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DIDELPHODUS CALORIS, NEW SPECIES (MAMMALIA, CIMOLESTA), FROM THE WASATCHIAN WA-0 FAUNA OF THE PALEOCENE-EOCENE THERMAL MAXIMUM, CLARKS FORK BASIN, WYOMING

ΒY

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Abstract — The Wasatchian Wa-0 mammalian fauna from the Paleocene-Eocene Thermal Maximum (earliest Eocene) is reasonably well sampled in North America, but mammals of small body size are still poorly known. Here we describe a new species of the insectivore *Didelphodus* based on a cranial rostrum, both dentaries, and a nearly complete upper and lower dentition, all found by screen-washing. The new species, *D. caloris*, is the oldest species of the genus known in North America. It differs from later early Eocene *Didelphodus* in being substantially smaller, in having relatively simple premolars, and in having a more reduced M₃ relative to preceding molars. Precursors of *Didelphodus* are not known with certainty, and the species *D. caloris* may be an immigrant to mid-continent North America. *D. caloris* is tentatively interpreted as a dwarfed form like other Wa-0 mammals because of its small size relative to the better-known successor species *D. absarokae*.

https://zoobank.org/urn:lsid:zoobank.org:pub:549A3715-0560-4220-AA54-CC75A41ADC24.

INTRODUCTION

Didelphodus is a relatively large insectivorous mammal found in Eocene deposits of North America and Europe. Edward Drinker Cope named the genus in 1882. Six names have been proposed for species-level taxa within *Didelphodus*. Here we describe and name an additional species based on an exceptionally complete specimen from a screen-wash site at University of Michigan locality SC-139 in the Clarks Fork Basin of northwestern Wyoming. The locality lies within both the Wa-0 biochron and the Paleocene-Eocene Thermal Maximum (PETM). The new species is the oldest, geologically, known for *Didelphodus*.

The first species of *Didelphodus* was named *Centetodon altidens* when it was published by Othniel Charles Marsh in 1872. This was based on a specimen, YPM 13516, of Bridgerian late early Eocene age that came from Henrys Fork in southwestern Wyoming (Marsh, 1872). William D. Matthew (1909) named another genus and species, *Phenacops incerta*, for a second Bridgerian specimen from Henrys Fork, AMNH 12091. Later

Matthew (1918) regarded *Didelphodus*, *Phenacops*, and other genera as doubtful in affinity and grouped them in Insectivora, tempering this interpretation by speculating that all may prove to be Creodonta. *Phenacops incerta* is now generally considered to be a synonym of *Didelphodus altidens* (McKenna et al., 1962).

The type species of *Didelphodus* was described by Cope (1881) as *Deltatherium absarokae*. The holotypic specimen, AMNH 4228, came from an unknown level in the Wasatchian early Eocene of the Bighorn Basin. It was published as an addendum to a note on the mesonychian *Triisodon quivirensis*, which Cope considered to be a creodont. Cope (1881) compared *Deltatherium absarokae* to *Deltatherium fundaminis*, named earlier in the year. A year later, Cope (1882) wrote that *De. absarokae* must be referred to the new genus *Didelphodus*. Then, two years later, Cope included *Didelphodus absarokae* in the order Creodonta and published stylized illustrations of the palate and dentaries (Cope, 1884, plate 24e, figs. 13–13a).

Matthew (1913) included a comparison and a composite drawing of *Didelphodus absarokae* in his description of *Palaeoryctes*, but the first real description of the type appeared

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later (Matthew, 1918). In addition, Matthew (1918) named two subspecies, *D. absarokae secundus* and *D. absarokae ventanus*. The first, *D. a. secundus*, was based on AMNH 16825 from the head of Ten Mile Creek in the Bighorn Basin, Wyoming. The age is uncertain, but it is probably late Graybullian or late middle Wasatchian, biochron Wa-5, early Eocene. The holotype of *D. a. secundus* is approximately the same age as the holotype of *D. a. a. absarokae* and generally considered to be a junior synonym (Van Valen, 1966).

