

INTRODUCTION

In 1850, Joseph Leidy published the first notice of North American rhinoceroses. In a few brief paragraphs, he described (but did not illustrate) some teeth he called *Rhinoceros occidentalis* (now referred to the rhinocerotid taxon *Subhyracodon occidentalis*)and *Rhinoceros nebraskensis*. In 1851, Leidy placed both *R. occidentalis* and *R. nebrascensis* (misspelled by Leidy and most later authors from this point onward with a "c" instead of a "k") in the European Oligocene-Miocene genus *Aceratherium*, because their teeth had cingula, unlike living *Rhinoceros*. Finally, in 1852 Leidy gave a full description and illustration of *R. nebrascensis*. He figured and discussed these specimens at length in his 1853 monograph on the "Ancient Fauna of Nebraska." In 1856, Leidy transferred *R. nebrascensis* to a new genus, *Hyracodon*, without a generic description or diagnosis, other than that it possessed "a greater number of teeth than any other known member of the *Rhinoceros* family." This refers to the fact that *Hyracodon* still has the incisors and canines that have been lost in most of the Rhinocerotidae.

Edward Drinker Cope described hyracodontids in 1873, when he proposed the species *Hyracodon arcidens* for fragments of two or three individuals from the Orellan Cedar Creek beds of Colorado.

While they were still undergraduates at Princeton, Scott and Osborn (1887) described some White River collections at the Museum of Comparative Zoology of Harvard University. They named two new species of *Hyracodon*. One was *H. major*, which was based on a partial skeleton of a large individual that cannot be compared to any taxon based on teeth. Sinclair (1922) recommended that this taxon be abandoned. The other was *H. planiceps*, which was actually a calf of *Subhyracodon*. Wood (1961) applied to the International Commission of Zoological Nomenclature for suppression of the name *planiceps*, and the name has been suppressed.

In the early part of this century, species names of rhinocerotoids continued to proliferate because most paleontologists considered every slight difference in premolars to be grounds for a new taxon. Lambe (1905) described *H. priscidens* from the Chadronian of Saskatchewan. Troxell (1921) proposed three new species of *Hyracodon*: *H. leidyanus*, *H. selenidens*, and *H. arcidens mimus* (misspelled "*minimus*" by some authors). Sinclair (1922) reviewed all the known species of *Hyracodon*, and recognized that all the Orellan species intergraded in size and morphology. Unfortunately, he did not use this argument to reduce the number of invalid names. Instead, he recognized four species groups: *H. nebrascensis*, *H. arcidens* (including *H. priscidens* and *H. selenidens*), *H. leidyanus*, and a new species, *H. apertus*. Abel (1926) reviewed the molarization of premolars in *Hyracodon*, showing their continuous intergradation. His diagram (Fig. 1) is misleading, because it gives the impression of a continuous chronocline in premolar crests. In fact, the first four specimens (I-V) all come from the early Orellan, and are thus part of a nearly contemporaneous population sample; the lower four specimens (VII-X) are also from the same level (the late Whitneyan) and represent variability within a single time frame. Based on this intergradation, he considered them to be "races" or subspecies of *H. nebrascensis*.

Horace Wood's first (1926) publication on rhinocerotoids erected yet another new species, *H. petersoni*. In 1927, Wood published his landmark review of Tertiary rhinoceroses and hyracodonts, but did not add any new species of *Hyracodon*.

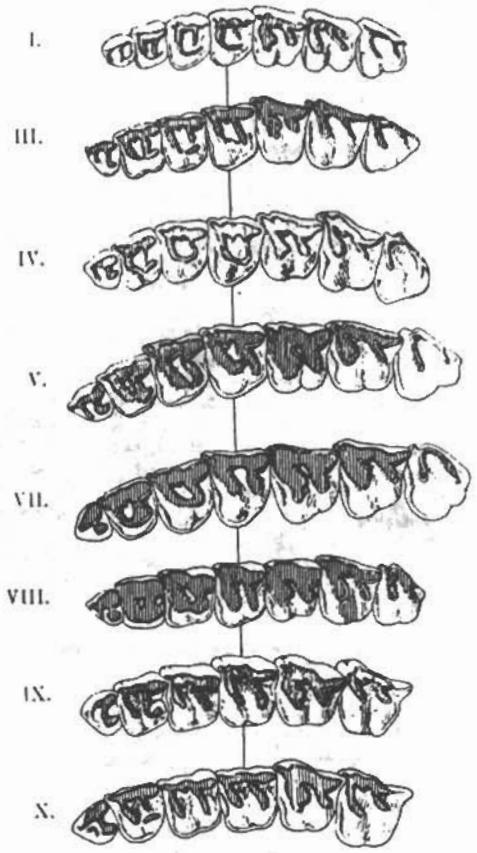

Figure 1. The molarization of upper premolars in *Hyracodon* cheek teeth, as originally shown by Abel (1926). The vertical line runs through the P4 in each specimen for reference. I is the type of *H. selenidens* (YPM 11173), as illustrated by Troxell (1921). III was referred to *H. nebraskensis* (YPM-PU 12687) by Sinclair (1922). IV was referred to *H. arcidens* (YPM-PU 12518) by Sinclair (1922). V was referred to *H. nebraskensis* (YPM-PU 12563) by Sinclair (1922). Although I-V are drafted to give the impression of a chronocline, all are from the early Orellan. VII is the type specimen of *H. apertus* (YPM-PU 10803) figured by Sinclair (1922). VIII was also referred to *H. apertus* (YPM-PU 12705) by Sinclair (1922). IX is the type specimen of *H. leidyanus* (YPM 11169) after Troxell (1921). X was also referred to *H. leidyanus* (YPM-PU 10802) by Sinclair (1922). VII-X also appear to be a chronocline, but all four are from the late Whitneyan.

The discovery of a large quarry sample of the early rhinocerotid *Trigonias* from the Chadronian Davis Ranch Quarry, Weld County, Colorado, provided the first evidence that primitive rhinocerotoid upper premolars were highly variable within a single population, and might not be reliable criteria for biological species. These specimens were described by Gregory and Cook (1928), who demonstrated that the entire sample was homogeneous in size and in all morphological features except for the molarization of upper premolars. Nevertheless, they followed the typological traditions of their time and recognized six species of *Trigonias* (four of them new) and called one specimen ?*Caenopus premitis*. In their paper, Gregory and Cook (1928, p. 4) commented on how plastic the variability of the population was, and suggested that this might be due to "hybridization of originally distinct races." It did not occur to them that the upper premolars might be meaningless in recognizing species. Apparently, the belief in the utility of premolar characters was too

deeply entrenched to be uprooted by this evidence.

William Diller Matthew's (1931) reaction to the Davis Ranch *Trigonias* sample was surprisingly modern. His critique of typological species concepts sounds as if it could have been written in the last decade. Matthew (1931, pp. 5-6) argued that, on ecological grounds, such a large number of closely related species in a single quarry was unlikely, and thus they were all the same species.

