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OF NORTHWESTERN WYOMING**

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ANN ARBOR

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Philip D. Gingerich, Director

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NEW SPECIES OF *TITANOIDES* (MAMMALIA, PANTODONTA)
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Abstract—Four specimens of a new pantodont species, *Titanoides nanus*, are described from two middle Clarkforkian localities in the Clarks Fork Basin of northwestern Wyoming. *T. nanus* is the smallest species of the genus, and comparison with other known specimens suggests, conservatively, that all may constitute a single evolutionary lineage. Within *Titanoides*, distinctive characteristics of *T. nanus* include its smaller tooth size and by inference body size, reduced canine dimorphism, smaller M³ lacking a well developed metacone, metastylids present on lower molars, and a cristid obliqua rising toward the protolophid rather than the metaconid. *T. nanus* is important in extending the range of *Titanoides* into middle Clarkforkian strata in the type area of the Clarkforkian land-mammal age.

Titanoides is one of the few large herbivorous mammals known from the late Paleocene of western North America. It is found in many localities, but is nowhere common. This complicates documentation of its variability in time and interpretation of its evolution through time. The species described here extends the chronological range of *Titanoides* from the Tiffanian land-mammal age well into the Clarkforkian land-mammal age. Thus the temporal range of *Titanoides* now spans virtually all of late Paleocene time.

The first species of *Titanoides* to be named, *T. primaevus*, was described by Gidley (1917), based on USNM 7934 from the Fort Union Formation of the Williston Basin near Buford, North Dakota (this interval is now regarded as Sentinel Butte Formation of the Fort Union Group). Gidley initially thought *Titanoides* might be related to titanotheres (hence the name), but soon recognized it to be an amblypod (pantodont) rather than a perissodactyl. Further collecting at the type locality yielded YPM-PU 16490, which Gazin (1956) and Simons (1960) reported as being part of the same individual animal as USNM 7934 (and hence part of the type). The type locality of *T. primaevus* has recently been relocated and restudied by Kihm and Hartman (1991) and Hartman and Kihm (1991, 1995), who have shown that its age is middle-to-late Tiffanian (late Paleocene) in the biochronology of Paleocene land-mammal ages. According to Hartman and Kihm, the type specimen of *T. primaevus* is from beds immediately overlying a locality yielding *Plesiadapis* similar to *P. churchilli* (Gingerich, 1976). Hartman and Kihm (1991, 1995) concluded that the type specimen of *T. primaevus* probably came from biochron Ti-4 within the Tiffanian (Gingerich, 1983).

Jepsen (1930) named a second species of *Titanoides*, *T. gidleyi*, based on YPM-PU 13235 from the Fort Union Formation on the southeast side of Polecat Bench in the northern Bighorn Basin near Powell, Wyoming. The type locality of *T. gidleyi*, as published by Jepsen, is in

Section 11, T56N, R99W, Park County, Wyoming, which is near Jepsen's 1928 field camp #3 on the southeast side of Polecat Bench. There are five University of Michigan localities in this section (SC-261, 262, 269, 339, and 340; Gingerich and Klitz, 1985), which was collected intensively to enable recognition of *Plesiadapis* biochrons in the Polecat Bench section. Three of the five localities in Section 11 have yielded the index fossil *Plesiadapis rex* (SC-261, 262, and 339), and interpretation in the context of *Plesiadapis* biostratigraphy (Gingerich, 1976, 1983) indicates that the type specimen of *T. gidleyi* came from biochron Ti-3 in the middle Tiffanian.

