



New species of *Peradectes* and *Swaindelphys* (Mammalia: Metatheria) from the Early Paleocene (Torrejonian) Nacimiento Formation, San Juan Basin, New Mexico, USA

Thomas E. Williamson and Louis H. Taylor

ABSTRACT

Three new metatherian taxa are reported from the early Paleocene (Torrejonian) of the Nacimiento Formation, San Juan Basin, New Mexico; two new species of *Swaindelphys*, *S. encinensis* and *S. johansoni*, and one new species of *Peradectes*, *P. coprexeches*. Most of the new specimens consist of isolated teeth. Both new species of *Swaindelphys* are larger than *S. cifellii*, previously the only reported species of *Swaindelphys*, and the first report of this genus outside of Wyoming. *S. johansoni* is approximately intermediate in size between *S. encinensis* and *S. cifellii*. *P. coprexeches* is nearly the same size as *P. elegans*, but differs in the more buccally expanded and convex outline of the upper molar metastylar lobe, and relatively larger stylar cusp C.

This provides new information on early Paleocene metatherian morphology and significantly increases their known diversity. New significant morphology reported here includes that of a dP3 not previously reported for early Paleocene metatherians. Moreover, this study helps to clarify taxonomic issues related to the validity of other Paleocene metatherians and is relevant to the origins and morphology of basal Herpetotheriidae and Peradectidae.

Thomas E. Williamson, New Mexico Museum of Natural History and Science, 1801 Mountain Road, NW, Albuquerque, New Mexico 87104-1375, USA. thomas.williamson@state.nm.us

Louis H. Taylor, Denver Museum of Nature and Science, 2001 Colorado Boulevard, Denver, Colorado 80205-5798, USA. taylorlh@aol.com

KEY WORDS: New species; metatheria; Paleocene; Torrejonian; San Juan Basin

INTRODUCTION

Early Paleocene metatherians from North America are poorly known. Recent studies (e.g., Sánchez-Villagra et al. 2007; Horovitz et al. 2009)

argued that crown clade marsupialia originated near the beginning of the Paleocene while the closest sister clade, Herpetotheriidae, has a Late Cretaceous origin. This conclusion did not address problems related to the generic identity and rela-

PE Article Number: 14.3.23A

Copyright: Society of Vertebrate Paleontology November 2011

Submission: 15 June 2007. Acceptance: 19 August 2011

Williamson, Thomas E. and Taylor, Louis H. 2011. New species of *Peradectes* and *Swaindelphys* (Mammalia: Metatheria) from the Early Paleocene (Torrejonian) Nacimiento Formation, San Juan Basin, New Mexico, USA. *Palaeontologia Electronica* Vol. 14, Issue 3; 23A:16p;
palaeo-electronica.org/2011_3/21_williamson/index.html

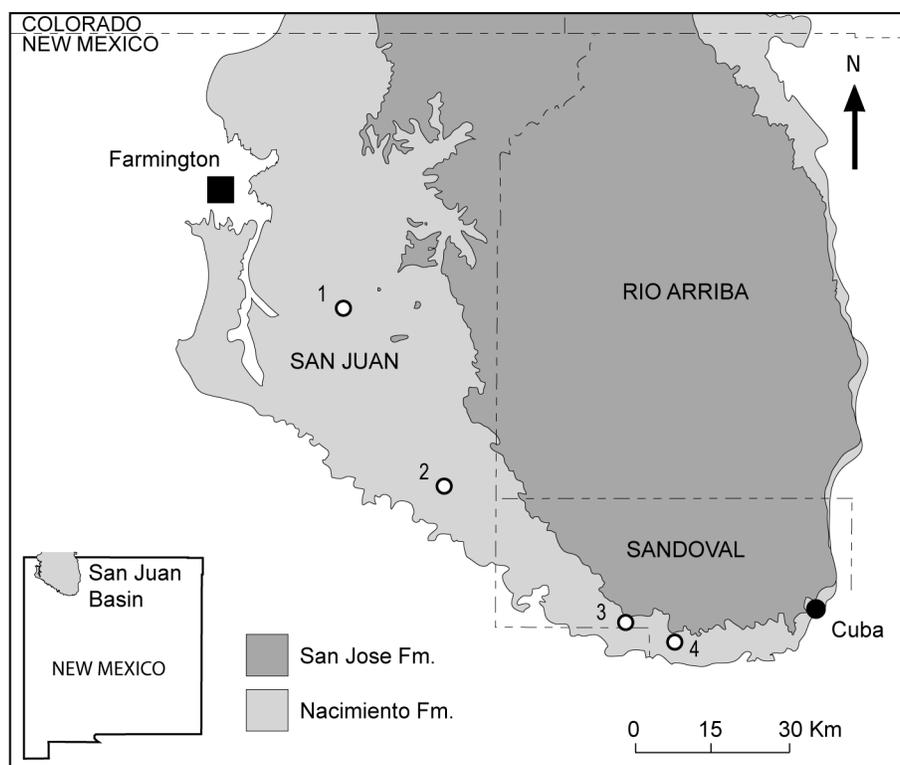


FIGURE 1. Map of the San Juan Basin, northwestern New Mexico showing the location of fossil localities yielding Torrejonian marsupial specimens documented here. A, NMMNH locality L-6398; B, L-5652; C, L-312, 1287, and 6898; D, L-1486, 2685, 6261, and 7583.

tionships of earliest Paleocene (Puercan) metatheria which remain contentious (Krishtalka and Stucky 1983; Johanson 1996a, 1996b; Clemens 2006). In addition, the conclusions regarding the relationship of purported Cretaceous herpetotheriids remain untested.

Until recently, herpetotheriids were not recognized from earlier than the basal Eocene (e.g., Krishtalka and Stucky 1983). Johanson (1996a) described a taxon from the early Paleocene (Torrejonian) of Wyoming, *Swaindelphys cifellii*, which is generally regarded as the oldest herpetotheriid from the Cenozoic of North America (Case et al. 2005; Martin et al. 2005; Korth 2007).

Here we report on three new metatherian taxa from the early Paleocene (Torrejonian) of the Nacimiento Formation, New Mexico. The first two of these represent two new species of *Swaindelphys*. This is the first report of *Swaindelphys* outside of the Wyoming. The third represents a new species of *Peradectes* and represents the only report of *Peradectes* from the Torrejonian of North America.

Geologic Setting

The majority of metatherian mammal specimens described here were recovered from microvertebrate fossil localities using screenwashing methods (e.g., Cifelli et al. 1996). These localities are widely distributed within the San Juan Basin (Figure 1) and span localities assigned to the *Pantolambda cavirictum* – *Mixodectes pungens* zone and *Mixodectes pungens* zone (Williamson 1996). The sites are middle to late Torrejonian in age (Lofgren et al. 2004; Figure 2).

Methods. Tooth nomenclature follows Davis (2007) All measurements are in mm and were made to the nearest 0.05 mm using a Wild™ measuring reticule and a Leica™ MZ 6 microscope.

Abbreviations for Descriptive Statistics. **DW** = distal width; **L** = length; **MW** = mesial width; **W** = width.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; UALP, University of Arizona Laboratory of Paleontology, Tucson.

TABLE 1. Correspondence of UALP and NMMNH specimen numbers for specimens included in this study.

| UALP | NMMNH |
|-------|-------|
| 8575 | 52885 |
| 9101 | 53928 |
| 9308 | 53935 |
| 9309 | 53932 |
| 10487 | 48543 |
| 10525 | 53927 |
| 14551 | 53933 |
| 14599 | 53936 |

Specimens that Taylor (1984) collected were originally deposited at the UALP. However, that collection was transferred to the NMMNH in 2005 (Williamson et al. 2006). All specimens from the UALP collection were assigned NMMNH specimen numbers (Table 1) and will be referred to by the NMMNH numbers in this report. All detailed locality information is on file at the NMMNH.

SYSTEMATIC PALEONTOLOGY

Family HERPETOTHERIIDAE Trouessart, 1879

Genus *SWAINDELPHYS* Johanson, 1996

SWAINDELPHYS JOHANSONI sp. nov.

(Figure 3, Table 2)

Holotype. NMMNH P-59304, left M3 from NMMNH locality L-7583.

Referred specimens. From NMMNH locality L-6398, NMMNH P-53926, partial left m?; 57342, partial left m4. From NMMNH locality L-7583, 59286, left dP3; 59293, right m2 or 3; 59303, left M2; 59304, left M3; 59345, left M4; 59378, right M1; 59389, left m2 or 3; and 59503, left M4.

Horizon and locality. NMMNH localities L-6898 and 7583, *Pantolambda cavirictum* – *Mixodectes pungens* Zone (Williamson 1996), Middle Torrejonian (To2) in age (Lofgren et al. 2004; Figure 2).

