A NEW SPECIES OF EXTINCT RHINOCEROS FROM THE LATE OLIGOCENE OF SOUTH DAKOTA

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Abstract—We describe a new species of rhinoceros, *Diceratherium marriottae*, from the upper Oligocene Sharps Formation (earliest Arikareean) in Badlands National Park, South Dakota. It is intermediate in size between the Whitneyan *D. tridactylum*, and the Arikareean *D. armatum*. Its morphology is also intermediate between those two species, especially in its distinctive low nasal ridges on the skull, which are not as large as those found in *D. armatum,* but much larger than those found in any known specimen of *D. tridactylum*. Thus, it represents a transitional species between those abundant and well-studied taxa.

INTRODUCTION

During the Oligocene, rhinoceroses were a significant component of the White River Chronofauna, although not very diverse compared to their later evolution in the Miocene. The most common Orellan (earliest Oligocene) species was *Subhyracodon occidentalis* (Leidy, 1850). In the Whitneyan, it evolved into the slightly larger *Diceratherium tridactylum* (Osborn, 1893). This taxon was formerly known as *Aceratherium tridactylum*, then *Subhyracodon tridactylum* (Prothero, 2005). Both of these species are known from hundreds of skulls and many other specimens. They are distinguished from each other not just by the larger size of *D. tridactylum,* but also by the fact that the male skulls of that species have the beginnings of the long rugose paired nasal ridges that eventually become very large in *Diceratherium armatum* in the early Arikareean, which has very large flange-like ridges forming a "V"-shaped pattern in male skulls. The only other rhinocerotids known from the Orellan-Whitneyan interval are *Amphicaenopus platycephalus* (Osborn and Wortman, 1894) and *Penetrigonias dakotensis* (Peterson, 1920), both of which have so far been reported from Chadronian and Whitneyan of South and North Dakota, but so far not found in the intervening Orellan.

In the early Arikareean, *D. tridactylum* was replaced by the large species *D. armatum* Marsh, 1875, and also by a smaller species *D. annectens* (Marsh, 1873), both of which had large flanges on their nasal bones in male skulls that probably supported some kind of paired nasal horns. In addition, there were a number of other isolated early Arikareean rhinos known from only a few specimens, or a single specimen. These include the small rhino *Skinneroceras manningi* Prothero 2005, from the earliest Arikareean "brown siltstone" at Roundhouse Rock, Morrill County, Nebraska (Swinehart et al., 1985; Tedford et al., 1996, 2004). Another is the peculiar short-faced rhinoceros *Woodoceros brachyops* Prothero 2005, known only from the late Whitneyan Blue Ash Channel, Harris Ranch, Fall River County, South Dakota. Prothero and Rasmussen (2008) also reported the huge species *Diceratherium radtkei*, from the earliest Arikareean Cabbage Patch beds of western Montana, as well as postcranials of that species from the earliest Arikareean of Wyoming.

In addition to these specimens, another specimen (F:AM 112171) was briefly mentioned and illustrated by Prothero (2005, p. 208, fig. 7.7), but not formally named or described. It was collected in 1950 by Morris Skinner and crew from the lower Sharps Formation in Shannon County, South Dakota. Additional specimens of this rhino have also been collected from the Sharps Formation, as discussed below. This specimen was originally not assigned to a new taxon, because only the isolated skull was known, but the addition of new material from the SDSM collections gives a much better idea of the overall morphology and variation in this species, and now a name for this species is justified.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, and F:AM, the Frick Collection of the AMNH; SDSM, South Dakota School of Mines Museum, Rapid City, SD.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Superfamily Rhinocerotoidea Owen, 1845
Family Rhinocerotidae Owen, 1845
Diceratherium Marsh, 1875

Rhinoceros Marsh, 1870 (*non* Linnaeus)
Diceratherium Marsh, 1875
Aceratherium Cope, 1879 (*non* Kaup)
Aceratherium Osborn, 1893 (in part)
Caenopus Hay, 1902 (in part)
Metacaenopus Cook, 1908
Epiaphelops Cook, 1912
Coenopus [*sic*] Gidley, 1924
Subhyracodon Wood, 1927 (in part)
Caenopus Wood and Wood, 1937 (in part)

Type species: *Diceratherium armatum* Marsh, 1875.