Despite Matthew's arguments, his contemporaries continued to name new species of rhinocerotoids based on slight variations of premolars. Peterson (1934) named *H. primus* for a specimen from the Duchesnean of Utah. Russell (1934) reviewed the Cypress Hills fauna first described by Lambe (1905, 1908). He reduced *H. priscidens* to synonymy with *H. arcidens*, and created a new species, *H. browni*. Schlaikjer (1935) described a number of new species from the early Chadronian Yoder l.f. of Goshen County, Wyoming, including *Caenopus yoderensis* and *Hyracodon ischyrolophus*.

In the White River monographs, Scott (1941) acknowledged the problem of the variability of upper premolars in rhinocerotoids, and reduced most of the species of *Hyracodon* (including *arcidens*, *selenidens*, *leidyanus*, and *apertus*) to synonymy. He did the same for *Trigonias*. Unfortunately, he still followed Wood in retaining the multiple invalid species of *Subhyracodon*.

After the White River monographs, almost 20 years passed before further research on hyracodonts was published. Green (1958) reported *Hyracodon* from the early Arikareean Sharps Formation of South Dakota. Radinsky (1967) published the first comprehensive review of the Hyracodontidae, revising the definition of the family and making comparisons to the Asian taxa for the first time. He agreed with Scott (1941) that the only valid species of *Hyracodon* was *H. nebraskensis*, and described a new genus and species, *Triplopides rieli*. However, Tanner and Martin (1976) disagreed, and recognized not only *H. nebraskensis* but also *H. priscidens*, *H. selenidens* (because of its supposed Chadronian provenience), *H. petersoni*, *H. primus*, *H. arcidens minimus* [*sic*], and a new species, *Hyracodon doddi*, from the late Chadronian of Sioux County, Nebraska.

In their review of *Forstercooperia*, Lucas, Schoch, and Manning (1981) also discussed the phylogeny of the rest of the Hyracodontidae. Russell (1982) reviewed the Cypress Hills rhinocerotoids, but failed to discuss several long-neglected taxa, including his own (1934) *Hyracodon browni*. Wilson and Schiebout (1984) described new material from the Duchesnean and Chadronian of the Trans-Pecos Texas region. On the basis of these additional specimens, they argued for the validity of *H. primus* and *H. petersoni*. Emry and Purdy (1984) showed that the type specimen of *Hyracodon nebraskensis* had long been misidentified, and determined which specimen was Leidy's original type.

The most recent research on North American hyracodontids was the rhino phylogeny of Prothero, Manning, and Hanson (1986), and the papers published in the perissodactyl symposium volume (edited by Prothero and Schoch, 1989). Prothero, Guérin, and Manning (1989) summarized the viewpoint on *Hyracodon* presented here. Lucas and Sobus (1989) reviewed the indricotheres. Heissig (1989) rejected the long-established view that indricotheres are distinct from rhinocerotids, and placed indricotheres within the Rhinocerotidae. In the American Museum Mongolian collections, he found a foot of *Juxia* that showed that primitive indricotheres had a functional fifth metacarpal. Apparently, he was unaware that the fifth metacarpal is a highly variable digit, disappearing and then re-appearing in several rhino genera (Prothero et al., 1986, p. 359). As a character, it is not sufficient evidence to outweigh all the other synapomorphies that support the distinction between the two families.

ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh, PA; F:AM, Frick Collection in the American Museum of Natural History, NY; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; NMC, National Museum of Canada, Ottawa, Ontario, Canada; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; SDSM, South Dakota School of Mines Museum, Rapid City, SD; SMNH P, Saskatchewan Museum of Natural History, Regina, Saskatchewan, paleontological collections; TMM, University of Texas Memorial Museum, Austin, TX; UNSM, University of Nebraska State Museum, Lincoln, NE; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; YPM, Yale Peabody Museum, New Haven, CT; YPM-PU, Princeton University collection, now housed at the YPM.

METHODS

The literature review above shows how taxonomic practices have changed over the years. Crucial to the controversy is the significance of the crests on the upper premolars. Before the advent of population thinking in the 1930s and 1940s, nearly all paleontologists were typologists who used almost any minor variation as the basis for a new taxon. As we have seen, however, Matthew (1931) and Scott (1941) were ahead of their time in realizing that rhinocerotoid upper premolars were highly variable within populations (first established by the Davis Ranch *Trigonias* sample). However, a thorough analysis of the variability of the upper premolars of *Hyracodon* has never been published. Radinsky (1967) assumed without discussion that all the species of *Hyracodon* were synonyms of *H. nebraskensis*; he did no detailed analysis of the large

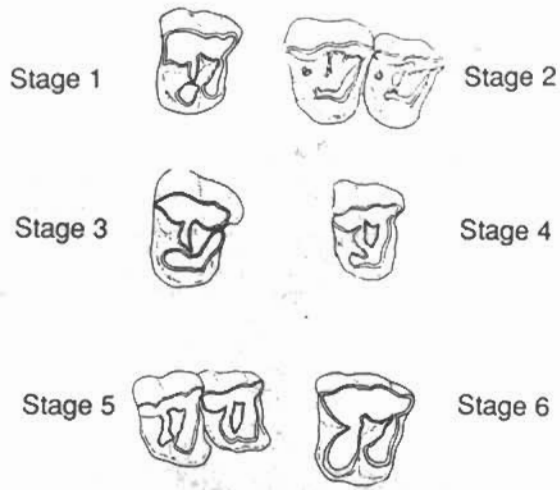

Figure 2. Coding system for the six standard stages of premolar molarization in *Hyracodon*. Figures modified from Gregory and Cook (1928).

samples of *Hyracodon* then available. In addition, most of the specimens discussed above come from the early Orellan. Relatively few analyses have been made of the variability of Duchesnean, Chadronian, or Whitneyan *Hyracodon* upper premolars.

Unlike the large quarry samples of *Trigonias* and *Subhyracodon*, however, there is apparently no similar quarry sample of *Hyracodon* than I have been able to locate. Although *Hyracodon* is very abundant in many museum collections from the late early Orellan "lower nodular zone" of the Big Badlands, they apparently did not die off in large numbers in a single place. Perhaps they lived in the open plains (as suggested by Clark et al., 1967), and so did not accumulate large masses of bones in river channels, as the larger-bodied, possibly more aquatic *Trigonias* and *Subhyracodon* did. Nixon and LaGarry-Guyon (1993) have described trackways from Toadstool Park, Nebraska, which seem to show that *Hyracodon* was solitary and *Subhyracodon* traveled in herds. Perhaps this explains the lack of quarry samples of *Hyracodon*. In the absence of a quarry, the best available sample is the late early Orellan "lower nodular zone" collection from a single area. For this study, I used the large sample from the western Big Badlands (Cottonwood Pass-Big Corral Draw-Quinn Draw area), collected for the Frick Laboratory by Morris Skinner and crews in the 1950s, and now curated in the American Museum of Natural History. Magnetic stratigraphy (Prothero and Swisher, 1992) shows that the lower nodular zone in this area is late early Orellan and spans the latter third of Chron C13n (33.1-33.5 Ma), and thus represents about 100,000-200,000 years of accumulation (not the 1100 to 11,000 years suggested by Clark et al., 1967).