Etymology. Named after Zerina Johanson for her contributions to Cretaceous and Paleogene metatherian studies.

Diagnosis. Over 10 percent larger than *Swaindelphys cifellii* in most dimensions and over 15 percent smaller than *S. encinensis* sp. nov. in most dimensions.

Description. All specimens referred to *Swaindelphys johansonii* consist of isolated teeth. A single partial tooth is tentatively identified as a dP3 of *S. johansonii* (Figures 3.1 and 3.3). It is missing the distobuccal corner of the tooth. It is smaller than permanent upper molars referred to *S. johansonii*, but is similar in size relative to the permanent

upper molars of other Paleogene metatherians such as *Peradectes louisii* (Crochet 1979) and *Amphiperatherium giselense* (Heller 1936) (Crochet 1980, figures 6 and 43, respectively). However, the dP3 of *Amphiperatherium goethei* (Crochet 1979) and *A. maximum* (Crochet 1979) are markedly larger relative to upper molars (Crochet 1980, figures 88 and 105, respectively). The protoconal lobe is rounded lingually with the conules placed symmetrically near the protocone on either side. The paraconule is larger than the metaconule. The paracone and metacone are subequal in height. The metacone is wider. The centrocrista is deflected buccally, with a shape resembling an obtuse inverted V. The parastylar lobe is relatively larger than those described for other Cretaceous and Paleogene metatherians. It projects mesially and is mesiolingually expanded so that the mesial margin of the tooth is deeply embayed between the parastylar and protoconal lobes. The intersection of these two lobes describes a nearly right angle at the mesial margin of the tooth. Styler cusp A is positioned at the mesial extremity of the parastylar lobe and is lingual to a line drawn between the paracone and metacone. A smaller styler cusp, styler cusp B (stylacone) is mesial to the paracone, positioned on a line drawn through the paracone and metacone. A low preparacrista extends from the mesial base of the paracone to styler cusp B. The styler shelf is narrow buccal to the paracone and expands buccal to the metacone. It supports several styler cusps. A cusp buccal to the intersection of the postpara- and premetacristae is interpreted to represent styler cusp C. It is larger than styler cusp B and smaller than styler cusp A. It is nearly conular, but mesiodistally elongate. A diminutive cusp is positioned close to and distal to styler cusp C.

Discussion. Nearly all specimens referred to *Swaindelphys johansonii* were collected from a single locality, NMMNH locality L-7583. Two additional specimens, both fragments of lower molars were collected from L-6398 and are tentatively referred to this taxon. Both of these localities are within the *Pantolambda cavirictum* – *Mixodectes pungens* Zone (Williamson 1996) and are Middle Torrejonian (To2) in age (Lofgren et al. 2004). — The upper dentition is represented by several isolated teeth. All four upper molars are significantly larger than the respective teeth of *Swaindelphys cifellii* (Johanson 1996a, table 1), and there is no overlap in tooth dimensions (Table 2).

A dP3 referred to *S. johansonii* is one of the few that has been described for any Cretaceous or

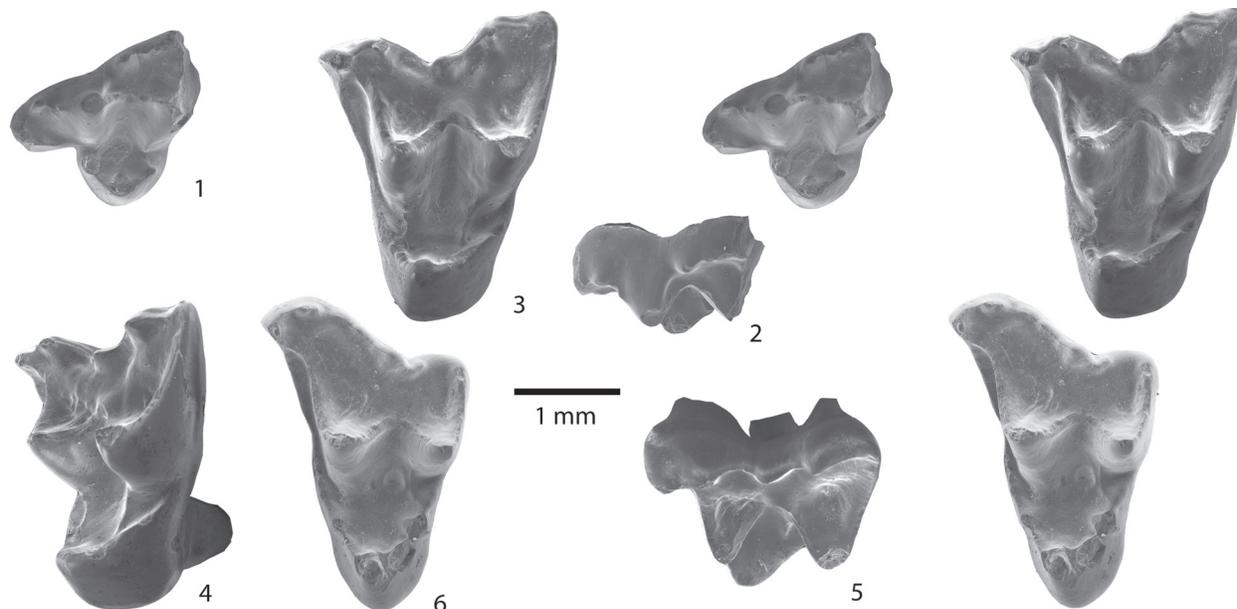


FIGURE 3. Upper dentition of *Swaindelphys johansonii* sp. nov. NMMNH P-59286, left dP3 in occlusal (1; stereopair) and buccal (2) views; 59304 (holotype), left M3 in occlusal (3; stereopair), disto-oblique (4), and buccal (5) views; 59345, left M4 in occlusal view (6, stereopair).

Paleogene metatherian taxa. A dP3 has been described and illustrated for several of these, including *Alphadon rhaister* (William A. Clemens, Jr. 1966, figure 11), *Didelphodon vorax* (Clemens 1966, figure 51), *Protolambda hatcheri* (Clemens 1966, figure 28), *Leptalestes krejci* (Lillegraven 1969, figure 23.5), *Glasbius twitchelli* (Archibald 1982, figure 49a-b), "*Peradectes*" cf. "*P.*" *pusillus* (Archibald 1982, figure 44a-b), *Peradectes californicus* (Rothecker and Storer 1996, figure 10), *Herpetotherium* sp. cf. *H. marsupium* (Rothecker and Storer 1996, figure 1A), and numerous Paleogene European metatherians (see Crochet 1980). An additional dP3 of a Cretaceous metatherian was described and illustrated by Eaton et al. (1999, figure 3E) as "*Pediomys* sp." based on an isolated tooth, UMNH VP 6894 (listed as UMNH VP 6594 by Eaton et al. (1999), from the Campanian Wahweap? Formation of Utah. Later, Eaton (2006, figure 13A) described this tooth as an M1 of "*Pediomyid* gen. and sp. indet." We agree with Davis (2007), that this tooth is a dP3 of "*Pediomys* sp." A number of the taxonomic identifications of other taxa reported above were considered doubtful or tentative. Regardless, these teeth share a similar overall shape in which the tooth is longer than wide, the protocone is relatively small with closely spaced conules, the parastylar lobe projects mesially, the paracone and metacone are

widely spaced, and the styler shelf is reduced or missing mesially and buccal to the paracone. Among these taxa, salient differences are the relative development of the styler shelf buccal to the paracone, relative size and development of the parastylar lobe, the relative size and placement of styler cusp B, which is absent from several taxa, and the relative size and placement of styler cusps C and D.

The styler shelf of the dP3 is reduced relative to the metastylar lobe in all metatherian taxa. It ranges in development from being present but narrow (e.g., *Turgidodon rhaister* and *Glasbius twitchelli*), present only as an ectocingulum on the buccal face of the paracone (e.g., *Peradectes californicus*), to being completely absent (e.g., *Swaindelphys johansonii*).