Simpson (1937) named a third species of *Titanoides*, *T. zeuxis*, based on AMNH 35201 from the Fort Union of the Crazy Mountain Basin near Melville, Montana. The type locality of *T. zeuxis*, as published by Simpson, is about 1,000 feet (ca. 300 m) above Scarritt Quarry. This is correlative with Simpson's Crazy Mountain Locality 13, type locality of *Plesiadapis rex* (see Krause and Gingerich, 1983, fig. 2). Thus the type of *T. zeuxis*, like that of *T. gidleyi*, came from Tiffanian biochron Ti-3 as indicated by *Plesiadapis* biostratigraphy (Gingerich, 1976). Simpson (1937), describing *T. zeuxis*, appears to have been most concerned with relationships of *Titanoides* to *Pantolambda* and *Barylamba*. His only comparative comment regarding other species of *Titanoides* in the diagnosis or elsewhere was that *T. zeuxis* is "much smaller than *T. primaevus* and slightly smaller than *T. gidleyi*" (p. 11) while "elevation of trigonids above talonids seems to be slightly greater than is usual in *Titanoides*" (p. 13). These differences are not enough to justify recognition of *T. zeuxis* as distinct from *T. gidleyi* when the two are now known to have lived in the same interval of Tiffanian time in the same intermontane structural trough of the emerging Rocky Mountains. Specimens from the Black Peaks Formation in Texas referred to *T. zeuxis* by Schiebout (1974) are early-to-middle Tiffanian in age and may belong in *T. gidleyi* as well.

Patterson (1939) named a fourth species, "*Sparactolambda*" *looki*, based on FMNH P15520 from about 80 feet (ca. 25 m) above the base of the Paleocene Plateau Valley beds, three miles west of DeBeque, in western Colorado. According to Kihm (1984) this locality, the *Sparactolambda* Quarry (locality 7-37), is in Section 31, T8S, R97W, Mesa County, Colorado. As best it can be determined, the type locality of "*S.*" *looki*, like other Plateau Valley localities, is either in Tiffanian biochron Ti-5 or Clarkforkian biochron Cf-1 (Gingerich, 1976, 1983; Kihm, 1984; Archibald et al., 1987; Thewissen and Gingerich, 1987). Gazin (1956, p. 47) synonymized *Sparactolambda* with *Titanoides*. Simons (1960) considered "*S.*" *looki* to be a junior synonym of *Titanoides primaevus*, but *T. looki* is smaller, younger geologically, and possibly worthy of recognition as a distinct species.

Finally, Simons (1960) named a fifth species, *T. major*, based on YPM-PU 16447. Simons (1960, p. 38) published the locality as Sage Point, which is on the southeast side of Polecat Bench, but unpublished records indicate that the type came from the SE $\frac{1}{4}$, NE $\frac{1}{4}$, Section 2, T56N, R99W, Park County, which is about 1 km southwest of Sage Point. This is in or near University of Michigan locality SC-264 (Gingerich and Klitz, 1985), which means that it is early Tiffanian in age (probably Ti-2). Simons (1960) named *Titanoides simpsoni* from Gidley Quarry in the Crazy Mountain Basin, but this has been synonymized with *Pantolambda intermedium* by Lucas (1982, 1984) and independently by Gingerich and Childress (1983). Thus *T. major* is the oldest known species of *Titanoides*.

There are presently two to four distinct species of Tiffanian *Titanoides*: early Tiffanian *T. major*, middle Tiffanian *T. gidleyi* (= *T. zeuxis* and possibly not distinguishable from *T. primaevus*), late Tiffanian *T. primaevus*, and late-Tiffanian-to-early-Clarkforkian *T. looki* (possibly not distinguishable from *T. primaevus*). Uncertainty about species distinctions results from limited sample sizes, with several species being based on single specimens. A new species of *Titanoides* is described here that is geologically younger than all others. It shares many similarities with earlier species, but as a sample differs in being smaller, having lower

molar metastylids, and in other details of molar form. This is the first record of *Titanoides* from Clarkforkian strata in the Clarks Fork Basin of northwestern Wyoming.

ABBREVIATIONS

Institutional abbreviations used here are as follows:

- AMNH — American Museum of Natural History, New York
 FMNH — Field Museum of Natural History, Chicago
 UM — Museum of Paleontology, University of Michigan, Ann Arbor
 USNM — U.S. National Museum, Washington
 YPM-PU — Princeton University collection at Yale Peabody Museum, New Haven

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA
 Order PANTODONTA Cope, 1873
 Family Titanoideidae Patterson, 1934

Gingerich and Childress (1983) grouped North American Paleocene *Pantolambda*, *Titanoides*, and *Barylambda* and its relatives in a single family Pantolambdidae, but a better appreciation of dental and especially postcranial differences (Patterson, 1939; Simons, 1960) indicates that *Titanoides* deserves to be placed in its own family.

