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ORIGINAL PAPER

Protungulatum, Confirmed Cretaceous Occurrence of an Otherwise Paleocene Eutherian (Placental?) Mammal

J. David Archibald · Yue Zhang · Tony Harper · Richard L. Cifelli

Abstract Neither pre-Cenozoic crown eutherian mammals (placentals) nor archaic ungulates ("condylarths") are known with certainty based on the fossil record. Herein we report a new species of the Paleocene archaic ungulate ("condylarth") *Protungulatum* from undisputed Late Cretaceous aged rocks in Montana USA based on an isolated last upper premolar, indicating rare representatives of these common early Tertiary mammals appeared in North America a minimum of 300 k years before the extinction of non-avian dinosaurs. The other 1200 mammal specimens from the locality are characteristic Late Cretaceous taxa. This discovery overturns the current hypothesis that archaic ungulates did not appear in North America until after the Cretaceous/Tertiary (K/T) boundary and also suggests that other reports of North American Late Cretaceous archaic ungulates may be correct. Recent studies, including ours, cannot determine whether *Protungulatum* does or does not belong to the crown clade Placentalia.

Keywords Eutheria · Placentalia · Archaic ungulate · *Protungulatum* · Late Cretaceous · Hell Creek Formation

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Introduction

The archaic ungulate or "condylarth" *Protungulatum donnae* was described from Bug Creek Anthills in northeastern Montana, U. S. A. (Sloan and Van Valen 1965). The sequence including Bug Creek Anthills and several other localities was thought to be Late Cretaceous in age, arguing for a gradual appearance of mammals otherwise known only from the Paleocene, and a gradual disappearance of typical Late Cretaceous mammals and dinosaurs (Sloan et al. 1986). This work argued that there were gradual rather than catastrophic extinctions at the Cretaceous/Tertiary (K/T) or Cretaceous/Paleogene (K/Pg) boundary. Although common co-occurrences of dinosaurs and Late Cretaceous mammals at Bug Creek Anthills argued for a Late Cretaceous age, subsequent work indicated the sites are Paleocene (Smit and Van der Kaars 1984) and fossils were reworked from Cretaceous sediments (Lofgren 1995). Thus, no archaic ungulates were known from Late Cretaceous localities.

Two Canadian Late Cretaceous sites were argued to include teeth of four archaic ungulate species (Fox 1989). Cifelli et al. (2004) discussed the issues surrounding the assessment of the age of these the faunas yielding these teeth. They assigned these faunas to the Puercan land mammal age (early Paleocene) but noted that other hypotheses are: some of these faunas are transitional assemblages of Cretaceous age, the beginning of the Puercan is diachronous between southern Canada and northern United States, or *Protungulatum* and a few other normally Paleocene mammals occur in the Late Cretaceous of southern Canada.

As noted above, *Protungulatum* has been regarded, almost universally, to be a "condylarth" or archaic ungulate. The meanings of the terms "condylarth" and "archaic ungulate" have varied from author to author. In more recent, broader studies such as Van Valen (1978), Condylarthra was used formally as an order. Prothero et al. (1988) argued that the concept of Condylarthra should be abandoned. Archibald (1998) followed this recommendation, referring to this assemblage as archaic ungulates. Archaic ungulates, again almost universally, have been regarded as including the ancestry of both extinct groups such as the South American meridiungulates as well as extant clades of hoofed mammals, notably perissodactyls and artiodactyls (including cetaceans) (e.g., Archibald 1998). Archaic ungulates would thus be at minimum a paraphyletic if not a polyphyletic group rather than a clade, but they also would reside within the crown clade Placentalia as they would share a more recent ancestry with some but not all placentals. This terminology follows the convention of treating Eutheria as the sister taxon of Metatheria (including Marsupialia), with the crown group of Eutheria being Placentalia (Rougier et al. 1998). As discussed later, whether *Protungulatum* belongs within the crown clade Placentalia or lies outside the crown clade is a matter of some debate.

The description here of a specimen referable to a new species of *Protungulatum* and recovered from definitively Late Cretaceous deposits raises anew questions about the timing and place of the origin of this traditionally recognized North American Paleocene eutherian species. It also speaks to the question of the pace of appearances and disappearances at and near the K/T boundary. This specimen does not address whether *Protungulatum* is or is not a placental mammal or whether placentals are known before the K/T boundary. We do, however, review the current arguments as to whether *Protungulatum* is or is not a placental mammal, which of course impinges on the question as to whether fossils of placental mammals are present in Cretaceous rocks.

