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On: 11 November 2011, At: 11:55

Publisher: Taylor & Francis

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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

First records of a triisodontine mammal, *Goniacodon levisanus*, in the late Paleocene of the northern Great Plains, North America

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Available online: 24 Mar 2010

To cite this article: Elizabeth M. St. Clair, Doug M. Boyer, Jonathan I. Bloch & David W. Krause (2010): First records of a triisodontine mammal, *Goniacodon levisanus*, in the late Paleocene of the northern Great Plains, North America, *Journal of Vertebrate Paleontology*, 30:2, 604-608

To link to this article: <http://dx.doi.org/10.1080/02724631003617902>

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FIRST RECORDS OF A TRIISODONTINE MAMMAL, *GONIACODON LEVISANUS*, IN THE LATE PALEOCENE OF THE NORTHERN GREAT PLAINS, NORTH AMERICA

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The Triisodontinae are a group of condylarths, including the early Paleocene genera *Eoconodon*, *Triisodon*, and *Goniacodon*, with molar morphology intermediate between that of arctocyonids and mesonychians (Szalay, 1969; Rose, 2006). Although Triisodontinae may be a paraphyletic group closely related to Mesonychia (Prothero et al., 1988; Williamson and Carr, 2007), the phylogenetic relationships of mesonychians, triisodontines, and arctocyonids remain poorly resolved (e.g., Williamson and Carr, 2007). Thus, we follow a traditional taxonomic scheme that includes Triisodontinae within Arctocyonidae (e.g., Matthew, 1937; Simpson, 1945; Van Valen, 1966, 1978; Szalay, 1969; O'Leary and Rose, 1995; O'Leary, 1998; Rose, 2006) pending more detailed phylogenetic studies.

Eoconodon has been recovered from deposits correlated to the Puercan North American Land Mammal 'Age' (NALMA), in localities as far apart as Montana and New Mexico (Clemens and Williamson, 2005). *Triisodon* has been identified only in the San Juan Basin, New Mexico, from strata of the Torrejonian NALMA (Taylor, 1981; Tomida, 1981; Williamson and Lucas, 1993). *Goniacodon* is best known from the Paleocene Nacimiento Formation of the San Juan Basin (e.g., Williamson, 1996), although it has also been recorded from early Paleocene localities in Wyoming (Gingerich, 1978; Rigby 1980; Rose, 1981a) and Utah (Robison, 1986; Tomida and Butler, 1980; Van Valen, 1966, 1978). Prior to this study, localities yielding *Goniacodon* have been assigned to either the late Puercan or Torrejonian NALMAs. Here we report the first known occurrences of *Goniacodon* from the Crazy Mountains Basin (CMB), Montana, from Bingo Quarry (Q) in the eastern CMB, and from a new locality in the western CMB. These sites are earliest Tiffanian (late Paleocene) in age. These new records represent the first known occurrences of triisodontines in the late Paleocene, and the most northerly occurrences of *Goniacodon* in North America.

The Bingo Q fauna is one of the oldest and best sampled in the Tiffanian (Ti) of the eastern CMB (Fig. 1; Hartman and Krause, 1993; Bloch et al., 2006). Bingo Q lies stratigraphically below Douglass Q, which is within the earliest Ti biochron, Ti1 (Krause and Gingerich, 1983), and above Donald Q, which is also early Ti (Bloch et al., 2006). It was discovered in 1989 but the fauna remains largely undescribed, with the exception of specimens of *Elphidotarsius* (Silcox et al., 2001) and *Gingerichia* (Zack et al., 2005). Taxa typical of the Ti that have been identified within the Bingo Q sample include *Ectocion* and *Nannodectes* (Bloch et al., 2006). *Aphronorus orieli* is also present, indicating an early Ti age (Gingerich et al., 1983). Unpublished paleomagnetic data indicate that Donald Q and Bingo Q are located within a reversed polarity zone, C26R, which is at least consistent with a Ti age (Fig. 1).

A new Paleocene mammal locality was discovered in the western part of the CMB in 2004. The stratigraphy in this region is not as clear as in the eastern part of the basin; however, the new site (informally referred to as the 'Plan B Locality') has yielded remains of *Ectocion* and *Aphronorus orieli* and appears similar to Bingo Quarry in faunal composition and, by inference, age. More detailed descriptions of new collections from the CMB are currently in preparation.