Titanoides Gidley, 1917

Titanoides nanus, new species
 Figs. 1-2

Holotype.—UM 80264, left and right C₁ (broken), left and right P₁, left dentary with P₄-M₁, right dentary with M₁₋₃, and associated bone fragments. Left and right dentaries were found by J. Yaroch on July 15, 1982. Additional pieces of the type, including the canines, P₁s, and P₄ (catalogued as UM 82376 before being combined with UM 80264) were collected by C. Childress on July 7, 1983. Pieces from one collection contact pieces of the other, and there is no question all represent the same individual animal.

Type locality.—UM locality SC-19 in the Clarks Fork Basin, Wyoming (see Rose, 1981, p. 15; Gingerich and Klitz, 1985).

Diagnosis.—Smallest species of *Titanoides*. Teeth of *T. nanus* differ from those of all other species in averaging 10-25% smaller in linear dimensions. Upper incisors differ from those of *T. primaevus* in having a more rounded occlusal edge and in having lingual cingula. In the upper dentition M³ differs from earlier species in being short anteroposteriorly, with a prominent protocone and paracone but little or no metacone. Lower molars appear to be a little higher-crowned, with sharper cusps and crests, a distinct metastylid, and a cristid obliqua joining the metastylid on M₁ or curving upward to join the protolophid buccal to the metaconid on M₂₋₃. The metastylid is a distinct cusp on all lower molars of the three specimens preserving these teeth; it is present on six out of six teeth (100%). Posterior upper and lower molars are smaller, relative to anterior cheek teeth, than in earlier species of *Titanoides*.

Referred specimens.—SC-19 (type locality): UM 98101, seven associated teeth including left I¹, left I³, right I², right I³, left C₁, trigonid of left P₄, and left M₃. SC-117: UM 87996,

TABLE 1—Measurements *Titanoides nanus*, new species, compared to those of type specimens of late Paleocene *Titanoides primaevus* Gidley and *Titanoides looki* (Patterson). Length [L] is measured mesiodistally. Width [W] is measured buccolingually. Measurements of M_{1-3} of *T. primaevus* are from Gidley (1917), and all measurements for *T. looki* are from Patterson (1939). Asterisks mark estimated lengths and widths.

	<i>T. primaevus</i>	<i>T. looki</i>	<i>Titanoides nanus</i>			
	Ti-3 to Ti-4	Ti-5 to Cf-1	Cf-2			
	USNM 7934 + YPM-PU 16490 Holotype Male	FMNH P15520 Holotype Male	UM 80264 (SC-19) Holotype Female	UM 87996 (SC-117)	UM 95865 (SC-117)	UM 98101 (SC-19) Male
Upper dentition						
I^1 L	6.7	--	--	--	--	6.4
W	--	--	--	--	--	5.4
I^2 L	8.8	--	--	--	--	8.5
W	5.4	--	--	--	--	6.3
I^3 L	8.8	--	--	--	--	8.7
W	5.8	--	--	--	--	5.3
M^3 L	19.7	19.5	--	--	12.8	--
W	31.4	32.4	--	--	24.1	--
Lower dentition						
C_1 L	--	43.0	14.2	--	--	20.0*
W	--	22.3	10.4	--	--	13.0*
P_1 L	--	12.8	11.1	--	--	--
W	--	8.0	5.4	--	--	--
P_4 L	--	14.7	12.7	--	--	--
W	--	15.0	12.3	--	--	--
M_1 L	22.5*	19.0	17.0	17.6 ¹	--	--
W	15.5	14.4	13.0	12.8 ¹	--	--
M_2 L	27.0	23.3	19.2	--	--	--
W	19.0	16.0	13.2	--	--	--
M_3 L	32.8	29.7	22.6	--	--	22.4
W	19.4	17.9	13.1	--	--	13.0*

¹This tooth is isolated and may be M_2

buccal half of left M_1 or M_2 and virtually complete right M_1 or M_2 ; and 95865, left M^3 . Both localities are at the 1370 m level in the Polecat Bench - Sand Coulee measured stratigraphic section.