The tooth here referred to *Swaindelphys johansonii* most closely resembles a fragmentary dP3 described by Archibald (1982) and tentatively referred to "*Peradectes*" cf. "*P.*" *pusillus*. As in *S. johansonii*, it has a relatively greatly expanded parastylar lobe. Moreover, the parastylar lobe is expanded mesiolingually so that styler cusp A which occupies a position near the mesial apex of this lobe, is positioned lingual to a line drawn through the paracone and metacone. A similar condition is observed for a tooth, UALP 2872 that Lillegraven (1969) doubtfully referred to *Leptalestes*

TABLE 2. Measurements of *Swaindelphys johansoni* sp. nov. *Approximate measurement.

| | | Length | MW | DW |
|---------|-------|--------|------|------|
| dP3 | 59286 | -- | 1.21 | |
| M1 | 59378 | 2.37 | 2.18 | 2.61 |
| M2 | 59303 | 2.18 | 2.42 | -- |
| M3 | 59304 | 2.27 | 2.64 | 2.88 |
| M4 | 59345 | 1.98 | 2.90 | 2.47 |
| | 59503 | -- | -- | 1.84 |
| m2 or 3 | 58849 | | -- | 1.51 |
| | 58948 | 2.37 | 1.55 | 1.45 |
| | 59293 | -- | -- | 1.40 |
| | 59389 | 2.27 | 1.45 | 1.31 |
| m4 | 57342 | -- | 1.21 | -- |

krejicii. However, in both taxa, the parastylar lobe is not as expanded as in *S. johansoni* and both also lack a stylar cusp B.

Clemens (1966), in describing the dP3 of *Turgidodon rhaister* and Archibald (1982) in describing a dP3 that he tentatively referred to *G. twitchelli*, identified the stylar cusp immediately distobuccal to the paracone as the stylar cusp B and reported that stylar cusp C was absent in these teeth. It is much more likely that the stylar cusp B is absent in these specimens and the cusp immediately mesiodistal to the paracone is stylar cusp C.

As in *Swaindelphys johansoni*, a diminutive stylar cusp B is present mesio Buccal to the paracone in the dP3 of *P. californicus*.

Swaindelphys encinensis sp. nov.
(Figures 4-5 Table 3)

"*Peradectes encinensis*" Taylor, 1984, p. 103, table 4.

Peradectes? n. sp. B. Williamson and Lucas, 1993 p. 120; Williamson, 1993 p. 101, 1996 p. 34.

Holotype. NMMNH P-21594, right partial maxilla with M3 from NMMNH locality L-2685.

Referred specimens. From NMMNH locality L-312, NMMNH P-00060, right m1; 01972, left m2 or 3; 57344, left M2; 58843, left partial M2; 58888, left m2 or 3; 58921, left m2 or 3; 58924, right m2 or 3; 58930, partial left m2 or 3 (talonid); 58948, left m2 or 3; 58970, right m1; 58982, left m4; 59004, left partial M4; 59023, right M1; 59028, partial left M3;

and 59256, partial left M4. From NMMNH locality L-1287, NMMNH P-54129, left M4. From NMMNH locality L-1486, NMMNH P-18587, right M3. From NMMNH locality L-6261, NMMNH P-53927, partial left m?; 53932, partial right lower molar; 53933, partial right lower molar (partial trigonid); 53935, partial right lower molar (talonid). From NMMNH locality L-6249, NMMNH P-48543, right partial M1 or 2. From NMMNH locality L-6282; NMMNH P-52885, partial right dentary with m1-2. From NMMNH locality L-6315, NMMNH P-53928, right m1. From NMMNH locality L-6898, NMMNH P-57342, partial left m4.

Horizon and locality. Numerous localities of the *Mixodectes pungens* zone (Williamson 1996), all located at the East and West Flanks of Torreon Wash, Nacimiento Formation, San Juan Basin, New Mexico, late Torrejonian (To3) in age (Lofgren et al. 2004).

Etymology. Named for Ojo Encino, the area from which the type and referred specimens were collected.

Diagnosis. Larger than *Swaindelphys johansoni*, over 15 percent larger in most dimensions; upper and lower molar cusps more inflated and upper molar protocone more mesiodistally expanded; M4 differs from *S. johansoni* in possessing a less buccally expanded metastylar lobe and in lacking an ectoflexus.

Description. As in other Paleogene marsupials, M1 of *Swaindelphys encinensis* is relatively less transverse than M2 or 3 and the stylar shelf is reduced mesially, giving it a canted appearance in occlusal view. Also, the protocone is less compressed mesiodistally. The M1 has only a shallow ectoflexus (Figure 4.1). It is progressively deeper in M2 (Figure 4.2) and M3 (Figure 4.3-4.4). In M3 the ectoflexus is relatively deep and smoothly indented, centered on stylar cusp C. In all upper molars the paracone is smaller than metacone. The para- and metacones have nearly flat buccal walls. The metacone has a slight expansion at its base buccally, giving this area a modest convexity. The paracone and metacone are separated by a deep and narrow cleft. The preparacrista intersects with stylar cusp B (= stylocone) in M1 and 2, but merges into the stylar shelf lingual to a position that is medial to the apex of stylar cusp B in M3. There is no contribution to the preparacrista from stylar cusp B in M3. Stylar cusp B is the largest of the stylar cusps, followed by stylar cusp D, stylar cusp C, and finally, stylar cusp A. Stylar cusp A is circular and subequal in height to stylar cusp B. A

TABLE 3. Measurements of *Swaindelphys encinensis* sp. nov. *Approximate measurement.

| | | Length | MW | DW |
|---------|-------|--------|------|-------|
| M1 | 59023 | 2.57 | 2.61 | 2.90 |
| M2 | 57344 | 2.61 | 2.90 | 3.00 |
| | 58843 | 2.37 | -- | -- |
| M3 | 18587 | -- | 3.12 | 3.29 |
| | 21594 | 2.76 | 3.34 | 3.58 |
| M4 | 54129 | 2.27 | 3.10 | 2.61 |
| | 59004 | 1.91 | -- | -- |
| | 59256 | 1.79 | -- | -- |
| p3 | 58849 | 1.22 | 0.68 | |
| m1 | 00060 | 2.53 | 1.36 | 1.46 |
| | 52885 | 2.30 | 1.30 | 1.30 |
| | 53928 | 2.55 | 1.35 | 1.45 |
| | 58970 | 2.46 | 1.26 | 1.41 |
| m2 | 52885 | 2.50 | 1.40 | 1.50 |
| m2 or 3 | 01972 | 2.49 | 1.45 | 1.48 |
| | 53934 | -- | -- | 1.61 |
| | 58921 | 2.64 | 1.55 | 1.65 |
| | 58924 | 2.42 | 1.45 | 1.33* |
| | 58888 | 2.57 | 1.65 | 1.57 |
| | 58930 | -- | -- | 1.69 |
| m4 | 58982 | 2.42 | 1.40 | 1.16 |
| | 53932 | -- | -- | 1.55 |
| | 53935 | -- | -- | 1.69 |

crista extends mesially from stylar cusp B, but a distinct notch separates this crista from stylar cusp A. Stylar cusp C is situated at the deepest part of the ectoflexus on the ectocingulum so that the ectoflexus is centered on stylar cusp C. Cusp D is represented by a single elongate and oval shape in NMMNH P-18517, but appears to be represented by several smaller cusps along the margin of the stylar shelf in NMMNH P-21594 (Figures 4.3-4.4). In unworn teeth, the paraconule is smaller than the metaconule. The postmetaconule crista terminates below the distolingual base of the metacone. The preparaconule crista extends buccally to the lingual base of stylar cusp A. A postparaconule crista is indistinct or absent. A premetaconule crista is present and extends buccally from the metaconule to the base of the metacone. The M4 (Figure 4.5) is reduced distally with a concomitant reduction in the

metacone and metastylar lobe. However, in M4, unlike the preceding molars, the metaconule is larger than the paraconule.

Numerous isolated lower teeth are referred to *S. encinensis*. These are all from localities or the same fossil horizons that yield upper teeth referable to *S. encinensis*, and so referral is not in doubt. In addition, a partial dentary with m1-2, NMMNH P-52885, is referred to this taxon.

The dentary P-52885 preserves the alveolus for the double-rooted p3 mesial to the m1. A single mental foramen is situated below the mesial root of m1.