The second subspecies named by Matthew (1918), *D. a. ventanus*, is based on AMNH 14747 from Alkali Creek in the Wind River Basin, Wyoming. The age is Lostcabinian or late Wasatchian, biochron Wa-7, in the early Eocene. Matthew wrote that the teeth of *D. ventanus* are somewhat smaller and narrower than those of *D. absarokae* (and *D. a. secundus*), with M₃ smaller in proportion to the preceding molars. *D. a. ventanus* is generally considered to be a synonym of *D. altidens* (Van Valen, 1966).

Didelphodus has been identified from several early Eocene sites in Europe, based on fragmentary specimens: Mutigny and Avenay in France (Rich, 1971), Rians in France (Godinot, 1981), Fournes in France (Marandat, 1991), and Abbey Wood in England (Hooker, 2010). These specimens have been compared to North American species of *Didelphodus*, but none has proven adequate for diagnosis as a distinct species.

Two species of *Didelphodus*, *D. serus* and *D. rheos*, were named by Storer (1984, 1995), based on isolated teeth from localities in Saskatchewan Province, Canada. These are Uintan and Duchesnian in age, spanning the long middle Eocene. The records constitute a substantial extension of the temporal range for *Didelphodus*—an insectivore with generalized teeth—and more complete specimens will be required to determine whether the Uintan and Duchesnian species really represent *Didelphodus*.

Wa-0 mammals of the Bighorn and Clarks Fork basins have been described by Matthew (1915), Granger (1915), Gingerich (1986, 1989, 1993), Strait (2001), Smith et al. (2002), Heinrich et al. (2008), Chester et al. (2010), and Rose et al. (2012). The Rose et al. (2012) study was the first to record *Didelphodus* sp. in a Wa-0 fauna, based on six isolated teeth. *Didelphodus* has not been reported from the Paleocene, and all of the previously named species are geologically younger than *Didelphodus caloris* described here.

MATERIAL AND METHODS

The *Didelphodus* specimen described here, UM 118709, is relatively large for an insectivore. It was found by screen-washing sediment from locality SC-139 in the Clarks Fork Basin. The first fragment, a piece of left dentary with fresh breaks, was found on a 5-mm-mesh screen. Then other fragments of the left and right dentaries were found, including pieces partially enclosed in carbonate nodules. Two broken isolated lower premolars were found on a 1-mm-mesh screen. Fragments of the skull were found exclusively in carbonate nodules, also collected by screen-washing. In the laboratory, the nodules and concretions with bones and dentaries were dissolved in acetic acid with a buffer of tricalcium phosphate. This technique allowed us to preserve all of the bony fragments in situ, including the very fragmentary M³. Surplus sediment was cleaned carefully from the bones with a tungsten carbide needle. Finally, all pieces were reassembled and glued using Paraloid B72 dissolved in acetone.

Photographs of UM 118709 included here were made at the Royal Belgian Institute of Natural Sciences using an FEI Quanta 200 FEG scanning electron microscope in low-vacuum environmental mode (ESEM).

INSTITUTIONAL ABBREVIATIONS

AMNH	 American Museum of Natural History,
	New York, New York, U.S.A.
UM	 University of Michigan Museum of
	Paleontology, Ann Arbor, Michigan, U.S.A.
USNM	 U. S. National Museum of Natural History,
	Washington, D.C., U.S.A.
YPM	 Peabody Museum of Natural History,
	Yale University, New Haven, Connecticut,

SYSTEMATIC PALEONTOLOGY

Order CIMOLESTA McKenna, 1975 Suborder DIDELPHODONTA McKenna, 1975 Family CIMOLESTIDAE Marsh, 1889

Didelphodus Cope, 1882

Centetodon (in part), Marsh, 1872, p. 214. *Deltatherium* (in part), Cope, 1881, p. 669. *Didelphodus* Cope, 1882, p. 522. *Phenacops* Matthew, 1909, p. 535.

U.S.A.

Didelphodus caloris, new species Figure 1

Didelphodus sp., Rose et al., 2012, p. 26, fig. 15.