Materials and Methods

Fossil Material The specimen described here is from the Spigot-Bottle locality, Carter County, southeastern Montana, which occurs in the uppermost Cretaceous, Hell Creek Formation. Spigot-Bottle is the richest of a number of localities discovered in the 1980s and 90s by field expeditions led by the first author. In 2002 a preliminary list of 23 species of mammal was published based on 874 specimens from Spigot-Bottle and four other localities (Hunter and Archibald 2002). This material was catalogued into the University of California Museum of Paleontology (UCMP), Berkeley, California. The fourth author led expeditions that collected many additional specimens from Spigot-Bottle. This material was catalogued into the Oklahoma Museum of Natural History (OMNH), Norman, Oklahoma. The species described here, based on an isolated last upper premolar, is from the latter collection. Based on studies of other eutherian mammals (e.g., Nessov et al. 1998), this tooth may be a P5; however, to avoid confusion with the referral of this tooth as P4 in other studies (e.g., Luo 1991), we identify it as the last upper premolar.

In 2009 the combined sample of over 1200 specimens, mostly from Spigot-Bottle formed the faunal study of the second author for his graduate research (Zhang 2009 unpubl. MSc thesis). In part because of the much larger sample, the number of mammalian taxa recognized in this new study was increased to 35 (Table 1). Spigot-Bottle and associated localities are the taxonomically richest in species diversity and the second richest in numbers of specimens known from the Late Cretaceous of North America. This explains why one might expect to find truly rare taxa such as the new species of *Protungulatum* described here. It is unusual, however, in that it is the only taxon listed in Table 1 that is not normally recovered from the latest Cretaceous. Although the vast majority of the specimens come from Spigot-Bottle, a few rarer taxa, the multituberculate *Essonodon browni* and the metatherian *Glabius intricatus*, are from much less rich localities in the region. The eutherian *Cimolestes magnus* has also been reported from another locality in the region (Clemens 1973).

Stratigraphic Setting and Age of the Locality Spigot-Bottle occurs about 61 m below the Hell Creek—Fort Union formational contact, which approximates the K/T (K/Pg) boundary (Belt et al. 1997: fig. 12). Paleofloral studies, and palynology in particular, place the K/T (K/Pg) boundary within the proximity of this lowest lignite at the Hell Creek—Fort Union formational contact (e.g., Johnson and Hickey 1990) in this area. Also, no dinosaur remains have been found above this lowest lignite.

Spigot-Bottle is within the Toe Bone Channelbelt, a well-studied, multistoried channel complex capped 45 m below the lowest lignitic coal (Belt et al. 1997: fig. 12) (Fig. 1). The C30n/C29r paleomagnetic reversal is about 10 m above the channel capping (Fig. 1), which places Spigot-Bottle a minimum of 300 k years before the K/T (K/Pg) boundary (Hicks et al. 2002; Gradstein et al. 2004).

Contamination from Tertiary sediments is not possible because the nearest such outcrops occur 2 km to the southeast and across several drainages. Further, these samples were collected in situ and screen-washed in screens used solely for Late Cretaceous sediments. The final tangential evidence that the tooth (OMNH 64985) is from the latest Cretaceous and is not a Paleocene contaminant

Table 1 Mammals, latest Cretaceous, Hell Creek Formation, SE Montana, after Zhang (2009 unpubl. MSc thesis)