Included species: *D. tridactylum* (Osborn, 1893); *D. annectens* (Marsh, 1873); *D. matutinum* (Marsh, 1870); *D. niobrarense* Peterson, 1906; *D. radtkei* Prothero and Rasmussen, 2008; and *D. marriottae* new species.

Diagnosis: (after Prothero, 2005, p. 49): "Moderate to large rhinocerotids with paired ridge-like subterminal nasal horns or rugosities in males; hornless in females. P2-4 nearly completely molariform. Molars with strong cingula, relatively simple crown patterns, nearly always lacking crochets or cristae. Skull relatively long, with long basicranial axis and flat dorsal profile. Limbs elongate, but metapodials relatively short. Distinguished from *Subhyracodon* by the presence of nasal rugosities in male skulls, molarized upper premolars, and larger size. Distinguished from *Menoceras* by the dolichocephalic skull with long basicranial region and flat dorsal profile, subterminal ridge-like paired nasal horns (not the terminal spherical horn bosses seen in *Menoceras*), relatively simple teeth with no crochets or cristae, and larger size."

Distribution: Early Whitneyan to ?late Hemingfordian of the High Plains, Montana, Oregon, and New Jersey.

Discussion: The complicated taxonomy of *Diceratherium*, and its frequent confusion with the unrelated European immigrant rhino *Menoceras*, were discussed by Prothero (2005, p. 49). Originally all paired-horned rhinoceroses in North America

were lumped under Marsh's (1875) genus *Diceratherium* from the John Day Formation of Oregon. When the Agate Springs rhino *Menoceras* was first described, it was mislabeled *Diceratherium cooki*, and thought to be representative of true *Diceratherium* (Marsh never illustrated his type specimen, so no one noticed how different its paired nasal ridges were from the spherical horn bosses of male *Menoceras* skulls). Troxell (1921) first distinguished and named the Agate Spring taxon as *Menoceras*, but was ignored by later workers. Tanner (1969) finally illustrated the two taxa side-by-side, with Marsh's type specimen of *D. armatum* compared to the Agate rhinoceros *M. arikarense*, showing how different their paired horns really were. Since that time the scientific community has come to accept them as distinct genera. In fact, as Prothero et al. (1986) point out, *Menoceras* is a much more derived rhinoceros than *Diceratherium*, with many features that unite it with Eurasian taxa such as *Pleuroceros*, and only the paired horns (which developed in two entirely different ways) seemed to unite them.

The Whitneyan species "*Aceratherium" tridactylum* had long been lumped in with the Orellan taxon *Subhyracodon occidentalis*. Prothero (2005, p. 49-50) pointed out that this made *Subhyracodon* paraphyletic, in that in many male specimens of *tridactylum*, there are rugose surfaces along their low nasal ridges (best demonstrated in AMNH 541) that anticipate the condition in *D. armatum*. For this reason, Prothero transferred *S. tridactylum* to *Diceratherium*, making the combination *Diceratherium tridactylum*. The new species discussed below is just slightly more derived than *D. tridactylum*, with slightly larger size and even more prominent and robust nasal ridges.

Diceratherium marriottae **n. sp.**
Figs. 1-4, Table 1

Diceratherium gregorii Green, 1958
Diceratherium gregorii Macdonald, 1963
Diceratherium gregorii Macdonald, 1970
Diceratherium armatum Prothero, 2005 (in part)
Diceratherium annectens Prothero, 2005 (in part)

Holotype: F:AM 112171, a partial skull (Fig. 1). The locality information is written directly on the specimen as follows: "Top of Cedar Pass. Zone: 107 feet above base of 1st white layer, and near base of 2nd white layer". These notes were written when the specimen was collected by Morris F. Skinner in 1950, and record his stratigraphy for the Sharps Formation in Badlands National Park, Jackson County, South Dakota (see Tedford et al., 1996, 2004). The "1st White Layer" in Skinner's notes had formerly been referred to the Rockyford Ash, but