Holotype.— UM 118709, a cranial rostrum with partial crowns or complete teeth of C_1 – M_3 in one or both maxillae; a lower incisor; and partial or complete crowns of C_1 – M_3 in one or both dentaries (Figs. 1–6).

Type locality and horizon.— UM 118709 came from a screen-wash site in University of Michigan locality SC-139. The locality is in the northwest quarter of section 14, T56N, R102W, in the Clarks Fork Basin of Park County, Wyoming. The wash site is at 44.83872° N and 109.11902° W (coordinates 648665 × 4966756 in UTM zone 12N). It occupies part of a broad shallow scour cutting the single prominent red bed running through the middle of locality SC-139.

Age and distribution.— Locality SC-139 is in the PETM and yields a Wa-0 earliest Eocene fauna. *Didelphodus caloris* is also known from the Sand Creek Divide area in the southern



FIGURE 1 — UM 118709, holotype of the new species *Didelphodus caloris*. Scanning electron micrograph of cranial rostrum with crowns of left P^2-M^3 . The rostrum is shown in left lateral (A), palatal (B), and dorsal (C) views. Anterior is at the left. Abbreviations: *iof*, left infraorbital foramen; *pp*, right postorbital process.

Bighorn Basin of Washakie County, Wyoming (Rose et al., 2012). Diagnosis.— Didelphodus caloris differs from *Didelphodus absarokae* in being significantly smaller (Fig. 7); in having upper premolars with a well-developed metastyle on

TABLE 1. Measurements of crown length, width, and height for the teeth of UM 118709, holotype of *Didelphodus caloris*. Measurements from the left and right side are averaged when both are available. Estimates are shown with an asterisk. Incisor crown length and width are labiolingual and mesiodistal, respectively. All measurements are in mm. Abbreviations: *Tri. wid.*, trigonid width; *Tal. wid.*, talonid width.

Upper dentition				Lower dentition				
Tooth	Length	Width	Height	Tooth	Length	Tri. wid.	Tal. wid.	Height
I ^x	_		_	Ix	0.79	0.83		_
C^1	3.26*	2.18*	_	C1	3.67	2.72		
\mathbf{P}^1	1.80*	1.12*	_	P_1	1.99	1.19		2.18
\mathbf{P}^2	2.21	1.60	_	P_2	2.73	1.73		3.33
P ³	2.65	2.52		P3	2.76	1.69		3.22
\mathbf{P}^4	2.70	3.34	2.00*	P ₄	3.11	1.66		3.02
M^1	3.42	4.36	1.77*	M_1	3.12	2.18	1.82	2.72
M^2	2.97	5.02	1.71*	M ₂	3.16	2.28	1.90	
M ³	1.89	3.83	1.45*	M ₃	2.59*	1.72	1.26	

P⁴; in having lower premolars with a simple apical protoconid, small and low anterior basal cusp, and no metaconid; in having a more centrally placed paraconid on M¹; and in having a reduced M₃. *Didelphodus caloris* is seemingly similar in size to poorly known *Didelphodus altidens*, but differs from it lacking a protocone on P³ (present in *D. altidens*; White, 1952); and lacking a rudimentary inner cusp (metaconid) on P³ (present in *D. altidens* = *D. a. ventanus*; Matthew, 1918).

Etymology.— caloris, L., warm or hot; acknowledging the 'thermal maximum' environment when *Didelphodus caloris* lived during the PETM (and several unusually warm days when the holotype was found in July, 2022).

Discussion.— Isolated teeth of *Didelphodus* sp. from the Wa-0 fauna of Sand Creek Divide were described and illustrated by Rose et al. (2012). Direct comparison indicates that the Sand Creek Divide teeth are indistinguishable from *D. caloris* (see below).