Species	Numbers of specimens	Percentage
MULTITUBERCULATA		
Mesodma hensleighi	56	4.68%
Mesodma formosa	225	18.81%
Mesodma thompsoni	248	20.74%
Cimolodon nitidus	27	2.26%
Cimolodon n. sp.	15	1.25%
Cimolomys gracilis	13	1.09%
Cimolomys sp. cf. *C. gracilis*	1	0.08%
Meniscoessus robustus	87	7.27%
Essonodon browni	6	0.50%
METATHERIA		
Pediomys elegans	161	13.46%
Leptalestes cooki	40	3.34%
Leptalestes krejcii	27	2.26%
Protolambda hatcheri	32	2.68%
Protolambda florencae	15	1.25%
Alphadon marshi	16	1.34%
Alphadon wilsoni	5	0.42%
Nortedelphys magnus	7	0.59%
Nortedelphys intermedius	13	1.09%
Nortedelphys minimus	3	0.25%
Albertatherium foxi	4	0.33%
Turgidodon rhaister	17	1.42%
Didelphodon vorax	21	1.76%
Protalphadon lulli	6	0.50%
genus and species undetermined A	1	0.08%
genus and species undetermined B	1	0.08%
Glasbius intricatus	5	0.42%
EUTHERIA		
Gypsonictops hypoconus	96	8.03%
Gypsonictops illuminatus	6	0.50%
cf. *Gypsonictops hypoconus*	4	0.33%
Paranyctoides n. sp.	2	0.17%
Cimolestes incisus	16	1.34%
Cimolestes propalaeoryctes	12	1.00%
Cimolestes stirtoni	3	0.25%
Batodon tenuis	4	0.33%
Protungulatum coombsi	1	0.08%
Total	1196	100%

comes from the specimen itself. The tooth, although almost morphologically identical to the similar tooth in *Protungulatum donnae*, is considerably larger than any known similar teeth for this earliest Paleocene species, indicating it cannot simply be referred to this species. The chances that a Paleocene specimen of a considerably larger size than any known for *P. donnae* happened to contaminate Spigot-Bottle can be qualitatively regarded as very remote, especially given the stratigraphic and sampling protocols discussed above.

We note that this discovery does not affect the first appearance datum (FAD) defining the beginning of the Puercan age if *Protungulatum donnae* (Cifelli et al. 2004) is used rather than simply *Protungulatum* (Lofgren et al. 2004).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
EUTHERIA Gill, 1872
?PLACENTALIA Owen, 1837
?ARCTOCYONIDAE Murray, 1866

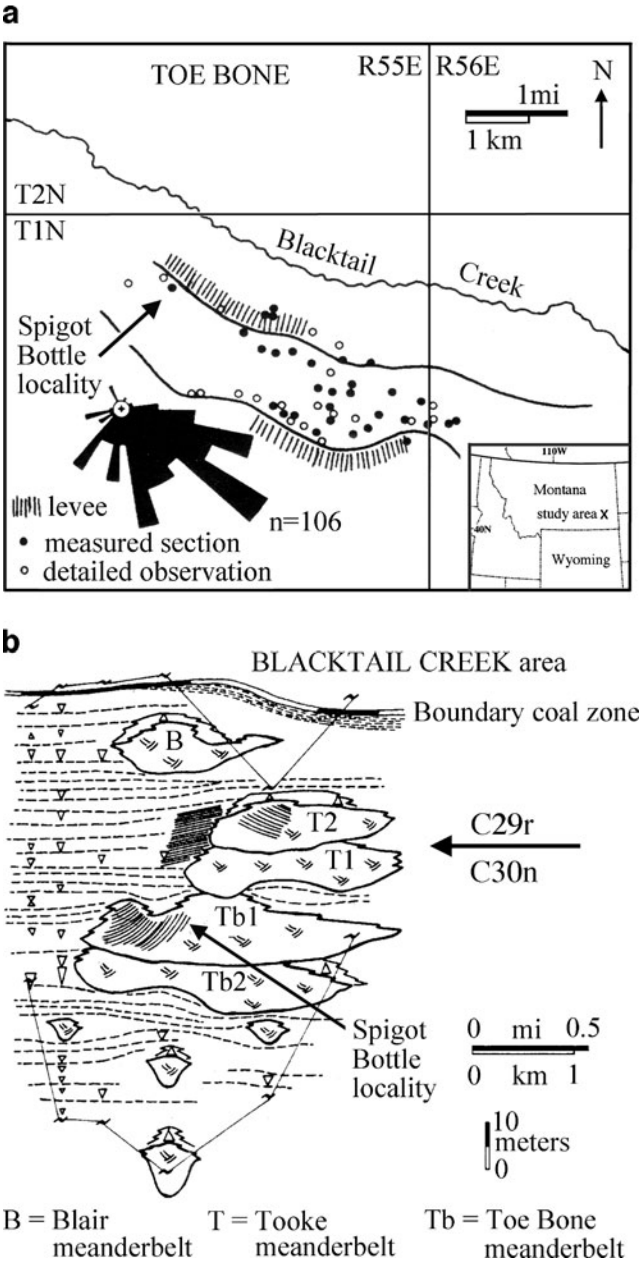

Fig. 1 **a** Map showing location and **b** stratigraphic position of the Spigot-Bottle locality within the Toe Bone Channelbelt, southeastern Montana (modifed after Belt et al. 1997)

PROTUNGULATUM Sloan and Van Valen, 1965

Protungulatum coombsi, new species
Figure 2

Holotype and only Known Specimen OMNH 64985, last left upper premolar.