Age and distribution.—Middle Clarkforkian, latest Paleocene, of northwestern Wyoming. *T. nanus* is known from two adjacent localities in the same narrow stratigraphic interval within

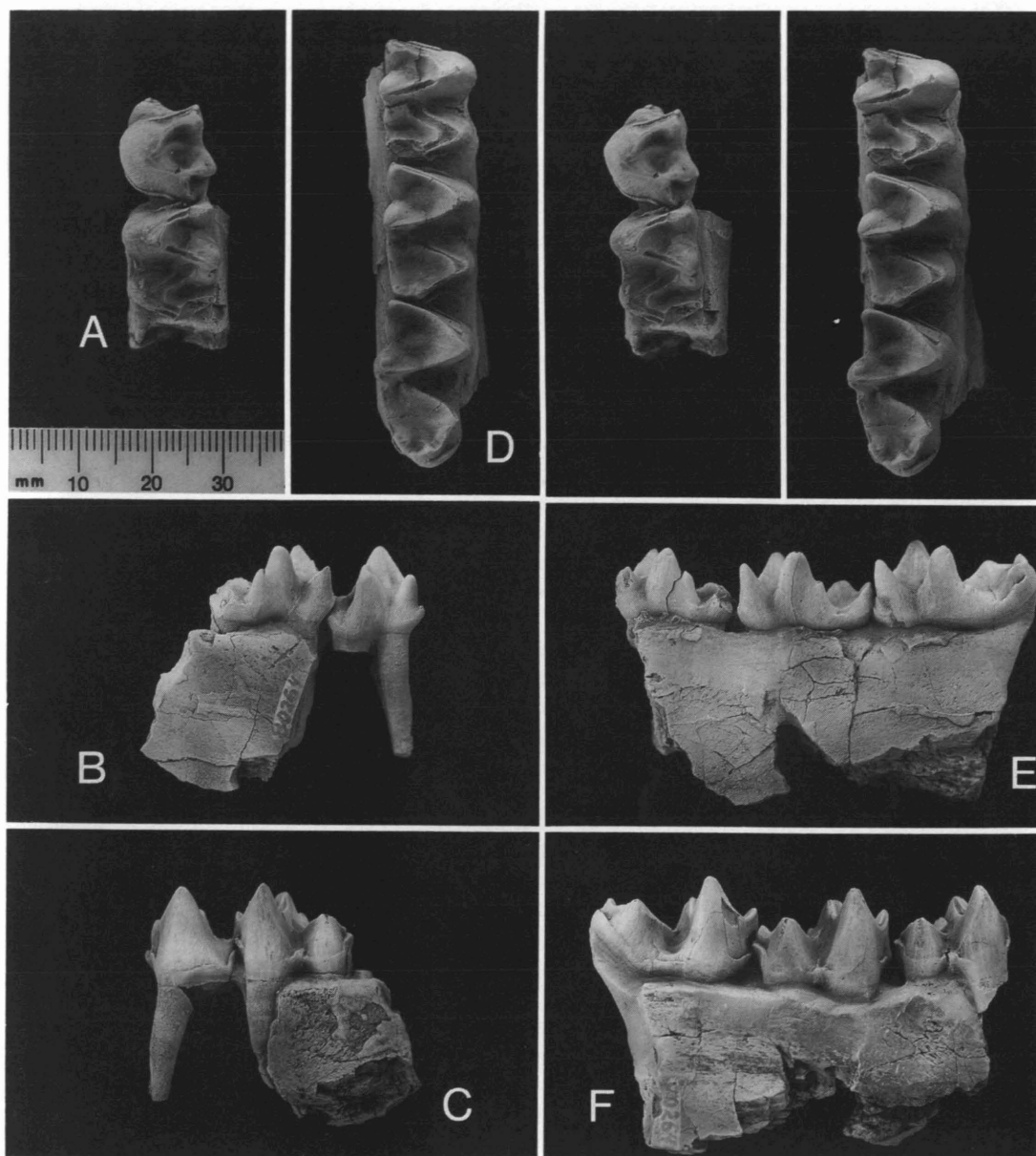


FIG. 1.—Lower cheek teeth of *Titanoides nanus*, new species (UM 80264, holotype), from UM locality SC-19 in the middle Clarkforkian, late Paleocene, of the Clarks Fork Basin, Wyoming. A-C, left dentary with P_4 - M_1 in occlusal, lingual, and buccal views. D-F, right dentary with M_{1-3} in occlusal, lingual, and buccal views. A and D are stereophotographs. Scale is in mm.

the *Plesiadapis cookei* zone (Cf-2) of the middle Clarkforkian land-mammal age, Clarks Fork Basin of northwestern Wyoming.