To quantify the variability in upper premolars, I coded the different cusp and crest configurations into six standard stages of increased molarization (Fig. 2). In stage 1, the protocone and hypocone are completely separated from the ectoloph, and merge with it only in the latest wear stages. In stage 2, the protoloph curves around the anterolingual margin of the tooth, but does not connect to the ectoloph except in the latest wear stages, and remains distinct from the hypocone. The metaloph, however, is larger than in stage 1, and may contact the hypocone. In stage 3, the protoloph connects to the ectoloph, and curves completely around the anterolingual margin of the tooth crown, merging with the hypocone. In stage 4, the protoloph contacts the metaloph from the early wear stages, but still has a posterolingual crest remaining in the hypocone position. In stage 5, the protoloph loses its lingual extension, forming two parallel crests (the protoloph and metaloph), which are still in contact at the lingual end. Finally, stage 6 premolars are fully molarized in the typical rhinocerotoid "π"-shaped pattern, with short, parallel protoloph and metaloph, and no closure of the valley between them.

Gregory and Cook (1928) developed their own scheme of coding the premolar variability in the Davis Ranch *Trigonias* sample. Although they coded the characters differently, their figures 4 and 5 show that all six of these premolar stages occur in this single population sample, and their Graph 4 shows that all six stages form an almost continuous frequency distribution.

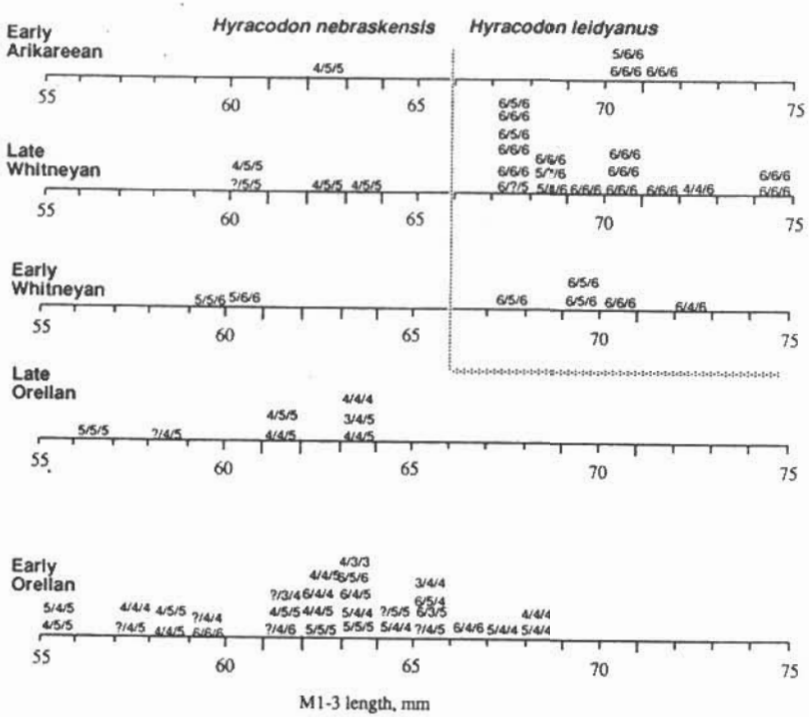

Figure 3. Size-frequency distributions (as measured by length of M1-3) of different specimens of *Hyracodon*, with their premolar stages (coded P2/P3/P4 in sequence) following the system shown in Figure 2. A question mark indicates that a particular premolar crown was missing, too damaged, or too worn to be assessed. Note that through the Orellan to early Arikareean, there is a series of samples with highly variable premolars, whose mean size is about 63 mm; these are referred to *H. nebraskensis*. In the Whitneyan and early Arikareean, there is a much larger lineage (mean size = 70 mm) with more advanced premolars; these are referred to *H. leidyanus*.

Thus, this range of upper premolar variability can be documented from a single homogeneous population, and clearly has less taxonomic significance than previously thought.

Each specimen was coded by stage of molarization for each of the three upper premolars (P2/P3/P4 in sequence) and plotted by size (as indicated by M1-3 length), as shown in Figure 3. The large sample from the lower nodular zone of the western Big Badlands forms a single unimodal size-frequency distribution. Inspection of the premolar stages within the sample shows extreme and continuous variability in each tooth. P2's in stages 4, 5 and 6 are equally common. P3's are typically stage 4 or 5, although there are few in stage 3 and 6. P4's are usually stage 4 or 5, with only a few in stage 6. This large range of variability includes not only the type specimen of *H. nebraskensis* (coded 6/4/5) from the ?early Orellan of South Dakota, but also the types of *H. arcidens* (3/3/5), and *H. selenidens* (4/3/3), which are from the early Orellan of Colorado (Galbreath, 1953).

Figure 3 shows, however, that the early Orellan to early Arikareean *Hyracodon* sample is not completely homogeneous or monospecific, contrary to Scott (1941) and Radinsky (1967). For example, in the Whitneyan and early Arikareean, there is a disjunctly larger (M1-3 length = 68-76 mm) species which is distinct from contemporary specimens referable to *H. nebraskensis*. These larger specimens nearly all have stage 6 P2s, stage 5-6 P3s, and stage 6 P4s. Many are coded 6/6/6 (completely molarized), a condition found in only one of the *H. nebraskensis* specimens. This sample seems to be referable to Troxell's (1921) species *H. leidyanus* from the Whitneyan of South Dakota (premolar stages of the type = 4/5/6). *H. apertus* (Sinclair, 1922) from the late Whitneyan *Protoceras* channels in Big Corral Draw in the Big Badlands, is also within this range of variation (premolar stages of the type = 4/5/6).

Although there are fewer Chadronian specimens that can be plotted in this fashion, many of these fall outside the range of variation of *H. nebraskensis*, and so some of the Chadronian taxa are considered valid as well (as discussed further below).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Superfamily RHINOCEROTOIDEA Owen, 1845
Family HYRACODONTIDAE Cope, 1879

Type Genus—*Hyracodon* Leidy, 1856

Included Genera—*Forstercooperia* Wood, 1939; *Juxia* Chow and Chiu, 1963; *Urtinotherium* Chow and Chiu, 1963; *Paraceratherium* Forster Cooper, 1911; *Triplopus* Cope, 1880; *Epitriplopus* Wood, 1927; *Ardynia* Matthew and Granger, 1923; *Triplopides* Radinsky, 1967; *Prohyracodon* Koch, 1897; *Ilianodon* Chow and Xu, 1961; *Eggysodon* Roman, 1911.