Locality Spigot-Bottle locality, Carter County, Montana, U. S. A. The locality occurs in the latest Cretaceous, Hell Creek Formation, Carter County, Montana. Exact locality data are available from the authors.

Etymology For Walter Coombs, discoverer of the Spigot-Bottle locality.

Diagnosis OMNH 64985 is identical to last upper premolars of *Protungulatum donnae*, except the former averages 21% (range 13 to 26%) longer, 18% (range 10 to 26%) wider anteriorly, and 18% (range 11 to 23%) wider posteriorly than a sample of 15 specimens of *P. donnae*, making its larger size statistically significant (Fig. 3). Compared to species of *Oxyprimus*, the last upper premolar of *Protungulatum* (only known in *P. coombsi* and *P. donnae*) is larger, has a deeper ectoflexus, and a protocone that is relatively larger in relation to the paracone. Compared to species of *Mimatuta*, in the last upper premolar of *Protungulatum* the protocone apex is more lingual and has a shorter, steeper lingual slope, and the ectoflexus is slightly deeper. Compared to latest Cretaceous eutherians, the labial margin of the last upper premolar in *Protungulatum donnae* and in OMNH 64985 are curved because para- and metastylar regions (Fig. 2: "p" and "m") are broader. This margin is straighter in the similarly sized *Cimolestes stirtoni* and *C. magnus*. Pre- and postcingula are common in *Protungulatum donnae*, occurring in OMNH 64985, but on occasion can be present among other taxa, especially in *C. magnus*. *Cimolestes stirtoni* and *C. magnus* have carnassial notches and central cristae lacking in *Protungulatum donnae* and OMNH 64985. Late Cretaceous zhelestid upper last premolars resemble those of *Protungulatum* more than those of *Cimolestes*, except as in *Cimolestes*, stylar regions are straighter (Nessov et al. 1998). The broken and worn last upper premolar known in the large Late Cretaceous taeniodont eutherian *Schowalteria* (Fox and Naylor 2003) differs from *P. coombsi* in the same ways as do these teeth of *Cimolestes stirtoni* and *C. magnus*.

Comments While naming a new species on the basis of one tooth is unusual, in this instance it is justified because the specimen in question bears a striking resemblance to the very distinctive last upper premolars of *Protungulatum*; yet it is unique in its significantly larger size compared to the numerous last upper premolars that have been identified for the earliest Paleocene species *P. donnae*. The larger earliest Paleocene species, *P. gorgun* (discussed below), is not known from the last upper premolar; thus the possibility of synonymy must await recovery of last upper premolars of *P. gorgun*. Although unfortunately unique, because the specimen comes from beds of unquestioned Late Cretaceous age, it has a direct bearing on the important questions of whether archaic ungulates ("condylarths") or crown eutherians (placentals) occur in the Late Cretaceous and did not simply appear suddenly at the K/T (K/Pg) boundary. Simply