For all lower molars, the protoconid is larger than the metaconid, and the paraconid is the smallest trigonid cusp. The metaconid is mesial and slightly posterior to the protoconid. A distinct notch is present in the paracristid. The paracristid proj-

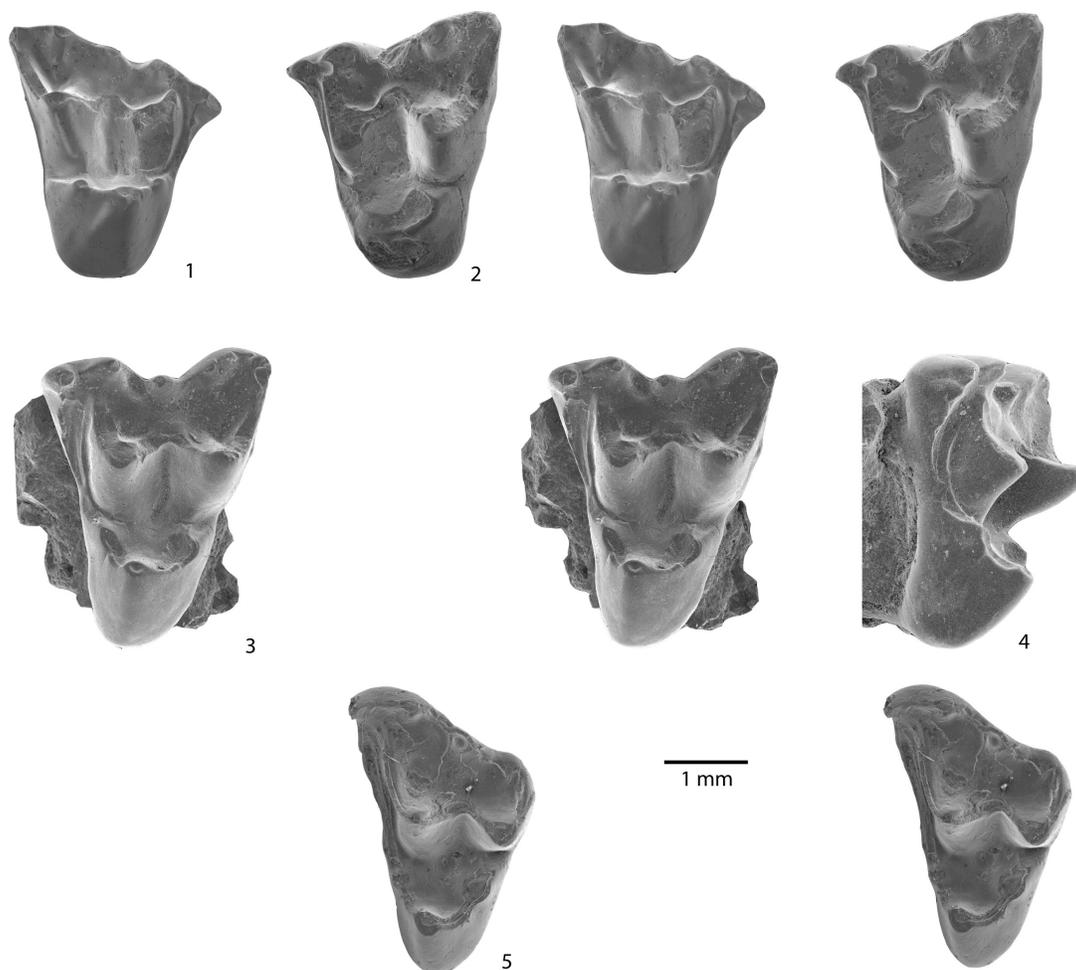


FIGURE 4. Upper dentition of *Swaindelphys encinensis* sp. nov. NMMNH P-59023, right M1 in occlusal view (1, stereopair); 57344, left M2 in occlusal view (2, stereopair); 21594 (holotype), partial maxilla with left M3 in occlusal (3; stereopair) and mesio-oblique (4) views; 54129, left M4 occlusal view (5, stereopair).

ects mesiolingually and terminates in a mesiolingual paraconid. The trigonid basin opens lingually as a groove between the metaconid and paraconid. A precingulid is present near the base of the tooth mesial and labial to the protoconid. The m1 trigonid is narrower than the talonid, and the paraconid and paracristid project more mesially than in the succeeding molars. For the m2 of NMMNH P-52885, the talonid is wider than the trigonid. The identity of many isolated teeth, whether they represent m2 or m3, remains uncertain. For m1-3, the trigonids and talonids are subequal in length (Figures 5.1-5.3.). The hypoconid is the largest of the talonid cusps. The hypoconulid and entoconid are positioned close together so that they are twinned. The entoconid is mesiodistally elongate and erect forming a blade that closes the talonid basin lingually. It is taller than the hypoconulid. The hypoco-

nulid is distobuccal to the entoconid and inclined distally. The cristid oblique meets the distal face of the talonid near the distal base of the protoconid. The postcingulid descends from the buccal side of the hypoconulid to the base of the tooth distal to the hypoconid.

A single complete m4, 58982 (Figures 5.4-5.6) possesses a trigonid similar to that of m2-3. The talonid is narrower than the trigonid and relatively more elongate than in preceding molars. The entoconid is lower and smaller than the hypoconulid.

Discussion. A small sample size available to study for both *S. encinensis* and *S. johansoni* hampers comparison. The holotype of *S. johansoni* (NMMNH P-59304), an M3 from locality L-7583, is over 14 percent smaller in buccolingual width than the holotype (21594) and a referred specimen

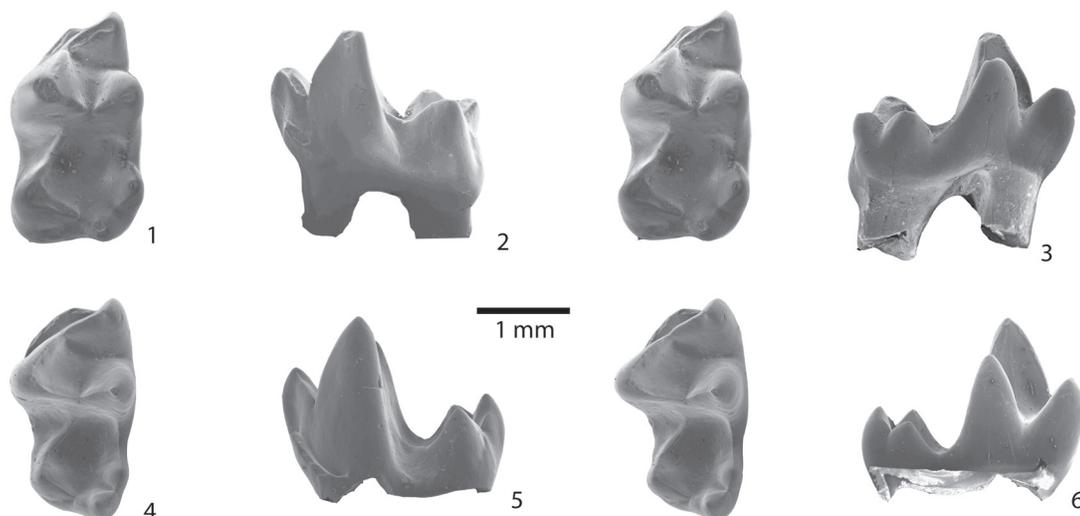


FIGURE 5. Lower dentition of *Swaindelphys encinensis* sp. nov. NMMNH P-1972, left m2 or 3 in occlusal (1; stereopair), buccal (2), and lingual (3) views; 58982, left m4 in occlusal (4; stereopair), buccal (5), and lingual (6) views.

(18587) of *S. encinensis*. A student T-Test of pooled m1-2 length (Tables 2-3) of *Swaindelphys encinensis* (n=4) and *S. johansoni* (n=2) results confirms that the difference between the two samples is statistically significant (P-Value = 0.0006). There is no overlap in tooth measurements between samples of these taxa.

Swaindelphys encinensis is the largest metatherian reported from the late early Paleocene (Torrejonian) of western North America and is subequal in size to the Puercan taxon *Thylacodon pusillus* and *T. cf. T. pusillus* (e.g., Standhardt 1980, table 5; Williamson, unpubl. data; Archibald 1982, table 24; Clemens 2006, table 1).

Johanson (Johanson 1996a) erected the genus *Swaindelphys* and described the species *S. cifelli* from Swain Quarry of northern Wyoming, noting that whereas the upper teeth possessed some characters typical of herpetotheriid metatherians such as a V-shaped centrocrista, the lower molars lacked some features typical of derived members of herpetotheriidae including such features such as a distally-directed hypoconulid that is located distal to the entoconulid. Johanson (1996a) further described the lower teeth of *S. cifelli* as being very similar in morphology, but smaller than those of *Thylacodon pusillus* or *T. cf. T. pusillus* described by Archibald (1982). The lower teeth of *S. encinensis* are similar in size to *T. pusillus*, but have lower, more robust trigonid cusps, a relatively lower, less trenchant entoconid, and an m4 entoconid that is smaller than the hypoconulid.

Family PERADECTIDAE Crochet, 1979
Genus PERADECTES Matthew and Granger,

1921

PERADECTES COPREXECHEs sp. nov.
(Figures 6-7, Table 4)

“*Peradectes coproxeches*” Taylor (1984), p. 109, table 5 (in part).

“*Peradectes?* n. sp. C” (Williamson and Lucas 1992), p. 120; (Williamson 1993), p. 102; (Williamson 1996), p. 34.

“*Peradectes?* n. sp. D” Williamson and Lucas, 1992, p. 120; Williamson, 1993, p. 102; Williamson, 1996, p. 34 (in part).

Holotype. NMMNH P-59512, right M3 from NMMNH locality L-7583.

