A New Puercan (Early Paleocene) Hyopsodontid “Condylarth” from New Mexico

Authors: Williamson, Thomas E., and Weil, Anne

Source: Acta Palaeontologica Polonica, 56(2) : 247-255

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.0147

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne’s community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne’s Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 07 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

A new Puercan (early Paleocene) hyopsodontid “condylarth” from New Mexico

THOMAS E. WILLIAMSON and ANNE WEIL

Williamson, T.E. and Weil, A. 2011. A new Puercan (early Paleocene) hyopsodontid “condylarth” from New Mexico. *Acta Palaeontologica Polonica* 56 (2): 247–255.

Isolated cheek teeth from the late Puercan (early Paleocene) Split Lip Flats local fauna, from the head of Willow Wash, Nacimiento Formation, San Juan Basin, represent a new genus and species of hyopsodontid “condylarth”, *Chacomylus sladei*. The teeth are small, bunodont, and are remarkable for the enlargement of the protocone, pronounced exodaenodonty, and high degree of attritional wear caused by transverse shearing or grinding. Although *C. sladei* bears a superficial resemblance to the apheliscine apheliscid *Gingerichia*, a preliminary phylogenetic analysis confirms that it is a hyopsodontid, closely related to the Puercan hyopsodontids *Valenia wilsoni* and *Litomylus orthronepius*.

Key words: Mammalia, Condylartha, Hyopsodontidae, Puercan, Paleocene, Nacimiento Formation, New Mexico.

Thomas E. Williamson [thomas.williamson@state.nm.us], New Mexico Museum of Natural History and Science, 1801 Mountain Rd, NW, Albuquerque, NM 87104;
Anne Weil [anne.weil@okstate.edu], Oklahoma State University Center for Health Sciences, Department of Anatomy and Cell Biology, 1111 West 17th St., Tulsa, OK 74107-1898.

Received 9 December 2009, accepted 2 August 2010, available online 16 August 2010.

Introduction

The Nacimiento Formation of the San Juan Basin, northwestern New Mexico, contains the most diverse early Paleocene mammal assemblages in the world (Williamson 1996). Efforts to collect fossil mammals from these deposits have a long history, extending over 125 years. Rich faunas from near the base of the Nacimiento Formation form the basis for the middle and late interval zones of the Puercan (Pu2–3) North American Land Mammal Age (NALMA). A new late Puercan locale was recently discovered near the head of Willow Wash (Fig. 1), north of the classic late Puercan locales of Barrel Springs and De-na-zin Wash and southeast of late Puercan locality of Gallegos Canyon (Lucas 1984). The local fauna from this locale was termed the Split Lip Flats Local Fauna (Williamson and Weil 2002; Williamson et al. 2011). Underwater screenwashing of this locale, NMMNH localities L-4723 and 4725 (precise locality information on file at the NMMNH), resulted in the recovery of many isolated teeth representing multituberculate, eutherian, and metatherian mammals. Here we report on a new genus and species of hyopsodontid “condylarth” (Archibald 1998) from the Split Lip Flats Local Fauna. The new taxon is remarkable for its small size relative to other hyopsodontids and for its unique combination of dental characters.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; KU, University of Kansas, Lawrence, USA; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; UALP, University of Alberta Laboratory of Palaeontology, Edmonton, Canada; UCMP, University of California, Museum of Paleontology, Berkeley, USA.

Other abbreviations.—cc, centrocrista; co, cristid obliqua; DW, distal width; ecg, ectocingulum; encd, entocristid; end, entoconid; etx, ectoflexus; hy, hypocone; hyd, hypoconid; hyld, hypoconulid; hyxd, hypoflexid; L, length; me, metacone; mec, postmetacrista; med, metaconid; msl, metastylar lobe; mtl, metaconule; MW, mesial width; pa, paracone; pac, preparacrista; pacd, paracristid; pad, paraconid; pmlc, premetaconule crista; prc, precingulum; prl, paraconule; pprc, preprotocrista; ps, parastyle; pscg, postcingulum; psl, parastylar lobe; psplc, postparaconule crista; psprc, postprotocrista; pplc, preparaconule crista; pr, protocone; prcd, protocristid; prd, protoconid; ps, parastyle; pscg, postcingulid; psl, parastylar lobe; psmlc, postmetaconular crista; st, stylocone; sts, stylar shelf; tb, talon basin; tdb, trigonid basin; tlb, talonid basin; W, Width.