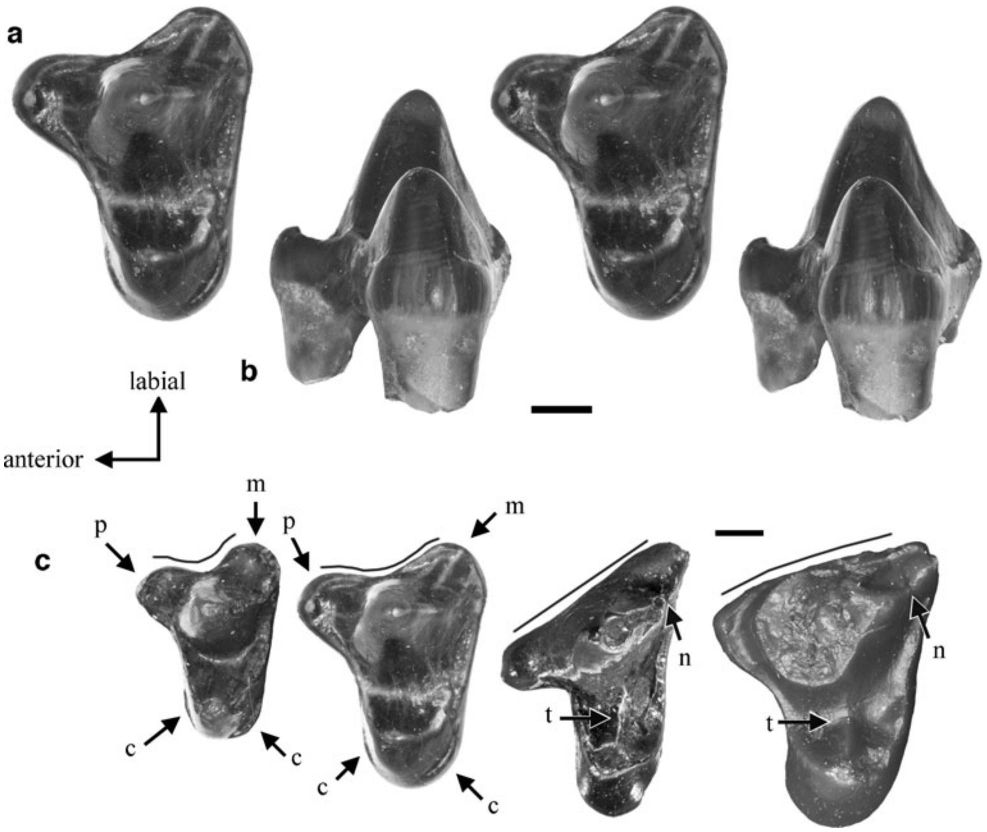

Fig. 2 Photographs of last upper premolars: **a** occlusal and **b** lingual views (stereo pairs) of OMNH 64985, holotype of *Protungulatum coombsi*. **c** From left to right, occlusal views of *Protungulatum donnae*, UCMP 125961 (in maxilla, view reversed); *Protungulatum coombsi*, OMNH 64985; *Cimolestes stirtoni*, UCMP 52189; and cast of *Cimolestes magnus*, UCMP 107743 (in maxilla, view reversed). Scales equal one millimeter. c, cingula; m, metastylar region; n, carnassial notch; p, parastylar region; t, central crista

referring to it as *Protungulatum* sp. would obscure both its differences in size and age.

Description and Comparisons

Protungulatum donnae was described from the earliest Paleocene Bug Creek Anthills site (Sloan and Van Valen 1965). In 1991, Luo argued that two other species, *Mimatuta morgoth* and *Oxyprimus erikseni*, were also present. Luo did not identify last upper premolars of these two taxa in his samples, although, the last lowest premolar was identified. In the sample of 15 last lowest premolars of *P. donnae* from Bug Creek Anthills used here (Table 2), neither *M. morgoth* nor *O. erikseni* could be identified, although there was some variation in size and robustness. For example, for complete specimens, ten have both a narrow pre- and postcingulum, three have only a postcingulam, and one has neither. In size, *P. coombsi* is statistically significantly larger than the sample of 15 last upper premolars of *P. donnae* (Table 3) (Fig. 3).

Three other species of *Protungulatum* have been proposed: *P. sloani* Van Valen, 1978, *P. gorgun* Van Valen, 1978, and *P. mckeeveri* Archibald, 1982. Lofgren (1995) provided convincing evidence that the last species, based on a single dentary, falls within the range of variation seen in *P. donnae*. Both *P. sloani* and *P. gorgun* are relatively poorly known; although upper molars were indicated, only lower dentitions were illustrated by Van Valen (1978). *Protungulatum sloani* was indicated as being similar in size to *P. donnae*, whereas *P. gorgun* was stated to be larger. Lofgren (1995) referred isolated upper and lower molars as well as associated lower premolars and molars to *P. gorgun,* but no upper premolars were described. His has been the only study to describe teeth of both *P. donnae* and *P. gorgun* from a single study area, the McGuire Creek localities. Based on these small samples available (one to six specimens per measurement), the M2 of *P. donnae* is from 8% (anterior width) to 17% (length) smaller than M2 of *P. gorgun*. For the last lower premolar (only one specimen each), *P. donnae* is from 13% (width) to 20% (length) smaller than *P. gorgun*. In only one instance is one of these measurements of *P. donnae* as much as 20% less than that of *P. gorgun*, whereas (as noted above) the last upper premolar of *P. donnae* ranges from 18% to 20% smaller in all comparable measurements of *P. coombsi*. Without additional material it would be imprudent to refer OMNH 64985 to the poorly known *P. gorgun*.