Range—Middle Eocene to early Miocene, Eurasia and North America.

Diagnosis—Small to gigantic cursorial hornless rhinocerotoids with long, slender metapodials. I3-1/3-1 C1-0/1-0 P4-3/4-3 M3/3. Incisors conical and pointed, approximately equal in size with each other. Premolars non-molariform to molariform. M3 triangular, retaining a lingually deflected metacone at the end of the ectoloph.

Discussion—Since the focus of most of the systematic papers in this volume is the White River Chronofauna, and since the Asian taxa were thoroughly reviewed by Radinsky (1967), I will not discuss them further here. *Triplopus* is currently being reviewed by R. Stucky (personal communication) *Forstercooperia* was discussed by Lucas et al. (1981) and is now being restudied by L. Holbrook (personal communication). No new material of *Epitriplopus* or *Triplopides* has been reported, so there is little to add to Radinsky's (1967) discussion. Only the genus *Hyracodon* is overdue for a revision.

Hyracodon Leidy, 1856

Rhinoceros Leidy, 1850 (*non* Linnaeus)(in part)
Hyracodon Leidy, 1856
Caenopus Schlaikjer, 1935

Type Species—*Hyracodon nebraskensis* (Leidy, 1850).

Included Species—Type and *H. leidyanus* Troxell, 1921; *H. priscidens* Lambe, 1905; *H. petersoni* Wood, 1926; *H. primus* Peterson, 1934.

Range—Late middle Eocene (late Duchesnean) to late early Oligocene (earliest Arikareean), North America.

Diagnosis—Small hyracodontids (length of P1-M3 = 108-149 mm) with posterolingually creased P3-4 protocone; reduced canines; deep rostrum; dp1 lost in adults; deciduous premolars retained into young adult life; molarization in upper premolars variable; coronoid process anteriorly inclined.

Discussion—As reviewed above, *Hyracodon* has been oversplit into 11 different species based on highly variable upper premolars. Most of the latest Chadronian and Orellan specimens fall within a single range of continuous variation that can be called *H. nebraskensis*. A larger, more advanced Whitneyan-Arikareean taxon seems distinct and is referred to *H. leidyanus*. Three Duchesnean and Chadronian taxa (*H. primus*, *H. petersoni*, and *H. priscidens*) are smaller than *H. nebraskensis*, and fall outside its range of premolar variability. For this reason, they are considered valid taxa.

Hyracodon primus Peterson, 1934

Hyracodon primus Peterson, 1934

Type—CM 11914, right maxillary fragment with P4-M2, Lapoint Member, Duchesne River Formation, Uinta Basin, Utah (Duchesnean).

Referred Material—Extensive sample from the late Duchesnean Porvenir l.f., Trans-Pecos Texas, listed by Wilson and Schiebout (1984, pp. 20, 22).

Diagnosis—Smallest species of *Hyracodon* (M1-3 length = 47-49 mm; see Table 1). No molarization of premolars; P2 in stage 1, P3 in stage 2-3, and P4 in stage 3. Prominent cristae on P3-4 and M1-2. Constricted protocone on upper molars. Differs from *Epitriplopus* in having shorter and wider M1, less molariform P4, and molar cristae. Differs from *H. petersoni* in its smaller size and much more primitive and unmolarized premolars.

Discussion—Wilson and Schiebout (1984) provided a thorough description of the material of *H. primus* from Texas. Although Radinsky (1967) considered the taxon to be indeterminate based on the type specimen, Wilson and Schiebout (1984) have clearly shown that *H. primus* is valid. Despite its primitive features, it also has the derived features of *Hyracodon*, including conical incisors, constricted symphysis, and strong premolar and molar cristae.

Hyracodon petersoni Wood, 1926

Hyracodon petersoni Wood, 1926
Hyracodon ischyrolophus Schlaikjer, 1935
Hyracodon petersoni Russell, 1982

Type—CM 3572, maxilla and premaxilla with most of the upper dentition, from the "*Titanotherium* beds, Badland Creek, Sioux County, Nebraska" (Chadronian).

Referred Material—From the early Chadronian

Table 1. Measurements of *Hyracodon* dentitions (in mm) *H. primus* after Wilson and Schiebout (1984, Tables 5-7); *H. petersoni* upper teeth based on type (CM 3572) and TMM 42156-4 (Wilson and Schiebout, Table 4), lower teeth after Russell (1982:13); *H. priscidens* based on type (NMC 6564) and four referred specimens; *H. nebraskensis* based on type and five referred specimens; *H. leidyanus* based on type (YPM 11173) and five referred specimens; *H. selenidens* type (YPM 11169) after Troxell (1921); *H. doddi* type (UNSM 1106) after Tanner and Martin (1976); *H. arcidens mimus* type after Troxell (1921); *H. apertus* type (YPM-PU 10803) after Sinclair (1922).