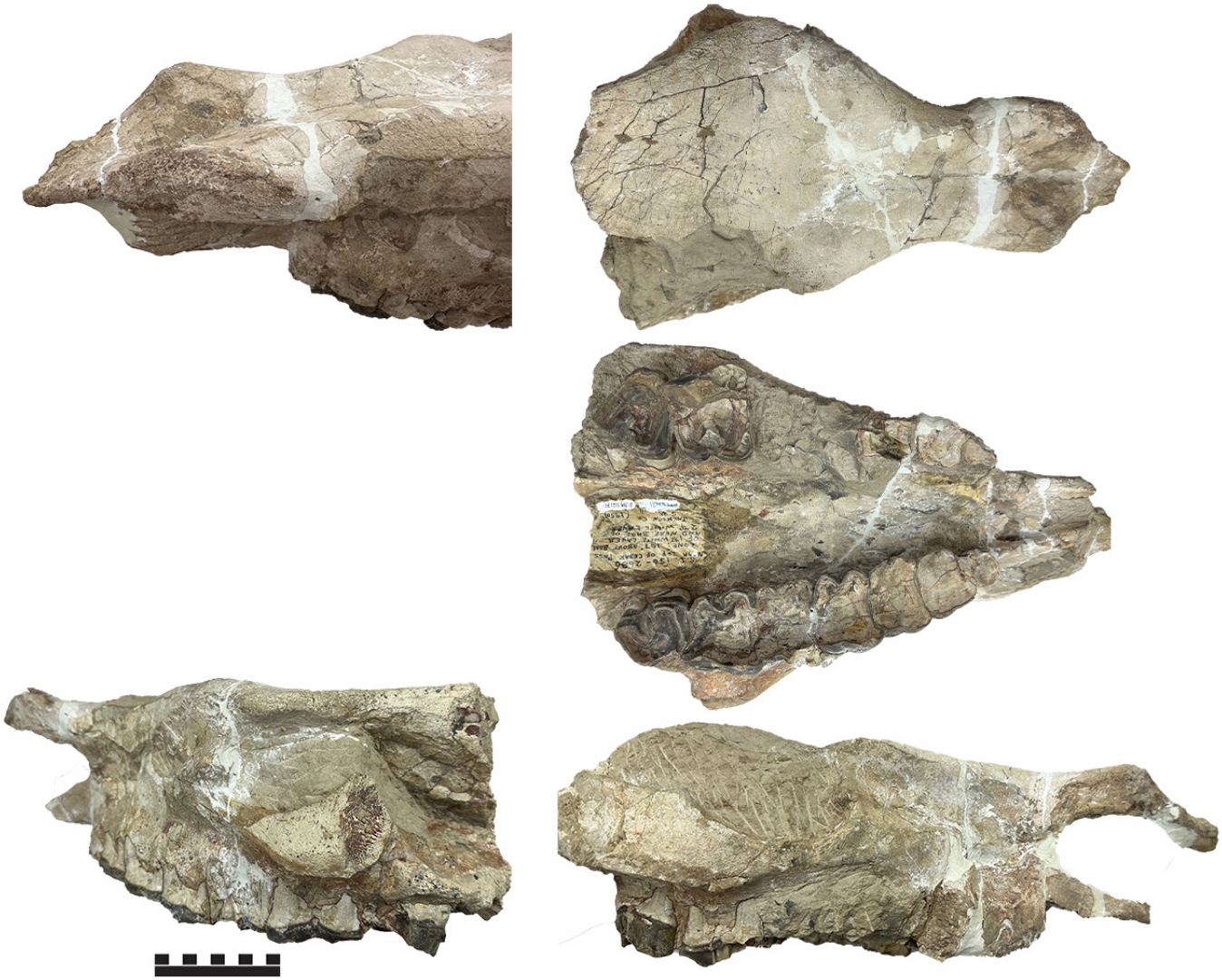

FIGURE 1. F:AM 112171, holotype skull of *D. marriottae*. Right column, top to bottom: dorsal, ventral, and right lateral view. Top left: oblique closeup of the nasal ridges from the left side. Bottom left: left lateral view. Scale bar in cm.