Abbreviations—AMNH, American Museum of Natural History; NMMNH, New Mexico Museum of Natural History, Albuquerque; UM, University of Michigan; USNM, United States National Museum (Smithsonian); YPM-PU, Yale Peabody Museum–Princeton University collection; CMB, Crazy Mountains Basin; Q, Quarry; Pu, Puercan; To, Torrejonian; Ti, Tiffanian; NALMA, North American Land Mammal 'Age.'

SYSTEMATIC PALEONTOLOGY

Family ARCTOCYONIDAE Giebel, 1855
Subfamily TRIISODONTINAE Trouessart, 1904
Genus *GONIACODON* Cope, 1888
GONIACODON LEVISANUS COPE, 1883
(Fig. 2)

Holotype—AMNH 3217, right dentary with p4 (fragment) and m1–2.

Revised Geographic and Temporal Range—Early Paleocene (late Puercan and Torrejonian) of the southern Great Basin and central Great Plains and late Paleocene (early Tiffanian) of the northern Great Plains, North America (biogeographic regions after Janis et al., 1998).

Referred Specimens—UM 51392, left m2 ('Plan B Locality,' western CMB); UM 51391, left m3 (Bingo Q, eastern CMB).

DESCRIPTION AND COMPARISONS

The crown of UM 51392, a left m2 (Fig. 2A), is intact and undamaged, with almost no wear on the cusps. UM 51391, a left m3 (Fig. 2B), is completely unworn but has a repaired crack separating the distolingual portion of the talonid from the remainder of the tooth, thus obscuring the morphology of the talonid notch.

The trigonid of m2 is tall and subequal in length and width relative to the talonid. The trigonid has three distinct cusps, with a small, low paraconid that is mesiolingual in position and linked to the protoconid by an externally convex, gently sloping preprotocristid. The metaconid and protoconid are subequal in height; the postprotocristid is oriented buccolingually and marked by a notch at its midpoint. The trigonid has a prominent, mesiobuccal cingulid. The cristid obliqua contacts the postvallid surface of the protoconid, creating a relatively shallow hypoflexid. The hypoconid is the largest talonid cusp, the entoconid is nearly equal in height, and the entoconid and small hypoconulid are distinct, but closely approximated. The entocristid reaches the

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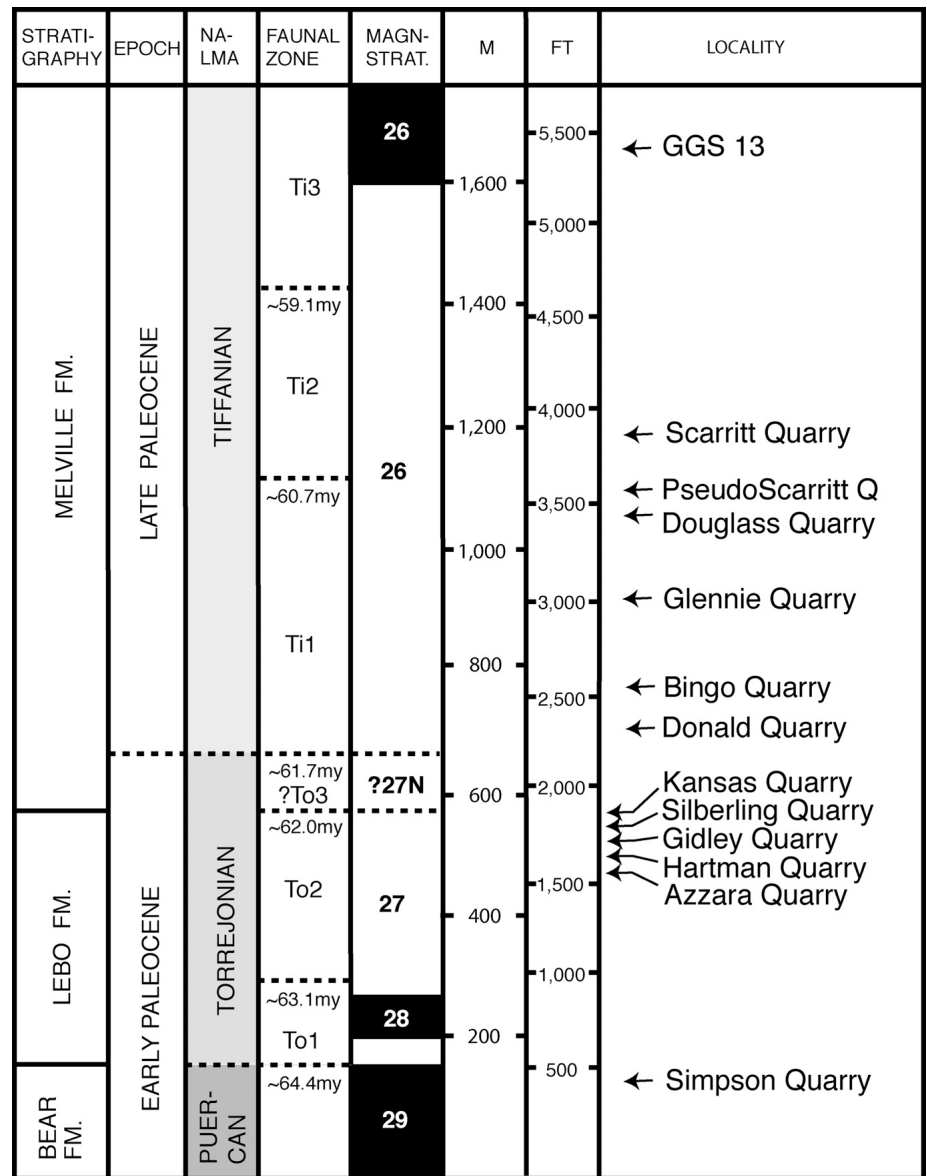