ZooBank.— This article conforms to requirements of the International Code of Zoological Nomenclature. It is available online at <u>https://deepblue.lib.umich.edu/handle/2027.42/41251</u>. The species name *Didelphodus caloris* is registered in ZooBank with a Life Science Identifier: urn:lsid:zoobank.org:pub:549A3715-0560-4220-AA54-CC75A41ADC24. The registration can be viewed at <u>https://zoobank.org/urn:lsid:zoobank.org:pub:549A3715-0560-4220-AA54-CC75A41ADC24.</u>

DESCRIPTION

The holotype of *Didelphodus caloris*, UM 118709, is a somewhat deformed cranial rostrum that retains much of the

permanent dentition. The dental formula was almost certainly 3.1.4.3 / 3.1.4.3, with the only uncertainty being the number of upper and lower incisors. The infraorbital foramen (*iof*) above P³ in the left maxilla measures 2.1×1.3 mm. A small postorbital process (*pp*) with a small foramen located just below it was possibly present on the right side of the skull (Fig. 1C) but this is now broken. Compression and breakage obscure other osteological details.

Upper dentition.— The upper dentition of the holotype includes, on the left side, a single large root for left C^1 , paired small roots for left P^1 , partial crowns of left P^{2-4} , and partial or complete crowns of left M^{1-3} (Fig. 1A-B). The right side preserves a single large root for right C^1 , and paired small roots for right P^1 and P^2 . Partial or intact crowns of right P^3-M^3 are present in a separate maxilla (Fig. 2A-C). The overall length of the maxillary dentition, from the front of C^1 to the back of M^3 , is approximately 24.1 mm. Measurements of individual teeth are listed in Table 1.

The upper canine crowns are not preserved, but a relatively large, vertically-implanted root for C^1 is present in each maxilla. C^1 is followed by a 1.1–1.2 mm diastema.

The crowns of left and right P^1 are missing, but each tooth is represented by a pair of small, closely-spaced roots. P^1 is followed by a 1.1–1.2 mm diastema.

The crown of P^2 is present on the left side. It is small, oval in occlusal outline, and bordered anteriorly, labially, and posteriorly by a narrow cingulum. P^2 is followed by a 0.8 mm diastema.

P³ is present in both the left and right maxillae. It is larger than P², and triangular in occlusal outline. The apical cusp of P³ is broken and missing on both sides. The crown is surrounded by a continuous narrow cingulum. A very small cusp on the lingual cingulum makes the occlusal outline triangular, but this is much



FIGURE 2 — UM 118709, holotype of the new species *Didelphodus caloris*. Scanning electron micrograph of right maxilla with crowns of P³–M³ in buccal (A), occlusal (B), and lingual (C) views. Anterior is at the right.

smaller than the well-developed protocone present on P^3 in later *Didelphodus absarokae* and *D. altidens*. There is no diastema between P^3 and P^4 .

P⁴ is well preserved in the right maxilla (Fig. 2), with the tip of the paracone somewhat worn. The crown is triangular in outline. Two cusps are prominent: one a well-developed medial protocone, and the other an even larger and more laterally positioned paracone. The paracone has a small swelling near the apex of the posterior surface that is an incipient metacone. There is a distinctly notched postmetacrista connecting the metacone

to the metastyle. The crown is surrounded anteriorly, labially, and posteriorly by a continuous cingulum. The cingulum has a well-developed parastyle at the anterolabial corner of the crown.

 M^1 is slightly worn but otherwise well preserved in the right maxilla. The crown is triangular in outline, with a broad stylar shelf. Three cusps are prominent on M^1 : the protocone is positioned lingually, and the paracone and metacone are positioned more centrally on the crown. The tip of the paracone is broken but this cusp appears to have been higher than the metacone. A small eroded paraconule is present between the



FIGURE 3 — UM 118709, holotype of the new species *Didelphodus caloris*. Scanning electron micrograph of left dentary with base of the crown of C_1 , and crowns of P_1 – M_3 in buccal (A, anterior at left) and lingual views (B, anterior at right). Abbreviations: *ap*, angular process; *mf*, mandibular foramen.

paracone and protocone, and a small eroded metaconule is present between the metacone and protocone. The paracone and metacone are connected to the corresponding parastyle and metastyle by well-developed crests of the preparacrista and postmetacrista, respectively. The metastylar lobe of the crown is more prominently developed than the parastylar lobe.