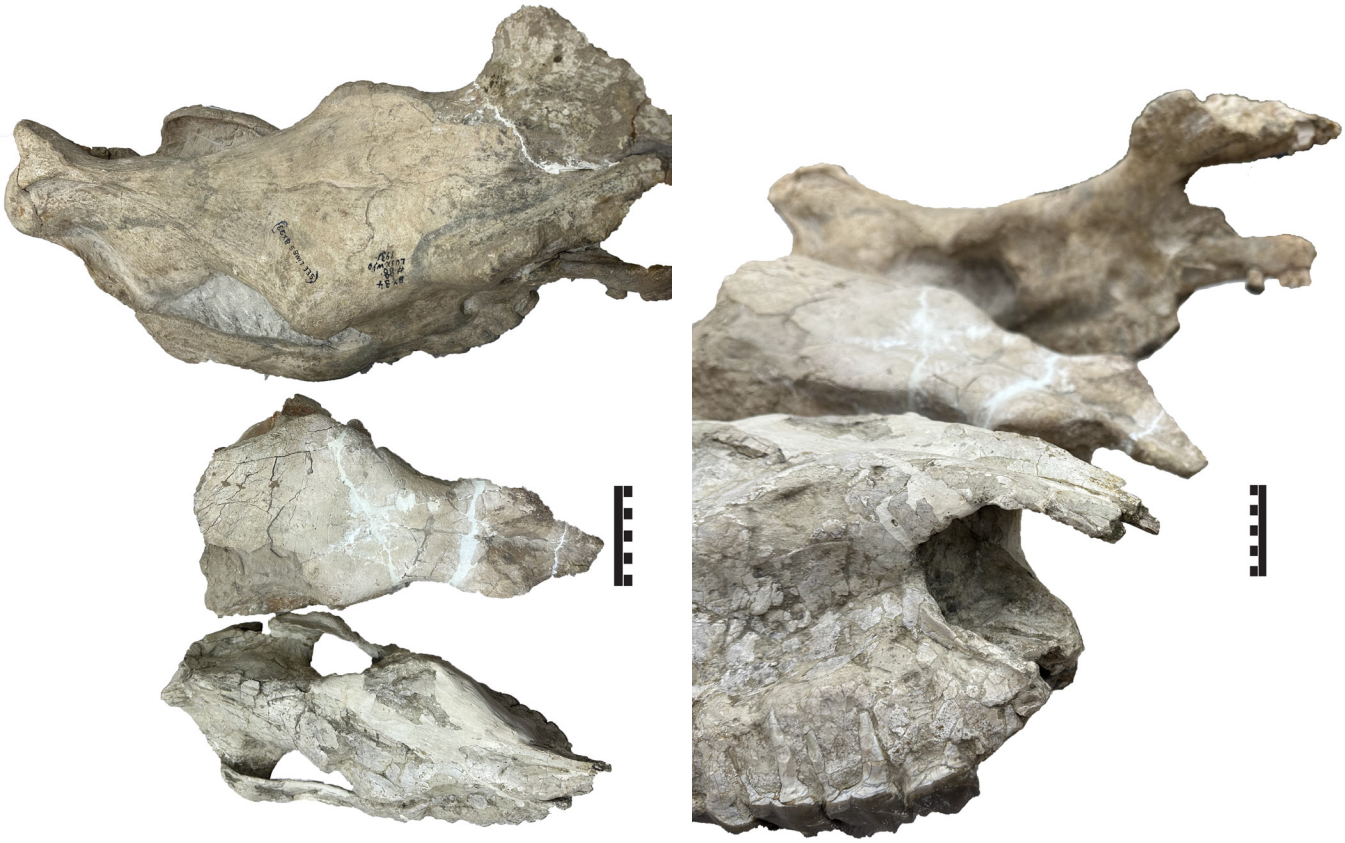

FIGURE 2. Two views comparing the nasal ridges in *Diceratherium*. The smallest skull (in the foreground or bottom of the image) is *D. tridactylum*, AMNH 541. In the middle is F:AM 112171, holotype of *D. marriottae*. C. In the background is the male skull of *D. armatum*, F:AM 112176, showing the huge flange-like nasal ridges on male skulls of this species. Scale bar in cm.