Material and methods

Tooth nomenclature (Fig. 2) follows Szalay (1969). All measurements are in mm and made to the nearest 0.05 mm using a Wild^{TM} measuring reticule and a Leica^{TM} MZ 6 microscope.

Acta Palaeontol. Pol. 56 (2): 247–255, 2011

doi:10.4202/app.2009.0147

Systematic paleontology

Order "Condylarthra" Cope, 1881

Family Hyopsodontidae Trouessart, 1879

Genus *Chacomylus* nov.

Etymology: Chaco, for Chaco Canyon of the San Juan Basin, New Mexico, and Latin mylus, millstone or grinder.

Type species: *Chacomylus sladei* sp. nov., only known species. Nacimiento Formation, Puercan, Paleocene, Willow Wash, San Juan Basin, New Mexico.

Diagnosis.—as for the type and only species.

Stratigraphic and geographic range.—As for the type and only known species.

Chacomylus sladei sp. nov.

Figs. 3–5, Table 1.

Etymology: In recognition of Warren Slade, long-time NMMNH volunteer and his contributions to New Mexico paleontology.

Holotype: NMMNH P-41208, right M1.

Type locality: NMMNH locality L-4723, head of Willow Wash, San Juan Basin, northwestern New Mexico.

Type horizon: Fossil horizon B (Williamson 1996), Nacimiento Formation (late Puercan, Pu3).

Material.—NMMNH P-34804, right P4; 38461, left P4; 44353, left M3; 51537, right partial M2; left p3?; 44345, right m2; 55397, left m3.

Diagnosis.—Similar to hyopsodontid and apheliscid "condylarths" (sensu Zack et al. 2005) in its small size and bunodont cheek teeth with a lower molar talonid that is at least about two-thirds the height of the trigonid. Similar in size to *Tiuclaenus minutus*, but smaller than other hyopsodontids (Table 1). Differs from all hyopsodontids (the upper dentition is unknown for *Tiznatzinia*, *Bomburia* unless *Platymastus palantir* is a synonym, see Williamson and Carr [2007], and *Oxytomodon*) by its lack of a P4 parastyle, rela-

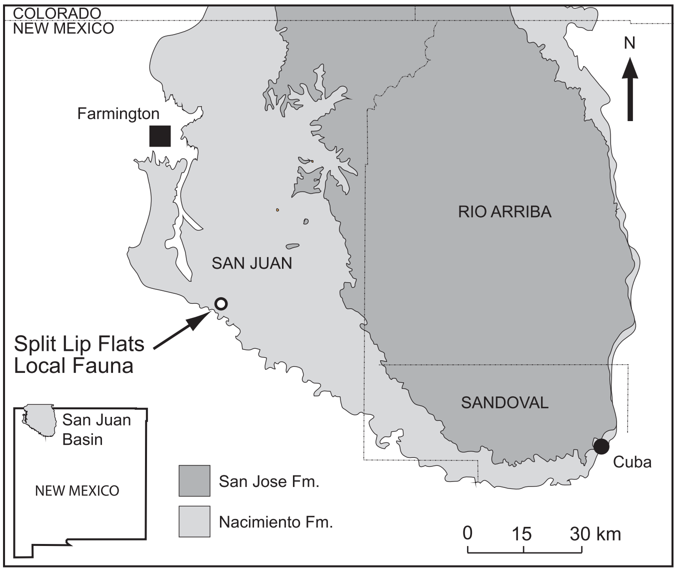

Fig. 1. Geologic map showing the the Paleocene Nacimiento Formation (Animas Formation in southern Colorado) and early Eocene San Jose Formation, San Juan Basin, New Mexico, and indicating the location of the Split Lip Flats Local Fauna.