 M^2 is also well preserved in the right maxilla. Here too the crown is triangular in outline, with a broad stylar shelf. Three cusps are prominent on M^2 : the protocone is positioned lingually, and the paracone and metacone are positioned more centrally on the crown. The paracone is a little larger and higher than the metacone. A small paraconule is present between the paracone and protocone, and a small metaconule is present between the metacone and protocone. The paracone and metacone are again connected to the corresponding parastyle and metastyle by well developed crests of the preparacrista and postmetacrista. However, here the parastylar lobe of the crown is more prominently developed than the metastylar lobe.

The crown of M^3 is missing its posterior margin, including the metacone and metastyle (if present). What remains is smaller but otherwise somewhat similar to the crown of M^2 . The protocone is positioned lingually, and the paracone is positioned more centrally on the crown. The paracone was probably higher and more prominent than the metacone. A small paraconule is present between the paracone and protocone, and a small metaconule is present as well. There is a wide stylar shelf buccal to the paracone, and this cusp is connected to the corresponding parastyle by a well-developed preparacrista. The parastylar lobe of the crown was undoubtedly more prominently developed than any remaining metastylar lobe.

Lower dentition.— The left dentary of UM 118709 includes the base of the crown of left C_1 , and crowns of left P_1 – M_3 (Figs. 3, 4D, 5). A single incisor (Fig. 4A-C) was found adhering to the rostrum, which we interpret as a lower incisor of uncertain position, possibly I₂. The right dentary includes the root of right C_1 , and crowns or partial crowns of right P_1 – M_2 (Fig. 6). The overall length of check teeth in the lower jaw, from the front of C_1 to the back of M_3 , is approximately 24.3 mm. Measurements of individual teeth are listed in Table 1.

The left dentary (Fig. 3) is more complete than the right dentary. Both are relatively straight and robust. Both dentaries have an anteriorly inclined mandibular symphysis, with a textured medial surface marking their articulation in life. This symphysis extends posteriorly to a point below the anterior roots of left and right P_3 . The joint itself was technically an amphiarthrosis or a slightly moveable joint linked by fibrocartilage. The left mandibular ramus is 6.7 mm deep on the lingual side and 3.0 mm thick below M_1 . The lateral surface of



FIGURE 4 — UM 118709, holotype of the new species *Didelphodus caloris*. Scanning electron micrographs of the lower incisor in lateral (A), anterior (B), and posterior view (C). Left dentary in anterior view (D) with the alveolus for left I₂ outlined. This alveolus is similar in size to the incisor root shown in A–C. Abbreviation: *a*, alveolus.

each dentary has a small mental foramen below the posterior root of P_1 and another below the posterior root of P_3 . The left dentary is broken posteriorly at the level of the mandibular foramen (*mf*), leaving a notch in the bone. A small fragment of the posterior part of the left dentary with an angular process (*ap*) is preserved, but this cannot be attached to the rest of the dentary because a small intervening fragment is missing. Here the angular process is rounded and moderate in size.

The incisor associated with UM 118709 is small. It has a straight root and appears to be a lower incisor. The incisor crown is swollen at the base and tapers to a transverselyoriented linear occlusal edge. The base of a single alveolus is visible on the anterior surface of the left dentary, seemingly for I₂, which appears to have had a slightly longer and more deeply implanted root than those for I₁ or I₃ (for which alveoli are poorly preserved).

The crown of the lower canine, C_1 , is not preserved, but the root present in both dentaries shows that the tooth was robust, with a narrow and slightly procumbent crown. A short 0.5 mm diastema separates P_1 from C_1 .

The crown of premolar P_1 is small, with a simple, narrow, pointed crown. The apex is above the anterior root, and there is a very small basal cusp at the posterior margin of the crown. There is again a short 0.5 mm diastema separating P_1 from P_2 .

