NEW GIANT RHINOCEROS FROM THE ARIKAREEAN (OLIGOCENE-MIOCENE) OF MONTANA, SOUTH DAKOTA AND WYOMING

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Abstract—Rhinoceros remains from the Arikareean Cabbage Patch beds of western Montana include additional specimens of the common forms *Diceratherium armatum* and *D. annectens*, new specimens referable to the tiny Nebraska rhino *Skinneroceras manningi*, and a mandible, a tooth and partial skeleton of a new giant rhinoceros. This new taxon was previously known only from three huge astragali and a humerus from the early Arikareean of eastern Wyoming, so it was not formally named. The Montana skeleton includes a partial skull and mandible indicative of a very large male *Diceratherium*. Based on their similar proportions and size, the giant rhinoceros specimens from the Arikareean of Montana are associated with a large rhinoceros previously described from South Dakota and the huge astragali and humerus from Wyoming; this taxon is herein named *Diceratherium radtkei* n.sp.

INTRODUCTION

Prothero (2005) reviewed the fossilized specimens of all North American rhinoceroses known before 2004. Most specimens were referred to named taxa, but in several cases there were specimens in the Frick Collection of the American Museum of Natural History (F:AM) that were distinctly different but not associated with cranial or dental material, so their taxonomic affinities were unclear. Among these were three astragali (F:AM 111846A-C) and a humerus (F:AM 111846D) from two localities in the late Arikareean Harrison Formation in eastern Wyoming: 77 Hill in Niobrara County, and Horse Creek in Goshen County (Figs. 1-2). Prothero (2005, p. 127-128) compared the specimens to known postcranials of the common Arikareean rhinoceros *Diceratherium*, and found that they were about 30% larger than astragali of the largest previously known species, *D. armatum* (Fig. 3). Likewise, the humerus was about 30% larger than the range of *D. armatum* humeri (Fig. 2). Since the sample of *D. armatum* bones is large and well characterized, these

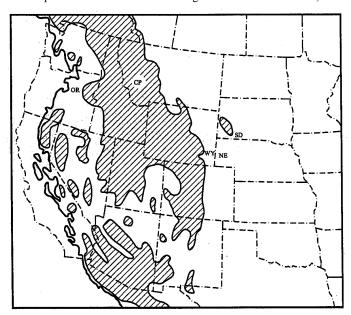


FIGURE 1. Index map showing the location of the Arikareean Cabbage Patch rhinos in western Montana (CP), and Arikareean rhinos in Oregon (OR), Wyoming (WY), Nebraska (NE), and South Dakota (SD). Hatching indicates upland and mountainous terrain. Map modified from R.C. Blakey website: http://jan.ucc.nau.edu/~rcb7/ (Paleogeography and Geologic History of North America. Paleogene Oligocene - 25Ma).

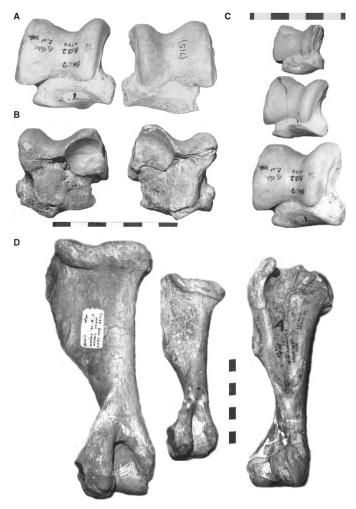


FIGURE 2. Postcranial material of rhinoceroses originally described by Prothero (2005). A-B. Astragali of *Diceratherium radtkei* (F:AM 114846A, left) from eastern Wyoming, compared with the indricothere *Juxia sharamurunese* (AMNH 715, right) from the Oligocene of Mongolia, in dorsal and plantar views. C. Comparison of astragalus of *D. radtkei* (bottom) with (top) *Diceratherium annectens* (F:AM 112188) and (middle) *D. armatum* (F:AM 112178). D. Humerus of *D. radtkei* (F:AM 111846D) on left, compared with *D. annectens* (F:AM 112188) in middle and *D. armatum* (F:AM 112178) on right. Scale bar in cm.

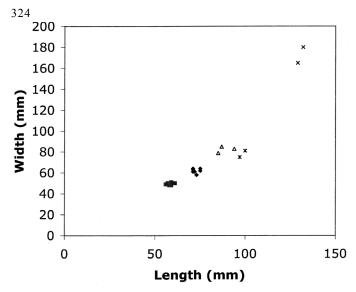


FIGURE 3. Plot of dimensions of astragali of representative samples of *D. annectens* (gray squares) and *D. armatum* (black diamonds) compared with *D. radtkei* (open triangles), *Juxia sharamurunese* (x with vertical slash), and the giant indricothere *Paraceratherium* (x).

unusually large specimens clearly fall outside the range of variation of any known species of Arikareean rhinoceros, and belong to a different taxon. Based on suggestions from Earl Manning, comparisons were made (Fig. 2) to the indricothere *Juxia sharamurunense* (Figs. 2, 3), which had similar-sized astragali. Unfortunately, with no other specimens available at that time, it was impossible to determine to what taxon this material belonged.

