NEW SPECIMEN REVEALS DELTATHEROIDAN AFFINITIES OF THE NORTH AMERICAN LATE CRETACEOUS MAMMAL *NANOCURIS*

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ABSTRACT—Deltatheroida is a small, mostly Asian, clade of Cretaceous mammals with a complicated systematic history and a poor North American fossil record. The recently described latest Cretaceous *Nanocuris improvida* is a relatively large, morphologically distinctive taxon with carnivorous adaptations; it was tentatively referred to its own family Nanocuridae within Eutheria. Here, we describe a new specimen from the uppermost Cretaceous Lance Formation of Wyoming that is referable to *Nanocuris improvida*, the second occurrence for the taxon. New morphological information from the specimen allows us to refer five additional Lancian specimens, some of which have been previously described as deltatheroidans, to *Nanocuris improvida* and ?*Nanocuris* sp. Results from a phylogenetic analysis remove *Nanocuris* from Eutheria and reveal strong support for its deltatheroidan affinities and for its nested position within Metatheria. As a result, we subsume Nanocuridae within the deltatheroidan family Deltatheridiidae. Within Deltatheridiidae, *Nanocuris* forms a clade with the only other North American deltatheroidan in the analysis, *Atokatheridium* from the Aptian-Albian of Oklahoma. With three Asian deltatheroidans as outgroups to the North American clade, we find support for the hypothesis that deltatheroidans originated in Asia by the Aptian-Albian and undertook a single dispersal event to North America by the Aptian-Albian.

INTRODUCTION

Deltatheroida is a small, mostly Asian, clade of Cretaceous mammals with a tangled systematic history that largely stems from their unique combination of primitive and derived dental features (for an excellent recent review, see Davis et al., 2008). Long regarded as eutherians close in ancestry to some 'insectivorans' and creodonts (Gregory and Simpson, 1926; Simpson, 1928; Van Valen, 1966; McKenna et al., 1971), deltatheroidans have recently been considered either a stem group of boreosphenidans outside of Eutheria and Metatheria (Butler and Kielan-Jaworowska, 1973; Fox, 1974, 1975; Kielan-Jaworowska, 1975; Kielan-Jaworowska et al., 1979; Cifelli, 1993a, 1993b; Fox and Naylor, 2006) or a sister taxon to a stem-based Marsupialia within Metatheria (Kielan-Jaworowska and Nessov, 1990; Marshall and Kielan-Jaworowska, 1992; Szalay, 1994; Muizon et al., 1997; Rougier et al., 1998, 2004; Luo et al., 2003; Kielan-Jaworowska et al., 2004; Sánchez-Villagra et al., 2007; Davis et al., 2008). Though this debate still lingers, we follow the recent phylogenetic analysis of Rougier et al. (2004) that recovers Deltatheroida as a basal clade within a well-supported Metatheria (21 synapomorphies; appendix 3).

Such recent analyses have benefited from an improved anatomical data set for deltatheroidans that is in large part drawn from dental, cranial, and postcranial remains recovered from the fossil-rich Campanian deposits of Mongolia (Gregory and Simpson, 1926; Kielan-Jaworowska, 1975; Rougier et al., 1998, 2004; Horowitz, 2000). The remainder of the Asian record of deltatheroidans includes less complete but nevertheless important material from the Coniacian of Uzbekistan (e.g., Nessov, 1985, 1987, 1993; Kielan-Jaworowska and Nessov, 1990) and Campanian of Kazakhstan (Averianov, 1997). The North American record, by contrast, is meager and restricted to a small number of isolated teeth of two genera from the Aptian-Albian of Oklahoma (Kielan-Jaworowska and Cifelli, 2001; Davis et al., 2008) and unnamed taxa from the Turonian of Utah (Cifelli, 1990), early Campanian (Judithian land mammal 'age') of Alberta, and late Maastrichtian (Lancian land mammal 'age') of Alberta and Wyoming (Fox, 1974).

Denver Museum of Nature & Science (DMNH) specimen 55343 adds significantly to the deltatheroidan record from North America. It is a dentulous mammal jaw fragment from the Lance Formation of eastern Wyoming (Fig. 1) that is referable to the morphologically distinctive *Nanocuris improvida*. This taxon, otherwise only known from the Frenchman Formation (Lancian) of Saskatchewan, Canada (Fig. 1), was previously placed in its own family, Nanocuridae, within Eutheria (Fox et al., 2007). It is relatively large by Mesozoic mammal standards (m3 length = 4.60 mm, equivalent to m2 position of Fox et al., 2007) and exhibits several features indicative of a carnivorous diet (Fox et al., 2007). The new specimen was collected in the 1970s by K. Donald Lindsey, then Curator of Paleontology at the DMNH, and his high school field assistant, Richard K. Stucky, who is now Curator of Paleoecology and Evolution at the DMNH. In 2007, Stucky showed the specimen to one of us (G.P.W.), who recognized its significance for its similarity to *Nanocuris*.

Herein, we (1) describe DMNH 55343, the new mandibular fragment of *Nanocuris*; (2) use the newly available morphological data to refer five additional Lancian specimens, some of which were previously described as deltatheroidans (Fox, 1974), to *Nanocuris improvida* and ?*Nanocuris* sp.; and (3) present results of a phylogenetic analysis that reassigns *Nanocuris* from Eutheria (Fox et al., 2007) to Delatheroida within Metatheria. As such, *Nanocuris*, known by isolated teeth and fragmentary jaws, is arguably North America's best-known deltatheroidan.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; **DMNH**, Denver Museum of Nature & Science (formerly Denver Museum of Natural History), Denver, Colorado, U.S.A.; **RSM P**,
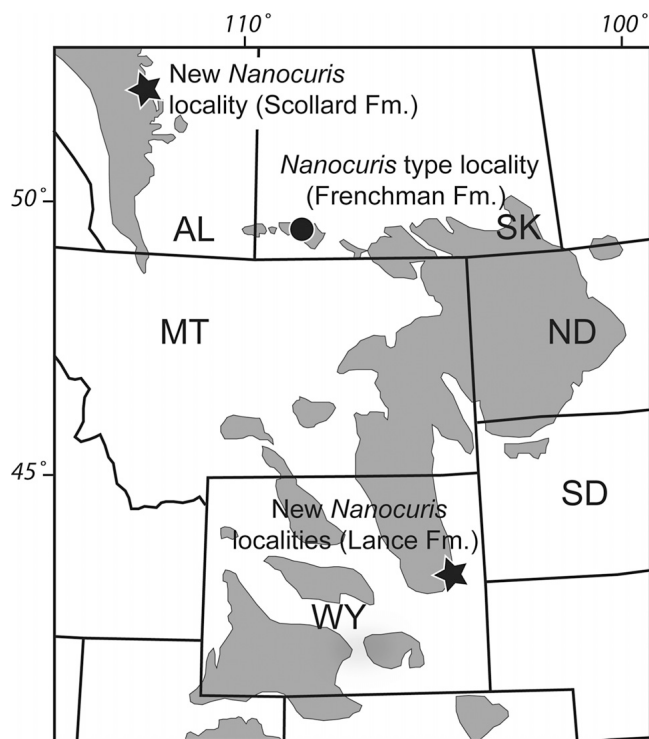
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FIGURE 1. Map of northwestern North America showing fossil sites that have yielded *Nanocuris* specimens. Filled circle represents the type locality for *Nanocuris improvida* (Fox et al., 2007). Filled stars represent localities of newly described and newly referred specimens of *Nanocuris* from this paper. Shaded areas show major depositional basins.

Palaeontological Collections of the Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; **UA**, University of Alberta, Edmonton, Alberta, Canada; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Measurements and Measurement Abbreviations—Therian dental measurements follow Lillegraven (1969) and Lillegraven and Bieber (1986). Specimens were measured using a Leica MZ9.5 binocular dissecting microscope with a custom measuring stage similar to that in Lillegraven and Bieber (1986). It has the capability of reading directly to 0.001 mm. Measurements are abbreviated as follows, L = length, ML = mesial length, DL = distal length, MW = mesial width, and DW = distal width.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
BOREOSPHENIDA Luo, Cifelli, and Kielan-Jaworowska, 2001
METATHERIA Huxley, 1880
DELTATHEROIDA Kielan-Jaworowska, 1982
DELTATHERIDIIDAE Gregory and Simpson, 1926
NANOCURIS Fox, Scott, and Bryant, 2007
NANOCURIS IMPROVIDA Fox, Scott, and Bryant, 2007
(Figs. 2, 3, 4A–C)

Referred Specimen—DMNH 55343, an incomplete right mandible that preserves a damaged penultimate molar and distal half of the ultimate molar.

Locality and Horizon—The specimen was found as float at DMNH loc. 982 (Lance General) in the area of Lance Creek, Wyoming (Fig. 1), in a gray mudstone of the Lance Formation just up slope from ceratopsian bones (Stucky, pers. comm., 2008). The Lance Formation is approximately coeval with the French-

man Formation of the holotype and corresponds to the latest Cretaceous, Lancian North American land-mammal 'age' (late Maastrichtian).

Comment—Fox et al. (2007) inferred from the holotype that *Nanocuris* had a standard eutherian lower cheek tooth formula of four premolars and three molars. Below (Morphological Reinterpretation of the Holotype), we contend that the fragmentary cheek tooth that those authors identified as the p4 talonid is more plausibly identified as that of the m1. By this arrangement, *Nanocuris* would have had a standard metatherian cheek tooth formula of four rather than three molars. We apply this change throughout the paper and, for example, refer to the penultimate and ultimate molars in the holotype, as m3 and m4, respectively.