OMNH 64985 also differs from other earliest Paleocene archaic ungulates in the same manner that *Protungulatum donnae* differs. In *Mimatuta minuial* (and to a lesser extent the more poorly known *M. morgoth*) relative to *P. donnae* and *P. coombsi*, the last upper premolar is shorter and slightly more inflated, and the protocone apex is shifted

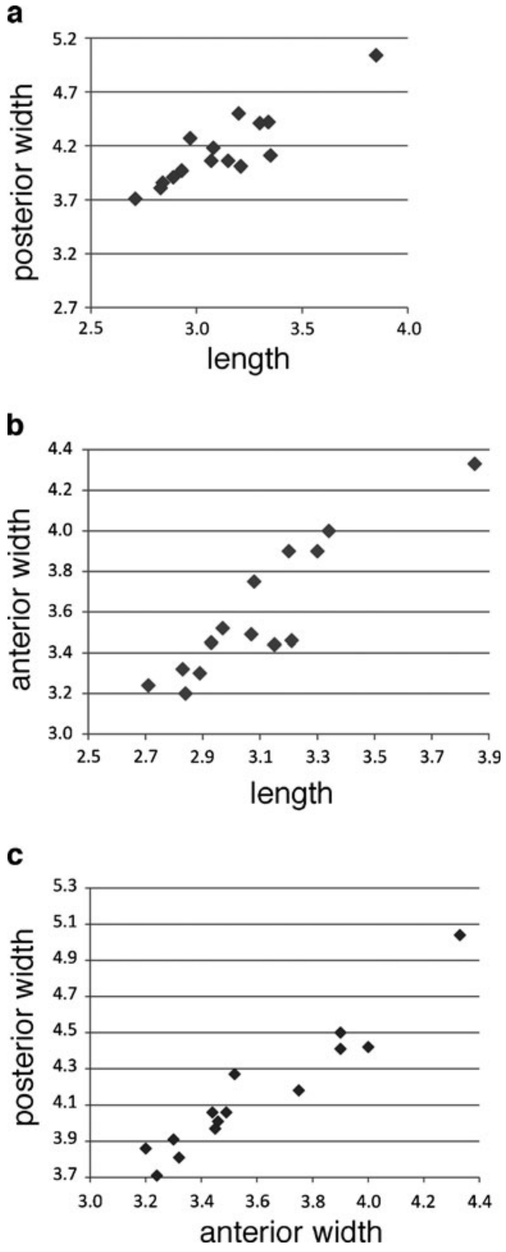

Fig. 3 Bivariate plots of measurements of the last upper premolar of *Protungulatm donnae* and *P. coombsi*: **a** length and posterior width, **b** length and anterior width, and **c** anterior width and posterior width (see Tables 2 and 3)

labially, which lengthens its lingual face (Archibald 1982 and examination of casts of these taxa). OMNH 64985 has none of these attributes and is accordingly more similar to *P. donnae* than to any species of *Mimatuta*.

Table 2 Measurements of length, anterior width, and posterior width of the last upper premolar of *Protungulatm donnae*. All specimens are from UCMP localities at Bug Creek Anthills (V65127 and V70201). All specimens are isolated last upper premolars, except UCMP 125961, which is a maxilla also preserving M1-3

Locality	UCMP #	Tooth side	Length	AW	PW
V65127	51800	left P4/	3.35	3.72	4.11
V65127	71796	left P4/		3.40	
V65127	71797	left P4/	3.21	3.46	4.01
V65127	71803	right P4/	3.08	3.75	4.18
V65127	71804	right P4/	2.93	3.45	3.97
V70201	91073	right P4/	2.83	3.32	3.81
V70201	91074	left P4/	2.89	3.30	3.91
V70201	100642	left P4/	2.97	3.52	4.27
V70201	100644	right P4/	2.71	3.24	3.71
V70201	100652	right P4/	3.34	4.00	4.42
V70201	100680	right P4/	3.30	3.90	4.41
V70201	100685	right P4/	3.15	3.44	4.06
V70201	102056	right P4/	3.20	3.90	4.50
V65127	105494	left P4/	2.84	3.20	3.86
V65127	125961	right max	3.07	3.49	4.06