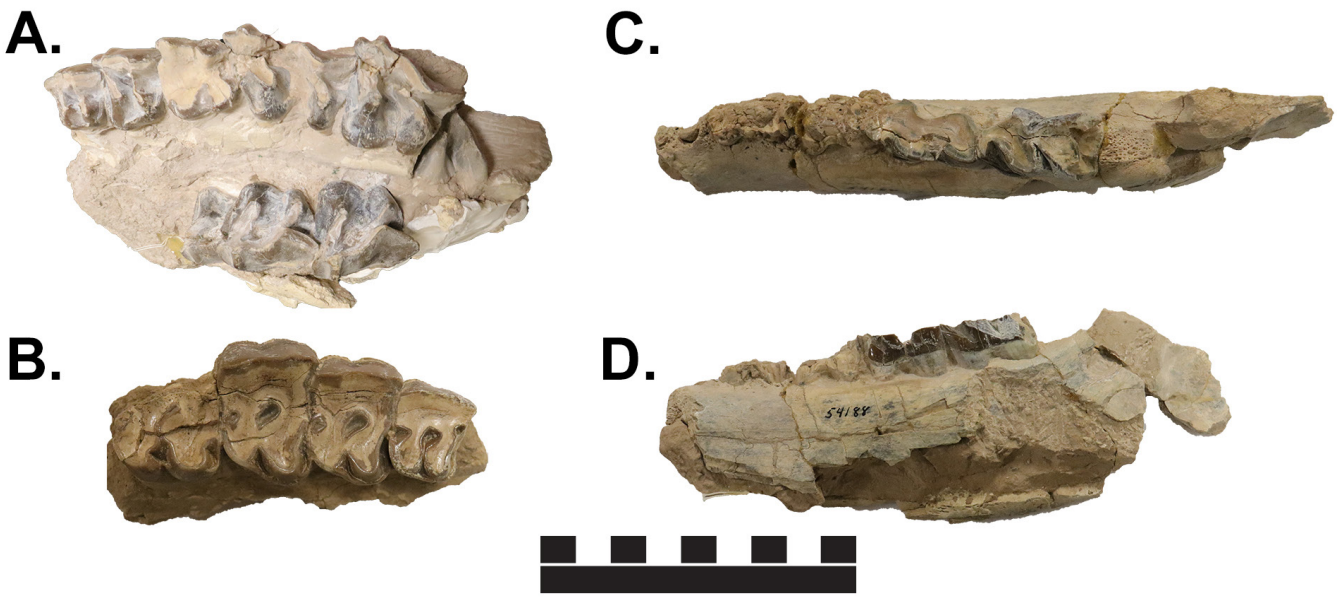

FIGURE 3. Referred specimens of *D. marriottae*. **A,** SDSM 54144, juvenile partial skull in crown view. **B,** SDSM 54339, adult palate in crown view. **C-D,** Crown and lateral views of SDSM 54188, left lower jaw. Scale bar in cm.

does not correlate with the type section of the Rockyford Ash at Sheep Mountain Table (Evanoff et al., 2010). However, any fauna retrieved and published from that interval or higher is a characteristic earliest Arikareean fauna (Parris and Green, 1962; Welsh et al., 2018).

Referred materials: All referred specimens are from the Wounded Knee Fauna of Macdonald (1963, 1970, Oglala-Lakota County (formerly Shannon County), South Dakota (see Green, 1958). From SDSM locality V5354: SDSM 54339, maxillary fragment with P2-M1 (Fig. 2B); 59111, various teeth and tooth fragments; From SDSM locality V542: SDSM 54165, M2; 54188, dentary fragment with m1-2 (Fig. 3C-D); 54198, mandible fragment with m1 not erupted; 54144, partial skull (Fig. 3A); From SDSM locality V543, an M2. These specimens come from the same beds as the type skull, and their size matches that of the type skull as well (Tables 1, 2). (Most of these specimens were listed by Macdonald, 1963, 1970, as "*Diceratherium gregorii*", which is an invalid junior synonym of *D. armatum*, *fide* Prothero, 2005).

Etymology: In honor of Katherine Marriott, for her many contributions to paleontology, and for her support of other paleontology students in advancing their careers.

Distribution: Sharps Formation (earliest Arikareean), South Dakota.V5354 is near the top of the Sharps, while V542 is just over 100 feet above the base of the Sharps Formation.

Diagnosis: Species of *Diceratherium* intermediate in size between *D. armatum* and *D. tridactylum* (M1-3 length = 111-120 mm). Rugose nasal ridges much more developed than those in male *D. tridactylum*, but not so large as those in *D. armatum* or *D. annectens*.

Description: The type skull, F:AM 112171 (Fig. 1), is broken just posterior to the M3, so it is not possible to measure total skull length, or describe any part of the skull posterior to the orbits. However, the skull is 330 mm wide at the midpoint of M2, and 90 mm wide at the diastema anterior to P2. In dorsal view, the skull roof is low and flat, with a narrowing over the preorbital region, and widens over the orbit with supraorbital crests. It then narrows in the postorbital region before the point at which the posterior skull is broken off. The nasals are partly damaged, but they clearly show prominent paired rugose nasal ridges that are larger than those found in *D. tridactylum*, but much smaller than the large flanges in *D. armatum* (Fig. 2).