In his unpublished doctoral dissertation, Rasmussen (1977, p. 412-413) described a partial skeleton (MPUM 1367) of a large rhinoceros from the Arikareean Cabbage Patch beds of Montana as Diceratherium cf. D. armatum and noted the material is from a larger rhinoceros than the type of D. armatum (YPM 10003). Rasmussen (1977, p. 413, table 64) pointed out the similarity in large size of the lower molars of MPUM 1367 to another large *Diceratherium* (SDSM 53484) from South Dakota, originally assigned by Green (1958, p. 591-594) to D. armatum. Rasmussen (1977) suggested the South Dakota rhinoceros is also a much larger rhinoceros than the type of D. armatum. Rasmussen's descriptions were never published but came to Prothero's attention in October 2004 after the rhino monograph went to press. As discussed below, the Montana specimens are comparable in size and age to the huge rhino postcranials from Wyoming (Prothero, 2005, p. 127-128) and the large skull and rami from South Dakota (Green, 1958, p. 591-594), and the large specimens from the Arikareean of Montana, South Dakota and Wyoming probably belong to the same taxon. The cranial and dental material of the large Cabbage Patch rhinoceros is complete enough to determine that it represents a large male Diceratherium and not an indricothere such as Juxia. In addition, rhinoceros specimens from the Cabbage Patch beds represent three other rhinocerotids known from the Arikareean of the High Plains and Oregon, including material that is probably referable to the tiny early Arikareean rhinoceros Skinneroceras manningi. All of the Cabbage Patch rhinoceros specimens are tied to known lithostratigraphic, biostratigraphic and magnetostratigraphic intervals as recently described and summarized by Rasmussen and Prothero (2003)

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY; F:AM, Frick Collection, American Museum of Natural History, New York, NY; KU. University of Kansas Museum of Natural History, Lawrence, KS; KU-Mt, Montana locality. University of Kansas Museum of Natural History, Lawrence, KS; MPUM, University of Montana Museum of Paleontology, Missoula, MT; MV, Montana locality. University of Montana Museum of Paleon-

tology, Missoula, MT; PM, University of Chicago paleontology collections, Field Museum of Natural History, Chicago, IL; SDSM, South Dakota School of Mines Museum of Paleontology, Rapid City, SD; USNM, United State National Museum, Smithsonian Institution, Washington, DC; YPM; Peabody Museum of Natural History, Yale University, New Haven, CT

GEOLOGIC SETTING

The Arikareean Cabbage Patch strata in the type area in the northern part of the Cenozoic Flint Creek Basin occur in scattered outcrops along the south flank of the Garnet Range in western Montana (see summary by Rasmussen and Prothero, 2003). The Cabbage Patch beds in western Montana are part of the Bozeman Group and equivalent to the Arikareean parts of the Renova Formation east of the Continental Divide in Montana (see summary by Rasmussen, 2003). The Cabbage Patch strata in the type area have been tilted, folded, faulted and deeply eroded but still can be traced into four adjacent intermontane basins in western Montana. The Cabbage Patch beds unconformably onlap an irregular topography of Precambrian to Mesozoic strata and locally onlap erosional remnants of Paleogene strata (unnamed Eocene and Oligocene strata) and early Arikareean volcanics (ignimbrite and lahar deposits in a paleovalley eroded into Cretaceous and older rocks). Upper Miocene through Holocene strata and sediments are locally present on top of the Cabbage Patch beds, sometimes filling paleovalleys or tributaries to paleovalleys. The Cabbage Patch strata were predominantly fluvio-lacustrine in origin with fluvial strata four-to-five times as abundant as lacustrine strata; paludal and eolian (ash falls) strata account for approximately 3% of the total Cabbage Patch strata (see Rasmussen, 1977, for additional details). The Cabbage Patch strata are dominated by fresh volcaniclastics and montmorillonitic mudstones. These tuffaceous strata are usually poorly bedded because of deposition and re-working in fluvial environments and the subsequent intense bioturbation by plants and invertebrates. Playa, lacustrine, lacustrine delta fill, and paludal deposits are well-bedded, contain thin pure ash beds, and locally may be highly fossiliferous with plants, invertebrates, and vertebrates. Conglomerates, arkose, and other coarse clastics are locally derived and occur as scattered lenses throughout the entire Cabbage Patch stratigraphic sequence. Large mammalian fossils, including rhinoceros remains, are predominantly found in fluvial overbank deposits within the Cabbage Patch beds. Water-worn teeth and bones of large mammals are rare in fluvial channel deposits. Fossils of smaller vertebrates occur in a wider variety of deposits in the Cabbage Patch beds.