FIGURE 1. Stratigraphy of Paleocene mammal localities in the eastern Crazy Mountains Basin, Montana (modified from Hartman and Krause, 1993). Paleomagnetostratigraphy is based on existing data for the eastern CMB; C27N has not yet been documented here. Dates for biochron boundaries follow Gradstein et al. (2004).

distal surface of the metaconid without marked mesial reduction in height.

The trigonid of m3 is similar to that of m2; the preprotocristid is distinctive in that it bears four or five small rounded cusps and the mesiobuccal cingulid is not as greatly developed as in m2. The trigonid and talonid are subequal in length, with slightly greater buccolingual width in the trigonid. The talonid of m3 is approximately oval in occlusal outline, with a short cristid obliqua. The entoconid and hypoconulid of m3 are not differentiated; there is a continuous ridge in this region bearing small cusps. There is no distinct hypoconulid lobe.

Comparisons with Arctocyonids—The morphology of UM 51392 and UM 51391 is similar to that of specimens of triisodontines known elsewhere from the early Paleocene, and is distinct from that of mammals of similar size and dental form already known from the To and Ti of the CMB (e.g., the arctocyonines *Arctocyon* and *Colpoclaenus*, and smaller arctocyonids such as *Chriacus* and *Mimotricentes*). Features shared with some or all triisodontines and not found in the above taxa include

fusion of the protoconid and metaconid at a height above that of the paraconid, a paraconid that is prominent and mesially positioned, presence of a shelf-like mesiobuccal cingulid, and a mesiodistally long trigonid that is relatively tall compared to the talonid. The m3 is particularly distinctive in lacking a pronounced hypoconulid lobe.

Comparisons with Mesonychians and Triisodontines—Mesonychian lower molar morphology differs from that of triisodontines in the reduction or disappearance of the talonid basin, and in the greatly increased size of the protoconid relative to the metaconid (Szalay, 1969). The molar morphology of *Oxyclaenus cuspidatus* (sensu Williamson and Carr, 2007; hypodigm previously referred to *Microclaenodon assurgens*) shares some features with triisodontines, such as the fusion of cusp bases of the metaconid and protoconid. In comparison to triisodontines, including the CMB specimens, lower molars referred to *Oxyclaenus cuspidatus* have taller trigonids and are buccolingually more compressed, possibly derived features shared with mesonychians (Szalay, 1969). In addition, lower