Revised Diagnosis—Differing from most basal boreosphenidans in the following features (+ = apomorphy; − = plesiomorphy): lower molars with a paraconid tall relative to metaconid (+), a well-developed paracristid and carnassial notch (+), and upper molars with a well-developed postmetacrista (+) (except deltatheroidans and stagodontids); reduction in size of the last lower molar (+) (except deltatheroidans and *Glasbius*); masseteric fossa on the mandible with a well-defined anteroventral margin distal to the tooth row (−), lower molars with a distal metacristid (−), a weak talonid basin with an absent or insignificant entoconid (−), and upper molars with a poorly developed protocone and conules (−) (except deltatheroidans and most stem boreosphenidans); and possession of four lower molars (−) (except metatherians and stem boreosphenidans). Differing from metatherians except deltatheroidans in: absence of a paraconid vertical keel and a hypoconulid postcingulid (−). Differing from all other deltatheroidans in: its larger size, p1 oriented oblique to the jaw axis (+) (except *Deltatheridium*; Kielan-Jaworowska, 1975), lower molars with a highly reduced metaconid (+), and upper molars with a procumbent protocone (+); upper molars with a shallower ectoflexus (+), smaller stylar shelf (+), and mesiodistally longer and transversely narrower protoconal region (+) (except *Sulestes*); and upper molars with a weak stylocone (+) and weak conules (−) (except *Atokatheridium*). Specifically, differing from *Sulestes* in: lower molars with a poorly developed or absent entoconid (−), narrower talonid (−), and greater height differential between trigonid and talonid (−). Differing from *Deltatheroides* in: p1 double-rooted (+). Differing from *Atokatheridium* and *Oklatheridium* in: much larger size and lower molars with greater height differential between trigonid and talonid (−). Differing from all mammals in: mandible with a large neurovascular (?) channel and foramen opening medial to the canine (Fox et al., 2007).

Description—DMNH 55343 is an incomplete right mandible that preserves the lingual wall of the distal alveolus of m2, a damaged m3, and the mesial root, trigonid base, and talonid of m4 (Fig. 2). The mandible is broken anteriorly; as a result, the mesial root of m3 is exposed buccally, but, on the lingual side, the lateral wall for the mesial alveolus of m3 and the distal alveolus of m2 is preserved. On the ventral side, breakage has exposed cross-sections of m3 roots, apices of m4 roots, and the mandibular canal. Based on the root cross-sections, the roots of m3 were longer than those of m4. The mesial root of m3, exposed in buccal view (Fig. 2C, D), descends vertically and slightly mesially; the portion below the level of the alveolar rim has a roughened surface due its cementum attachment. Its cross-section is subcircular, though in mesial view the root is somewhat flattened along its length. The m3 distal root has a greater mesiodistal length than the mesial root, and, in cross-section, it is laterally compressed. It descends vertically and slightly distally, whereas the path of descent for the mesial root of m4 is nearly vertical and that for the distal root of m4 is vertical and slightly mesial. The distal root of m4 has a greater mesiodistal length than that of the mesial root of m4, as is the case for m3.
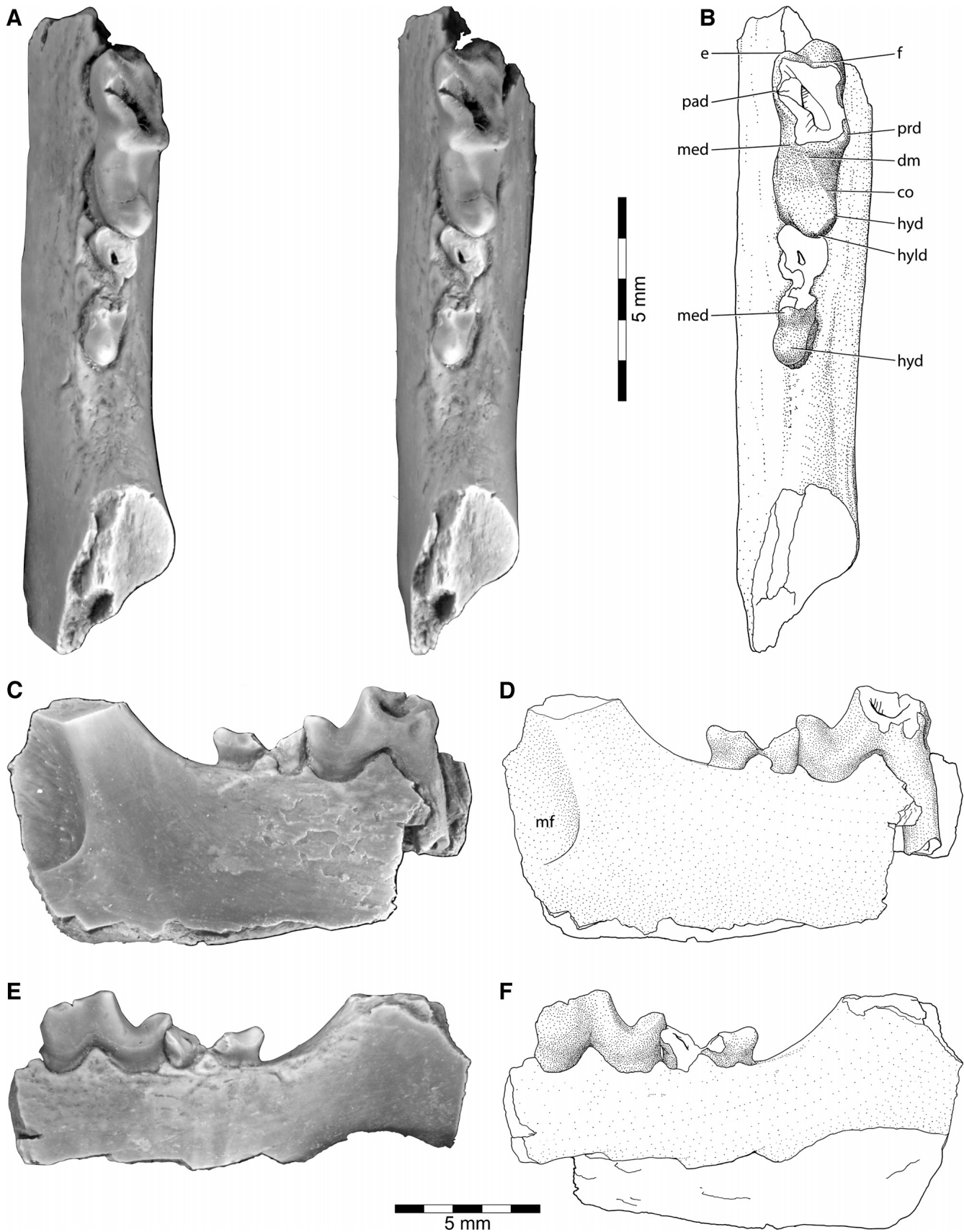
FIGURE 2. Digital images and stipple illustrations of DMNH 55343, a fragmentary mandible of *Nanocuris improvida*, **A**, **B**, in stereo occlusal view, **C**, **D**, in buccal view, and **E**, **F**, in lingual view. Because part of the fragmentary ventral margin of the mandible was obstructed by wax, it was digitally removed from **E**. **Abbreviations**: **co**, cristid obliqua; **dm**, distal metacristid; **e**, cuspule e; **f**, cuspule f; **hyd**, hypoconid; **hyld**, hypoconulid; **med**, metaconid; **mf**, masseteric fossa; **pad**, paraconid; **prd**, protoconid. Scale bars equal 5 mm.

The posterior end of the mandibular fragment preserves the base of the ascending ramus and the anterior portion of the masseteric fossa. The holotype preserves a greater portion of the posterior mandible, but the bone surface in DMNH 55343 appears to be in better condition. The ascending ramus of the coronoid process is robust and rises from the horizontal at a point distal to the m4 and at an angle of ∼130°. The masseteric fossa strongly resembles that in the holotype. It is deep with a well-defined rim that forms a rounded outline in buccal view that does not extend beyond the level of the coronoid process; it terminates well before the tooth row and it does not reach the ventral border. A buccal mandibular foramen is not evident, though in the anteroventral-most part of the fossa, the rim houses a deep pocket. Below the masseteric fossa, the small preserved portion of the mandible flares somewhat laterally. On the lingual side, a barely perceptible posterior depression suggests a shallow pterygoid fossa might have existed farther posteriorly on the mandible. Likewise, due to the incomplete nature of the specimen, we cannot confirm whether a lingual mandibular foramen was present or whether it lacked a meckelian groove, as noted in the holotype. The mandibular fragment is 15.89 mm in length and the maximum depth of the preserved portion of the horizontal ramus is 5.95 mm on the buccal side and 3.65 mm on the lingual side.

The molars of DMNH 55343 are fragmentary; a significant portion of the trigonid cusps of m3 have been sheared off at a buccoventral angle such that the pulp cavity of the tooth is exposed, and on the m4, nearly the entire mesial half of the crown is missing. The enamel of what remains of the m3 and m4 is in fair condition and preserves the coronal morphologies in greater detail than in the holotype specimen.

The crowns are sectorial in overall form: they are laterally compressed, the talonids form a trenchant ridge and lack basins for crushing, and the trigonid is considerably taller than the talonid on m3 and presumably on m4. The m3 is almost one and one-half times longer than the m4 (see Table 1 for measurements). Among Mesozoic boreosphenidans, this degree of size reduction of the ultimate lower molar is otherwise only found in *Glasbius* and deltatheroidans, both metatherians (Kielan-Jaworowska et al., 2004). Although the m3 trigonid is damaged, the cusp arrangement is discernible from the cusp outlines and lateral aspects of the trigonid. The protoconid was the largest of the trigonid cusps, though its base and the bases of the other cusps do not bulge laterally. The distal face of the trigonid is only slightly oblique to the transverse plane, but based on the buccal curvature of the trigonid and the indications from the broken enamel band, we infer that the apex of the protoconid was buccal and somewhat mesial to the metaconid. We estimate the true height of the metaconid was only slightly greater than that preserved in DMNH 55343. The paraconid is well separated from the metaconid, and we estimate that the main trigonid cusps form an angle of ∼67°. The convexities evident on the lingual aspect of the trigonid indicate that the paraconid was a considerably larger and taller cusp than the metaconid and that both were uninflated. The enamel band that is exposed by breakage and visible in occlusal view (Fig. 2A, B) further reveals the morphology of the metaconid. Just mesial to the metaconid, it jogs sharply buccally before expanding lingually to outline the paraconid. The metaconid and protoconid are positioned such that their bases were probably connected medially for much of the height of the metaconid. As a result, the trigonid probably had a short protocristid with only a minor shearing role, and there was probably little to no transverse motion of the jaw during occlusion. The paracristid is not preserved, but based on occlusal outline, it was likely high and elongate and formed the major lower molar blade in a postvallum-prevallid shearing mechanism. Below the paracristid and mesial to the paraconid is a pillar-like mesiolingual cuspule (cuspule e) that shows little or no separation from the base of the paraconid. A more prominent vertical mesiolingual crest descending from near the apex of the