In ventral view (Fig. 1), the teeth of F:AM 112171 are so worn that no crown pattern remains. However, their measurements are given in Table 1. The P1 is present but represented by a small circular crown, with the crown pattern completely worn off. (P1 is often missing in rhinos, because in many cases it is a retained dP1). The premaxilla anterior to P1 has long lateral ridges on their ventral exterior edges, and then they are broken on the anterior end, so no anterior teeth are preserved. The palate is flat, and the rest of the base of the skull is missing just posterior to M3.

In lateral view (Fig. 1), the skull is incompletely prepared, so there is still lots of matrix filling the orbital region and zygomatic arch, as well as in the narial notch. Presumably, the latter was left by the preparators to protect the fragile nasal bones from being broken off. As in other species of *Diceratherium*, the narial notch is fairly shallow and ends anterior to the P1. The premaxillae are long and delicate, but in this specimen, none of the anterior teeth are preserved. The right and left sides of the skull are only partially prepared, so there is too much matrix covering the bone to describe the orbit or zygomatic arch in detail. Only the broad surface of the malar part of the zygomatic arch is still visible above the matrix. Much of the maxillary is damaged, exposing the roots of the molars. As stated before, none of the postorbital part of the skull has been preserved.

Because the teeth of the holotype, F:AM 112171, are so worn, the crown pattern of less worn upper teeth can be seen better in SDSM 54144 (Fig. 3A) and SDSM 54339 (Fig. 3B). SDSM 54144 is a juvenile specimen, with dP2-4 still in place, and M3 just beginning to erupt. On this specimen, the dP2 and dP3 are very lightly worn, so the crests of the protoloph and metaloph are thin and narrow. The dP2 does not seem to show the peculiar three-lobed pattern found in many extinct rhinos. The crests on dP3 in SDSM 54144 remain parallel and unconnected in SDSM 54144, which is less worn. However, dP4 is completely molariform and also completely worn down, typical of specimens which are about to start shedding their deciduous dentitions.

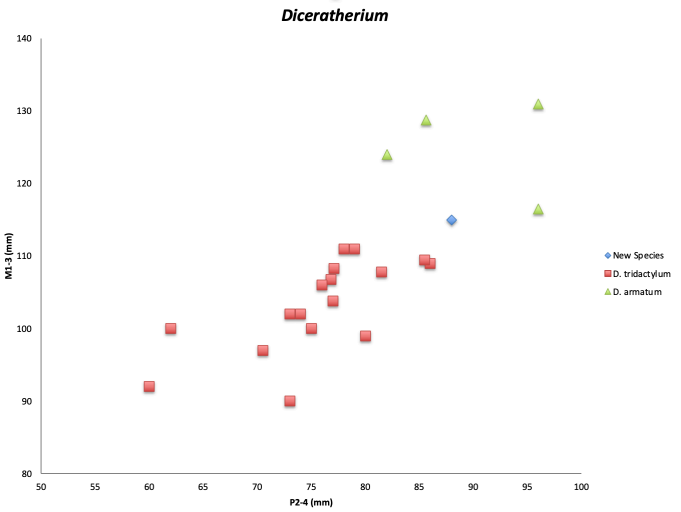

FIGURE 4. Bivariate plot of P2-4 vs. M1-3 of three species of *Diceratherium*, showing their relative size.

SDSM 54339 (Fig. 3B), on the other hand, is a partially worn adult maxilla, so the P2 and P3 are much more worn. The protoloph and metaloph form areas of dentin surrounded by outer rims of enamel, with narrow crests connecting the metaloph and protoloph to the ectoloph, and a broad circular lake of enamel where the protocone and metacone would be. This trend is even stronger in P3 in SDSM 54339, where the wear on the protoloph and metaloph has caused these crests to converge at the base. P4 is even more pronounced in this trend, with a completely molariform shape and the convergence of the protoloph and metaloph on the lingual side forming a lake of enamel in the middle of the tooth.

In both SDSD 54144 and SDSM 54339, the M1 is erupted and undergoing wear. It shows the classic "π" shape of rhino upper cheek teeth, with only moderate wear in SDSM 54144, while in SDSM 54339, the tooth is deeply worn and the ectoloph is broken off. M2 is preserved only in SDSM 54144, where it is moderately worn with strong metaloph crests, and posteriorly deflected protolophs and metalophs. M3 is present only in SDSM 54144, where it is just beginning to erupt from its crypt. It shows the classic rhinocerotid "V"-shaped pattern of protoloph and metaloph, with only a short ectoloph, and no metastyle on the posterolabial side.