Table 1. Measurements (in mm) of *Chacomylus sladei* gen. et sp. nov.

		L	MW	DW
P4	NMMNH P-34804	2.35	3.25	
	NMMNH P-38461	2.50	2.95	
M1	NMMNH P-41208 (holotype)	2.80	4.00	3.95
M2	NMMNH P-51537	–	4.00	4.00
M3	NMMNH P-44353	1.85	3.20	2.50
p3?	NMMNH P-34838	2.15	1.55	
m2	NMMNH P-44345	2.60	2.25	2.15
m3	NMMNH P-55397	2.80	1.90	1.65

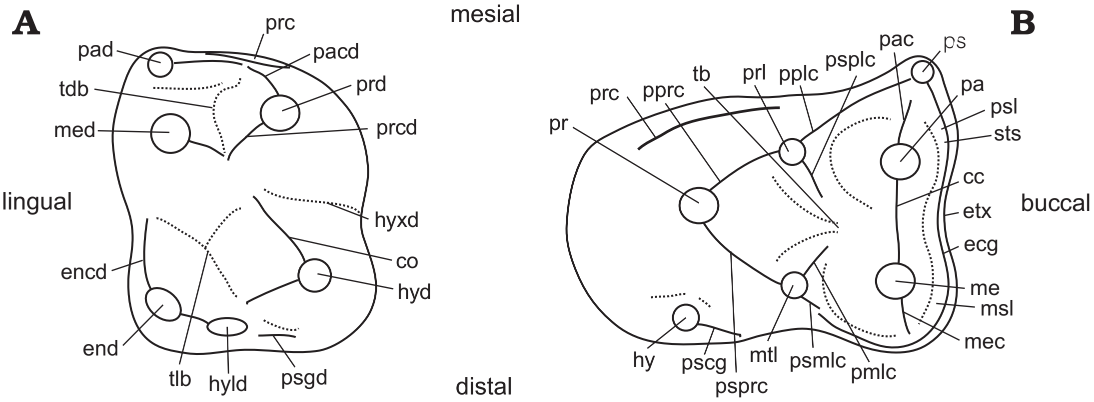

Fig. 2. Outlines of right lower molar (**A**) and left upper molar (**B**) of *Chacomylus sladei* gen. et sp. nov. showing tooth nomenclature used in the text. Abbreviations.—cc, centrocrista; co, cristid obliqua; ecg, ectocingulum; encd, entocristid; end, entoconid; etx, ectoflexus; hy, hypocone; hyd, hypoconid; hyld, hypoconulid; hyxd, hypoflexid; me, metacone; mec, postmetacrista; med, metaconid; msl, metastylar lobe; mtl, metaconule; pa, paracone; pac, preparacrista; pacd, paracristid; pad, paraconid; pmlc, premetaconule crista; prc, precingulum; prl, paraconule; pprc, preprotocrista; ps, parastyle; pscg, postcingulum; psl, parastylar lobe; psplc, postparaconule crista; psprc, postprotocrista; pplc, preparaconule crista; pr, protocone; prcd, protocristid; prd, protoconid; ps, parastyle; pscg, postcingulid; psl, parastylar lobe; psmlc, postmetaconular crista; st, stylocone; sts, stylar shelf; tb, talon basin; tdb, trigonid basin; tlb, talonid basin.