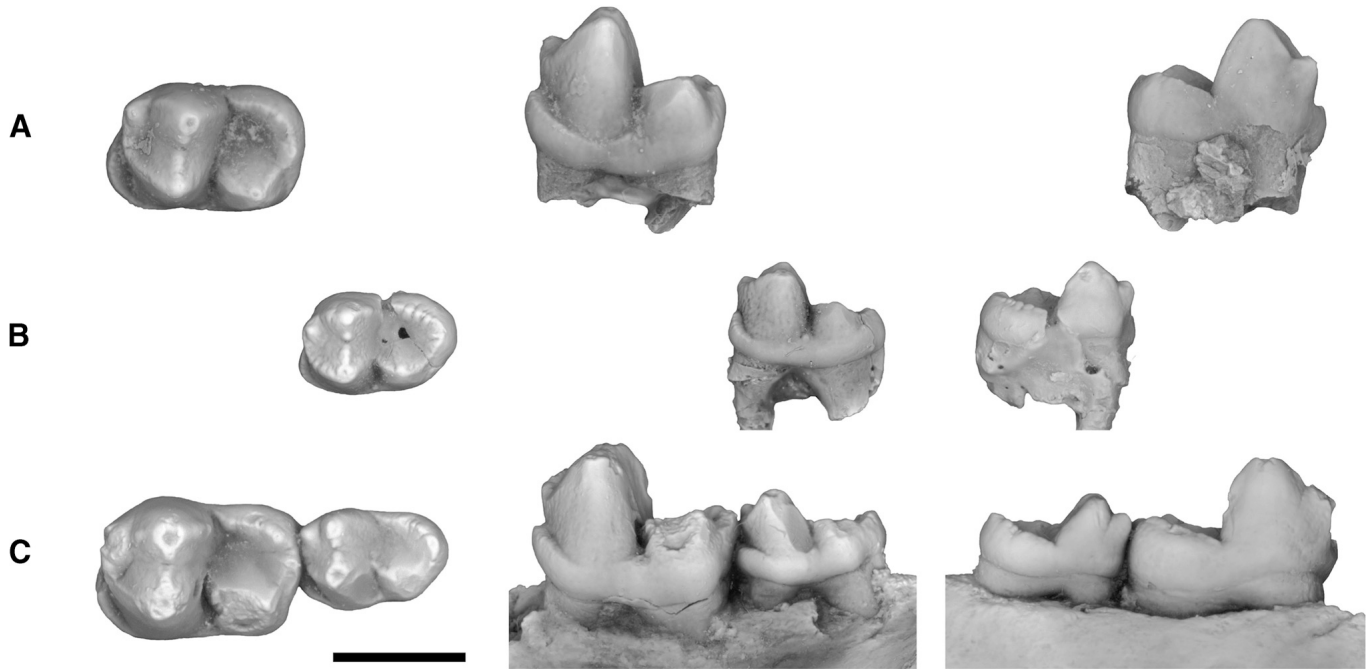


FIGURE 2. Lower molars of *Goniacodon levisanus* in occlusal (left), buccal (middle), and lingual (right) views. **A**, UM 51392, left m2 from 'Plan B Locality' western Crazy Mountains Basin, Montana; **B**, UM 51391, left m3 from Bingo Quarry, eastern CMB; **C**, YPM-PU 17497 (cast), left dentary with m2-3 from Rock Bench Quarry, Bighorn Basin, Wyoming. Scale bar equals 5 mm.

molars of *O. cuspidatus* differ from those of the CMB specimens in that the entocristid declines sharply mesial to the entoconid, leaving the talonid basin open lingually (Williamson and Carr, 2007), and in the greater development of the hypoconulid (particularly in m3).

Goniacodon is distinguished from other triisodontines (i.e., *Triisodon*, *Eoconodon*) by its more triangular upper molars and by relative reduction in size of both m3 and M3 (Gingerich, 1978; Kondrashov and Lucas, 2006). These parameters cannot be assessed on the CMB specimens, but comparative observations and measurements (Table 1) indicate that the morphology described for the CMB specimens is more consistent with that of *Gonia-*

codon levisanus from the Bighorn Basin (Rock Bench Q, YPM-PU 17497; Gingerich, 1978) and the San Juan Basin (e.g., AMNH 3218, USNM 408053) than any other triisodontine examined, including *Triisodon crassiscuspis*, which has been referred to *Goniacodon* by some authors (e.g., Van Valen, 1978; Williamson and Carr, 2007).