paraconid, which is present in members of the clade of *Kokopelia* + crown marsupials but absent in deltatheroidans (Cifelli and Muizon, 1997; Luo et al., 2002), is absent on the m3 of DMNH 55343. Between the mesiolingual cuspule and a less prominent mesiobuccal cuspule (cuspule f), there is a well-developed groove that extends vertically to the base of the crown. This interlocking mechanism received the distal aspect of the preceding tooth, as evidenced by attritional wear along the groove and the partially preserved relationship of the m3 and m4. This mesial groove is consistent with morphology recognized by Fox et al. (2007) for the fragmentary m3 of the holotype (their m2; see fig. 3A). Distal to the mesiobuccal cuspule and mesial to the base of the protoconid is a shallow but defined depression (Fig. 2C, D). Its dorsal margin is broken but its rounded ventral margin flares laterally. We infer that during the final phase of occlusion, after the metacone sheared past the paracristid, its distal aspect was in part received in this depression. In lateral view (Fig. 2C–F), the interalveolar bony wall that separates the roots of m3 is mesial to the metaconid and at the level of the protoconid. It projects dorsally above the level of the alveolar rims and at the height of the mesial and distal bases of the crown. The distal aspect of the trigonid is steeply sloped and nearly vertical. It preserves a prominent distal metacristid that descends from the apex of the metaconid in a ventrobuccal direction (Fig. 2A, B). Buccal to the distal metacristid, a shallow concavity that is more evident low on the trigonid presumably reflects occlusion with the paracone of the opposing upper molar, though no wear facet is evident. Lingual to the distal metacristid, the distal face of the trigonid is flat. At the level of the talonid, the steep path of the distal metacristid sharply meets the slightly shallower slope of the cristid obliqua. In lateral view, the junction of these cristids is V-shaped and indicates a shearing function (Fig. 2C–F). The trenchant cristid obliqua divides the talonid into a small steeply sloped buccal side and a broader more shallowly sloped lingual side. The cristid obliqua extends distally and slightly buccally to a prominent, rounded talonid cusp that we interpret as the hypoconid. Its beveled surface indicates slight attritional wear. The cristid continues distolingually from the hypoconid to the distal-most part of the talonid and a faint swelling that we interpret as the hypoconulid. Between the hypoconid and hypoconulid, the cristid shows slight wear. From the hypoconulid, a postcristid fades as it descends mesiolingually. If an entoconid was present, it was small and has since been obliterated by wear. Within the small fishhook-shaped ring formed by the cusps and cristids is a very shallow linguoventrally sloped depression that shows minor wear; a small protocone presumably occluded into this lingually open talonid basin. The narrow distal base of the talonid fits in the vertical groove along the mesial base of m4, and as a result of this interlocking, m3 significantly overlaps m4. A postcingulid, a feature found within the clade of *Kokopelia* + crown marsupials but not in deltatheroidans (Cifelli, 1993; Luo et al., 2002), is not evident on the m3 of DMNH 55343.

The m4 suffered postmortem damage that removed most of the mesial half of the crown (Fig. 2); small portions of the mesial and buccal bases of the trigonid and a thin bridge to the well-preserved distal half of the crown remain. Important morphological details on the mesial half of the crown confirm observations from the m3. In general, the m4 is similar in form to the m3; for example, based on its outline, the trigonid was somewhat wider than the talonid and notably longer. The most obvious difference between the two crowns is that m4 is considerably smaller than m3. Also, m3 has a slightly oblique overall orientation, aligned along a mesiolingual-distobuccal axis, whereas m4 appears to be aligned along a slight mesiobuccal-distolingual axis.

On the mesial aspect of the m4 crown, there is evidence of two basal cuspules that are separated by a vertical groove that receives the m3 talonid. The groove is not as pronounced as in m3, but it is also not as well exposed (Fig. 2A, B). The apex of

TABLE 1. Dental measurements of specimens referred to *Nanocuris improvida* and ?*Nanocuris* sp.

	L	ML	DL	MW	DW
Nanocuris improvida					
UCMP 46359					
m1	4.07	2.35	1.72	1.99	1.42
AMNH 59482					
m1	—	2.42	—	1.93	—
UCMP 82563					
m2 or m3	—	2.68	—	2.00	—
DMNH 55343					
m3	4.60	2.88	1.72	1.91	1.23
m4	∼ 3.36	∼ 2.35	1.01	∼ 1.15	0.83
RSM P2523.260					
m4	3.2	—	—	—	—
UA 4085b					
M2	3.95	—	—	4.30	4.60
?*Nanocuris* sp.					
AMNH 59451					
?M1	3.52	—	—	2.83	3.71

Measurements for RSM P2523.260 and UA 4085b were taken from Fox et al. (2007) and Lillegraven (1969), respectively. All other specimens were measured according to methods described in the text. **Abbreviations**: **L** = length; **ML** = mesial length; **DL** = distal length; **MW** = mesial width; **DW** = distal width. All measurements are in millimeters.

the mesiolingual cuspule is not preserved, only its base is. On the holotype, this cuspule corresponds to what Fox et al. (2007) recognized as the lingual wall of the groove just mesial to the paraconid. The m4 of DMNH 55343 does not preserve the paraconid. Distal to the mesiobuccal cuspule on the buccal aspect of the trigonid base is the ventral part of a small rounded depression that has a low rim (Fig. 2C, D). It corresponds to the similar but larger depression on the buccal base of the m3 trigonid. A thin bridge of dentine extends distally from the buccal side of the mesial half of the crown across the interalveolar bony wall to the distal half of the crown. The distal half of the crown is low, laterally compressed, and forms a finger-like projection, resembling the more worn m4 of the holotype. A small, blunted surface is evident mesiolingually on the distal fragment of the crown (Fig. 2A, B); mesial to it is a broken enamel band that in occlusal view jogs sharply in the buccal direction before it turns lingually and is truncated by breakage. We interpret the blunted surface as the metaconid or the distal aspect of the metaconid; the distinct path of the enamel band is reminiscent of that just mesial to the metaconid and distal to the paraconid of m3. The positioning of the metaconid also corresponds to the swelling that Fox et al. (2007) recognized as the metaconid on the m4 of the holotype. This interpretation would lend support to Fox et al.'s (2007) strongly obtuse angle (∼180°) for the m4 trigonid, and would contrast with a more acute angle for the m3 trigonid. Distal to the metaconid is the distal metacristid that descends distally and slightly buccally and shows evidence of minor wear along its buccal surface. Buccal to the distal metacristid is a distinct depression, as in m3, that presumably occluded with the paracone of M4 (Fig. 2C, D). Most of the mesial margin of this depression is broken, but at the mesiobuccal base a slight lateral expansion of the crown is preserved that corresponds to the base of the protoconid. At the level of the talonid, the distal metacristid connects to the cristid obliqua; it is not as trenchant as in m3 and extends in a distal rather than distobuccal direction (Fig. 2A, B). An ovate dentine exposure and slight swelling distally along the dorsal surface of the cristid is interpreted as the hypoconid. Fox et al. (2007) considered the corresponding cusp on the holotype as the hypoconulid, but it more likely corresponds to the dominant talonid cusp of the m3, which is mesiobuccal to a faint cusp we interpret as the hypoconulid. This interpretation of cusp ho-

mologies on the reduced m4 talonid follows from Butler (1990), Martin (2002), and Lopatin and Averianov (2006) that consider the single cusp buccal to the incipient talonid basin in more basal taxa homologous with the hypoconid. A talonid basin is not present and no other cusps or wear facets are evident on the m4 of DMNH 55343. As shown in lateral view (Fig. 2C–F), the talonid extends distally beyond the distal root.

DMNH 55343 is confidently assigned to *Nanocuris improvida*, previously known only from the Frenchman Formation of Saskatchewan. Our specimen is similar in size to the holotype (Table 1: m4 of RSM P2523.260) and possesses many of its distinctive dental and mandibular features (Fox et al., 2007), such as a reduced m4, a simple m4 talonid, laterally compressed molars, and a sharply defined masseteric fossa. The presence of other notable features of RSM P2523.260, like a neurovascular canal and robust canine, cannot be determined in the Lance specimen due to its fragmentary nature. Several other distinctive morphological features of DMNH 55343 that are not discernible or preserved in the holotype (e.g., m3 with a distal metacristid and at least two talonid cusps) enable us to refer five previously described Lancian specimens to *Nanocuris improvida* and ?*Nanocuris* sp.

Additional Referred Specimens—UCMP 46359, left m1; AMNH 59482, mesial fragment of left m1; and UCMP 82563, mesial fragment of right m2 or m3, all from the type area of the Lance Formation, east-central Wyoming (Lancian); UA 4085b, right M1 or M2, from the Scollard Formation, Alberta (Lancian).

Comments—The Lance Formation specimens (UCMP 46359, AMNH 59482, UCMP 82563) were first described and illustrated by Clemens (1973:figs. 26–27). He suggested that they were likely all from the same species, which had resemblances to borhyaenids and miacids. The Scollard Formation specimen (UA 4085b) was first described and illustrated by Lillegraven (1969:fig. 35–1). He tentatively identified it and a potentially associated tooth in a maxillary fragment (UA 4085a) as deciduous premolars (P4 and P3, respectively) of *Cimolestes magnus*. His identifications were based on their large size, carnivorous adaptations, and their lack of resemblances to known permanent molar morphologies. Fox (1974) later suggested that all of these specimens (except UCMP 82563 and UA 4085a, both of which he did not consider) and UA 4248 (see ?*Nanocuris* sp.) were attributable to a single species or closely related species within Deltatheridiidae, though some have considered this referral uncertain (e.g., Kielan-Jaworowska et al., 1979; Rougier et al., 2004). The following descriptions are based on direct examination of the lower molar specimens and descriptions and illustrations of UA 4085b from the literature.