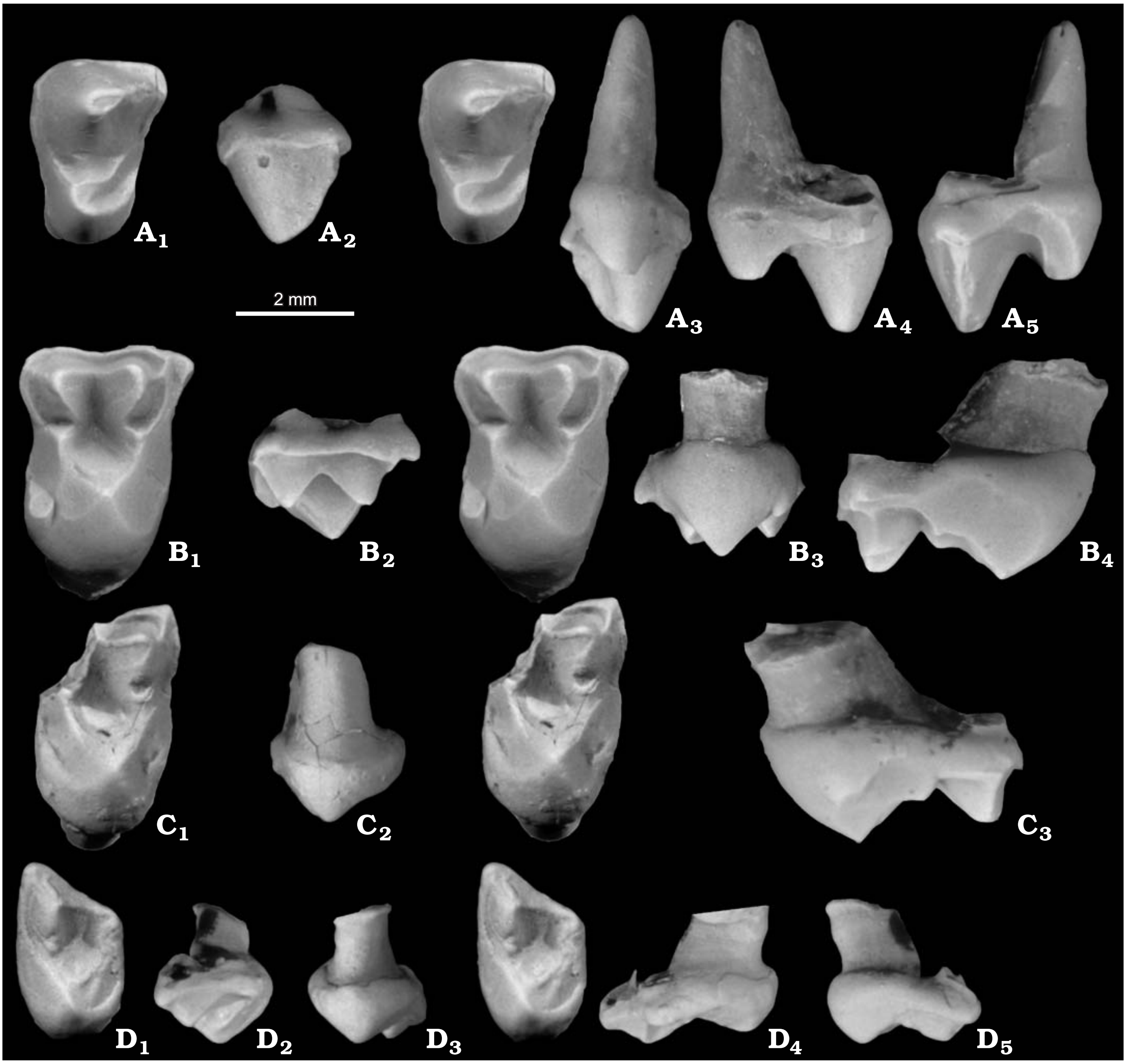

Fig. 3. Upper dentition of the hyopsodontid "condylarth" *Chacomylus sladei* gen. et sp. nov., Nacimiento Formation, lower Paleocene (late Puercan, Pu3), San Juan Basin, New Mexico. **A**. NMMNH P-38461, left P4 in occlusal (A_1, stereopair), buccal (A_2), lingual (A_3), mesial (A_4), and distal (A_5) views. **B**. 41208 (holotype), right M1 in occlusal (B_1, stereopair), buccal (B_2), lingual (B_3), mesial (B_4), and distal (B_5) views. C. 51537, left partial M2? in occlusal (C_1, stereopair), and lingual (C_2) views. **D**. 44353, left M3 in occlusal (D_1, stereopair), buccal (D_2), lingual (D_3), mesial (D_4), and distal (D_5) views.