FOSSIL LOCALITIES

MV6558: The small rhinoceros remains (MPUM 13230, 13231; KU 18670, 18678) at this site are from a fluvial, overbank, shelly, greenish-gray siltstone (Rasmussen, 1969, p. 166-167) in the lower part of the Cabbage Patch beds (unit 2 of measured section B-I – KU-Mt-25, Rasmussen, 1977, p. 520). Paleomagnetic data from the measured section though this site (Rasmussen and Prothero, 2003) indicate a correlation with the middle of normal polarity Chron C9n in the late Oligocene (~27.5 Ma). This site has one of the most diverse fossil assemblages known in the Cabbage Patch beds, with several undescribed new taxa. MV6554: The isolated rhinoceros teeth (MPUM 1490, 2269) at this site are from fluvial channel, yellowish-gray siltstone (Rasmussen, 1969, p. 155) in the lower part of the Cabbage Patch beds (unit 3 of measured section A-III - MV6554, Rasmussen, 1977, p. 506). Paleomagnetic samples were not obtained from the measured section at this site, but lithostratigraphic and biostratigraphic data indicate an approximate correlation with stratigraphic unit 2 of MV6558 (middle of normal polarity Chron C9n as reported by Rasmussen and Prothero, 2003). This site is the richest fossil site in the Cabbage Patch beds, with bones of amphibians and small mammals concentrated into cross-bedded, 2-10 cm-thick lenticular beds that form dark bands across the face of the outcrop.

Isolated teeth, jaws and bones of larger mammals are mixed into the conglomerate lenses of this fluvial channel deposit.

MV6547 (=KU-Mt-46): A large rhinoceros mandible (PM 3103) discovered in the Cabbage Patch beds by Dick Konizeski and Jim Orr in 1956 was referred to *Diceratherium* cf. *armatum* (Konizeski and Donohoe, 1958, p. 49). Their fossil site was rediscovered in 1965 by Rasmussen (1969, p. 132), and the new bone and tooth fragments were later found to fit on the same *Diceratherium* mandible collected in 1956 (Rasmussen, 1977, p. 480). The *Diceratherium* mandible is from a shelly, yellowishgray mudstone in the middle part of the Cabbage Patch beds (laterally equivalent to the fluvial overbank mudstone in unit 19 of measured section B-II – MV6504; Rasmussen, 1977, p. 525). Paleomagnetic data from the nearby measured section in MV6504 (Rasmussen and Prothero, 2003) indicate this site is in the later normal polarity part of Chron C7n in the late Oligocene (~ 24.8–25.2 Ma).

MV6504-1: Skeletal remains of the large *Diceratherium* (MPUM 1367) at this site are from fluvial overbank, dusky yellowish-gray mudstone (Rasmussen, 1969, p. 173-174) in the middle part of the Cabbage Patch beds (top part of unit 1 of measured section B-II – MV6504, Rasmussen, 1977, p. 528-529). Paleomagnetic data from the measured section through this site (Rasmussen and Prothero, 2003) indicate a correlation with the early reversed polarity part of Chron C7r in the late Oligocene (~25.8 Ma). See discussion on taphonomy below for additional details of this site.

MV6504-4: The large *Diceratherium* astragalus (MPUM 1462) at this site is from fluvial overbank, shelly, dusky-yellow mudstone (Rasmussen, 1969, p. 173) in the middle part of the Cabbage Patch beds (top part of unit 4 of measured section B-II – MV6504; Rasmussen, 1977, p. 527-528). Paleomagnetic data from the measured section very close to this site (Rasmussen and Prothero, 2003) indicate a correlation with the middle reversed polarity part of Chron C7r in the late Oligocene (~25.5 Ma). This site is very rich with mollusks, especially large slugs, amphibians and small mammals. The *Diceratherium* astragalus is the only large mammal specimen from this site.