Description—UCMP 46359 is the most complete of the lower molars, although, as noted by Clemens (1973), some enamel is missing from the coronal surface and cusp apices are slightly worn (Fig. 3A–D). The size and arrangement of the trigonid cusps are generally as inferred from the m3 of DMNH 55343, except that the cusps form a slightly less acute angle of ∼75° and the protoconid is in a more mesial position relative to the metaconid. The paraconid is, as expected for deltatheroidans, considerably larger than the spur-like metaconid. The bases of the paraconid and metaconid do not make contact, and, as a result, the lingual side of the trigonid is open (Fig. 3D). The paracristid has a strong carnassial notch (Fig. 3C). Below the paraconid, cuspule e is represented as a laterally compressed ridge extending down to the base of the crown. Cuspule f is low and more cuspate. Slight wear is evident in the shallow groove between these cuspules. Distal to cuspule f is a slight depression (Fig. 3C), but less pronounced than that on the m3 of DMNH 55343. The protocristid is poorly defined and receives little contribution from the metaconid. The distal metacristid, though largely worn away, is still discernible (Fig. 3B) and resembles that in the m3 of DMNH 55343. Whereas the trigonid is considerably taller than the talonid, the difference is less than that estimated for the m3 of DMNH 55343. The
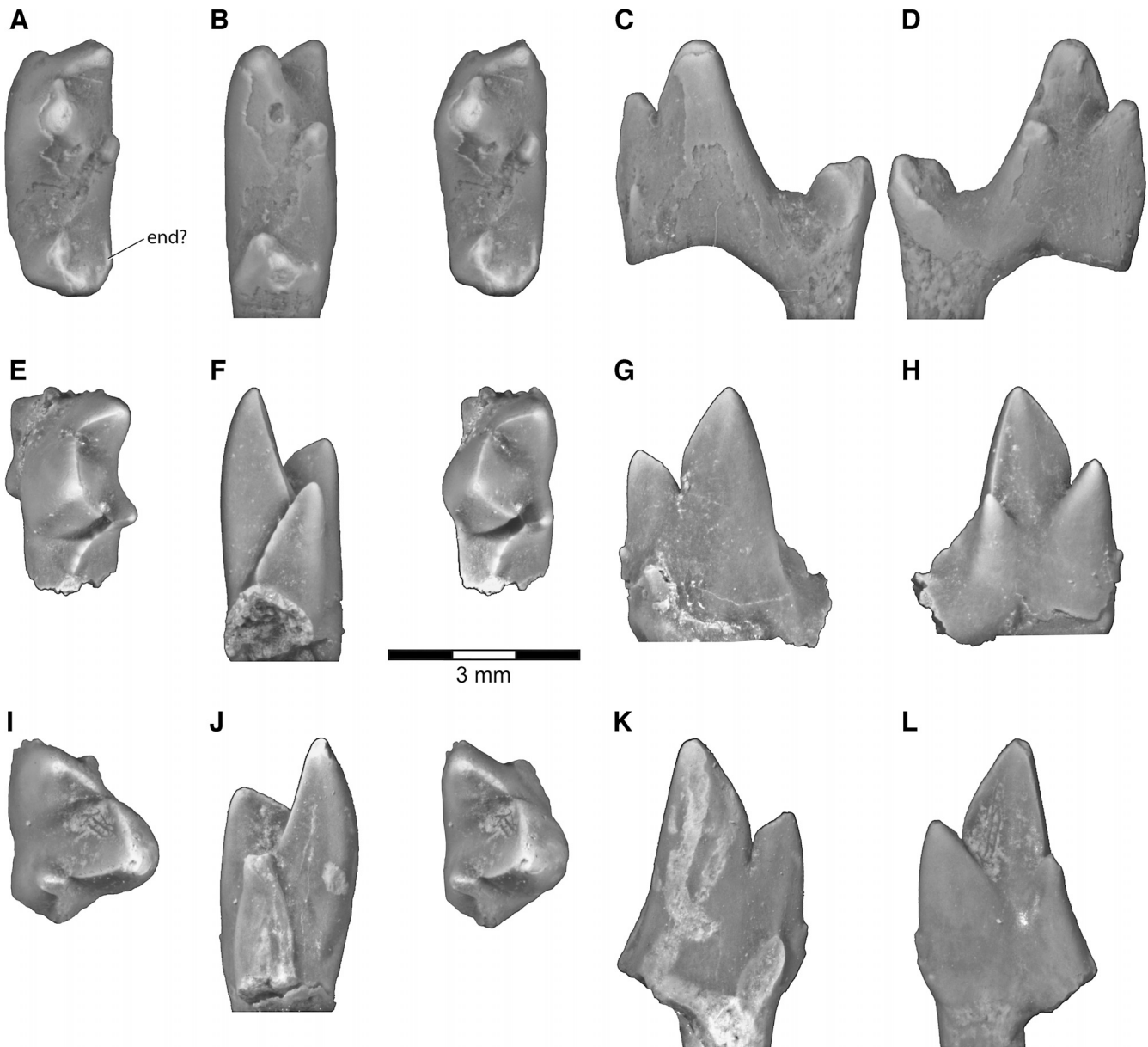
FIGURE 3. Digital images of additional specimens referred to *Nanocuris improvida*. UCMP 46359, a left m1, **A**, in stereo occlusal view, **B**, in distal view, **C**, in buccal view, and, **D**, in lingual view. AMNH 59482, mesial fragment of a left m1, **E**, in stereo occlusal view, **F**, in distal view, **G**, in buccal view, and, **H**, in lingual view. UCMP 82563, mesial fragment of a right m2 or m3, **I**, in stereo occlusal view, **J**, in distal view, **K**, in buccal view, and, **L**, in lingual view. **Abbreviation**: **end**, entoconid. Scale bar equals 3 mm.

structure of the talonid is similar to that on the m3 of DMNH 55343, but is slightly broader and has a barely discernible swelling along the postcristid that may be an entoconid or an artifact of breakage (Table 1, Fig. 3A). These slight differences and slightly smaller size of the crown relative to the m3 of DMNH 55343 imply that UCMP 46359 is likely from a more anterior position in the molar row, tentatively m1.

AMNH 59482 is a mesial fragment of a left lower molar that we tentatively identify as an m1 (Fig. 3E–H). There is breakage along the base of the trigonid, but the remainder of the trigonid is intact and unworn. The size and arrangement of the trigonid cusps is most similar to that in UCMP 46359, though the cusps are less worn; the angle formed by the trigonid cusps is ~74°. The mesial cuspules (e and f) are better preserved than in UCMP

46359, and a slight depression distal to cuspule f is also evident (Fig. 3G). The carnassial notch on the paracristid is deep. The distal metacristid is unworn and strongly developed, such that the distal face of the protoconid is mesial to the distal face of the metaconid (Fig. 3F). The estimated height differential between the trigonid and talonid is similar to UCMP 46359 and less than in UCMP 82563.

UCMP 82563 (Fig. 3I–L) is a lower molar trigonid fragment that more closely approximates the size and morphology of the m3 of DMNH 55343. The size differential between the paraconid and metaconid is greater than in UCMP 46359 and AMNH 59482 (Fig. 3J, L), a pattern expected for posterior molars of deltatheroidans. The trigonid cusps form an angle of ~63°, which is close to the 67° estimated for the m3 of DMNH 55343.

The carnassial notch on the paracristid is pronounced (Fig. 3K), whereas the metaconid makes no contribution to the protocristid (Fig. 3J). The distal metacristid is evident and slightly worn (Fig. 3J). The trigonid of UCMP 82563 is larger in overall size than that in UCMP 46359 (see Table 1), and though the talonid of UCMP 82563 is missing, the estimated height differential between it and the trigonid is greater than that in UCMP 46359. Differences with UCMP 46359 and similarities to the m3 of DMNH 55343 lead us to tentatively identify UCMP 82563 as an m2 or m3.

UA 4085b is a right upper molar from the Scollard Formation of Alberta (Fig. 4A–C). Whereas upper molars of *Nanocuris* are previously unknown, the specimen is consistent with the size and morphology predicted from an occlusal relationship with the isolated lower molars that Fox (1974) referred to Deltatheridi-idae and we now refer to *Nanocuris*. The crown cusps exhibit moderate apical wear, but most morphological details are discernible from the published illustrations (Lillegraven, 1969:fig. 35–1; Fox, 1974:fig. 1a). The occlusal outline of the crown forms an isosceles triangle with a long, broad stylar shelf and a mesiodistally short protoconal region. The buccal margin of the stylar shelf is bordered by a distinct ectocingulum with a shallow ectoflexus. From the illustrations, the ectocingulum appears to carry at least a few stylar cuspids or swellings, including a stylocone (contra Rougier et al., 2004). The metastylar region is buccally expanded relative to the smaller parastylar region, a feature suggestive of an anterior molar position. The MW:DW ratio is 0.93, which is similar to M2s of other deltatheroidans, for example, *Atokatheridium* and *Oklatheridium* (0.90, 0.94, respectively; Davis et al., 2008). The paracone is taller than the metacone, and these two cusps are joined at their bases for almost half of their height. Extensive wear is evident on the apex of the metacone and along the distobuccally directed postmetacrista. The wear reflects a dominant postvallum-prevallid shearing mechanism, as is found in deltatheroidans and consistent with the well-developed paracristids on the lower molars of *Nanocuris*. The protocone of UA 4085b is low, mesiodistally narrow, and mesially procumbent (Rougier et al., 2004). The apex of the protocone and the protocristae exhibit considerable wear; the patterns of wear suggest that two small conules (meta- and para-) might have been present along the pre- and postprotocrista and situated near the protocone. The postprotocrista terminates at the lingual base of the metacone, and the preprotocrista continues past the mesial base of the paracone to the parastylar region, though the wear along this crista is interrupted.

Although Lillegraven (1969) noted the possible association of UA 4085b with UA 4085a, a maxillary fragment with a tooth that he tentatively identified as a DP3 of *Cimolestes magnus*, we presently refrain from referring UA 4085a to *Nanocuris improvida* because details of its coronal morphology and its association with UA 4085b are uncertain.

Morphological Reinterpretation of the Holotype—We note two differences from Fox et al. (2007) in our morphological interpretations of the type specimen and thus, *Nanocuris*. The first difference bears critically on the cheek tooth formula and by consequence, the higher-level taxonomic affinities of *Nanocuris*. They identify the first tooth on the posterior mandibular fragment of RSM P2523.260 as a p4. Only the talonid of this tooth is known, and limited by its poor preservation, Fox et al. (2007:825) estimated that the talonid was "originally robustly developed." Our examination of their figure 3 concurs with this assessment. Rather, we point out that although Cretaceous eutherians possess submolariform to molariform p4s with multiple trigonid cusps, few have robustly developed talonids; *Gypsonictops* is an exception (Kielan-Jaworowska et al., 2004). An equally parsimonious interpretation is that this tooth represents an m1. Fox et al. (2007) rejected this hypothesis because it would mean that *Nanocuris* would be a marsupial and that m2 would then be the largest lower molar in its tooth row, a condition found in only one

other Cretaceous marsupial, *Glasbius intricatus*. However, other Cretaceous boreosphenidans that also possess four molars (e.g., deltatheroidans, *Kielantherium*; Kielan-Jaworowska et al., 2004) exhibit alternative molar size trends (see below). Moreover, new evidence for a distal metacristid on the lower molars of *Nanocuris* indirectly conflicts with their interpretation. That is, we know of no Cretaceous eutherians that retain a distal metacristid (Fox, 1975; Kielan-Jaworowska et al., 2004); yet, this feature regularly occurs in stem boreosphenidans and deltatheroidans, both of which are known to have four molars.