	primus	*petersoni*	*priscidens*	*nebraskensis*	*leidyanus*	*selenidens* type	*doddi* type	*arcidens* type	*apertus* type
P2-M3	—	97.0	106.0-116.0	115.0±5.2	123.3±4.2	—	—	—	144
M1-3	47.7	52.0-55.0	59.3-63.0	62.5±1.4	69.5±1.9	—	—	—	72
P2L	10.0	13.6-14.5	14.6-16.0	17.0±1.2	19.4±1.1	14	—	16	20
P2W	11.4	15.6-16.5	17.5-21.0	20.3±1.8	21.9±0.9	16	—	19	21
P3L	10.6	14.4-16.2	15.6-18.1	18.0±0.2	19.7±1.1	15	—	18	21
P3W	15.0	18.5-18.8	20.7-23.3	23.1±1.5	24.8±2.1	19	—	23	24
P4L	13.0	14.7-17.4	17.3-18.5	18.2±0.9	21.9±1.5	16	15.3	20	23
P4W	17.5	19.3-20.6	19.1-25.3	25.5±2.6	27.8±2.6	21	22.1	26	28
M1L	14.8-17.0	17.3-19.6	19.9-22.0	20.3±1.2	21.8±1.8	19	16.4	—	24
M1W	16.5-17.3	20.2-20.6	22.2-24.5	23.6±1.6	26.2±2.1	21	20.5	—	27
M2L	16.9-18.3	18.5-22.7	21.1-23.5	22.0±1.8	18.5±0.9	20	—	—	24
M2W	18.5-20.4	21.7-23.6	23.0-28.0	25.2±2.0	27.8±1.6	21	22.6	—	27
M3L	14.4-16.3	16.2-17.0	19.1-21.1	20.5±1.3	22.3±1.4	17	—	—	23
M3W	17.8-19.2	22.7-22.7	20.4-25.1	22.9±1.2	25.2±0	21	—	—	28
p2-m3	80.0	—	106.0-114.3	117.9±1.9	128.8±5.4	—	—	—	—
m1-3	46.0-49.7	—	64.0-66.0	62.9±1.8	68.2±1.2	—	—	—	—
p2L	10.8	12.6	14.2-15.7	17.0±2.0	18.9±0.5	—	—	—	—
p2W	7.4	8.8	9.3-10.0	11.8±0.5	12.4±1.6	—	—	—	—
p3L	12.5	14.9	15.3-19.0	19.1±0.9	22.8±0.7	—	—	—	—
p3W	8.9	12.0	11.6-13.1	14.9±0.9	15.5±2.1	—	—	—	—
p4L	12.6-14.3	15.3	16.5-20.0	19.6±0.4	23.2±1.1	—	—	—	—
p4W	9.6-10.9	11.9	12.0-14.0	15.5±1.3	16.9±1.0	—	—	—	—
m1L	13.7-16.0	13.8	17.7-20.0	19.4±0.4	22.8±1.3	—	—	—	—
m1W	9.9-10.2	12.1	12.4-15.0	14.1±1.4	14.9±0.9	—	—	—	—
m2L	15.0-18.9	19.5	20.0-22.8	22.5±0.6	24.3±0.5	—	—	—	—
m2W	10.0-12.5	12.9	13.0-14.0	14.0±1.4	15.5±1.3	—	—	—	—
m3L	17.3-18.3	19.9	24.2-24.6	23.5±0.9	23.0±1.9	—	—	—	—
m3W	10.3-11.2	13.1	13.1-13.7	13.1±1.2	14.0±0.9	—	—	—	—

Southfork l.f., Cypress Hills, Saskatchewan (Russell, 1982; this volume, Chapter 12): SMNH P1179.1, right maxillary fragment with P3-M3; SMNH P1179.2, right maxillary fragment with P3-M3; SMNH P1204.1, mandible. From the early Chadronian "Yoder Formation," Goshen County, Wyoming: SDSM 8748, type of *H. ischyrolophus* Schlaikjer, 1935. From the early Chadronian Coffee Cup and Airstrip l.f., Trans-Pecos Texas (Wilson and Schiebout, 1984, pp. 30-32): TMM 42153-4, skull fragment with P1-M3, and associated lower jaw fragment with partial m2 and m3; TMM 40501-1, M1.

Range—Early Chadronian of Wyoming, Nebraska, Saskatchewan, and Texas.

Diagnosis—Small species of *Hyracodon* (M1-3 length = 52-55 mm), slightly larger than *H. primus*, but smaller than *H. priscidens*. Differs from *H. priscidens* in that the P3-4 metaloph curves posteriorly, keeping the medial valley of P3-4 open posteriorly even in advanced stages of wear. Differs from *H. primus* in its larger size and more advanced upper premolars (4/3/3, except for the posteriorly-curved metaloph).

Discussion—*H. petersoni* is clearly distinct from the *H. priscidens* in its smaller size and peculiarly deflected P3-4 metalophs (not seen to this degree in any specimen of *H. priscidens*). The validity of *H. petersoni* was reaffirmed by Russell (1982), who showed that the Cypress Hills Chadronian *Hyracodon* could be separated into two groups, *H. petersoni* and *H. priscidens*.

Hyracodon ischyrolophus was named by Schlaikjer (1935) for an isolated left M3 from the early Chadronian Yoder l.f., Goshen County, Wyoming. As Schlaikjer (1935, fig. 8) shows, it is identical in size to *H. petersoni*, and distinguished only in having a slightly larger metaloph. However, this condition is seen in some of the referred material of *H. petersoni* (e.g., TMM 42153-4, shown in Wilson and Schiebout, 1984, fig. 20), so it is clearly within the normal range of variation of *H. petersoni*. Schlaikjer (1935, p. 86) named a new species on such an inadequate specimen because it allegedly filled the gap between *Triplopus* and *Hyracodon*.

Hyracodon priscidens Lambe, 1905

Hyracodon priscidens Lambe, 1905
Hyracodon browni Russell, 1934

Type—NMC 6564, left and right maxillae missing left P4 and right P3; plesiotype: NMC 66561, mandibular symphysis with left ramus. Both are from "Bone Coulee" (Conglomerate Creek Valley), now called the Calf Creek l.f., middle Chadronian, Cypress Hills, Saskatchewan (see Storer, this volume, Chapter 12).

Referred Material—From the Calf Creek l.f., Saskatchewan: SMNH P1634.1, mandible; ROM 23195, mandible (Russell, 1982). From the Pipestone Springs l.f., Jefferson County, Montana: AMNH 9708, mandible with right p1-3; 9710, right m3; 9855; isolated teeth; 9711, isolated teeth; 9709, right ramus with m1-3. From the McCarty's Mountain l.f., Madison County, Montana: F:AM 112166, left lower molar. From the Flagstaff Rim area, Natrona County, Wyoming (Emry, 1973, 1992): F:AM 111850, from Dry Hole Quarry; F:AM, 111849, 44 feet below Ash B; 111853, from 75 feet above Ash B, and over a dozen uncatalogued specimens from levels between these specimens. From the Ledge Creek area, Natrona County, Wyoming: F:AM 112167, 111852, 111854, from the "Red Fauna." Additional uncatalogued specimens ranging from 30 feet below the 160 Ash to 50 feet below the 310 Ash (Skinner and Gooris, 1968; Prothero, 1985). Much additional material from Chadron Formation collections in many museums could be referred to this taxon.

Range—Early to middle Chadronian, Wyoming, Nebraska, Montana, and Saskatchewan.

Diagnosis—Medium-sized *Hyracodon* (length M1-3 = 59-63 mm) with unmolarized upper premolars (P2 typically in stage 3-4; P3 in stage 2-3; P4 in stage 3-4). Strong protoloph on P2-4 curves posterolingually to hypocone. Metaloph on P3-4 does not connect to protoloph, leaving median valley open posteriorly. Posterior extension of metaloph on M3 is short and reflected posterolabially.

Discussion—*H. priscidens* is the common early-middle Chadronian hyracodont found in most localities of this age. It is slightly larger than *H. petersoni*, and lacks the strong posterior deflection of the metalophs on P3-4. Although it overlaps the size range of *H. nebraskensis*, *H. priscidens* has much less molarized premolars (typically stage 3 in P3-4), and never connects the protoloph or metaloph to enclose the medial valley (as is typical of *H. nebraskensis*).