Referred specimens. From NMMNH locality L-312, NMMNH P-57803, left M2; 58826, left m1; 58846, right M1; 58849, left p3; 58854, right m1; 58927, left m2 or 3; 58933, right m1; 59014, right m4; 59015, left M1; 59062, left M3; 59094, left m4; 59195, partial right M3; 59228, partial right M1; and 59342, left m1. From NMMNH locality L-5652, NMMNH P-43089, left m1. From NMMNH locality L-6315, NMMNH P-53929, left m4. From NMMNH locality L-6398, NMMNH P-53881, right m1; 53936, partial right M2. From NMMNH locality L6898, NMMNH P-56974, right m2 or 3; 56976, partial left m2 or 3; 56977, right m2 or 3; 57819, right M3; and 57820, left M2. From NMMNH locality L-7583, NMMNH P-59050, right m1; 59059, partial right m2 or 3 (taloid); 59063, left M1; 59283, left m1; 59284, left m1; 59288, right M2; 59291, partial right m2 or 3; 59292, right partial M3; 59313, left M2; 59319, left M2; 59334, right m2 or 3; 59338, right m1; 59341, left m4; 59342, left m1; 59344, left m2

TABLE 4. Measurements of *Peradectes coprexeches* sp. nov. *Approximate measurement.

| | Length | MW | DW | | Length | MW | DW | |
|----|--------|-------|-------|---------|--------|-------|-------|------|
| M1 | | | | | 59050 | 1.38 | 0.68 | -- |
| | 58846 | 1.35* | 1.14* | 1.29* | 59283 | 1.06 | -- | -- |
| | 59015 | 1.55 | 1.36 | 1.45 | 59284 | 1.02* | -- | 0.48 |
| | 59063 | 1.69 | 1.50 | 1.55 | 59342 | 1.67* | 0.77* | 0.82 |
| | 59228 | -- | -- | 1.45 | 59407 | -- | -- | 0.87 |
| | 59508 | 1.48 | 1.33 | 1.52 | 59482 | -- | 0.68 | 0.73 |
| M2 | | | | m2 or 3 | | | | |
| | 53936 | 1.50 | -- | -- | 56974 | 1.26 | 0.73 | 0.73 |
| | 57803 | 1.40 | 1.52 | 1.60 | 56976 | 1.50 | 0.82 | 0.77 |
| | 57802 | 1.40 | 1.45 | 1.50 | 56977 | 1.50 | 0.82 | 0.77 |
| | 59288 | 1.26 | 1.40 | 1.69 | 58927 | 1.45 | 0.87 | 0.80 |
| | 59313 | -- | 1.36 | -- | 59059 | -- | -- | 0.58 |
| | 59319 | 1.45 | 1.55 | 1.74 | 59291 | -- | -- | 0.68 |
| | 59459 | 1.45 | 1.45 | 1.79 | 59334 | 1.28 | 0.73 | 0.68 |
| | 59484 | 1.50 | 1.69 | 1.82 | 59344 | 1.50 | 0.87 | 0.73 |
| | 59499 | -- | 1.55* | -- | 59380 | 1.55 | 0.82 | 0.82 |
| | 59509 | 1.57 | 1.69 | 1.84 | 59391 | 1.45 | 0.75 | -- |
| | | | | | 59405 | -- | 0.87 | 0.70 |
| M3 | | | | | 59408 | 1.50 | 0.77 | 0.75 |
| | 59062 | 1.40 | 1.74 | 1.84 | 59460 | -- | 0.73 | 0.73 |
| | 59292 | 1.26* | -- | -- | 59496 | 1.40 | 0.77 | 0.77 |
| | 59483 | 1.40 | 1.74 | 1.84 | 59507 | -- | 0.82 | 0.70 |
| | 59512 | 1.50 | 1.69 | 1.86 | 59541 | 1.45 | 0.85 | 0.75 |
| | 59537 | 1.33 | -- | -- | 59542 | 1.55 | 0.90 | 0.87 |
| M4 | | | | | 59545 | 1.55 | 0.92 | 0.82 |
| | 59458 | 1.36 | -- | -- | m4 | | | |
| m1 | | | | | 53929 | 1.31 | 0.75 | 0.53 |
| | 43089 | 1.50 | 0.77 | 0.70 | 59014 | 1.45 | 0.87 | 0.68 |
| | 53881 | 1.36 | 0.68 | 0.63 | 59094 | 1.33 | 0.77 | 0.63 |
| | 58826 | -- | 0.68 | 0.73 | 59341 | 1.36 | 0.77 | 0.53 |
| | 58854 | 1.48 | 0.92 | 0.77 | 59450 | 1.26 | .063 | 0.56 |
| | 58933 | 1.31 | 0.58 | 0.58 | | | | |

or 3; 59380, left m2 or 3; 59391, left m2 or 3; 59405, left m2 or 3; 59407, right m1; 59408, left m1; 59422, left m4; 59450, left m4; 59458, partial left M4; 59459, right M2; 59460, left m1; 59465, partial left M3; 59482, right m1; 59483, left M3; 59484, right M2; 59485, partial left M?; 59486, left partial dentary with m4; 59496, left m1; 59499, partial left M2 or 3; 59507, left m1; 59508, right M1; 59509, right M2; 59537, partial left M3; 59541, right m2 or 3; 59542, right m2 or 3; and 59545, left m2 or 3.

Horizon and locality. From several localities of the Nacimiento Formation, San Juan Basin, New Mexico, distributed within fossil zones included in both the *Pantolambda carivictum* – *Mixodectes pungens* and *Mixodectes pungens* zones (Williamson 1996) and considered to be middle through late Torrejonian (To2-3) in age (Lofgren et al. 2004, Figure 2).

Etymology. Combines kopros, (Greek, dung) with exoche (Greek, point) after Coprolite Point (NMMNH locality L-6398) from which the first specimens were collected (Taylor 1984).

Diagnosis. Smaller than *P. elegans* (Matthew and Granger 1921), *P. pauli* (Gazin 1956), and *P. californicus* (Stock 1936); differs from all species of *Peradectes* including *P. minor* by more expanded and buccally more strongly convex metastylar lobe, deeper ectoflexus, relatively larger stylar cusp C, larger and more distinct conules and internal conular wings; further differs from *P. minor* by possessing a relatively more elongate m4 trigonid and narrower m4 talonid.

Description. *Peradectes coprexeches* is represented by numerous specimens, all consisting of isolated teeth or small jaw fragments with single teeth. M1 is triangular in occlusal view with a stylar