A second related difference in our interpretation of the holotype centers on the molar size trend along the tooth row. Fox et al. (2007) stated that the mesiodistal length of m2 (their m1) is greater than that of m3 (their m2), and that of m3 is much greater than that of m4. Thus, they indicate that there is a trend of decreasing size along the molar row. Our measurements from their figures 2 and 3 do not support this assertion; instead, the two molars, both of which no longer have fully preserved crowns and are consequently difficult to accurately measure, are more conservatively interpreted as subequal in length. We interpret a pattern of increasing rather than decreasing molar size along the tooth row. Support for this interpretation comes from UCMP 46359. This lower molar is significantly smaller than both the m3 of DMNH 55343 and the estimated size of m2 in the holotype; it is too large and its talonid too well developed to be an m4; and the possibility that it represents a second slightly smaller species of *Nanocuris* in the Lance Formation is considered unlikely. Based on this rationale and some characteristic morphological differences along the tooth row (e.g., paraconid lower in height), we identified UCMP 46359 as an m1. On these grounds, we interpret *Nanocuris* as having four molars that increase in size from m1 to m2 and m3 followed by a strongly reduced m4.

<div align="center">

?*NANOCURIS* Fox, Scott, and Bryant, 2007
?*NANOCURIS* sp.
(Fig. 4D–H)

</div>

Referred Specimens—AMNH 59451, right M1, from the type area of the Lance Formation, east-central Wyoming (Lancian).

Comments—AMNH 59451, from the Lance Formation, was first described by Clemens (1973:fig. 26a, b). In his comments, he considered that this distinctive upper molariform might be a molar referable to miacids, creodonts, or borhyaenids or alternatively, a deciduous P3 of a cimolestid. Additionally, he suggested that AMNH 59451 might belong to the same species as UCMP 46359, which we have referred to *Nanocuris improvida*. The following description is based on direct examination of AMNH 59451 and descriptions and illustrations in Clemens (1973:fig. 26a, b). We also note that UA 4248, a lower molar talonid fragment from the Dinosaur Park Formation (Oldman Formation of previous usage) of Alberta (Judithian), was included among the North American specimens that Fox (1974) assigned to Deltatheridi-idae. He suggested that these specimens were probably referable to a single species or closely related species. Of those specimens that we have examined, all are confidently assigned to *Nanocuris improvida* (see above); however, because we have not directly examined UA 4248 or illustrations of the specimen, we presently refrain from referring this specimen to *Nanocuris* and extending the temporal range of this taxon into the Judithian.

Description—AMNH 59451 is a well-preserved right molariform tooth that shows some attritional wear on the major cusp apices and cristae. There is also slight breakage mesial to the base of the paracone (Fig. 4E). The occlusal outline of the specimen approaches the shape of an equilateral triangle with a long stylar shelf, a short protoconal length, and a narrow crown width (Fig. 4D). The width of the stylar shelf is highly asymmetrical with a broad metastylar region and a very reduced parastylar region. The MW:DW ratio (0.76) is slightly less than that found in M1s of other deltatheroidans, for example, *Atokatheridium*
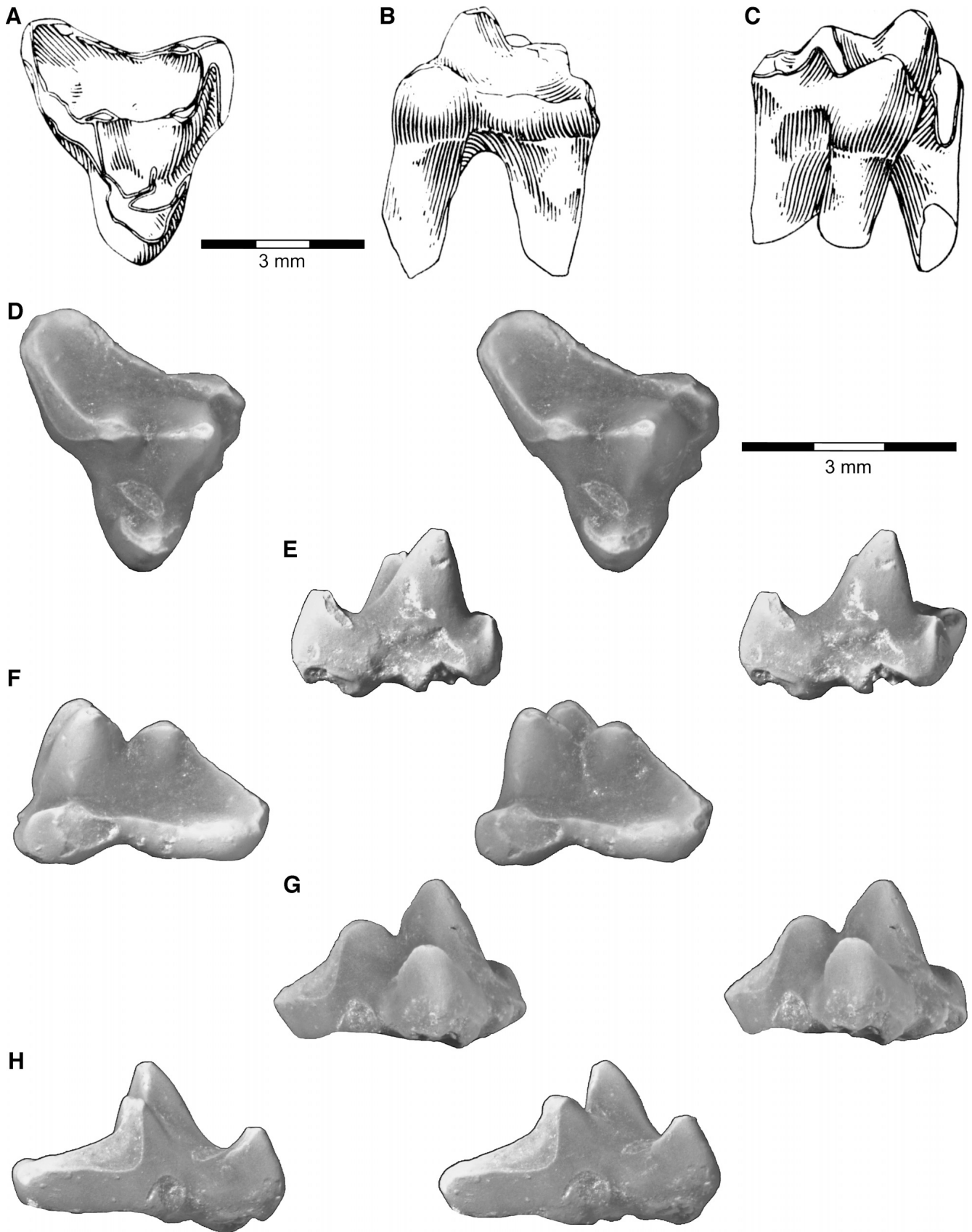
FIGURE 4. Line drawings of UA 4085b, a right M2, referred to *Nanocuris improvida*, **A**, in occlusal view, **B**, in buccal view, and, **C**, in lingual view. Reproduced from *The University of Kansas Paleontological Contributions* courtesy of and ©1969, The University of Kansas, Paleontological Institute. Scale bar equals approximately 3 mm. Digital images of AMNH 59451, a right ?M1, referred to ?*Nanocuris* sp., **D**, in stereo occlusal view, **E**, in stereo mesial view, **F**, in stereo buccal view, **G**, in stereo lingual view, and, **H**, in stereo distal view. Scale bar equals 3 mm.

and *Oklatheridium* (0.85, 0.81, respectively; Davis et al., 2008). The ectocingulum that borders the stylar shelf forms a rim similar to that in UA 4085b with small swellings and a distinct stylocone. The paracone is distinctly taller than the metacone, and both cusps are joined at their bases for almost half of their height. The apex of the paracone and the sharp centrocristae show some wear, whereas the apex of the metacone and the postmetacrista show considerable wear. The mesiobuccal aspect of the paracone is rounded and only shows development of a preparacrista near its base at the level of the stylocone. The preparastylar region is rounded and buccally bordered by a tall rim that has a swelling at its mesial edge that may be a slight parastyle. Although there is damage to the mesial base of the paracone that obscures the morphology in this area, it does not appear that there was a paracingulum (Fig. 4E). The protocone is small and narrow and shows significant apical wear that extends to the protocristae (Fig. 4D, G). Both protocristae terminate well before the lingual bases of the buccal cusps. Conules are not present. In overall form, the upper molar is primitive in a number of features (e.g., protocone morphology, lack of conules) and is reminiscent of a deciduous premolar; however, we are not aware of deciduous premolars that exhibit the same degree of attritional wear, particularly on the postmetacrista. Thus, we contend that AMNH 59451 is a permanent molar, and the degree of development of the postmetacrista indicates that it may be referable to a deltatheroidan. In size, the molar is smaller than UA 4085b of *Nanocuris improvida*, but it may be an acceptable size difference for an M1 versus an M2. As a conservative measure, we refrain from referring this specimen to *Nanocuris improvida*, until larger sample sizes are available.

DISCUSSION

Fox et al. (2007) brought to light an important but incomplete specimen (RSM P2523.260) with morphological features unknown among North American Mesozoic mammals. Their erection of a new taxon, *Nanocuris*, for this specimen and assignment of this taxon to a new family within Eutheria was a well-reasoned interpretation of the previous data. In their considerations of the phylogenetic affinities of *Nanocuris*, Fox et al. (2007) came to two key conclusions that now serve as working hypotheses. First, struck by the simple talonid morphology of the m4 (their m3) of *Nanocuris* relative to other latest Cretaceous mammals, the authors considered the possibility that the new taxon was a non- or pre-tribosphenic mammal (e.g., eutriconodontan, 'eupantothere'). They went on to discount this possibility on the basis of two primary concerns: (1) the length of the talonid relative to the rest of the m4 crown is longer than that found in the molars of pre-tribosphenic mammals; and (2) the temporal range extension implied by such an identification is much greater than expected (the youngest definitive record of a pre-tribosphenic mammal is from the Early Cretaceous; Kielan-Jaworowska et al., 2004; Lopatin and Averianov, 2006). They concluded that *Nanocuris* is more likely a therian mammal that had secondarily lost its talonid basin through substantial modification of the tribosphenic molar pattern. Second, on the basis of a hypothesized cheek tooth formula of four premolars and three molars and a pattern of decreasing molar size for *Nanocuris*, they argued that, among therians, it more likely belonged among eutherians than metatherians and that resemblances to mesonychians were convergent. The addition of DMNH 55343 and four other specimens to *Nanocuris improvida* provides new morphological data with which to re-evaluate these hypotheses and formulate new ones. Specifically, three of the specimens now referred to *Nanocuris* were previously assigned to the Deltatheridiidae by Fox (1974). The other specimens, including the holotype, also possess morphological features characteristic of deltatheroidans, such as a reduced last molar, an enlarged paraconid, a reduced metaconid, a well-developed paracristid, a narrow talonid, a distal metacristid,

and a large height differential between the talonid and trigonid (Luo et al., 2002; Kielan-Jaworowska et al., 2004; Rougier et al., 2004).