The lower molars of *Triisodon quiverensis*, *Eoconodon coryphaeus*, and *E. gaudrianus* are considerably larger than those of UM 51392 and 51391 (Table 1). Compared to the CMB specimens, *Triisodon quiverensis* has: (1) marked narrowing of m1-2 between the trigonid and talonid in occlusal view; (2) an m3 with a greater difference in buccolingual width between the trigonid

TABLE 1. Measurements of CMB specimens compared to descriptive statistics of *Goniacodon levisanus* (AMNH 2396, 2397, 3217, 3218, 3221, 3223, 4018, 16561, 16728, 16729, 128019, casts of USNM 408053 and YPM-PU 17497), and with measurements of *Triisodon* and *Eoconodon*.

Species		m2 length	m2 trigonid width	m2 talonid width	m3 length	m3 trigonid width	m3 talonid width
<i>Goniacodon levisanus</i>	Range	7.1-8.2	5.0-5.6	4.5-5.3	4.8-5.8	3.3-4.3	2.9-3.6
	Mean (SD)	7.57 (.361)	5.32 (.223)	4.99 (.298)	5.32 (.385)	3.79 (.385)	3.25 (.269)
	n	11	11	11	7	7	7
	UM 51392	7.7	5.0	4.8			
UM 51391				6.0	3.9	3.6	
<i>Goniacodon crassiscuspis</i>	AMNH 3225	13.6	7.4	n/a			
<i>G. crassiscuspis</i>	AMNH 3178			8.7	11.8	8.4	≥5.9
<i>Triisodon quiverensis</i>	AMNH 3352	15.6	10.6	10.1			
<i>T. quiverensis</i>	AMNH 16559				15.6	10.8	8.0
<i>T. (Sarcothraustes) antiquus</i>	AMNH 3174	18.7	12.1	10.8	15.3	10.5	9.0
<i>Eoconodon coryphaeus</i>	Range	11.4-13.7	7.0-11.2	7.2-11.0	11.5-14.4	7.0-10.3	6.3-9.0
<i>E. gaudrianus</i> (inc. cf. <i>gaudrianus</i>)	Range	8.9-10.1	6.3-7.7	5.8-7.6	8.0-9.5	5.3-6.5	4.6-5.6
<i>E. nidhoggi</i>	Range	6.8-7.4	4.6-4.8	4.4-4.6	7.4-7.6	4.4-5.6	3.7-4.7
<i>E. ginibitohia</i>	NMMNH	7.0	4.6	4.2	6.9	4.3	3.3
	P-21622						

Measurements of *Goniacodon* and *Triisodon* specimens taken with digital calipers or from digital images captured with calibrated Zeiss microscope. *Eoconodon* data from Clemens and Williamson (2005). Measurements in mm.

and talonid; (3) molars with greater crest development and higher cusps in both trigonid and talonid; and (4) a talonid basin that opens lingually with an entocristid that declines sharply in height mesial to the entoconid.

Lower molars of *Eoconodon coryphaeus* have a protoconid larger than the metaconid, and narrowing between the trigonid and talonid, though not as strongly as in *T. quiverensis*. Although Williamson and Carr (2007) score the talonid basin as being closed by the entocristid in *E. coryphaeus*, the entocristid declines in height mesial to the entoconid and reaches the lingual surface of the metaconid creating a lingually open basin. The molar morphology of *Eoconodon gaudrianus* is more similar to that of the CMB specimens, but it also has an entocristid reaching the lingual surface of the metaconid. Smaller species of *Eoconodon* are more comparable in molar size to the CMB specimens, but like the larger species, their molars have a sharply sloping entocristid with lingually open talonid basins (Clemens and Williamson, 2005), and lack the prominent mesiobuccal cingulid observed in the CMB specimens.