tively more transverse upper molars, and larger protocones. Differs in lower molar morphology from all hyopsodontids, except *Litomylus orthronepius* and *Oxytomodon*, in possessing lower molar exodaenodonty. Differs from *Litomylus orthronepius* in having narrower molar stylar shelves and relatively wider molars. Differs from *Oxytomodon* in having a more transverse orientation of the distal wall of the trigonid and in having an entocristid that closes the talonid basin lingually. Differs from all hyopsodontids in having development of wear facets that indicates greater enhancement of transverse shearing during mastication. Differs from apheliscids in having the upper molar postcingulum higher above the base of the crown than the precingulum, a relatively less developed hypocone, molar paraconid is lingually positioned, basally fused with, and closely appressed to, the metaconid, and the hypoconulid is lingual to the midline of the tooth and basally fused to the entoconid.

Description.—*Chacomylus sladei* is known only from isolated teeth. The isolated teeth described in this report are referred to *Chacomylus sladei* based on size, morphology, pat-

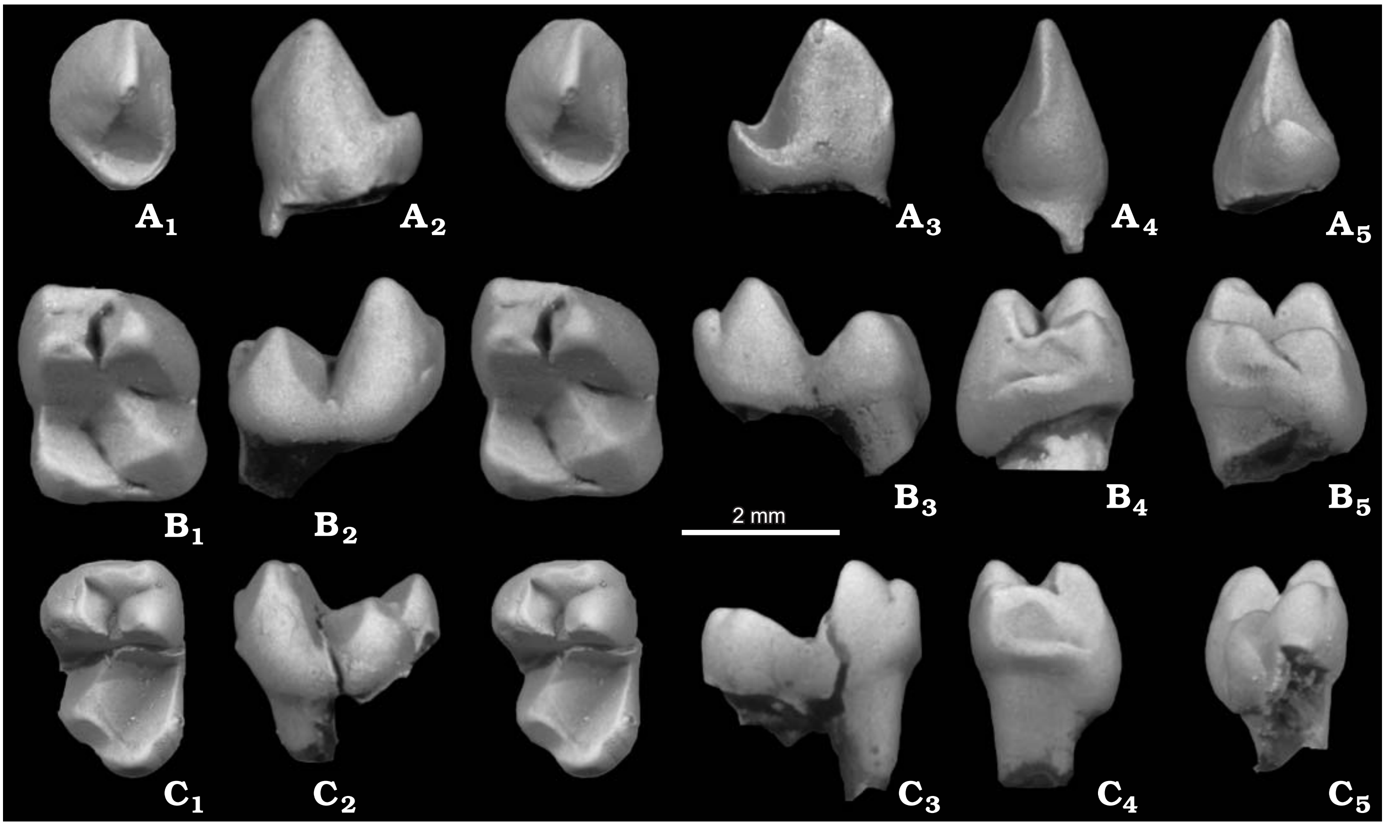

Fig. 4. Lower dentition of hyopsodontid "condylarth" *Chacomylus sladei* gen. et sp. nov., Nacimiento Formation, lower Paleocene (late Puercan, Pu3), San Juan Basin, New Mexico. **A**. NMMNH P-34838, left p3? in occlusal (A_1, stereopair), buccal (A_2), lingual (A_3), mesial (A_4), and distal (A_5) views. **B**. 44345, right m2 in occlusal (B_1, stereopair), buccal (B_2), lilngual (B_3), mesial (B_4), and distal (B_5) views. **C**. 55397, left m3 in occlusal (C_1, stereopair), buccal (C_2), lingual (C_3), mesial (C_4), and distal (C_5) views.

terns of attritional wear, and occlusal fit. The upper dentition is represented by two P4's, an M1, a probable M2, and an M3. The lower dentition is represented by an isolated premolar, probably a p3, an m2, and an m3.