Phylogenetic Analysis

Methods—To test the above hypotheses, we performed a phylogenetic analysis using the restricted data matrix of Rougier et al. (2004) that includes 42 taxa and 156 craniodental characters. Two taxa were added to the matrix, *Atokatheridium* from the Aptian-Albian of Oklahoma that was included in Rougier et al.'s (2004) expanded analysis and *Nanocuris*, for a total of 44 taxa. Appendix 1 provides the morphological character descriptions and scores for *Nanocuris* that were compiled by direct study of specimens available to us and by inspection of figures and descriptions in the literature (Lillegraven, 1969; Clemens, 1973; Fox, 1974; Rougier et al., 2004; Fox et al., 2007). Character 54 ('Entoconid') was treated as absent for *Nanocuris* in light of the lack of an entoconid on DMNH 55343 and a barely discernible swelling that may be an entoconid on UCMP 46359. Character scoring for other included taxa can be found in Rougier et al. (2004:appendices 1 and 2).

We performed a heuristic search in PAUP* 4.0b10 (Phylogenetic Analysis Using Parsimony; Swofford, 2002) with tree bisection-reconnection branch swapping and 1000 random addition sequence replicates. Settings for the analysis were as in Rougier et al. (2004). We defined *Amphitherium* as the outgroup and designated 12 multiple state characters as ordered (1, 4, 7, 12, 14, 35, 36, 47, 50, 51, 52, 116); the remaining characters were unordered. Taxa scored as having multiple states for a character were treated as polymorphic for that character. The analysis generated 263 most parsimonious trees with a tree length of 586 steps, a consistency index of 0.449, and a retention index of 0.672. Figure 5 shows the strict consensus of those shortest trees. A manual decay analysis was performed and the results are shown above each node. An analysis was also run with all characters unordered, but it did not affect the topology of Deltatheroida or its position within Boreosphenida.

Results—The results of the analysis are as in Rougier et al. (2004), with a few exceptions: (1) the basal branches of our consensus tree are more resolved than in Rougier et al. (2004); (2) *Pappotherium* is in a more basal position relative to *Slaughteria* (but see Kobayashi et al., 2002, regarding possible synonymy); (3) there is a basal metatherian dichotomy between Deltatheroida and (*Holoclemensia* + all other metatherians), instead of a trichotomy; and (4) although the basal split between *Sulestes* and the remaining deltatheroidans was recovered again, a trichotomy exists among *Deltatheridium*, *Deltatheroides*, and (*Atokatheridium* + *Nanocuris*). Most relevant to this study, *Nanocuris* is strongly nested within Deltatheroida rather than Eutheria, and, intriguingly, it is sister taxon to *Atokatheridium*, the only other North American deltatheroidan included in the analysis, though the decay analysis does not provide strong support for this clade.

Systematic and Paleobiogeographic Implications

The results of our phylogenetic analysis provide strong support for the removal of *Nanocuris* from Eutheria and its placement within Deltatheroida among metatherians. The original referral of *Nanocuris* to Eutheria and comparisons with miacids, creodonts, and mesonychians only to eventually be re-assigned a position within basal Metatheria bears a conspicuous parallel to the systematic history of its parent clade, Deltatheroida (Kielan-Jaworowska et al., 2004; Davis et al., 2008). Within the Deltatheroida, the trichotomous relationship of *Deltatheridium*, *Deltatheroides*, and *Atokatheridium* + *Nanocuris* lead us to place *Nanocuris* with *Atokatheridium* in the family Deltatheridiidae. We also subsume Nanocuridae within Deltatheridiidae pending
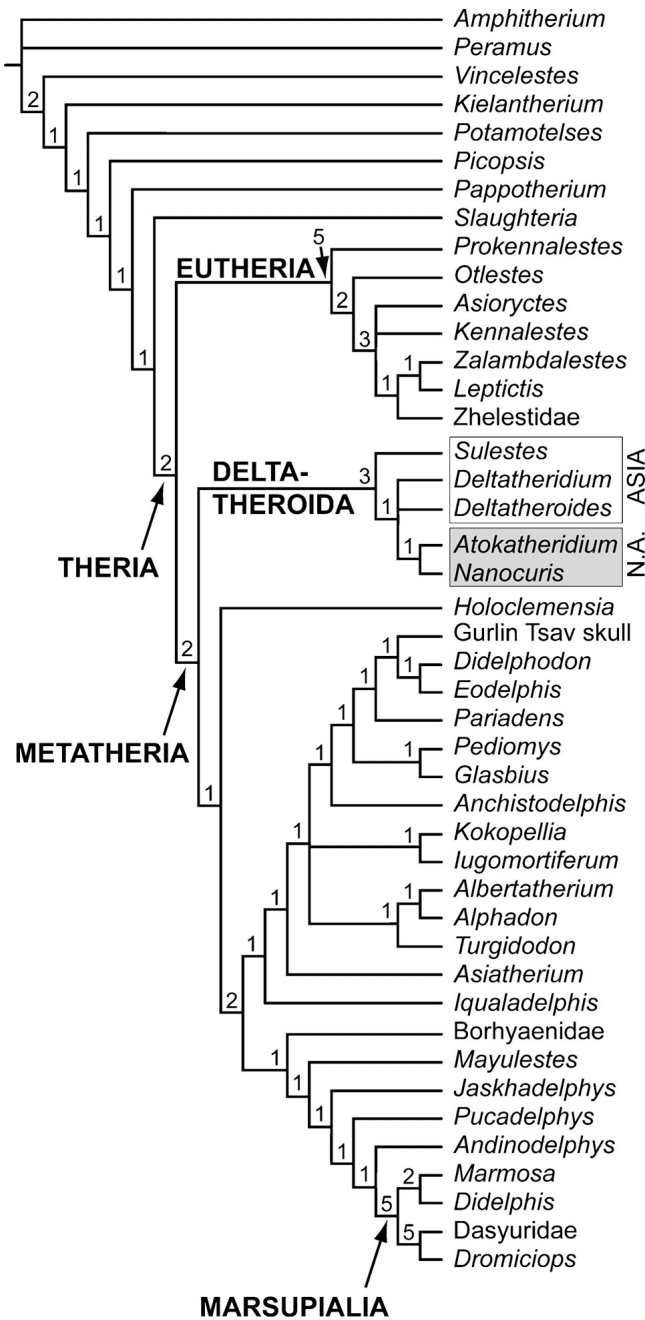
FIGURE 5. The strict consensus tree of the 263 most parsimonious trees generated from the phylogenetic analysis in this paper. The length of each individual tree is 586 steps, the consistency index is 0.449, and the retention index is 0.672. Decay indices are shown above each node.

better resolution and support for the phylogenetic relationships of the clade.

Within the family Deltatheridiidae, the two North American taxa, *Nanocuris* and *Atokatheridium*, form a clade to the exclusion of their Asian counterparts, *Deltatheridium* and *Deltatheroides*. This phylogenetic relationship, though lacking strong support, spurs consideration of its paleobiogeographic implications. Due to the history of discovery in Mongolia and the nature of its fossil record, Deltatheroida has traditionally been thought to originate in Asia (Kielan-Jaworowska and Nessov, 1990; Cifelli, 2000). Yet, the trickle of deltatheroidan fossils from

North America over the past 35 years has begun to cast doubt on this paleobiogeographic scenario (e.g., Kielan-Jaworowska and Cifelli, 2001; Davis et al., 2008). Now that *Atokatheridium* and *Oklatheridium* from the Aptian-Albian of Oklahoma have been confidently referred to Deltatheroida, they replace *Sulestes* and *Deltatherus* from the Coniacian of Uzbekistan as the stratigraphically oldest deltatheroidans and garner support for a North American origin of the clade (Davis et al., 2008).

Although the temporal disparity is compelling, our analysis supports a phylogenetic split between the North American deltatheridiids and the Asian deltatheridiids (Fig. 5) that implies ghost lineages for the Asian deltatheridiids that date back to the Aptian-Albian (i.e., the age of *Atokatheridium*). Likewise, the more basal split between *Sulestes* and Deltatheridiidae implies the same for *Sulestes*. Mapping geographic areas onto the tree topology demonstrates that Asia is the primitive state for the clade. Thus, presently the most parsimonious hypothesis to explain the pattern is that Deltatheroida originated in Asia followed by a single dispersal event to North America by the Aptian-Albian. This would imply that deltatheroidans were continuously present in North America from the Aptian-Albian until their extinction at the end Maastrichtian. Presently, occurrences and tentative occurrences of deltatheroidans are only known from the Aptian-Albian, Turonian, early Campanian (Judithian), and late Maastrichtian (Lancian). However, we contend that the poor temporal sampling of deltatheroidans may be explained by their true rarity in North American Cretaceous mammalian faunas. This point is illustrated by the University of California Museum of Paleontology's collection of mammals from the type Lance Formation. With over 4400 specimens and more than 3500 identified to genus, only 2 have been referred to *Nanocuris improvida*—a relative abundance of less than 0.1%. In this context, a spotty temporal record of deltatheroidans in North America is not surprising. However, with modest support for the phylogenetic relationships within Deltatheroida, we consider this paleobiogeographic hypothesis provisional and expect that new fossil data of both *Atokatheridium* and *Oklatheridium* (Davis et al., 2008) that became available to us after our analysis may help resolve some uncertainties.