Even less can be said for the three species of *Oxyprimus* named by Van Valen (1978). Lofgren (1995) indicated that *O. erikseni* and *O. galadrielae* appear to be valid species, but *O. putorius* is questionable. Based on casts and comments of various authors (Van Valen 1978; Archibald 1982; Luo 1991; Lofgren 1995), the species of *Oxyprimus* and especially that of the geologically oldest, *O. erikseni*, relative to species of *Protungulatum* tend to be smaller and have more rectangular and somewhat more transverse upper molars. The upper molars and the last upper premolar are somewhat more gracile. Luo (1991) noted that some smaller molars from Bug Creek Anthills are referable to *O. erikseni*. Similarly, this may be the case for some of the smaller and more gracile of the last upper premolars here labeled *P. donnae* (e.g., Table 2). OMNH 64985 has none of these attributes and is accordingly more similar to *P. donnae* than to any species of *Oxyprimus*.

Table 3 T-tests comparing the length, anterior width, and posterior width of the last upper premolar of *Protungulatm donnae* and *P. coombsi*

P. donnae	Length	AW	PW
N of Cases	14	15	14
Arithmetic Mean	3.062	3.539	4.091
Standard Deviation	0.205	0.254	0.240
P. coombsi	3.85	4.33	5.04
t-value	3.85	3.11	3.95
2-tailed p value	0.0020	0.0076	0.0016

The *t*-value used was the difference in the measured values of OMNH 64985 from the mean of the sampled *P. donnae* specimens, divided by the standard deviation of the sampled specimens. The probability of finding this value or one more extreme (e.g., a two-tailed test) was then calculated using the standard t distribution function (TDIST) in Microsoft Excel®

For all measurements the isolated tooth OMNH 64985 is significantly larger than previously described material referred to *P. donnae*

Discussion

The two Canadian Late Cretaceous sites yielded a reported four species of archaic ungulate (Fox 1989). Although our study does not directly address the issue of whether these Canadian sites were contaminated by Paleocene material, it does demonstrate that at least one species of archaic ungulate was in the latest Cretaceous of North America.

Ongoing studies have attempted to recognize "alien" or "immigrant" versus "resident" mammalian species from latest Cretaceous through mid-Paleocene sites in the northern Western Interior of North America (Weil and Clemens 1998; Clemens 2002, 2010). *Protungulatum* was recognized as a Paleocene "alien" or "immigrant," thought to have appeared in North America with no clear pre-Paleocene antecedent. Our study shows that *Protungulatum* appeared at least 300 k years earlier in the latest Cretaceous of North America. This shows that archaic ungulates were present in North America before the K/T extinctions although their radiation did not begin until after the K/T extinctions (Archibald 2011). Whereas our study demonstrates that archaic ungulates existed in the latest Cretaceous of North America, it cannot answer the question of whether *Protungulatum* in particular is a member of the crown Placentalia or belongs to a more basal eutherian clade.

Until a 2007 review, *Protungulatum* was regarded not only as an archaic ungulate but also as a placental mammal. This study, which included most Late Cretaceous eutherians and a number of Tertiary eutherians and placentals, found that there is no evidence of placentals in the Cretaceous (Wible et al. 2007). The authors did not argue that placentals could not be in the Cretaceous but rather that their analyses did not show this, based on the current fossil record. One unusual result was placement of the early Paleocene *Purgatorius* (conventionally considered a primate or primatomorph) and the two Paleocene archaic ungulates ("condylarths") *Protungulatum* and *Oxyprimus* outside of but near the origin of Placentalia. All preceding studies placed these taxa within placental clades (e.g., Kielan-Jaworowska et al. 2004; Silcox et al. 2005). Interestingly, the 2007 study found that the three other archaic ungulates included in the analysis (*Hyopsodus*, *Phenacodus*, and *Meniscotherium*) did cluster with placental mammals rather than being just basal to them. Using a Templeton test, Wible et al. (2007) could not significantly reject the grouping of *Purgatorius* with Primates, and Paleocene and Eocene "condylarths" with Cetartiodactyla, meaning the placement of *Purgatorius*, *Protungulatum,* and *Oxyprimus* in Placentalia could not be statistically rejected.