Etymology.—*nanos*, Gr., dwarf, in recognition of the small size of this species, and what appears to be a general trend toward smaller size in evolution of the *Titanoides* lineage.

Description.—UM 98101 is a group of associated teeth that includes four upper incisors, left I^1 , left I^2 , right I^1 , and right I^3 (Fig. 2A-F; identified by comparison with incisors of *Titanoides primaevus* and *Coryphodon proterus*). These resemble incisors of *Coryphodon* and differ from incisors of earlier *Titanoides* in having rounded occlusal edges and distinct lingual cingula. All are small (see Table 1 for measurements). I^1 is the smallest of the three, I^2 is the largest, and I^3 is distinctive in being a little longer mesiodistally and narrower buccolingually than either I^1 or I^2 . There are no interproximal facets on any of the upper incisors, indicating that they were spaced in the premaxilla like incisors of *T. primaevus* (PU 16490 holotype; see Simons, 1960, fig. 14). These incisors were found in association with cheek teeth of *T. nanus*, and they are much too small to be deciduous incisors of contemporary *Coryphodon*.

The only upper cheek tooth of *Titanoides nanus* is UM 95865, an isolated left M^3 (Fig. 2I). This has a broadly flattened protocone and a strongly V-shaped paracone with a prominent parastyle and a distinct mesostyle, as is typical of the genus, but it differs from described *Titanoides* in having little or no metacone. M^3 in *T. nanus* is much shorter anteroposteriorly than M^3 in earlier species.

Lower canines are preserved in two specimens, one the type UM 80264 and the other UM 98101. The type includes the base of the crown of both left (Fig. 2G) and right canines, and these are almost D-shaped in cross-section, with the flat surface being lingual and the convex surface labial. The anterior edge is a little flatter than the posterior edge of the crown, and the posterior edge is a little more keeled. These canines are relatively small compared to other cheek teeth (see Table 1), and the type individual is consequently interpreted as being female. UM 98101 includes a left lower canine (Fig. 2H), and this differs in being much more elongated anteroposteriorly, with a pronounced posterior blade or wing (Simons, 1960, p. 31). This referred individual is interpreted as a male. If these two specimens are representative, it appears that canine dimorphism in *Titanoides nanus* is less pronounced than that in *T. primaevus*.

Left and right P_1 are preserved in UM 80264. These are small double-rooted teeth, with anteroposteriorly-symmetrical elongated crowns bearing two small accessory cusps anterior and posterior to the apical cusp. They show no wear that might be attributed to honing of the upper canine, but it is possible that a developmentally-older male specimen would show such wear. The only other lower premolar known is P_4 in the type (Fig. 1A-C). It has prominent protoconid, paraconid, and metaconid cusps symmetrically arranged about a transverse plane through the middle of the trigonid (the paraconid is a little weaker than the metaconid), with almost no talonid.

Lower molars are almost perfectly preserved, with slight wear, in the right dentary of the holotype (Fig. 1D-F). All three molars, M_{1-3} , have high delicate trigonid cusps connected by thin sharp crests. There is a well developed metastylid on M_1 , and this is weaker but distinctly present on M_2 and M_3 . The cristid obliqua joins the protolophid on the back of the trigonid buccal to the metaconid. The talonid on M_1 is relatively short, that on M_2 is longer, and M_3 has the largest talonid. The entoconid and hypoconulid are connate on M_2 , and connected but distinct on M_3 .

The only postcranial element known for *Titanoides nanus* is what appears to be part of the midshaft of a humerus associated with the type specimen. This measures about 25.5 by 32.5 mm in cross-section.

Measurements of the teeth of *Titanoides nanus* in Table 1 show them to be distinctly smaller than the type specimens of Tiffanian *T. primaevus* and *T. looki* (which are closer in size to *T. major* and *T. gidleyi*).