TAPHONOMY

Bones of rhinoceroses and other large mammals in the Cabbage Patch beds were almost always disturbed prior to final burial and rarely occur as skeletons. In one quarry site (see MV6504-1 above), the skull (partially eroded when found), rami, and partial postcranial skeleton of a large rhinoceros (Diceratherium, MPUM 1367), the skull and partial postcranial skeleton of a large oreodontid (Megoreodon, MPUM 1365), and the partial skeleton of a small pleurolicine gopher (*Pleurolicus*, MPUM 2046) were found together in the same stratum. The skull of the large Diceratherium was upside down and separated vertically 20 cm above the rami, which were found lying on their side. Other fragmentary bones of the skeleton, including the premaxillary and a partially eroded humerus, lay at various angles next to the skull and rami. The upright skull, humerus, calcaneum, innominate, and two cervical vertebrae of the large Megoreodon were found together in a small area about 1.2 m from the Diceratherium. The partially articulated skeleton of the small Pleurolicus was found beneath the tusks of the Diceratherium. Death of the Diceratherium and Megoreodon was approximately contemporaneous, and subsequent burial was gradual over a period of time as seen by layers of finely laminated mudstone in the rock surrounding the bones. However, the deposition of mudstone was not continuous but intermittently disturbed as seen by mudstone laminations broken and oriented at many different angles. Hoof-marks, abundant small root burrows, and occasional large root burrows (and possible crayfish or tiny mammal burrows) are present throughout the rock matrix and cut across the disturbed laminated mudstone. The disarticulation of the skeletons of the Diceratherium and Megoreodon suggest scavenging by large carnivores, which separated and spread the bones from the carcasses, and the odd orientation of the bones and the disturbed mudstone suggest that the

remaining bones were trampled down into the mud (in a mud hole on a fluvial floodplain) by the carnivores and other large mammals. The presence of diatoms and freshwater sponge spicules in the laminated mudstone suggest the mud hole was periodically flooded with standing water. The gopher probably died much later in a burrow beneath the buried rami of the *Diceratherium*, although evidence of the actual burrow was destroyed by the subsequent intense growth of roots through the mud and soil prior to lithification. Other rhinoceros specimens from the Cabbage Patch beds discussed below were found as isolated elements within strata originally deposited in fluvial environments.

PALEOCLIMATE

Climatic conditions during deposition of the Cabbage Patch strata have been determined from plants, vertebrates and mollusks (as summarized by Rasmussen and Prothero, 2003, p. 490). The presence of sequoia leaf fossils throughout the Cabbage Patch strata suggests that the climate was sufficiently wet enough in the area to provide the habitat required by these large trees. Wet conditions are also indicated by the dominant presence of root burrows in the fluvial and lacustrine-margin sediments of the Cabbage Patch strata. Grass phytoliths recovered by Caroline Stromberg (personal communication to Rasmussen, 2004) from the siltstone matrix encasing the upper molar tooth of a small rhinoceros (MPUM 13231) in unit 2 of the measured section at MV6558 suggest that some or most of the smaller root burrows were by grasses. Terrestrial snails, large slugs, opossums, moles, hedgehogs, and abundant rodents suggest sufficient moisture for soft soils and abundant vegetation. Aquatic snails, clams and fish indicate sufficient precipitation to continuously supply at least some through-flowing streams within the area. Tortoise (Testudo) remains suggest mild winters without frost or with very infrequent short periods of freezing conditions. Estivating toads (Henrici, 1994) suggest seasonally drier conditions during part of each year. Bedded gypsum, gypsum cement and mud cracks seen in some lacustrine strata also indicate periods of dryness with some freshwater lakes becoming saline and forming playa lakes. Pierce (1993, p. 989-990) concluded from the terrestrial and aquatic mollusks that "the MAT (mean annual temperature) of the intermontane basin areas of western Montana was at least 2°C warmer than at the present ... probably 10°C, or greater, with a January (winter) mean temperature probably not less than 5°C and a July (summer) temperature probably 15-20°C." Pierce (1993) likewise determined that the MAP (mean annual precipitation) may have been 50 cm or less during semiarid conditions (lower and upper Cabbage Patch strata) and 75 cm or more during more humid conditions (middle Cabbage Patch strata). Climatic conditions during the Arikareean for the intermontane basins of western Montana were probably adequate to support all-year-long browsing and grazing by rhinoceroses and the other ungulates known from the Cabbage Patch beds.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758 Order Perissodactyla Owen, 1848 Family Rhinocerotidae Owen, 1845 Diceratherium Marsh, 1875 Diceratherium radtkei n.sp. Figs. 2-7, Tables 1-2

Diceratherium armatum Green, 1958:591-594 Diceratherium cf. armatum Konizeski and Donohoe, 1958:49 Diceratherium cf. armatum Rasmussen, 1977, p. 412-413 Diceratherium armatum Prothero, 2005, p. 51

Holotype: MPUM 1367, posterior portion of skull, left premaxillary with I1 and alveolus for I2, left and right rami with all teeth, and a poorly preserved humerus, from University of Montana locality MV6504-1, in the middle Arikareean Cabbage Patch beds, western Mon-

tana. The left premaxillary was stolen from the Museum of Natural History at the University of Kansas in 1973.

Referred material: From the early to middle Arikareean Cabbage Patch beds, western Montana: PM 3103, partial left mandible with p2-m3 (Konizeski and Donohoe, 1958, p. 49), from University of Montana locality MV6547 (middle Arikareean); MPUM 1490, right m3 (Rasmussen, 1977, p. 414), from University of Montana locality MV6554, unit 3 (early Arikareean).