The crown of P_2 is slightly higher than crowns of the other lower check teeth, but it is virtually identical in shape to the crown of P_3 . The small anterior and posterior basal cuspules are less developed than those on P_3 . There is a short 0.4 mm diastema separating P_2 from P_3 .

Premolars P_3 and P_4 have simple, high, pointed crowns covered with smooth enamel showing no occlusal wear. P_3 has a single apical cusp, the protoconid, with a slightly convex crest or preprotocristid descending anteriorly from the apex to small cuspule at the anterior base of the crown. P_3 has a straighter crest descending posteriorly from the apex to a similarly small cuspule at the base of the crown. There is no diastema separating P_3 from P_4 .

 P_4 has a crown like that of P_3 , but the basal cusps at the anterior and posterior margins of the crown are larger. The posterior cusp is on a rudimentary talonid. P_4 has a faint trace of a posterolabial cingulid that is not present on P_3 .

The first lower molar, M_1 , is well preserved in the left dentary. It is tritubercular, with a moderately high trigonid bearing distinct paraconid, protoconid, and metaconid cusps. The protoconid is the highest cusp. The paraconid is the lowest of the trigonid cusps, and it is centrally placed at the anterior margin of the crown. The protoconid and paraconid are connected by a worn paracristid, and the protoconid and metaconid are connected by a worn protocristid. There is a narrow cingulid at the anterobuccal base of the trigonid. The talonid of M_1 is narrower than the trigonid and shallowly basined. It is better preserved on right M_1 , where there is a distinct hypoconid and the entoconid and hypoconulid are confluent. The trigonid of right M_1 was broken in life and the trigonid base heavily worn before death.

The crown of M_2 is well preserved in both dentaries. M_2 is generally similar to M_1 , but the crown may be slightly larger. M_1 and M_2 both have a narrow cingulid at the anterobuccal base of the trigonid. The trigonid of M_2 differs from that of M_1 in having the paraconid placed a little more lingually relative to the protoconid and metaconid. M_2 also differs from M_1 in having a slightly shorter talonid, with the cristid obliqua positioned more lingually.

 M_3 is preserved in the left dentary. It resembles M_2 but has a shorter crown that is notably reduced in both height and width. The paraconid is lingually placed on the trigonid, and there is a narrow cingulid at the anterobuccal base of the trigonid. The talonid is narrow but still basined, with a labially positioned hypoconid. The entoconid and hypoconulid are damaged and their confirmation is unclear.

DISCUSSION

We follow McKenna and Bell (1997) in classifying *Didelphodus* in the order Cimolesta and family Cimolestidae. This is plausible because *Didelphodus* has cheek teeth that resemble those of some cimolestids (see, for example, *Altacreodus magnus* of Clemens and Russell, 1965; Fox, 2015). The family ranges temporally from the latest Cretaceous to at least the middle Eocene, and ranges geographically across all three northern continents and northern Africa. The North American middle Paleocene cimolestids *Acmeodon* and *Gelastops* have been linked somewhat tentatively to *Didelphodus* (Simpson, 1937). It is plausible that *Didelphodus* expanded its range northward from a more equatorial locale in North America to reach present-day Wyoming during the



FIGURE 5 — UM 118709, holotype of the new species *Didelphodus caloris*. Scanning electron micrograph of left dentition with base of the crown of C₁, and crowns of P₁–M₃ in buccal (A, anterior at left), occlusal (B, anterior at right), and lingual views (C, anterior at right).



FIGURE 6 — UM 118709, holotype of the new species *Didelphodus caloris*. Scanning electron micrograph of right dentary with crowns of P_1 – M_2 and roots of M_3 in buccal (A, anterior at right), occlusal (B, anterior at right), and lingual views (C, anterior at left). Note occlusal wear on the anterior portion of M_1 indicating that the trigonid was broken in life.