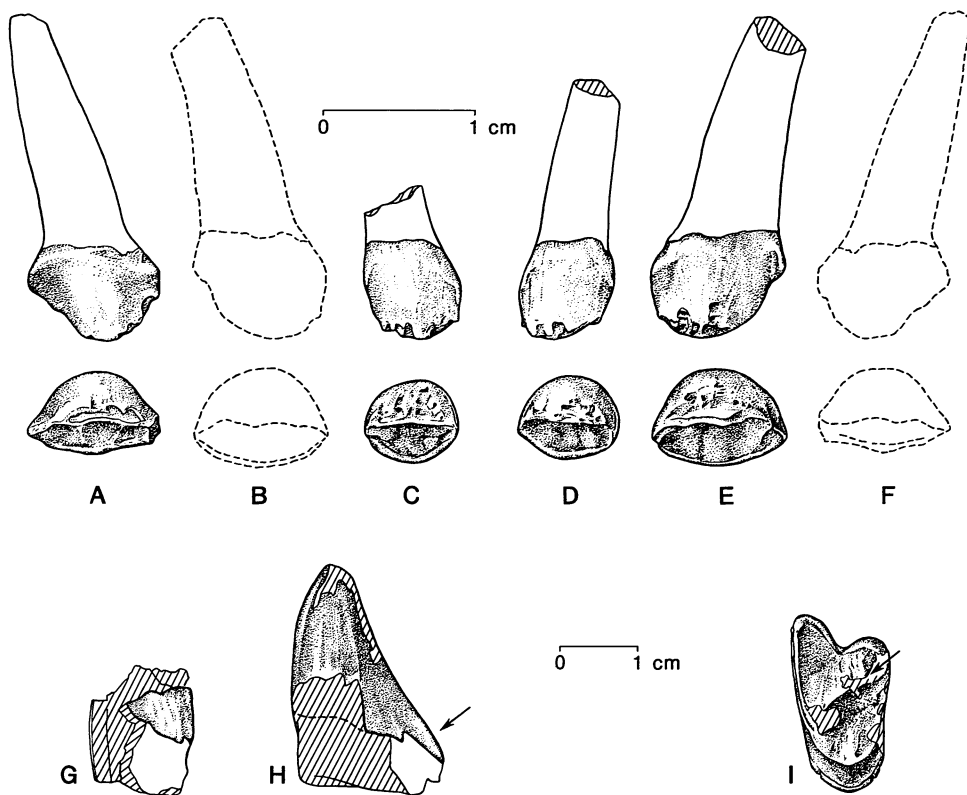


FIG. 2.—Incisors, canines, and M^3 of *Titanoides nanus*, new species, from UM locality SC-19 in the middle Clarkforkian, late Paleocene, of the Clarks Fork Basin, Wyoming. A, right I^3 . B, reflected outline of left I^2 . C, right I^1 . D, left I^1 . E, left I^2 . F, reflected outline of right I^3 . A-F are parts of UM 98101; each is shown in labial and occlusal views at $2 \times$ natural size. Note presence of a distinct lingual cingulum on all. G, left C_1 of female UM 80264 (holotype) in lateral view. H, left C_1 of male UM 98101 in lateral view. Note anteroposteriorly longer crown and distinct posterior blade or wing (arrow) that are characteristic of male *Titanoides*. I, left M^3 , UM 95865, in occlusal view. Note presence of a prominent mesostyle (arrow), but great reduction or absence of metacone. G-I are shown natural size. Scales are in cm.

FMNH P15551

Field Museum of Natural History specimen P15551 includes parts of two Plateau Valley *Titanoides* individuals that were collected in 1937 by J. H. Quinn. These were found at locality 76-37 (specimen label) or at locality 72-37 "Coffee Pot" (Kihm, 1984), one mile north of D. Harris ranch in Section 8, T10S, R96W, Mesa County, Colorado (these are listed as FMNH specimens P15550-51 in Kihm, 1984). This locality is 45 m above the base of the Atwell Gulch Member of the DeBeque Formation, and is the highest and hence youngest of DeBeque localities yielding *Titanoides* (Kihm, 1984). FMNH P15551 is similar in size to specimens of *Titanoides nanus* described here, but resembles the type of *T. looki* in lacking metastylids on lower molars (most lower molars of FMNH P15551 are not well preserved, but of the two that are, a right M_1 and a right M_3 , both lack a metastylid). Simons (1960, pp. 35-37) regarded FMNH P15551 as representing *T. zeuxis*, otherwise known only from Montana, because of its small size. However, Simons noted that FMNH P15551 resembles the type of