From the early Arikareean Sharps Formation, Shannon County, South Dakota: SDSM 53484, left maxilla with P2-M3, right maxilla with I2, P2-4, left ramus with c, p3-m3, right ramus with c, p2-m3 (Green, 1958, p. 591-594).

From the late Arikareean Harrison Formation in Wyoming (77 Hill Quarry in Niobrara County and Horse Creek in Goshen County): F:AM 111846A-C, three astragali, F:AM111846D, humerus (Prothero, 2005, p. 127-128).

Etymology: In memory of the late Marvin Radtke of Hall, Montana, rancher and landowner of several Cabbage Patch localities, whose courteous cooperation and interest in fossils aided Rasmussen in his efforts to collect the specimens described herein.

Known distribution: Early to late Arikareean of Montana, Wyoming, and South Dakota.

Diagnosis: Largest species of *Diceratherium*, about 30% larger than *D. armatum*, the largest species previously known. More massive basal part of the occiput; larger hypoglossal foramen which opens laterally rather than in condyloid fossa; larger postglenoid and mastoid processes; and a higher and more massive zygomatic arch, compared to other species of *Diceratherium*.

Description: Although the type skull (MPUM 1367) is fragmentary, enough parts are preserved to ascertain that the skull is referable to *Diceratherium*. The premaxilla (Figs. 4-5) contains a highly worn blunt knoblike I1, which shows the thegosis facets for wear with the lower i2 tusk. The anteroposteriorly elongated cylindrical shape of the I1 is characteristic of rhinocerotids, and found in many specimens of *Diceratherium*, such as F:AM 112176 (Prothero, 2005, fig. 4.16E-F). It is completely unlike the conical shape of the I1 found in indricotheres (Forster-Cooper, 1923; Radinsky, 1967; Lucas and Sobus, 1989). There is also a round alveolus for I2 on the premaxilla of MPUM 1367, which is rarely preserved in most specimens, but is known to be a simple knoblike tooth with a single blunt cusp (e.g., F:AM 112176, shown in Prothero, 2005, fig. 4.16E-F). In contrast, the I2 is absent in most indricotheres (Forster-Cooper, 1923; Radinsky, 1967; Lucas and Sobus, 1989).

The posterior portion (Figs. 4, 6) of the skull of MPUM 1367 also has features characteristic of *Diceratherium* and not of indricotheres. The occiput (Fig. 6) bears a high, rounded, flaring lambdoid crest, and a prominent sagittal crest that rises up from the flat dorsal profile of the skull above the orbits. These are all features seen in less distorted skulls of D. armatum, such as F:AM 112176 (Prothero, 2005, fig. 4.16E-F), although they are not as apparent in the dorsoventrally crushed type specimen of D. armatum, YPM 10003. In contrast, larger indricothere skulls (Forster-Cooper, 1923; Radinsky, 1967; Lucas and Sobus, 1989) often have a dorsally domed skull profile and a relatively low, flat occiput with less prominent lambdoid and sagittal crests than found in MPUM 1367, or in specimens of D. armatum. The width of the occipital condyle in MPUM 1367 is 117.9 mm, much wider than the 107.0 mm of YPM 10003. The basal part of the occiput of MPUM 1367 is more massive than in D. armatum specimens such as YPM 10003 or F:AM 112176. The hypoglossal foramen in MPUM 1367 is larger than that found in D. armatum, and opens on the side of the occipital, rather than in the condyloid fossa as in YPM 10003. The paramastoid process lies closer to the glenoid process in MPUM 1367 than it does in most specimens of D. armatum, such as YPM 10003 or F:AM 112176, although this feature can be highly variable in rhinocerotids (Prothero, 2005, p. 97). The postglenoid process and mastoid process are larger in MPUM 1367 than they are in specimens of D. armatum, and the zygo-

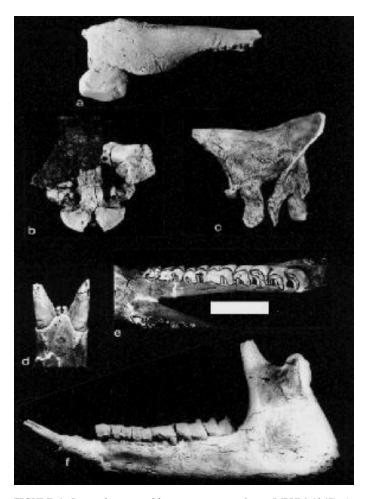


FIGURE 4. *Diceratherium radtkei* n.sp., type specimen (MPUM 1367). A. Lateral view of left premaxillary with I1. B. Posterior portion of skull in ventral (B) and left lateral (C) views. (D-F). Mandible. (D) Dorsal view of anterior dentition. (E) Occlusal view of cheek teeth. (F) Left lateral view of mandible. Scale bar = 10 cm.

matic arch in MPUM 1367 is more massive and higher than in most specimens of *D. armatum*. Unfortunately, the nasals of MPUM 1367 are not preserved; they might be expected to show the broad nasal flanges that supported the horns characteristic of a male skull of *Diceratherium*.