H. priscidens was erroneously synonymized with *H. arcidens* by Sinclair (1922), who misinterpreted the morphology shown in Lambe's clear illustration. Wood (1926, 1927) followed Sinclair in this synonymy. Apparently neither saw the type specimen, but relied on figures. Scott (1941) and Radinsky (1967) considered *H. priscidens* to be a synonym of *H. nebraskensis*. But Tanner and Martin (1976) considered *H. priscidens* a valid species, and Russell (1982) showed that it was distinct from all other species of *Hyracodon*.

Hyracodon browni was named by Russell (1934) based on two P3's from the Cypress Hills Chadronian. These teeth differ from *H. priscidens* from the same beds only in their lack of a metaloph, a feature seen in no other rhinocerotoid. In size and in the rest of the morphology, *H. browni* cannot be distinguished from *H. priscidens*. Curiously, in his review of the Cypress Hills rhinos, Russell (1982) did not comment on *H. browni*, even though he had originally described it from the same fauna 48 years earlier. Given the enormous variability of upper premolars in *Hyracodon* documented so far, I see no reason to base a separate species on such limited material of what is almost certainly an aberrant individual.

Hyracodon nebraskensis (Leidy, 1850)

Rhinoceros nebraskensis Leidy, 1850 (*non* Linneaus)
Aceratherium nebrascense Leidy, 1851 (*non* Kaup)
Hyracodon nebrascensis Leidy, 1856
Hyracodon arcidens Cope, 1873
Hyracodon selenidens Troxell, 1921
Hyracodon arcidens mimus Troxell, 1921
Hyracodon apertus Sinclair, 1922 (in part, not type)
Hyracodon apertus Green, 1958
Hyracodon doddi Tanner and Martin, 1976

Type—USNM 336207, partial skull and mandible missing the rostrum, the incisors and canines, and the braincase (see Emry and Purdy, 1984), from the "Mauvaises Terres, Nebraska Territory" (presumably from the Orellan, Big Badlands, South Dakota). Figured by Emry and Purdy (1984, figs. 1 and 2); original figures in Leidy (1852, Plate 12A, fig. 6; 1853, Plate 14, figs. 1, 2).

Referred Material—Virtually all the abundant *Hyracodon* specimens from the late Chadronian and Orellan are referable to this species. In addition to the type and other specimens described by Leidy (e.g., USNM 138, 336208), they include a large number of specimens from the late Chadronian *Chadronia* Pocket (see Ostrander, 1985), Sioux County, Nebraska: AMNH 82925, 82595, 82923, 82910, 82924, 82985, 92984, 86201, 86200; over a hundred catalogued specimens from the late early Orellan "lower nodular zone," Scenic Member of the Brule Formation, Big Badlands, South Dakota, in the American Museum collections; dozens of catalogued specimens, including the types of *H. "arcidens"* (AMNH 6318) and *H. "selenidens"* (YPM 11173) from the Orellan Cedar Creek Member of the Brule Formation, Logan and Weld Counties, Colorado, in the American Museum Collection, and in the University of Kansas collections (see Galbreath, 1953). From the late Orellan "middle Oreodon beds,"

Badlands of South Dakota, including AMNH 12305, 12306, 9783, 1165, and 1176. From the late Orellan Frank Kostelecky Ranch, Stark County, North Dakota: F:AM 112168. From the Whitneyan Poleslide Member, Big Badlands, South Dakota: AMNH 560. From the late Whitneyan Pussy Springs locality, Morrill County, Nebraska: F:AM 111866. From the late Whitneyan Redington Gap area, Scottsbluff County, Nebraska: F:AM 111805. From the early Arikareean Sharps Formation, Washabaugh County, South Dakota: F:AM 111869 (50 feet above the Rockyford Ash).

Range—Late Chadronian to early Arikareean of the High Plains (the Dakotas, Nebraska, Colorado, Wyoming).

Diagnosis—Medium-sized *Hyracodon* (M1-3 length = 55-70 mm). Molarization of upper premolars is highly variable. P2 ranges from stages 4-6; P3 typically stage 4-5; P4 typically stage 4-5. Most specimens are larger than the sample of *H. priscidens* and have more advanced prêmolars. Distinguished from *H. leidyanus* by its smaller size and less advanced premolars.

Discussion—As discussed above, the *nebraskensis-arcidens-apertus-selenidens* morphotypes intergrade completely in size and morphology. As Scott (1941, p. 841) put it, "It is quite out of the question that four separate species of *Hyracodon* should have lived together in the same area which is now South Dakota and Nebraska, nor is the problem rendered any less difficult by calling these variations subspecies. Several Recent subspecies do not occur together, but each one has its own range, though with some overlapping on the borders of the ranges. Nor is a stratigraphic separation possible . . . For zonal purposes the species are of little value, as they range through considerable thickness of beds, and the same is true of size variants."

Tanner and Martin (1976) described a new species, *H. doddi* (UNSM 1106) from the late Chadronian (18 feet below the Upper Purplish White layer), Sioux County, Nebraska. In having a fully molarized (= stage 6) P4, it is virtually identical in morphology with the type of *H. apertus* from the Whitneyan, and differs only in its slightly smaller size and its Chadronian age. However, there are numerous specimens in the late Chadronian and early Orellan collections in the American Museum collections (e.g., AMNH 9788) which also show the morphology of *H. doddi*, so there is no reason to separate it from the highly variable sample of *H. nebraskensis*. Tanner and Martin (1976) justified the distinction of *H. doddi* from *H. nebraskensis* and *H. apertus* on the grounds that there were no specimens in the Nebraska collections older than the Whitneyan with a fully molarized P4. The larger collections in the American Museum, however, have completely encompassed this range of variation, so there is no longer any basis for retaining *H. doddi*.

Tanner and Martin (1976, p. 211) also argued for the validity of *H. selenidens* distinct from *H. arcidens* and *H. nebraskensis* because the types of the latter species were both "about 20% larger than *H. selenidens* and both are geologically younger (Orellan?)." They argued that the type of *H. selenidens* is Chadronian because it was apparently associated with brontothere material in the Yale collection. Tanner and Martin did not examine the full range of sizes shown by *H. nebraskensis*, or they would have seen that *H. selenidens* is at the small end of the frequency distribution of *H. nebraskensis* (which also ranges into the late Chadronian). As Sinclair (1922) showed, *H. selenidens* cannot be distinguished from *H. arcidens*, and the fact that one is late Chadronian and the other early Orellan should have no bearing on systematic decisions.

Hyracodon leidyanus Troxell, 1921

Hyracodon leidyanus Troxell, 1921
Hyracodon leidyanus Sinclair, 1922
Hyracodon apertus Sinclair, 1922 (in part)
Hyracodon leidyanus Wood, 1927
Hyracodon nebraskensis Scott, 1941 (in part)
Hyracodon nebraskensis Radinsky, 1967 (in part)

Type—YPM 11169, left maxilla with P1-M3, from "Crow Buttes, South Dakota." Sinclair (1922) and Wood (1926, 1927) argued that it is probably from the "*Protoceras* beds" (Whitneyan) in age.