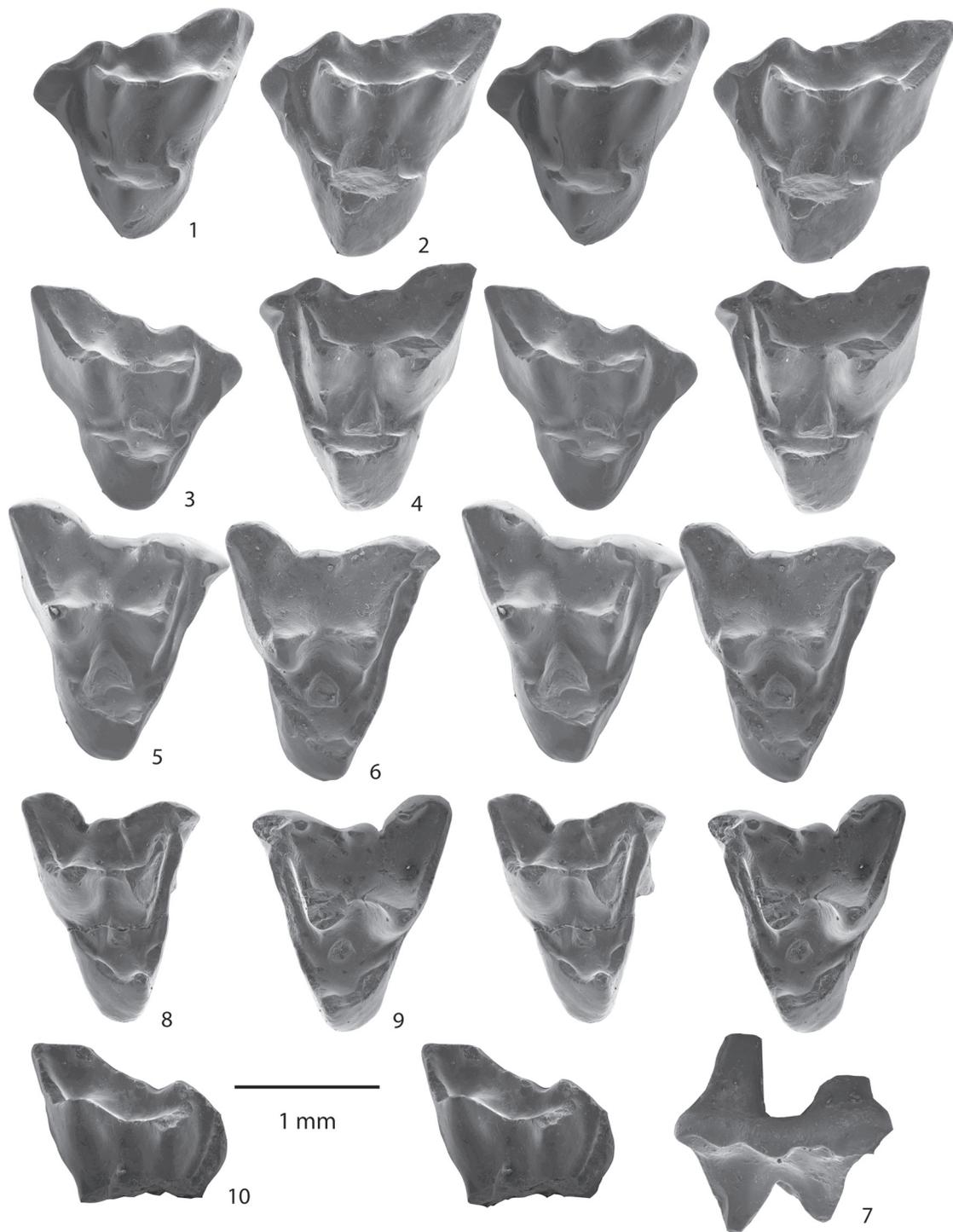


FIGURE 6. Upper dentition of *Peradectes coprexeches* sp. nov. NMMNH P-59015, left M1 in occlusal view (1; stereopair); 59063, left M1 in occlusal view (2; stereopair); 59508, right M1 in occlusal view (3; stereopair); 59319, left M2 in occlusal view (4, stereopair); 59509, right M2 in occlusal view (5, stereopair); 59512 (holotype), right M3 in occlusal (6; stereopair) and buccal (7) views; 57819 right M3 in occlusal view (8, stereopair); 59062, left M3 in occlusal view (9, stereopair); 59458, partial left M4 in occlusal view (10, stereopair).

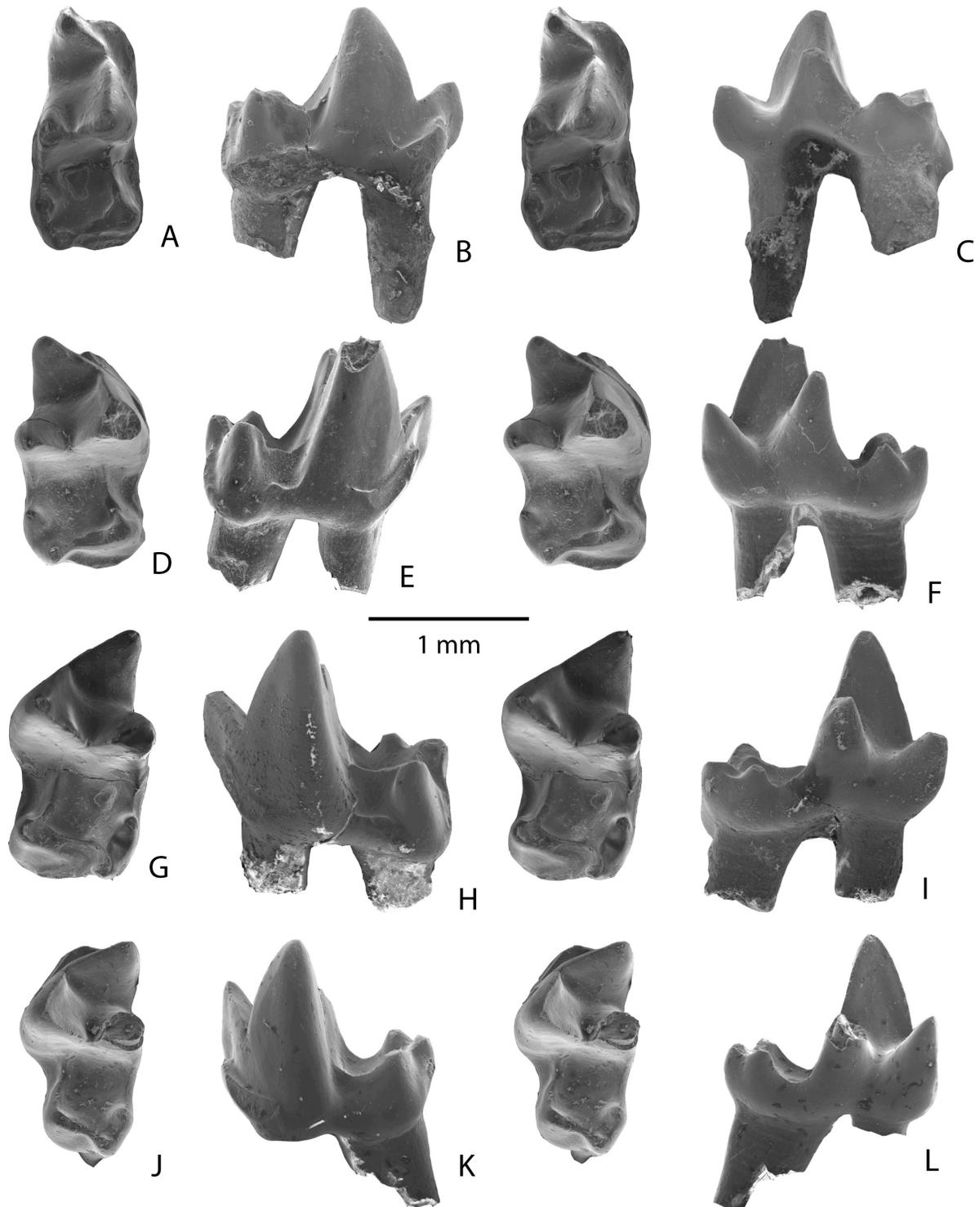


FIGURE 7. Lower dentition of *Peradectes coprexeches* sp. nov. NMMNH P-59338, right m1 in occlusal (1; stereopair), buccal (2), and lingual (3) views; 59541, right m2 or 3 in occlusal (4; stereopair), buccal (5), and lingual (6) views; 59545, left m2 or 3 in occlusal (7; stereopair), buccal (8), and lingual (9) views; 59341, left m4 in occlusal (10; stereopair), buccal (11), and lingual (12) views.

shelf that narrows mesially. A triangular parastylar lobe projects mesial to the paracone. The buccal margin of the tooth is nearly straight with a shallow ectoflexus distal to stylar cusp B. Stylar cusp B is the highest of the stylar cusps, followed by stylar cusps D, C, and A. Stylar cusp C is present as an elongated cusp along the margin of the stylar shelf in most specimens, but is represented as two smaller, closely appressed cusps in one specimen (59063; Figure 6.2), similar to what Clemens (2006) described for *P. minor*. The metacone is higher and longer than the paracone. The centracrista is straight. The preparacrista is short and extends buccally to the mesial base of stylar cusp B. The conules are subequal in size, and the internal conular wings are small, but distinct. The post-metaconular crista descends to near the distolingual base of the metacone.

M2 is more transverse than M1 with a wider stylar shelf buccal to the paracone. The ectocingulum of the metastylar lobe expands buccally in a convex arc, and the three mesial stylar cusps, A, B, and C form a nearly straight line that is directed nearly mesially.

M3 differs from M2 in having a more buccally expanded parastylar lobe and a relatively deeper ectoflexus. Both are buccally rounded in occlusal view and the ectoflexus is approximately centered on stylar cusp C. In some specimens (e.g., 57819 and 59062; Figs. 6.5 and 6.6, respectively), a deep notch is present, in occlusal view, immediately distal to stylar cusp C. However, in one specimen (59512; Figure 6.4) no such notch is present.

A partial M4 (Figure 6.10) possesses a reduced metastylar lobe, lacks a distinct stylar cusp C, and has a shallow ectoflexus.

Lower teeth are represented by a single p3 and numerous lower molars. The p3 closely resembles that of the holotype of *P. elegans* (AMNH 17376). The principle cusp is high with a convex mesial border. Distally, a crest descends to a narrow talonid, which supports a single blade-like median cusp. Mesially, a crest descends and curves lingually to the base of the crown where it merges with a lingual cingulid. In buccal view, the face of the tooth is convex.

The m1 (Figure 7.1-7.3) has a narrow trigonid with a mesially projecting paraconid. The protoconid is the highest trigonid cusp followed by the metaconid and the paraconid. The talonid is rectangular in occlusal view. The hypoconid is the largest talonid cusp followed by the entoconid and then the hypoconulid. The hypoconulid is positioned lingually, and the entoconid is higher, longer, and

compressed buccolingually. The cristid oblique intersects the distal face of the trigonid buccal to the protocristid notch, below the apex of the protoconid. A mesiodistally elongate precingulid resides near the base of the mesiobuccal face of the tooth below the paracristid notch. An ectocingulid is present within the ectoflexid. A postcingulid descends buccally from the hypoconulid.