Further confirmation of the generic identity of MPUM 1367 can be seen in the mandible (Fig. 4D-F). It is large and robust, and bears tiny peg-like first lower incisors, and a long tusk-like i2, which indicates that MPUM 1367 comes from a male individual, since female i2 tusks in rhinocerotids are short and blunt with a distinct cingulum around the crown (Prothero, 2005, fig. 2.3). This type of tusk is well known on lower jaws of male specimens of *D. armatum* (e.g., F:AM 112176, shown in Prothero, 2005, fig. 4.16G-H). By contrast, indricotheres have a short, conical i2 tusk, which looks entirely different from that found in rhinocerotids (Forster-Cooper, 1923; Radinsky, 1967; Lucas and Sobus, 1989). This is proof that the largest rhinocerotid specimens from the Arikareean of Wyoming, Montana, and South Dakota belong to *Diceratherium* and not to an indricothere such as *Juxia*.

Discussion: Other than robustness, the chief diagnostic feature of *D. radtkei* is its much larger size. In its postcranials (e.g., Fig. 3) or teeth (e.g., Fig. 7), all specimens referred to *D. radtkei* are disjunctly larger than the cluster for *D. armatum*, and, in most cases, they are at least 30% larger. To test this hypothesis, the coefficients of variation (100 x SD/Mean) of samples of *Diceratherium* were calculated. For a large sample of *D. armatum* from 77 Hill Quarry, the CV of the m2 length is 4.1 and for m2 width it is 5.5 (Table 2). These are values that are

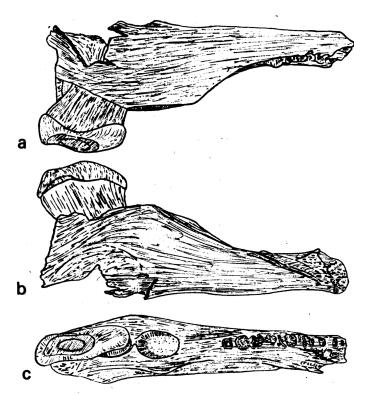


FIGURE 5. Sketch of the left premaxilla of the type specimen (MPUM 1367) of *Diceratherium radtkei*, showing the worn I1 and alveolus for I2, in (A) lateral; (B) medial; and (C) occlusal view.

reasonable for a single species (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974). When specimens of the larger rhino were added to this sample, the CV for m2 length is 14.8 and for m2 width it is 9.5. These values are too large to represent a single population, whose CVs of most dental features are typically around 4-5, and nearly always less than 10 (Kurten, 1953; Simpson et al., 1960; Yablokov, 1974). The coefficients of variation have also been documented in population samples of other species of rhinocerotids, and they are nearly always less than 10 (Table 2; see also Prothero, 2005). Thus, the specimens we refer to *D. radtkei* are too large to be simply large individuals of *D. armatum*, but apparently represent a different species.

In addition to the type specimen, a number of other specimens are referred to *D. radtkei* based on size. These include MPUM 1490, a broken right m3, whose width of 31 mm is identical to the m3 measurements of MPUM 1367; and PM 3103, a left ramus with p2-m3, whose measurements are also typical of *D. radtkei* (Table 1). Green (1958, p. 591-594) referred an exceptionally large rhino maxilla and mandible (SDSM 53584) from the early Arikareean Sharps Formation in South Dakota to *Diceratherium armatum*, and thought that it might just be a large individual within the range of variation of *D. armatum* (this specimen was again referred to *D. armatum* by Prothero, 2005, p. 51). However, the measurements (Table 1; see also Green, 1958, table 4) are clearly too large to belong to the known range of *D. armatum* as it is now understood, and instead fit within the size range of *D. radtkei* (Fig. 7).

Diceratherium armatum Marsh, 1875

Referred material: From the early to middle Arikareean Cabbage Patch beds, western Montana: MPUM 1462, astragalus (Rasmussen, 1977, p. 412), from University of Montana locality MV6504-4 (middle Arikareean); MPUM 2269, right p1 (Rasmussen, 1977, p. 414), from University of Montana locality MV6554, unit 3 (early Arikareean).

Discussion: In addition to the giant species *D. radtkei*, there are a number of fossils that fall within the size range of the large species, *D. armatum*. These include MPUM 2269, a right p1 that is too small to



FIGURE 6. Posterior view of the occiput of the type specimen of *Diceratherium radtkei* (MPUM 1367), showing the characteristic flare of the lambdoid crest.

belong to *D. radtkei* but closely matches *D. armatum* (Prothero, 2005, Table 4.4), and an astragalus, MPUM 1462, whose measurements (64 mm wide, 67 mm high) fall within the range a variation of *D. armatum* (Prothero, 2005, Table 5.3).