CONCLUSIONS

The incomplete dentulous jaw collected by Lindsey and Stucky in the 1970s and described in this paper (DMNH 55343) provides a key combination of features that allowed us to place *Nanocuris* among the known Mesozoic mammal diversity by parsimony of all phylogenetically informative characters. On the one hand, the resemblances of the partial m4 of DMNH 55343 to the more complete but poorly preserved m4 of the type specimen were unmistakable. On the other hand, the damaged m3 of DMNH 55343 preserved enough distinctive features (distal metacristid, talonid morphology, trigonid outline) to spark comparisons with the enigmatic deltatheroidans and, specifically, the specimens from the same and coeval deposits in North America that Fox (1974) had referred to the Deltatheridiidae. Detailed inspection of these and other Lancian specimens led to their referral to *Nanocuris* and to a phylogenetic analysis that confirmed Fox's earlier assessment of these specimens, and now *Nanocuris*, as members of the family Deltatheridiidae within the metatherian clade Deltatheroida. These data add significantly to a sparse North American fossil record of the Deltatheroida, composed mostly of isolated teeth; they confirm the survival of the clade up to the Cretaceous-Tertiary extinction event; and they point to a trend of increasing size in the clade through the Cretaceous. As the most complete deltatheroidan from North America, *Nanocuris* also provides better resolution of the phylogenetic relationships within the Deltatheridiidae and support for a paleobiogeographic hypothesis that postulates an Asian origin

of the clade and a single dispersal to North America by the late Early Cretaceous.

Moreover, the re-discovery of DMNH 55343 offers a salient reminder of how much is left to learn about North America's latest Cretaceous mammalian diversity, even from its most intensively sampled and most thoroughly monographed mammalian fauna, that of the Lance Formation, Wyoming (e.g., Marsh, 1889a, 1889bb; Osborn, 1893; Hatcher, 1896; Simpson, 1929; Clemens, 1964, 1966, 1973; Whitmore, 1985; Whitmore and Martin, 1986). We suspect that additional fossils of *Nanocuris* and other rare taxa lurk in museum collections of other Lancian and possibly Judithian faunas but have thus far been overlooked or misidentified as the 'usual suspects'. Uncovering records of these rare fossil taxa in museum collections or through continued field work will not only significantly improve estimates of mammalian diversity (most species in a community are of low relative abundance; Magurran, 1988), but may also contribute important insights on several paleoecological fronts: (1) the rarity of a taxon or its low population density in a fauna may reflect information about the extremes of its physiological and ecological tolerances (Gaston, 1994); (2) low fossil abundance of a taxon may be due to a historical failure to sample particular paleoenvironments (McKinney, 1996), and thus rare taxa may add to our understanding of landscape heterogeneity; (3) rare taxa may provide key data affecting phylogenetic and paleobiogeographical relationships within or among clades, as demonstrated above; and (4) because ecological specialists tend to have low population numbers in modern communities (Brown, 1995), discovery of rare fossil taxa may disproportionally increase our knowledge of the ecological diversity of a fauna. This last point is epitomized by the discovery of *Nanocuris*. Large by Mesozoic mammal standards and possessing dental traits clearly indicative of a carnivorous lifestyle, *Nanocuris* combines with taxa like *Didelphodon vorax*, a contemporary metatherian and possible semi-aquatic durophage, to underscore recent observation that Mesozoic mammals evolved greater ecological diversity than generally appreciated (Luo, 2007).

LITERATURE CITED

Averianov, A. 1997. New Late Cretaceous mammals of southern Kazakhstan. Acta Palaeontologica Polonica 46:243–256.
Brown, J. H. 1995. Macroecology. University of Chicago, Chicago, Illinois, 270 pp.
Butler, P. M. 1990. Early trends in the evolution of tribosphenic molars. Biological Reviews 65:529–552.
Butler, P. M., and Z. Kielan-Jaworowska. 1973. Is *Deltatheridium* a marsupial? Nature 245:105–106.
Cifelli, R. L. 1990. Cretaceous mammals of southern Utah. III. Therian mammals from the Turonian (early Late Cretaceous). Journal of Vertebrate Paleontology 10:332–345.
Cifelli, R. L. 1993a. Early Cretaceous mammal from North America and the evolution of marsupial dental characters. Proceedings of the National Academy of Sciences of the United States of America 90:9413–9416.
Cifelli, R. L. 1993b. Theria of metatherian-eutherian grade and the origin of marsupials; pp. 205–215 in F. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials. Springer-Verlag, New York.
Cifelli, R. L. 2000. Cretaceous mammals of Asia and North America. Paleontological Society of Korea Special Publication 4:49–84.
Cifelli, R. L., and C. de Muizon. 1997. Dentition and jaw of *Kokopellia juddi*, a primitive marsupial or near marsupial from the medial Cretaceous of Utah. Journal of Mammalian Evolution 4:241–258.
Clemens, W. A. 1964. Fossil mammals of the type Lance Formation, Wyoming: Part I. Introduction and Multituberculata. University of California Publications in Geological Sciences 48:1–105.
Clemens, W. A. 1966. Fossil mammals of the type Lance Formation, Wyoming: Part II. Marsupialia. University of California Publications in Geological Sciences 62:1–122.
Clemens, W. A. 1973. Fossil mammals of the type Lance Formation, Wyoming: Part III. Eutheria and summary. University of California Publications in Geological Sciences 94:1–102.
Davis, B. M., R. L. Cifelli, and Z. Kielan-Jaworowska. 2008. Earliest evidence of Deltatheroida (Mammalia: Metatheria) from the Early Cretaceous of North America; pp. 3–24 in E. J. Sargis and M. Dagosto (eds.), Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer, Dordrecht.
Fox, R. C. 1974. *Deltatheroides*-like mammals from the Upper Cretaceous of North America. Nature 249:392.
Fox, R. C. 1975. Molar structure and function in the Early Cretaceous mammal *Pappotherium*: Evolutionary implications for Mesozoic Theria. Canadian Journal of Earth Sciences 12:412–442.
Fox, R. C., and B. G. Naylor. 2006. Stagodontid marsupials from the Late Cretaceous of Canada and their systematic and functional implications. Acta Palaeontologica Polonica 51:13–36.
Fox, R. C., C. S. Scott, and H. N. Bryant. 2007. A new, unusual therian mammal from the Upper Cretaceous of Saskatchewan, Canada. Cretaceous Research 28:821–829.
Gaston, K. J. 1994. Rarity. Chapman and Hall, London, 205 pp.
Gregory, W. K., and G. G. Simpson. 1926. Cretaceous mammal skulls from Mongolia. American Museum Novitates 225:1–20.
Hatcher, J. B. 1896. Some localities for Laramie mammals and horned dinosaurs. American Naturalist 30:112–120.
Horovitz, I. 2000. The tarsus of *Ukhaatherium nessovi* (Eutheria, Mammalia) from the Late Cretaceous of Mongolia: an appraisal of the evolution of the ankle in basal therians. Journal of Vertebrate Paleontology 20:547–560.
Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 43:649–662.
Kielan-Jaworowska, Z. 1975. Evolution of therian mammals in the Late Cretaceous of Asia. Part I. Deltatheridiidae. Acta Palaeontologica Polonica 33:103–132.
Kielan-Jaworowska, Z. 1982. Marsupial-placental dichotomy and paleogeography of Cretaceous Theria; pp. 367–383 in E. Montanaro Galitelli (ed.), Palaeontology, Essential of Historical Geology. S.T.E.M. Mucci, Modena, Italy.
Kielan-Jaworowska, Z., and R. L. Cifelli. 2001. Primitive boreosphenidan mammal (?Deltatheroida) from the Early Cretaceous of Oklahoma. Acta Palaeontologica Polonica 46:377–391.
Kielan-Jaworowska, Z., R. L. Cifelli, and Z.-X. Luo. 2004. Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. Columbia University Press, New York, 700 pp.
Kielan-Jaworowska, Z., J. G. Eaton, and T. M. Bown. 1979. Theria of metatherian-eutherian grade; pp. 182–191 in J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens (eds.), Mesozoic Mammals: The First Two-Thirds of Mammalian History. University of California Press, Berkeley, California.
Kielan-Jaworowska, Z., and L. A. Nessov. 1990. On the metatherian nature of the Deltatheroida, a sister group of the Marsupialia. Lethaia 23:1–10.
Kobayashi, Y., D. A. Winkler, and L. L. Jacobs. 2002. Origin of the tooth-replacement pattern in therian mammals: evidence from a 110 Myr old fossil. Proceedings of the Royal Society, London 269:369–373.
Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. The University of Kansas Paleontological Contributions 50:1–122.

Lillegraven, J. A., and S. L. Bieber. 1986. Repeatability of measurements of small mammalian fossils with an industrial measuring microscope. Journal of Vertebrate Paleontology 6:96–100.

Linnaeus, C. 1758. Systema naturae per regna triae naturae, secundum classis, ordines, genera, species cum characteribus, differentis, synonyms locus; Edito decima, reformata, Volume 1. Laurentii Salvi, Stockholm, 824 pp.

Lopatin, A., and A. Averianov. 2006. Revision of a pretribosphenic mammal *Arguimus* from the Early Cretaceous of Mongolia. Acta Palaeontologica Polonica 51:339–349.

Luo, Z.-X., Q. Ji, J. R. Wible, and C.-X. Yuan. 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940.

Luo, Z.-X. 2007. Transformation and diversification in early mammalian evolution. Nature 450:1011–1019.

Luo, Z.-X., R. L. Cifelli, and Z. Kielan-Jaworowska. 2001. Dual origin of tribosphenic mammals. Nature 409:53–57.

Luo, Z.-X., Z. Kielan-Jaworowska, and R. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47:1–78.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey, 179 pp.

Marsh, O. C. 1889a. Discovery of Cretaceous Mammalia. American Journal of Science 38:81–92.

Marsh, O. C. 1889b. Discovery of Cretaceous Mammalia. Part II. American Journal of Science 38:177–180.

Marshall, L. G., and Z. Kielan-Jaworowska. 1992. Relationships of the dog-like marsupials, deltatheroidans and early tribosphenic mammals. Lethaia 25:361–374.

Martin, T. 2002. New stem-line representatives of Zatheria (Mammalia) from the Late Jurassic of Portugal. Journal of Vertebrate Paleontology 22:332–348.

McKenna, M. C., J. S. Mellett, and F. Szalay. 1971. Relationships of the Cretaceous mammal *Deltatheridium*. Journal of Paleontology 45:441–442.

McKinney, M. L. 1996. The biology of fossil abundance. Revista Española de Paleontología 11:125–133.

Muizon, C. de, R. L. Cifelli, and R. Céspedes. 1997. The origin of dog-like borhyaenoid marsupials of South America. Nature 389:486–489.