T. looki from the same beds in Colorado and differs from *T. gidleyi* (here regarded as a senior synonym of contemporary *T. zeuxis*) in having smaller paraconids relative to the metaconids on lower premolars and molars. A partial crown of a lower canine is very similar to that of UM 98101 described here. After considering various possible interpretations, FMNH P15551 is here referred to *Titanoides looki*. It is smaller than other specimens of Plateau Valley *T. looki* but important in supporting the intermediacy of the Plateau Valley sample between earlier *T. primaevus* and later *T. nanus*. This supports interpretations cited in the introduction that the known Plateau Valley faunas lived close in time to the Tiffanian-Clarkforkian boundary (i.e., in biochrons Ti-5 and/or Cf-1).

DISCUSSION

Clarkforkian strata of the Clarks Fork Basin have been studied for eighty years by field parties from the American Museum of Natural History led by Walter Granger, field parties from Princeton University led by Glenn Jepsen, and by my own expeditions from the University of Michigan: it is surprising to discover a new species as large as *Titanoides nanus* after so many years of prospecting. The first specimen, the holotype, was found in 1983 shortly after publication of Rose's (1981) review of Clarkforkian mammals. It was found lying on a bright red mudstone that passes through the middle of locality SC-19 in the center of the Clarks Fork Basin, which may help to explain why *Titanoides* was not found previously. Granger carried out the first survey of the basin, and understandably expended most effort on the margins of the basin and on formational boundaries. Jepsen considered red coloration to mark sediments of Eocene age, which he avoided because he was interested in the Paleocene. Many fossil mammals were found at SC-19 and SC-117 by University of Michigan collectors during the 1970s and early 1980s, and it must be a simple matter of chance that no *Titanoides* were found then while four specimens turned up subsequently.

Discovery of *Titanoides nanus* means that three pantodont genera and species, placed in three families, are now known from Clarkforkian sediments of northwestern Wyoming: small *Cyriacotherium psamminum* (Cyriacotheriidae; Rose and Krause, 1982), medium-sized *Titanoides nanus* (Titanoididae), and large *Coryphodon proterus* (Coryphodontidae; Simons, 1960). *Barylambda churchilli* is present in late Tiffanian zone Ti-4 (Gingerich and Childress, 1983) and *B. faberi* is present in Ti-5 (UM 73601), but *Barylambda* has not been found in the Clarkforkian of northwestern Wyoming.

Titanoides appears to have some utility biostratigraphically in the Tiffanian and Clarkforkian in that distinct species have now been named from three of the five commonly recognized Tiffanian biochrons, one has been named from the Tiffanian-Clarkforkian transition, and now a species is known from the middle Clarkforkian biochron. The best known species are *T. primaevus* from Ti-4, which is known from the most specimens, and *T. looki* from Ti-5 and/or Cf-1, which is known from the most complete skeletal remains (Patterson, 1939; Simons, 1960). Lower canines from Croc Tooth Quarry (Ti-4) in the Bighorn Basin (PU and UM collections) show that *T. primaevus* was strongly dimorphic, even more so than *T. nanus*, and sexual dimorphism complicates identification and comparison of individual specimens in small samples. Whatever the biostratigraphic utility of *Titanoides* in the Tiffanian, *T. nanus* is distinctly different from all earlier species, and it appears to be a reliable, if rare, index species for the middle Clarkforkian land-mammal age.

The earliest species of *Titanoides* appears to have been the largest species of the genus, *T. major* from early Tiffanian zone Ti-2 (Simons, 1960). The smallest species is clearly *T. nanus* described here from middle Clarkforkian zone Cf-2. There is at present no indication that more than one lineage of *Titanoides* lived in the Western Interior of North America during the late Paleocene, and it appears that an important trend in this lineage was the evolution of

smaller body size (countering the often-quoted generalization, Cope's rule, that lineages evolve toward larger body size).

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