Wood (1933) described an isolated partial skull (USNM 11682) of a male *D. armatum* from unnamed Arikareean strata in Gallatin County, Montana, that is very close in measurements with the holotype (YPM 10003). Koerner (1940), in his report on new fossil vertebrates from the Arikareean Fort Logan beds in Meagher County, MT, made no mention of the numerous specimens of *Diceratherium*, including specimens of *D. armatum*, collected in the 1930s while Koerner was a student at Yale University (these uncatalogued specimens are now at the University of Colorado Museum, Boulder, CO). Additional unpublished *Diceratherium* specimens from various sites in Montana, including specimens of *D. armatum*, have been catalogued at the University of Montana Museum of Paleontology, in Missoula, MT.

Diceratherium annectens (Marsh, 1873)

.Referred material: From the early Arikareean Cabbage Patch beds, western Montana: MPUM 13230, right ramus with 3 teeth (?p4-m1-m2?), from University of Montana locality MV6558, unit 2.

Discussion: Although this specimen is very incomplete, its size allows us to assign it to *D. annectens*. Three molariform cheek teeth are preserved. They probably represent p4-m2, based on wear sequence. The first tooth (?p4) is 23 mm long by 12 mm wide; the second tooth (?m1) is 34 mm long by 15 mm wide; and the third tooth (?m2) is 33 mm long by 15 mm wide. These measurements best fit within the range of variation of *D. annectens* (Prothero, 2005, Table 4.4) and are too small for *D. armatum* and too large for *S. manningi*. Thus, three species of *Diceratherium* are presently known in the Cabbage Patch beds. The co-occurrence of *D. armatum* and *D. annectens* is not surprising, because they co-occur in nearly every locality where they are known, including 77 Hill Quarry in Wyoming, and many other localities in the Arikaree Group of Nebraska, Wyoming, and South Dakota, as well as in the Turtle Cove Member of the John Day Formation in Oregon and the Toledo Bend local fauna in Texas.

TABLE 1. Measurements of lower jaws and teeth of *Diceratherium radtkei* (in mm).

	PM 3103	2D2M	53584
Left Right	Left	Left	Right
Length of symphysis 116.6	_	_	_
Width of symphysis 86.3	_	_	_
Depth jaw below m1 81.0 80.7	66.0	_	_
i1, anteroposterior 8.1 8.2	_	_	_
i1, transverse 9.6 8.6	_	_	_
i1, height 7.9 6.6	_	_	_
i2, transverse 36.3 36.1	_	27.4	
i2, height — 87.1	_	_	_
p1, anteroposterior — —	6.6	_	_
p1, transverse — —	5.4	_	_
p2, anteroposterior 29.3 31.2	26.6	_	31.7
p2, transverse 17.6 19.8	16.0		23.4
p3, anteroposterior 39.7 35.1	34.2	42.5	40.2
p3, transverse 22.8 24.3	21.5	25.5	29.3
p4, anteroposterior 37.9 37.2	37.7	49.9	46.3
p4, transverse — 27.1	24.2	30.0	31.4
m1, anteroposterior 41.9 41.9	42.1	49.3	50.6
m1, transverse 28.8 30.8	28.9	35.5	31.7
m2, anteroposterior — 50.6	_	59.0	62.0
m2, transverse — 33.5	_	34.8	37.7
m3, anteroposterior 54.6 53.8	_	60.7	_
m3, transverse 31.2 30.9		32.4	34.4

TABLE 2. Population statistics of *Diceratherium* molars (measurements in mm).

TAXON	m2 length	m2 width
D. armatum (77 Hill Qua	rry)	
Mean	44.8	30.4
Standard Deviation	1.8	1.7
CV	4.1	5.5
D. armatum + D. radtkei		
Mean	49.4	32.2
Standard Deviation	7.3	3.1
CV	14.8	9.5
D. annectens (77 Hill Qua	arry)	
Mean	35.0	24.0
Standard Deviation	2.0	1.0
CV	5.7	4.2

Skinneroceras manningi Prothero, 2005

Referred material: From the early Arikareean Cabbage Patch beds, western Montana: MPUM 13231, upper molar; KU 18670, partially erupted m3, lacking anterior metalophid (Rasmussen, 1977, p. 415); KU 18678, lower molar. All three from University of Montana locality MV6558, unit 2