Nessov, L. A. 1985. [Rare osteichthyans, terrestrial lizards and mammals from the estuaries and coastal plain zones of the Cretaceous of the Kyzylkum Desert]. Ezegodnik vsesouznogo Paleontologiceskogo Obsestva 28:199–219. [Russian]

Nessov, L. A. 1987. [Results of search and study of Cretaceous and early Paleogene mammals on the territory of SSSR]. Ezegodnik vsesouznogo Paleontologiceskogo Obsestva 30:119–218. [Russian]

Nessov, L. A. 1993. [New Mesozoic mammals of middle Asia and Kazakhstan, and comments about evolution of theriofaunas of Cretaceous coastal plains of ancient Asia]. Trudy Zoologicheskogo Instituta RAN 249:105–133. [Russian]

Osborn, H. F. 1893. Fossil mammals in the upper Cretaceous beds. I: The multituberculates. II: The trituberculates. III: Faunal relations of the Laramie mammals. Bulletin of the American Museum of Natural History 5:311–330.

Rougier, G. W., J. R. Wible, and M. J. Novacek. 1998. Implications of *Deltatheridium* for early marsupial history. Nature 396:459–463.

Rougier, G. W., J. R. Wible, and M. J. Novacek. 2004. New specimen of *Deltatheroides cretacicus* (Metaheria, Deltatheroida) from the Late Cretaceous of Mongolia. Bulletin of the Carnegie Museum of Natural History 36:245–266.

Sánchez-Villagra, M., S. Ladevèze, I. Horowitz, C. Argot, J. J. Hooker, T. E. Macrini, T. Martin, S. Moore-Fay, C. d. Muizon, T. Schmelzle, and R. J. Asher. 2007. Exceptionally preserved North American Paleogene metatherians: adaptations and discovery of a major gap in the opossum fossil record. Biology Letters 3:318–322.

Simpson, G. G. 1928. Affinities of the Mongolian Cretaceous insectivores. American Museum Novitates 330:1–11.

Simpson, G. G. 1929. American Mesozoic Mammalia. Memoirs of the Peabody Museum of Yale University 3:1–235.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Szalay, F. 1994. Evolutionary history of the Marsupials and an Analysis of Osteological Characters. Cambridge University Press, Cambridge, U.K., 481 pp.

Van Valen, L. 1966. Deltatheridia, a new order of mammals. Bulletin of the American Museum of Natural History 132:1–126.

Whitmore, J. L. 1985. Fossil mammals from two sites in the Late Cretaceous Lance Formation in northern Niobrara County, Wyoming. Dakoterra 2:353–367.

Whitmore, J. L., and J. E. Martin. 1986. Vertebrate fossils from the Greasewood Creek locality in the Late Cretaceous Lance Formation of Niobrara County, Wyoming. Proceedings of the South Dakota Academy of Sciences 65:33–50.

APPENDIX 1. List of morphological characters for placing deltatheroidan and other basal eutherians and metatherians among early mammalian clades: originally published by Rougier et al. (1998) as the online supplementary information (www.nature.com), and updated and revised by Rougier et al. (2004). In this analysis of *Nanocuris*, we included two additional taxa, *Nanocuris* and *Atokatheridium* (in the Rougier et al., 2004, expanded analysis), and we have adopted the same search parameters as Rougier et al. (1998, 2004), and the same matrix scorings for the comparative taxa (other than *Nanocuris*).

Scoring: Only those characters that can be observed on *Nanocuris* are listed here with our interpretation of the character states of *Nanocuris*. For brevity, the characters known from other boreosphenidans for phylogeny of metatherians and eutherians but are not known on the more limited materials of *Nanocuris* are scored as '?.' The full scorings of all characters (either known, or unknown) for *Nanocuris* is presented in the matrix table at the end of this list (character numbers following Rougier et al., 2004, original sequence).

4. Number of molars: more than four (0), four (1), or three (2). Ordered.
   Nanocuris = 1
5. Molar cusp form: sharp, gracile (0) or inflated, robust (1). (Cifelli, 1993)
   Nanocuris = 0
6. Size of molars increasing posteriorly: absent (0), moderate posterior increase (1), or marked posterior increase (2). [All molars considered in lower jaw, and all but the last considered in upper jaw]
   Nanocuris = 1
7. Number of postcanine tooth families: eight or more (0), seven (1), or less than seven (2). Ordered.
   Nanocuris = 1
16. Upper molar outline in occlusal view: does (0) or does not (1) approach isosceles triangle.
   Nanocuris = 1
17. Stylar shelf: uniform in width, 50% or more of total transverse width (0), uniform in width, but less than 50% of total transverse width (1), slightly reduced labial to paracone (2), strongly reduced labial to paracone (3), or strongly reduced or absent (4). [Penultimate molar considered when present]
   Nanocuris = 0
20. Stylar cusp A: distinct, but smaller than B (0), subequal to larger than B (1), or very small to indistinct (2). [Penultimate molar considered when available]
   Nanocuris = 2
21. Preparastyle: absent (0) or present (1).
   Nanocuris = 0
22. Stylar cusp B size relative to paracone: smaller but distinct (0), vestigial to absent (1), or subequal (2).
   Nanocuris = 0
23. Stylar cusp C: absent (0) or present (1).
   Nanocuris = 0

24. Stylar cusp D: absent (0), smaller or subequal to B (1), or larger than B (2).
Nanocuris = 0

25. Stylar cusp E: directly lingual to D or D position (0), distal to D (1), or small to indistinct (2).
Nanocuris = 2

26. Preparacingulum: absent (0), interrupted between stylar margin and paraconule (1), or continuous (2). [Penultimate molar considered when available]
Nanocuris = 2

27. Metacone size relative to paracone: noticeably smaller (0), slightly smaller (1), or subequal to larger (2).
Nanocuris = 1

28. Metacone position relative to paracone: labial (0), approximately at same level (1), or lingual (2).
Nanocuris = 1

29. Metacone and paracone shape: conical (0) or subtriangular, with labial face flat (1).
Nanocuris = 0

30. Metacone and paracone bases: adjoined (0) or separated (1).
Nanocuris = 0

31. Centrocrista: straight (0) or V-shaped (1).
Nanocuris = 0

32. Salient postmetacrista—weakly developed (0) or strongly developed, with paraconid enlarged and metaconid reduced on lower molars (1). (Cifelli, 1993)
Nanocuris = 1

33. Preprotocrista: does not (0) or does (1) extend labially past base of paracone (double rank prevallum/postvallid shearing). (Cifelli, 1993)
Nanocuris = 1

34. Postprotocrista: does not (0) or does (1) extend labially past base of metacone (double rank prevallum/postvallid shearing). (Cifelli, 1993)
Nanocuris = 0

35. Conules: absent (0), small, without cristae (1), or strong, labially placed, with wing-like cristae (2). Ordered. (Modified from Cifelli, 1993)
Nanocuris = A (0, 1)

36. Protocone on upper molars: lacking (0), small, without trigon basin (1), small, with distinct trigon basin (2), somewhat expanded anteroposteriorly (3), or with posterior portionexpanded (4). Ordered.
Nanocuris = 2

37. Procumbent protocone: absent (0) or present (1).
Nanocuris = 1

38. Protocone height: low (0) or tall, approaching para- and/or metacone height (1).
Nanocuris = 0

39. Protocingula: absent (0) or pre- and/or postcingulum present (1).
Nanocuris = 0

40. Lingual root position: supporting paracone (0) or supporting trigon (1).
Nanocuris = 1

44. Roots on lower canine: biradiculated (0) or uniradiculated (1).
Nanocuris = 1

45. First lower premolar: oriented in line with jaw axis (0) or oblique (1).
Nanocuris = 1

48. Trigonid configuration: open, with paraconid anteromedial (0), more acute, with paraconid more posteriorly placed (1), or anteroposteriorly compressed (2).
Nanocuris = 0

49. Lower molar talonid: small heel (0) or multicuspidated basin (1). (Cifelli, 1993)
Nanocuris = 1

50. Talonid width relative to trigonid: very narrow, subequal to base of metaconid, developed lingually (0), narrower (1), or subequal to wider (2). Ordered.
Nanocuris = 1

51. Lower molar cristid obliqua: incomplete, with distal metacristid present (0), complete, attaching below notch in metacristid (1), or complete, labially placed, at base of protoconid (2). Ordered. (Modified from Cifelli, 1993)
Nanocuris = 0

52. Hypoconulid: absent (0), in posteromedial position (1), or lingually placed and 'twinned' with entoconid (2). Ordered. (Modified from Cifelli, 1993)
Nanocuris = 1

53. Hypoconulid of last molar: short and erect (0) or tall and sharply recurved (1).
Nanocuris = 0

54. Entoconid: absent (0), smaller than (1), or subequal to larger than hypoconid and/or hypoconulid (2).
Nanocuris = 0

55. Labial postcingulid: absent (0) or present (1).
Nanocuris = 0

56. Paraconid and metaconid: metaconid at extreme lingual margin (0) or aligned (1).
Nanocuris = 1

57. Metacristid orientation to lower jaw axis: oblique (0) or transverse (1).
Nanocuris = 0

58. First lower molar metaconid, low and confluent with precingulid: absent (0) or present (1).
Nanocuris = 0

59. Protoconid height: tallest cusp on trigonid (0) or subequal to para- and/or metaconid (1).
Nanocuris = 0

60. Paraconid height relative to metaconid: taller (0), subequal (1), or shorter (2). [Molars other than the first considered when available]
Nanocuris = 0

61. Last lower molar size relative to penultimate lower molar: subequal (0) or smaller or lost (1).
Nanocuris = 1

63. Space between last lower molar and coronoid process: present (0) or absent (1).
Nanocuris = 1

70. Labial mandibular foramen: present (0) or absent (1)
Nanocuris = 1

74. Mandibular foramen: below (0) or posterior to anterior edge of coronoid process (1).
Nanocuris = 1

75. 'Meckelian' groove: present (0) or absent (1).
Nanocuris = 1

76. 'Coronoid' facet: present (0) or absent (1).
Nanocuris = 1

Below are the scorings of *Nanocuris* for the morphological characters in the phylogenetic analysis. Scorings of all comparative taxa correspond to those in Rougier et al. (2004). Code for polymorphism: A = (0, 1).

Nanocuris

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???1011??? ????110??2 0000221100 0110A21001
???11??011 0100010000 1?1?????1 ???111????
?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????
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