Lower molars of *Goniacodon crassiscuspis* are larger than those of the CMB specimens and differ particularly in the morphology and proportions of m3, having a much larger trigonid relative to the talonid (particularly in buccolingual diameter) and a protoconid that is larger compared to the other cusps, though this is not seen on m1–2. The mesiobuccal cingulid is much less developed in the molars of *G. crassiscuspis* than in the molars of the CMB specimens. The CMB specimens share the following features with specimens of *G. levisanus*: (1) metaconid and protoconid subequal in height in both m2 and m3; (2) shelf-like mesiobuccal cingulid (variable in *G. levisanus* from the San Juan Basin); (3) talonid and trigonid of m3 close to equal in buccolingual diameter; (4) lack of distinct hypoconulid with no hypoconulid lobe on m3; and (5) talonid basin closed lingually by the entocristid, which reaches the distal surface of the metaconid. This final feature is unclear in the CMB m3, given the damage in this region, but the preserved morphology is consistent with that of m2. The measurements of the CMB specimens either fit within the range of *G. levisanus*, or expand it only slightly (m3 length). *G. levisanus* is the only known triisodontine species that could accommodate both CMB individuals within its size range, due to the reduced m3 in this species. For example, whereas the CMB m2 is 0.3 mm longer than the largest m2 of *E. nidhoggi* measured by Clemens and Williamson (2005), the m3 is 1.4 mm shorter than the smallest specimen of *E. nidhoggi*.

DISCUSSION

The occurrences of *Goniacodon* recorded here represent a temporal range extension into the Tiffanian, and a significant northerly range extension. Interestingly, the genus *Acmeodon* has a similar pattern of occurrence, common in more southerly Torrejonian deposits and appearing in the CMB during the To-Ti transition. *Acmeodon* is known from early Tiffanian localities in the CMB (Krause and Maas, 1990; Bloch et al., 2006) but, like *Goniacodon*, is absent from Torrejonian localities in this region (e.g., Simpson, 1937; Rose, 1981a). These occurrences may indicate some reduction of a north-south separation during the To-Ti transition, either through altered landscape configuration leading to the reduction of a geographic barrier or through range shifts in response to climatic variation. Based on analysis of species diversity in the large quarry samples of Paleocene mammals then available, Rose (1981a, 1981b) argued that there was a shift from a subtropical-adapted fauna in the Torrejonian to a warm temperate-adapted fauna in the Tiffanian. Likewise, Gingerich (1976, 1985) predicted that the Tiffanian fauna might show range shifts to the south, in response to inferred cooler climate in the first part of the late Paleocene (e.g., Haq et al., 1977; Buchardt, 1978; Wolfe, 1978; Hickey,

1980). However, northerly range extensions of some taxa in this transitional period provide contrary evidence and support the inference that this purported late Paleocene climatic cooling was not a feature of the To3-Ti1 boundary, as indicated by the relatively high taxonomic diversity found in more recently collected, large samples from early Tiffanian localities such as Douglass Q in the CMB (Krause and Maas, 1990) and especially the Cochrane 2 locality in Alberta (Fox, 1990; Scott et al., 2002).

The To-Ti transition has been difficult to document in the CMB due to the large previously unsampled section between the two published quarries that represent the latest To and earliest Ti. In the Hanna Basin, Wyoming, an overlap zone in which To and Ti taxa co-occur has been documented (Higgins, 2003). The presence of a typically To taxon such as *Goniacodon* in one of the earliest Ti localities in the CMB (Bingo Q) could also be cited as evidence of a more gradual transition between NALMAs than previously known. However, the occurrence of To taxa not sampled from the earlier CMB quarries indicates that the To-Ti transition in this region is more complex than a simple overlapping of species ranges across the To-Ti boundary, and deserves closer scrutiny. Further description and analysis of the fossils from Bingo Q and new localities in the CMB will augment understanding of the early-late Paleocene transition in North American mammalian faunas, including biogeographic connections and paleoecological comparisons with other regions.

ACKNOWLEDGMENTS

We thank the CMB landowners who granted access over decades of collection work, in particular the Kremer family who own the land on which Bingo Q is situated; G. Gunnell and P. Gingerich for access to casts in the UM collection; M. Jin, C. Norris, and J. Galkin for access to comparative material at the AMNH; N. Kley for the use of his microscope for photographs; and two anonymous reviewers whose comments greatly improved the manuscript. NSF grants BSR-8722539 and EAR-0308902 supported field work in the CMB.

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Submitted July 2, 2008; accepted May 31, 2009.