Lower teeth and jaws are rare in this species. The best preserved is SDSM 54188, a partial left ramus (Fig. 3C-D). The tooth crowns are worn and badly broken, but they still show the curved "L"-pattern that forms the trigonid and talonid of each molar. Measurements of the lower teeth are given in Table 1.

DISCUSSION

As can be seen from the measurements, and the condition of the nasal ridges, *D. marriottae* represents a good intermediate between *D. tridactylum* and *D. armatum* (Fig. 2). This is even more striking when the tooth row measurements are plotted (Fig. 4). The holotype, F:AM 112171, falls exactly in the gap

TABLE 1. Measurements of upper teeth of *Diceratherium* (in mm). All the data in the first 5 columns are for *D. marriottae*. Means for *D. tridactylum* and *D. armatum* from Prothero (2005, table 4.4). SD = standard deviation.

	F:AM112171	SDSM54339	SDSM54144	Mean	SD	*D. tridactylum*	*D. armatum*
P2-M3	200.7	—	—	200.7	—	176.0	234.0
P2-4	88.0	—	—	88.0	—	73.0	102.0
M1-3	115.0	—	—	115.0	—	103.0	132.0
Length P1	22.2	—	—	22.2	—	—	—
Width P1	23.2	—	—	23.2	—	—	—
Length P2	27.0	24.5	27.9	26.5	1.8	25.0	28.0
Width P2	26.5	29.5	27.5	27.8	1.5	32.0	37.0
Length P3	31.3	27.7	30.7	29.9	1.9	29.0	30.0
Width P3	44.9	37.8	33.2	38.6	5.9	40.0	45.0
Length P4	31.9	29.8	32.3	31.3	1.3	32.0	32.0
Width P4	45.9	43.1	33.5	40.8	6.5	44.0	48.0
Length M1	35.7	—	41.3	38.5	3.9	34.0	39.0
Width M1	43.4	—	35.1	39.3	5.8	43.0	51.0
Length M2	38.8	37.5	43.6	39.9	3.2	37.0	57.0
Width M2	45.4	42.7	49.4	42.5	3.0	45.0	56.0
Length M3	38.8	—	—	38.8	—	37.0	46.0
Width M3	33.2	—	—	33.2	—	40.0	51.0

TABLE 2. Measurements (in mm) of lower teeth of *D. marriottae.*

	SDSM54144	SDSM 54188	SDSM 54198
Length p3	28.7	—	—
Width p3	18.7	—	—
Length p4	30.8	—	—
Width p4	19.5	—	—
Length m1	33.2	35.5	28.5
Width m1	21.1	18.5	15.3
Length m2	36.4	—	31.7
Width m2	21.9	—	17.8

between the cluster of specimens of *D. tridactylum* and the cluster of *D. armatum.* The holotype is the only specimen that can be plotted this way, because the referred material does not include any complete tooth rows. The intermediate condition of *D. marriottae* can also be seen in the measurements of the teeth (Table 1), where the means of the *D. marriottae* measurements are almost exactly between typical range of variation of *D. tridactylum* and *D. armatum.* Thus, it is clear that *D. marriottae* can be justified as a separate species, and not just an aberrantly large individual of *D. tridactylum* with larger nasal horn ridges. The sample size of *D. tridactylum* is quite large, and the range of variation of nasal ridges in this species is well known, and *D. marriottae* does not fall within that range of variation.

CONCLUSION

We describe a new species of extinct fossil rhino, *Diceratherium marriottae*, from the late Oligocene (earliest Arikareean) of South Dakota. It is intermediate in size, and in the development of its elongate rugose nasal horn ridges, between Whitneyan (late early Oligocene) *D. tridactylum* and Arikareean *D. armatum.* Although known from only a few specimens, its low nasal horn ridges in the type specimens show the transition between the tiny nasal ridges in male skulls of *D. tridactylum* and the large ridges of male specimens of *D. armatum.* With this new taxon, the diversity of early Arikareean rhinos is increased to six species. In addition to *D. marriottae*, there are *D. annectens, D. radtkei,* and *D. armatum,* as well as the peculiar rhinos *Skinneroceras manningi* and *Woodoceras brachyops*.

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