Referred Material—From the Poleslide Member of the Brule Formation, Big Badlands, South Dakota: YPM 11168 (paratype), lower jaw and some postcranial fragments; YPM-PU 10802, 10144, two skulls; F:AM 111856, skull and jaws; F:AM 111857, skull; F:AM 111858, palate; F:AM 111859, partial skull and jaws; YPM-PU 10803, type of *H. "apertus."* From the Vista Member, Logan County, Colorado: AMNH 8821, palate and mandible; 8813, skull and jaws. From the Harris Ranch-Slim Buttes area, Fall River County, South Dakota (see Simpson, 1985): F:AM 111860, 111861, 111862, 111863, all skulls with jaws and associated postcranials. From Roberts Ranch, Scottsbluff County, Nebraska: F:AM 111864, skull and jaws. From Redington Gap, Morrill County, Nebraska: F:AM 111867, skull. From the basal Sharps Formation, Shannon and Washabaugh Counties, South Dakota: F:AM 111870, maxilla with right P1-4 (15 feet above the Rockyford Ash); F:AM 111868, maxilla with M1-3, and SDSM 54141 (referred by Green, 1958, to *H. apertus*), both found 5 feet above the Rockyford Ash.

Range—Whitneyan to earliest Arikareean of South Dakota, Nebraska, and Colorado.

Diagnosis—Largest species of *Hyracodon* (M1-3 length = 66-75 mm). P3-4 completely molariform or nearly so (mostly stage 6, a few stage 5), with parallel protoloph and metaloph and no connection blocking the valley between them. P2 not completely molariform, but the hypocone is connected to the metaloph, and separate from the protoloph. Crochets and cristae are occasionally present in the upper molars. Teeth slightly more hypsodont than in *H. nebraskensis*. Skull and skeletal features are very robust, reflecting its large size.

Discussion—The large sample of Whitneyan *Hyracodon* in the Frick Collection (Fig. 3) separates into two clusters of morphology: a smaller *H. nebraskensis-H. apertus* group that remains stable in size and range of morphologies throughout the late Chadronian to early Arikareean, and a disjunctly larger group that first appears in the early Whitneyan. In most skulls the upper premolars are fully molarized, as in the type of *H. leidyanus*. It is unlikely that these larger *Hyracodon* represent sexual dimorphs, since earlier *Hyracodon* show no such dimorphism, and the premolars of these larger specimens are consistently more advanced than contemporary small *H. nebraskensis*. These morphological and size gaps are adequate justification for recognizing *H. leidyanus*. This species apparently split off from *H. nebraskensis* in the early Whitneyan and co-existed with it until they both became extinct in the early Arikareean.

SUMMARY

The variability of the upper premolars in *Hyracodon* has led to tremendous taxonomic confusion. In the last century, researchers have gone back and forth from oversplitting (e.g., Troxell, Wood, Tanner and Martin) to excessive lumping (e.g., Scott, Radinsky). I believe that the large sample now available in the Frick Collection suggests an intermediate solution. There are five valid species of *Hyracodon*. The Duchesnean *H. primus* and early Chadronian *H. petersoni* are clearly valid taxa, although their available sample is still small. In the early and middle Chadronian, the common hyracodont was *H. priscidens*. Most of the specimens of *Hyracodon* from the late Chadronian-early Arikareean are encompassed within the highly variable type species, *H. nebraskensis*. These include the types and most specimens referred to *H. apertus, H. selenidens, H. arcidens*, and *H. doddi*. However, in the Whitneyan and early Arikareean, another larger species, *H. leidyanus*, persists alongside *H. nebraskensis*. *Hyracodon* disappears from the fossil record in the early Arikareean along with a number of other taxa characteristic of the White River Chronofauna. This is part of the "faunal reorganization" of the late early Arikareean discussed by Tedford et al. (1985, 1987; this volume, Chapter 15).

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LITERATURE CITED

Abel, O. A. 1926. Die Molarisierung der Oberen Prämolaren von *Hyracodon nebrascensis* Leidy. Palaeontologische Zeitschrift 8(3): 224-245.

Clark, J., J. R. Beerbower, and K. K. Kietzke. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology of the Big Badlands of South Dakota. Fieldiana: Geology Memoir 5:1-158.

Cope, E. D. 1873. Second notice of extinct Vertebrata from the Tertiary of the Plains. Paleontological Bulletin 15: 1-2.

Emry, R. J. 1973. Stratigraphy and preliminary biostratigraphy of the Flagstaff Rim area, Natrona County, Wyoming. Smithsonian Contributions to Paleobiology 18.

Emry, R. J. 1992. Mammalian range zones in the Chadronian White River Formation at Flagstaff Rim, Wyoming; pp. 106-115 *in* D. R. Prothero and W. A. Berggren (eds.), Eocene-Oligocene Climatic and Biotic Evolution, Princeton University Press, Princeton, NJ.

Emry, R. J., and R. W. Purdy. 1984. The holotype and would-be holotypes of *Hyracodon nebraskensis* (Leidy 1850). Notulae Naturae of the Academy of Natural Sciences, Philadelphia 460: 1-18.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata 4.

Green, M. 1958. Arikareean rhinoceroses from South Dakota. Journal of Paleontology 32:587-594.

Gregory, W. K., and H. J. Cook. 1928. New material for the study of evolution: a series of primitive rhinoceros skulls (*Trigonias*) from the lower Oligocene of Colorado. Proceedings of the Colorado Museum of Natural History 8(1): 3-39.

Hanson, C. B. 1989. *Teletaceras radinskyi*, a new primitive rhinocerotid from the late Eocene Clarno Formation, Oregon; pp. 379-398 *in* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.

Heissig, K. 1989. The Rhinocerotidae; pp. 399-417 *in* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.

Kihm, A. J. 1987. Mammalian paleontology and geology of the Yoder Member, Chadron Formation, east-central Wyoming. Dakoterra 3:28-45.