The m2-3 (Figure 7.4-7.9) differs from m1 in having relatively shorter and wider trigonids with a paraconid that is positioned near the mesiolingual corner of the tooth. The entoconid is relatively lower and shorter so that it is subequal in size to the hypoconulid or smaller. It is conular rather than buccolingually compressed.

The m4 (Figure 7.10-7.12) is smaller than m2 or 3, but with a relatively more elongate protoconid. The talonid is narrower than the trigonid, but as in the m2 or 3, the entoconid and hypoconulid are subequal. However, the postcingulid is relatively weaker and an ectocingulid is lacking from the ectoflexid.

Discussion. All specimens of *Peradectes coprexeches* were recovered using screenwashing methods. This material comes from several localities, and most specimens are from a single locality, L-7583. Three specimens, NMMNH P-59508, 59509, and 59512, representing an M1, M2, and M3, respectively, were recovered from the same small batch of screenwashing matrix and likely come from a single individual.

Peradectes coprexeches differs from other species of *Peradectes* by its more expanded metastylar lobe, deeper ectoflexus, and relatively larger stylar cusp C. The buccal margin of the metastylar lobe is strongly convex in occlusal view and expands buccally beyond the parastylar lobe, whereas the metastylar lobe of *P. elegans* is relatively flat and does not extend buccally significantly beyond the parastylar lobe.

Taylor (1984) reported an unpublished metatherian taxon, "*Peradectes coprexeches*," from a single locality (NMMNH locality L-6398; "Coprolite Point") in Kutz Canyon of the northern San Juan Basin (Figure 1). Most of the specimens that he referred to this taxon were unavailable for this study. However, we refer one specimen available to us from this locality, a partial M2 (NMMNH P-53936; = UALP 14599, Table 1). It closely resembles M2s referred to this taxon recovered from other localities in the southern San Juan Basin in the distinctive shape of the buccal margin of the tooth, with a relatively pronounced ectoflexus compared to other species of *Peradectes*,

and the relatively large size of styler cusp C. A fragment of a lower tooth from this locality (53881) is tentatively referred to this taxon. Taylor (1984) referred an additional specimen, a partial M1, (UALP 10498 from UALP locality 7671) to "*P. coprexeches*." This specimen was not available to study, but based on the measurements reported for this specimen (Taylor 1984, table 5; width = 2.1), it falls outside of the size range for this taxon. Based on the measurement, it might be referable to *Swaindelphys johansonii* (above).

A single lower tooth, an m1 (NMMNH P-43089) from locality L-1870, is also tentatively referred to this *Peradectes coprexeches*. It is similar in size and morphology to m1s referred to *Peradectes coprexeches* recovered from other localities reported here.

CONCLUSIONS

Two new species of *Swaindelphys*, *S. encinensis* and *S. johansonii* and one new species of *Peradectes*, *P. coprexeches*, represent the first metatherians to be identified and described from the late early Paleocene (Torrejonian) of the Nacimiento Formation, San Juan Basin, New Mexico. These taxa significantly increase the taxonomic and morphological diversity of Paleocene metatherians. Metatherians have previously been generally poorly known, constituting minor components of Paleogene faunas of western North America (see Krishtalka and Stucky 1983; Korth 2007). However, data presented here indicate they were at least locally abundant members of the mammalian fauna in the late early Paleocene of the San Juan Basin of northwestern New Mexico. At one locality, L-7583, for example, metatherian specimens referable to *Swaindelphys johansonii* and *Peradectes coprexeches* constitute over 25% (n = 50) of the generically identifiable mammal specimens (n = 189). This approaches the total number of identifiable multituberculate specimens (n = 68) from the same locality and exceeds that of any other taxon of therian mammal. Of the metatherians, *P. coprexeches* predominates (n = 41). Preliminary calculations of the minimum number of individuals (MNI) indicates that *P. coprexeches* [MNI = 10] constituted over 30% of the total therian mammal abundance [MNI ~ 31]. *S. johansonii* is relatively more rare [MNI = 2] and didn't exceed about 6%.

Swaindelphys was previously represented by a single species, *S. cifellii*, from the middle Torrejonian (To2) of Swain Quarry, "Fort Union Formation," northern Wyoming. The new species

described here are significantly larger than *S. cifellii* and add new morphological information to this taxon. One of these new taxa, *S. johansonii*, includes a dP3 that has not previously been described for any early Paleocene metatherian. It differs significantly from those described for other Paleogene metatherians including *Peradectes* and *Herpetotherium*.

Swaindelphys has been considered a basal herpetotheriid by numerous workers (e.g., Johanson 1996a; Korth 2007; Hooker et al. 2008). However, some workers have proposed that certain Cretaceous taxa represent older representatives of Herpetotheriidae (Case et al. 2005; Martin et al. 2005). These putative Cretaceous herpetotheriids formed the basis for extending the origin of Herpetotheriidae to the Late Cretaceous by recent studies on the origins and relationships of Herpetotheriidae and crown-clade marsupials (Sánchez-Villagra et al. 2007; Horovitz et al. 2008). However, we note that neither *Swaindelphys* nor putative Cretaceous herpetotheriids have been included in the phylogenetic analyses accompanying these studies that would test these conclusions.

The morphology of *Swaindelphys* has important relevance to questions regarding the taxonomy of earliest Paleocene (Puercan) metatherians. Johanson (1996a) noted that the lower dentition of *Thylacodon pusillus* or taxa referred to *T. cf. T. pusillus*, closely resemble that of *Swaindelphys cifellii*. This might imply a possible close relationship between *Thylacodon* and *Swaindelphys* and would perhaps nullify the validity of *Thylacodon pusillus* as the holotype consists of a partial dentary with lower molars (see Clemens 2006). Others have suggested that *Thylacodon* is a synonym of *Peradectes* (Clemens 1979; Archibald 1982; Clemens 2006). The taxonomic validity of *Thylacodon* remains unresolved (e.g., Clemens 2006), and examining this issue is beyond the scope of this study. However, based on the new specimens described here, we are able to confirm that while the teeth of *S. encinensis* overlaps in size with those of *T. pusillus*, they differ significantly, especially in features of the molar talonid cusps. We find that the lower teeth of these taxa can be readily distinguished. This finding lends support to the suggestion that *Thylacodon* is a valid taxon (e.g., Krishtalka and Stucky 1983) rather than a synonym of *Swaindelphys*.

Peradectes coprexeches is the first peradectid metatherian to be described from Torrejonian age strata. However, a similar unidentified

metatherian is described from the Wagonroad locality of the North Horn Formation, central Utah (Tomida and Butler 1980) based on an isolated lower molar. This tooth is slightly larger than lower molars referred *P. coprexeches*. An undescribed metatherian is present from the Gidley Quarry of the Fort Union Formation, Crazy Mountain Field, Montana, based on a partial dentary with p3-m2 (AMNH 35956). Metatherians have not been reported in previous faunal summaries of the Gidley Quarry fauna (Rose 1981, table 39; Williamson 1996, table 7). This new occurrence suggests that peradectids were present and widespread throughout North America for at least part of the Torrejonian. We further suggest that their absence from many faunas is largely due to sampling biases due to their small size.

Based on the results reported here, all Nacimiento Formation early Paleocene (Torrejonian) metatherian taxa are restricted to the latter part of the Torrejonian (Figure 2). *Peradectes coprexeches* is limited to fossil horizons G and H of Williamson (Williamson 1996) and therefore is present only within the *Pantolambda cavirictum* – *Mixodectes pungens* and *Mixodectes pungens* zones of the Nacimiento Formation (latter part of To2-To3; Lofgren et al. 2004). *Swaindelphys johansonii* has been documented only in the *Pantolambda cavirictum* – *Mixodectes pungens* Zone and *S. encinensis* is reported only from the *Mixodectes pungens* Zone. Few microvertebrate localities are known for earlier Torrejonian sites of the Nacimiento Formation, and therefore the absence of small mammals such as metatherians from strata below fossil horizon G is likely due to collecting biases.