In a follow-up publication, Wible et al. (2009) made some amendments to the taxon-character matrix of their earlier work. We performed additional analyses on the same data set from their 2009 study using the program MrBayes to test whether it was significantly more unlikely to place *Purgatorius*, *Protungulatum,* and *Oxyprimus* within or outside Placentalia. The analysis is described in the Appendix. We found that, as in the 2007 study, *Purgatorius*, *Protungulatum,* and *Oxyprimus* are, as a group, outside the crown clade Placentalia. We did not further test whether any of the taxa individually is more likely to be a placental.

A recent study examined the relationships of cetaceans to various other placentals (Spaulding et al. 2009). The study included some extant and extinct placentals as well as *Protungulatum*, and was rooted with the extant afrotherian tubulidentate *Orycteropus afer.* As no stem eutherians (other than possibly *Protungulatum*) were included, the question of whether *Protungulatum* is or is not a placental could not be addressed. Nevertheless, *Protungulatum* was not found to be sister to most or all other in-group placentals, but rather, in one analysis it occurred in a polytomy that was sister to the clade including extinct and extant Perissodactyla and Artiodactyla (including Cetacea) (Spaulding et al. 2009: fig. 2). In another analysis *Protungulatum* was embedded within an artiodactyl clade exclusive of cetaceans (Spaulding et al. 2009: fig. 5). In both analyses, other extinct placentals as well as members of the extant clades Carnivora and Erinaceomorpha were found to be successively more distant sister taxa to the clades including *Protungulatum*.

Conclusions

Whether or not *Protungulatum* is in fact a placental mammal and thus the first definitive placental from the Cretaceous, the discovery reported here demonstrates that archaic ungulates ("condylarths") lived during the Late Cretaceous in North America.

Latest Cretaceous sites in northern Montana, U. S. A., and Alberta and Saskatchewan, Canada, have the greatest diversity of eutherians, whereas more southern sites of similar age have fewer eutherians but more metatherians and multituberculates. Thus, the rare occurrence of a eutherian archaic ungulate such as *Protungulatum* is not unexpected. Undoubtedly archaic ungulates appeared before non-avian dinosaur extinction in North America, possibly earlier in the north. As witnessed in North America, the explosive Paleocene radiation of 70+ species of archaic ungulates was actually ignited in the latest Cretaceous (Archibald 2011).

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Appendix

A reanalysis of the Nexus formatted data matrix compiled by Wible et al. (2009), using the program Mr.BAYES accessed through the Cyberinfrastructure for Phylogenetic Research (CIPRES) portal 2.0 website, was preformed to determine relationships and quantify support values for alternate topologies of the crown group Placentalia, specifically to examine the placental affinities of the latest Cretaceous and/or early Paleocene taxa *Protungulatum*, *Oxyprimus*, and *Purgatorius*. A constrained treesearch was used to force the taxa *Protungulatum* and *Oxyprimus* into a clade with the placental ungulates *Gujaratia*, *Hyopsodus*, *Meniscotherium*, and *Phenacodus*; while the genus *Purgatorius* was forced into a clade with the primatomorph taxa *Plesiadapis*, *Northarctus*, and *Adapis*. A second treesearch was run completely unconstrained, and the likelihood values of these topologies were compared using a Bayes factors test (Kass and Raftery 1995). All treesearches used the same matrix of 69 taxa and 408 unordered characters and were run for ten million generations with sampling every 1000 generations, generating a stable distribution of parameter estimates. Likelihood values were saved, after a 10% burn in, and used an Mk model of character change with alpha values (rates of evolution) estimated by a Gamma distribution binned into four categories (Lewis 2001; Prieto-Marquez 2010). This distribution of alpha values was chosen over one assuming strictly equal rates of evolution after both types of models were run using the constrained and unconstrained data described above; in both cases the Mk+G models generated significantly higher likelihood values compared to their constant rate counterparts.

The harmonic means of the log likelihood values for both the constrained and unconstrained analyses are, respectively:

Constrained + Gamma harmonic mean= −8520.87
Unconstrained + Gamma harmonic mean= −8499.48

The large difference between these two values when compared with a Bayes factors test (difference=42.78) suggests that the unconstrained analysis is truly a better explanation of the data given the model parameters, and that the taxa *Purgatorius*, *Protungulatum*, and *Oxyprimus* cannot confidently be placed inside the crown group Placentalia.

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