Discussion: This tiny diceratheriine rhinoceros was originally described by Prothero (2005, p. 58-59) based on a skull and jaws (F:AM 111843) of a presumed female individual from the earliest Arikareean Roundhouse Rock locality on the Wildcat Ridge in Scotts Bluff County, Nebraska. It was previously known only from the type specimen, which is distinct not only in its size but also in its well developed parasagittal crests, flat dorsal skull profile, and strong antecrochets on the molars. The specimens listed above are all smaller than typical *D. annectens* (Prothero, 2005, Table 4.4) and fall close to the dimensions of the type specimen of *S. manningi* (Fig. 7). These include MPUM 13231, a partially prepared upper molar which is 31 mm wide and 29 mm long; KU 18670, a partially erupted m3, whose length is about 25 mm and width is 18 mm; and KU 18678, another isolated lower molar, whose length is 26

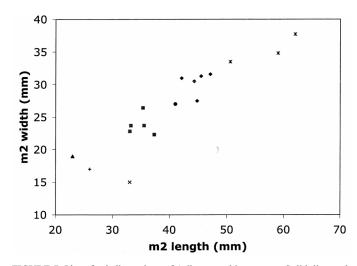


FIGURE 7. Plot of m2 dimensions of Arikareean rhinoceroses. Solid diamonds = *Diceratherium armatum* from 77 Hill Quarry, Wyoming; gray squares = *D. annectens* from 77 Hill Quarry, Wyoming; x with vertical slash = *D. radtkei*; solid triangle = type specimen of *Skinneroceras manningi*; + = KU 18678, referred to *S. manningi*; x = MPUM 13230, referred to *D. annectens*; solid circle = Montana *D. armatum*.

mm and width is 17 mm. All of these specimens are close in dimensions to the type of *S. manningi*, and too small to fall within the range of variation of *D. annectens*. Thus, although the material is highly fragmentary, based on the size of the specimens and their early Arikareean age, they are probably referable to *S. manningi*. This extends the range of this taxon from its type locality in Roundhouse Rock, Nebraska, to western Montana.

CONCLUSIONS

Rhinoceros specimens from the Arikareean Cabbage Patch beds in the Flint Creek intermontane basin of western Montana include four species of rhinoceros previously known from other Arikareean localities in the Great Plains. These include the more common species Diceratherium armatum and D. annectens (also found together in Oregon, Texas, Florida and elsewhere), plus the rare dwarf rhino Skinneroceras manningi (previously known only from the type locality at Roundhouse Rock in western Nebraska). In addition, fragmentary skull and jaw material of a giant Diceratherium from the Cabbage Patch beds allows identification of the mysterious giant rhino postcranials previously known only from the late Arikareean of Wyoming (Prothero, 2005, p. 127-128), and a more specific identification of a poorly preserved large rhinoceros from the early Arikareean of Shannon County, South Dakota (Green, 1958, p. 591-594). These specimens are now considered to pertain to one taxon, a giant species of Diceratherium, D. radtkei. Specimens of D. armatum and D. annectens were previously known from other Arikareean localities in Montana (mostly as uncatalogued and undescribed specimens) but the Cabbage Patch S. manningi and D. radtkei were previously known only from a few specimens in Nebraska, South Dakota, and Wyoming. Thus, the Cabbage Patch specimens represent a considerable geographic range extension of these taxa into the intermontane terrain of the northern Rocky Mountains.

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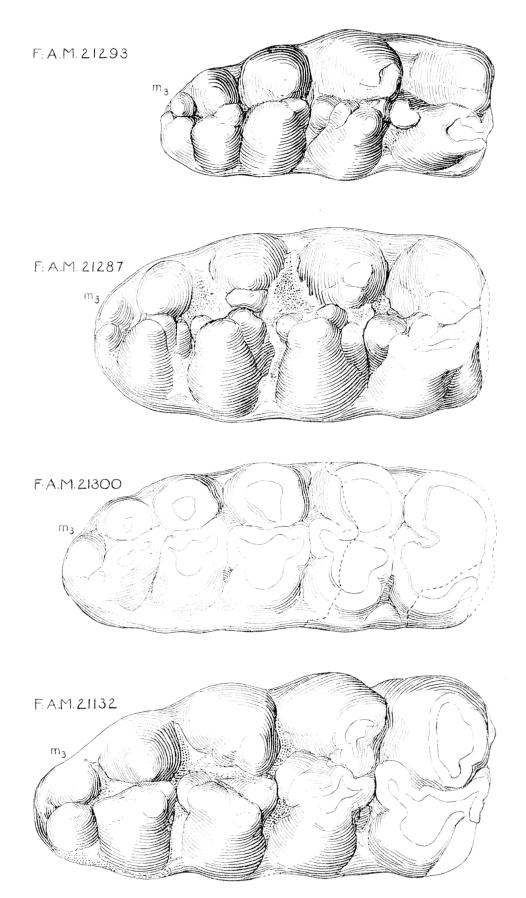


Fig. 25. Longirostrine m₃s from the late Tertiary of New Mexico.