FIGURE 7 — Stratigraphic position of UM 118709, holotype of the new species *Didelphodus caloris* (filled diamond). The type locality is University of Michigan locality SC-139 in the Clarks Fork Basin of northwestern Wyoming. This is a Wa-0 early Wasatchian locality lying within the Paleocene-Eocene Thermal Maximum (PETM). Wa-0 specimens of *Didelphodus* M₁ or M₂ described by Rose et al. (2012) are from Sand Creek Divide in the southern Bighorn Basin (open diamonds; USNM 533578, 533580, and 540166). Stratigraphically higher *Didelphodus absarokae* specimens are known from the Clarks Fork Basin (filled circles) and from the northern and central Bighorn Basin (open circles). Solid line for *D. caloris* and gray shading for *D. absarokae* show the expected ±2 standard deviation range and 95% confidence interval for each species, centered on successive sample means. *D. caloris* is older geologically and smaller in size than all known *D. absarokae* specimens. *Didelphodus altidens* (not shown) is a later and less well known latest Wasatchian and Bridgerian age descendent of *D. absarokae*. *Didelphodus absarokae* specimens plotted here are in the University of Michigan Museum of Paleontology collection.

PETM. It is also plausible that *Didelphodus* immigrated into North America from Europe (Smith et al., 2006) or possibly Asia (Beard, 1998) during the PETM. However, there is as yet no evidence of *Didelphodus* or a direct ancestor in the Paleocene of North America, Europe, or Asia.

Didelphodus caloris and *D. absarokae* differ slightly in age (Fig. 7). Associated mammals show *D. caloris* from SC-139 to be part of a Wa-0 fauna, and *D. absarokae* to belong to later Wa-1 through Wa-6 faunas. As noted in the diagnosis, *D. caloris* differs from *D. absarokae* in being smaller (Fig. 7). Measurements of M_1 size for specimens of each species lie outside the expected ± 2 standard deviation range of M_1 size in the other species. *D. caloris* also differs from *D. absarokae* in having: (a) very simple lower premolars with no traces of metaconids; and (b) a relatively small M_3 .

Comparison with much younger late Wasatchian and Bridgerian *D. altidens* is more difficult because there are few good specimens of the latter. Matthew (1918) described the best mandibular dentition as the holotype of *D. absarokae ventanus*, and White (1952) described the best maxillary dentition of *D*.

altidens under the name *D. ventanus*. *D. caloris* is seemingly similar in size to *D. altidens*, but here again there are few comparable specimens. *D. altidens* can be traced as a lineage getting smaller while evolving from *D. absarokae* (Bown and Schankler, 1982), meaning that the small size of *D. altidens* was achieved independently. While similar in size, *D. caloris* differs from *D. altidens* in lacking a protocone on P^3 (present in *D. altidens*; White, 1952), and in lacking a rudimentary metaconid on P_3 (present in *D. altidens*; Matthew, 1918). No crown of P_4 has been described for *D. altidens* so the degree of development of the metaconid on P_4 is unknown.

Some PETM mammals are smaller than both their immediate pre-PETM ancestors and their post-PETM descendants (Gingerich, 1989). As a consequence, the PETM species are plausibly interpreted as dwarfed forms, and the dwarfing can be attributed, directly or indirectly, to PETM climate change (Gingerich, 2003; Secord et al., 2012). However, dwarfing is difficult to demonstrate when the mammals are immigrants and their immediate ancestors are unknown. *Didelphodus caloris* falls in this category (Fig. 7). *Macrocranion junnei* is another even smaller PETM insectivore succeeded by a larger species following the PETM (Smith et al., 2002; Rose et al., 2012). Both fit the common pattern of notably small size during the PETM, but a dwarfing interpretation is necessarily speculative because we do not know the size of the immediate ancestor.

CONCLUSIONS

Didelphodus caloris is a new species of insectivorous mammal found at a Wa-0 wash site in the PETM of the Clarks Fork Basin of northwestern Wyoming. It is the oldest species of *Didelphodus* known anywhere. The holotype is a cranial rostrum with much of the upper and lower dentition. *D. caloris* is tentatively interpreted as a dwarfed form like other Wa-0 mammals because of its small size relative to its immediate successor *Didelphodus absarokae*.

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