ACKNOWLEDGMENTS

We thank P. Hester and S. Landon of the U.S. Bureau of Land Management for permits and providing field assistance. We also thank U. Denetclaw, L.J. Flynn, R. Haskin, S. Libed, W. Slade, Y. Tomida, K. Tremaine, A. Weil, S. Williams, R. Williamson, and T. Williamson for field and lab assistance. Numerous personnel including R. Fox and C. Scott, of the University of Alberta, Edmonton, J. Meng and J. Galkin of the AMNH, F. Jenkins and J. Cundiff of the MCZ, Harvard, A. Henrici and A. Tabrum of the Carnegie Museum of Natural History, Pittsburgh, P. Holroyd, W. Clemens of the UCMP, E.H. Lindsay of the University of Arizona, and D. Bohaska of the National Museum of Natural History, Washington, D.C. provided discussion,

hospitality, and access to specimens, and for that we are grateful. We thank K. Davies and R. Cifelli, University of Oklahoma, Norman, for casting and M. Spilde, University of New Mexico for assistance with the SEM. T.D. Carr provided discussion and important feedback on an earlier draft. This research was supported by an NSF grant (EAR 0207750 To TEW).

REFERENCES

- Archibald, J.D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. *University of California Publications in Geological Sciences*, 122:1-286.
- Case, J.A., Goin, F.J., and Woodburne, M.O. 2005. "South American" marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. *Journal of Mammalian Evolution*, 11:223-255.
- Cifelli, R.L., Madsen, S.K., and Larson, E.M. 1996. Screenwashing and associated techniques for the recovery of microvertebrate fossils. *Oklahoma Geological Survey Special Publication 96-4*:1-24.
- Clemens, W.A. 1979. Marsupialia, p. 192-220. In Lillegraven, J.A., Kielan-Jaworowska, Z., and Clemens, W.A. (eds.), *Mesozoic Mammals, the First Two-thirds of Mammalian History*. University of California Press, Berkeley, California.
- Clemens, W.A. 2006. Early Paleocene (Puercan) peradectid marsupials from northeastern Montana, North American Western Interior. *Palaeontographica Abteilung A*, 27:19-31.
- Clemens, W.A., Jr. 1966. Fossil mammals of the type Lance Formation, Wyoming; Part II, Marsupialia. *University of California Publications in Geological Sciences*, 62:1-122.
- Crochet, J.Y. 1979. Diversité systématique des Didelphidae (Marsupialia) Européens Tertiaires. *Géobios*, 12:365-378.
- Crochet, J.Y. 1980. Les Marsupiaux du tertiaire d'Europe. *Éditions de la Fondation Singer-Polignac*, Paris, France.
- Davis, B.M. 2007. A revision of "pediomyid" marsupials from the Late Cretaceous of North America. *Acta Palaeontologica Polonica*, 52:217-256.
- Eaton, J.G. 2006. Late Cretaceous mammals from Cedar Canyon, southwestern Utah. *New Mexico Museum of Natural History and Science Bulletin*, 35:373-402.
- Eaton, J.G., Diem, S., Archibald, J.D., Schierup, C., and Munk, H. 1999. Vertebrate paleontology of the Upper Cretaceous rocks of the Markagunt Plateau, southwestern Utah, p. 323-333. In Gillette, D.D. (ed.), *Vertebrate Paleontology in Utah*. Utah Geological Survey, Salt Lake City, Utah.
- Gazin, C.L. 1956. Paleocene mammalian faunas of the Bison Basin in South-Central Wyoming. *Smithsonian Miscellaneous Collections*, 131:1-57.

- Heller, F. 1936. Neue Beuteltierreste aus der mitteleuropäischen Braunkohle des Geiseltales bei Halle (Saale). *Nova Acta Leopoldina*, 4:311-316.
- Hooker, J.J., Sanchez-Villagra, M.R., Goin, F.J., Simons, E.L., Attia, Y., and Seiffert, E.R. 2008. The origin of Afro-Arabian 'didelphimorph' marsupials. *Palaeontology*, 51:635-648.
- Horovitz, I., Ladeveze, S., Argot, C., Macrini, T.E., Martin, J.E., Hooker, J.J., Kurz, de Muizon, C., and Sánchez-Villagra, M.R. 2008. The anatomy of *Herpetotherium* cf. *fugax* Cope, 1873, a metatherian from the Oligocene of North America. *Palaeontographica (A)*, 284:109-141.
- Horovitz, I., Martin, T., Bloch, J.I., Ladevèze, S., Kurz, C., and Sánchez-Villagra, M.R. 2009. Cranial Anatomy of the earliest Marsupials and the origin of opossums. *PLoS ONE*, 4:e8278.
- Johanson, Z. 1996a. New marsupial from the Fort Union Formation, Swain Quarry, Wyoming. *Journal of Paleontology*, 70:1023-1031.
- Johanson, Z. 1996b. Revision of the Late Cretaceous North American marsupial genus *Alphadon*. *Palaeontographica Abteilung A*, 242:127-184.
- Korth, W.W. 2007. Marsupialia, p. 39-47. In Janis, C.M., Gunnell, G.F., and Uhen, M.D. (eds.), *Evolution of Tertiary Mammals of North America, Vol. 2*. Cambridge University Press, Cambridge, UK.
- Krishtalka, L. and Stucky, R.K. 1983. Paleocene and Eocene marsupials of North America. *Annals of Carnegie Museum*, 52:229-263.
- Kuiper, K.F., Deino, A., Hilgen, F.J., Krijgsman, W., Renne, P.R., and Wijbrans, J.R. 2008. Synchronizing rock clocks of Earth history. *Science*, 320:500-504.
- Lillegraven, J.A. 1969. Latest Cretaceous mammals of the upper part of Edmonton Formation of Alberta, Canada, and review of Marsupial-Placental dichotomy in mammalian evolution. *The University of Kansas Paleontological Contributions*, 12:1-122.
- Lofgren, D.L., Lillegraven, J.A., Clemens, W.A., Gingerich, P.D., and Williamson, T.E. 2004. Paleocene biochronology; the Puercan through Clarkforkian land mammal ages, p. 43-105. In Woodburne, M.O. (ed.), *Late Cretaceous and Cenozoic mammals of North America*. Columbia University Press, New York, New York.
- Martin, J.E., Case, J.A., Jagt, J.W.M., Schulp, A.S., and Mulder, E.W.A. 2005. A new European marsupial indicates a Late Cretaceous high-latitude transatlantic dispersal route. *Journal of Mammalian Evolution*, 12:495-511.
- Matthew, W.D., and Granger, W. 1921. New genera of Paleocene mammals. *American Museum Novitates*, 13:1-13.
- Rose, K.D. 1981. The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. *University of Michigan Papers on Paleontology*, 26:1-197.
- Rothecker, J., and Storer, J.E. 1996. The Marsupials of the Lac Pelletier Lower Fauna, Middle Eocene (Duchesnean) of Saskatchewan. *Journal of Vertebrate Paleontology*, 16:770-774.
- Sánchez-Villagra, M., Ladeveze, S., Horovitz, I., Macrini, T.E., Martin, J.E., Morre-Fay, S., De Muizon, C., Schmeizle, T., and Asher, R.J. 2007. Exceptionally preserved North American Paleogene metatherians: Adaptations and discovery of a major gap in the opossum fossil record. *Biological Letters*, 3:318-322.
- Standhardt, B.R. 1980. *Early Paleocene mammals of the Black Toe Local Fauna, Nacimiento Formation, New Mexico*, Unpublished M.S. Thesis, The University of Arizona, Tucson, Arizona, USA.
- Stock, C. 1936. Sespe Eocene didelphids. *Proceedings of the National Academy of Sciences*, 22:122-124.
- Taylor, L.H. 1984. *Review of Torrejonian mammals from the San Juan Basin, New Mexico*. Unpublished Ph.D. Thesis, The University of Arizona, Arizona, USA. Tucson.
- Tomida, Y. and Butler, R.F. 1980. Dragonian mammals and Paleocene magnetic polarity stratigraphy, North Horn Formation, central Utah. *American Journal of Science*, 280:787-811.
- Trouessart, E. -L. 1879. Catalogue des mammifères vivants et fossiles. *Revue et Magasin de Zoologie*, 7:219-285.
- Williamson, T.E. 1993. *The beginning of the age of mammals in the San Juan Basin; biostratigraphy and evolution of Paleocene mammals of the Nacimiento Formation*. Unpublished Ph.D. Thesis, University of New Mexico, Albuquerque, New Mexico, USA.
- Williamson, T.E. 1996. The beginning of the age of mammals in the San Juan Basin, New Mexico; biostratigraphy and evolution of Paleocene mammals of the Nacimiento Formation. *New Mexico Museum of Natural History and Science Bulletin*, 8:1-141.
- Williamson, T.E., Hester, P.M., and Bednarski, S.P. 2006. Transfer of UALP San Juan Basin vertebrate collection to the NMMNH. *New Mexico Geology*, 28:62-63.
- Williamson, T.E. and Lucas, S.G. 1992. Stratigraphy and mammalian biostratigraphy of the Paleocene Nacimiento Formation, southern San Juan Basin, New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 43:265-296.