Lambe, L. M. 1905. A new species of *Hyracodon* (*H. priscidens*) from the Oligocene of the Cypress Hills,

Assiniboia. Transactions, Royal Society of Canada, Series 2 11(Section 4):37-42.
Lambe, L. M. 1908. The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. Contributions to Canadian Palaeontology 3(4):5-64.
Leidy, J. 1850. [First descriptions of *Rhinoceros nebraskensis, Agriochoerus antiquus, Palaeotherium proutii,* and *P. bairdii.*] Proceedings of the Academy of Natural Sciences of Philadelphia 5: 119.
Leidy, J. 1851. [Remarks on *Aceratherium occidentale* and *A. nebrascense.*] Proceedings of the Academy of Natural Sciences of Philadelphia 5:331.
Leidy, J. 1852. Description of the remains of extinct Mammalia and Chelonia, from Nebraska Territory; pp. 535-572 *in* D. D. Owen, Report on the geological survey of Wisconsin, Iowa, and Minnesota; and incidentally of a portion of Nebraska Territory. Lippincott, Grambo & Co., Philadelphia.
Leidy, J. 1853. The ancient fauna of Nebraska; or a description of remains of extinct Mammalia and Chelonia, from the Mauvaises Terres of Nebraska. Smithsonian Contributions to Knowledge 6(7): 1-126.
Leidy, J. 1856. Notices of several genera of extinct Mammalia, previously less perfectly characterized. Proceedings of the Academy of Natural Sciences of Philadelphia 8: 91-92.
Lucas, S. G., R. M. Schoch, and E. Manning. 1981. The systematics of *Forstercooperia*, a middle to late Eocene hyracodontid (Perissodactyla, Rhinocerotoidea) from Asia and western North America. Journal of Paleontology 55: 826-841.
Lucas, S. G., and J. Sobus. 1989. The systematics of indricotheres; pp. 358-378 *in* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.
Matthew, W. D. 1931. Critical observations on the phylogeny of rhinoceroses. University of California Publications in Geological Sciences 20: 1-8.
Nixon, D. A., and H. E. LaGarry-Guyon. 1993. New trackway sites in the White River Group type section at Toadstool Park, Nebraska: paleoecology of an Oligocene braided stream, riparian woodland, and adjacent grassland. Journal of Vertebrate Paleontology 13 (supplement to number 3):51A.
Ostrander, G. E. 1985. Correlation of the early Oligocene (Chadronian) in northwestern Nebraska; pp. 205-231 *in* J. E. Martin (ed.), Fossiliferous Cenozoic deposits of western South Dakota and northwestern Nebraska. Dakoterra, Museum of Geology, South Dakota School of Mines 2.
Peterson, O. A. 1934. List of species and descriptions of new material from the Duchesne River Oligocene, Uinta Basin, Utah. Annals of the Carnegie Museum 23: 373-389.
Prothero, D. R. 1985. Chadronian (early Oligocene) magnetostratigraphy of eastern Wyoming: implications for the Eocene-Oligocene boundary. Journal of Geology 93: 555-565.
Prothero, D. R., C. Guérin, and E. Manning. 1989. The history of the Rhinocerotoidea; pp. 322-340 *in* D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Oxford University Press, New York.
Prothero, D. R., E. Manning, and C. B. Hanson. 1986. The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). Zoological Journal of the Linnean Society of London 87:341-366.
Prothero, D. R., and R. M. Schoch (eds.) 1989. The Evolution of Perissodactyls. Oxford University Press, New York.
Prothero, D. R., and C. C. Swisher III. 1992. Magnetostratigraphy and geochronology of the terrestrial Eocene-Oligocene transition in North America; pp. 46-74 *in* D. R. Prothero and W. A. Berggren (eds.), Eocene-Oligocene Climatic and Biotic Evolution, Princeton University Press, Princeton, N.J.
Radinsky, L. B. 1967. A review of the rhinocerotoid family Hyracodontidae (Perissodactyla). Bulletin of the American Museum of Natural History 136(1): 1-45.
Russell, L. S. 1934. Revision of the Lower Oligocene vertebrate fauna of the Cypress Hills, Saskatchewan. Transactions, Royal Canadian Institute 29(1), no. 43:49-67.
Russell, L. S. 1982. Tertiary mammals of Saskatchewan. Part VI: The Oligocene rhinoceroses. Life Sciences Contributions, Royal Ontario Museum 133:1-58.
Schlaikjer, E. M. 1935. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. III. A new basal Oligocene formation. Bulletin of the Museum of Comparative Zoology, Harvard University 74(3): 71-93.
Scott, W. B. 1941. The mammalian fauna of the White River Oligocene. Part V. Perissodactyla. Transactions of the American Philosophical Society 28(5): 747-980.
Scott, W. B., and H. F. Osborn. 1887. Preliminary account of the fossil mammals from the White River Formation contained in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology 13(5): 151-171.
Simpson, W. F. 1985. Geology and paleontology of the Oligocene Harris Ranch badlands, southwestern South Dakota; pp. 303-333 *in* J. E. Martin (ed.), Fossiliferous Cenozoic deposits of western South Dakota and northwestern Nebraska. Dakoterra, Museum of Geology, South Dakota School of Mines 2.
Sinclair, W. J. 1922. Hyracodons from the Big Badlands of South Dakota. Proceedings of the American Philosophical Society 61: 65-79.
Skinner, S. M., and R. J. Gooris. 1966. A note on *Toxotherium* (Mammalia, Rhinocerotidae) from Natrona County, Wyoming. American Museum Novitates 2261: 1-12.
Tanner, L. G., and L. D. Martin. 1976. New rhinocerotoids from the Oligocene of Nebraska; pp. 210-219 *in* C. S. Churcher (ed.), Athlon: Essays in paleontology in honour of Loris Shano Russell. Royal Ontario Museum, Life Sciences, Miscellaneous Publications.
Tedford, R. H., T. Galusha, M. F. Skinner, B. E. Taylor, R. W. Fields, J. R. Macdonald, J. M. Rensberger, S. D. Webb, and D. P. Whistler. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene epochs) in North America; pp. 153-210 *in* M. O. Woodburne (ed)., Cenozoic Mammals of North America, Geochronology and Biostratigraphy, University of California Press, Berkeley, California.
Tedford, R. H., J. B. Swinehart, R. M. Hunt, Jr., and M. R. Voorhies. 1985. Uppermost White River and lowermost Arikaree rocks and faunas, White River Valley, northwestern Nebraska and their correlation with South Dakota; pp. 335-352 *in* J. E. Martin (ed.), Fossiliferous Cenozoic deposits of western South Dakota and northwestern Nebraska. Dakoterra, Museum of Geology, South Dakota School of Mines 2.
Troxell, E. L. 1921. New species of *Hyracodon*. American Journal of Science II: 34-40.
Wilson, J. A., and J. A. Schiebout. 1984. Early Tertiary vertebrate faunas, Trans-Pecos Texas: Ceratomorpha less Amynodontidae. Pearce-Sellards Series, Texas Memorial Museum 39: 1-47.
Wood, H. E., II. 1926. *Hyracodon petersoni*, a new cursorial rhinoceros from the Lower Oligocene. Annals of the Carnegie Museum 16(7): 315-318.
Wood, H. E., II. 1927. Some early Tertiary rhinoceroses and hyracodonts. Bulletins of American Paleontology 13(50): 5-105.
Wood, H. E., II. 1961. *Planiceps* Scott & Osborn, 1887 (*Hyracodon*): Proposed suppression under the plenary powers as a *nomen dubium* (Mammalia). Bulletin of Zoological Nomenclature 18(3):28.