P4.—The P4 (Fig. 3A) is wider than long. The paracone is the tallest cusp and is elongated mesiodistally. A smaller swelling on the crest descending distally from the paracone likely represents the metacone. A low ectocingulum bounds the tooth buccally and widens distally. Mesially, the ectocingulum is narrow. The P4 lacks a parastyle. The protocone is distinct and separated from the paracone by a cleft. A low preprotocrista extends mesiobuccally to the mesial base of the paracone. On the distal face of the protocone, wear has breached the enamel, forming an elongate exposure of dentine ringed by enamel that extends distobuccally. The remnant of a narrow postcingulum is present lingual to this facet on the distal face of the protocone. This obliterates any evidence of a metaconule, if one was originally present. A paraconule is not developed.

M1.—The M1 (Fig. 3B) is wider than long. The paracone and metacone are subequal in size, closely spaced, and partially fused at their base. The stylar shelf is undeveloped, with only the low ectocingulum bordering the buccal margin of the crown. The parastylar lobe extends mesially and the parastyle has been beveled by wear. The paraconule and metaconule are subequal in size and positioned close to the paracone and metacone. The protocone is large and subequal in height to the para- and metacone. A hypocone is present as a distinct cusp distal to the apex of the protocone. The postmetaconule crista extends to the metastyle. The postcingulum terminates lingual to the metaconule.

Planar wear facets have beveled the mesial and distal sides of the protocone. Similar facets have also truncated the distal face of the paracone and the mesial face of the metacone, forming a V-shaped notch into the centrocrista; the original shape and orientation of the centrocrista have been obliterated. A precingulum may have been present, but this can no longer be determined because of wear to this region of the tooth.

M2.—A probable M2 (Fig. 3C), missing the metacone and distobuccal corner of the tooth, is represented by NMMNH P-51537. It is similar to the M1, but differs in that the pre- and postcingulum are not completely obliterated by wear. The precingulum originates lingually at a position buccal to the apex of the protocone. It is significantly lower on the protocone than the postcingulum. The postcingulum is expanded distal to the apex of the protocone, but does not support a distinct hypocone. The paracrista extends mesiobuccally from the paracone to the stylocone near the mesio-

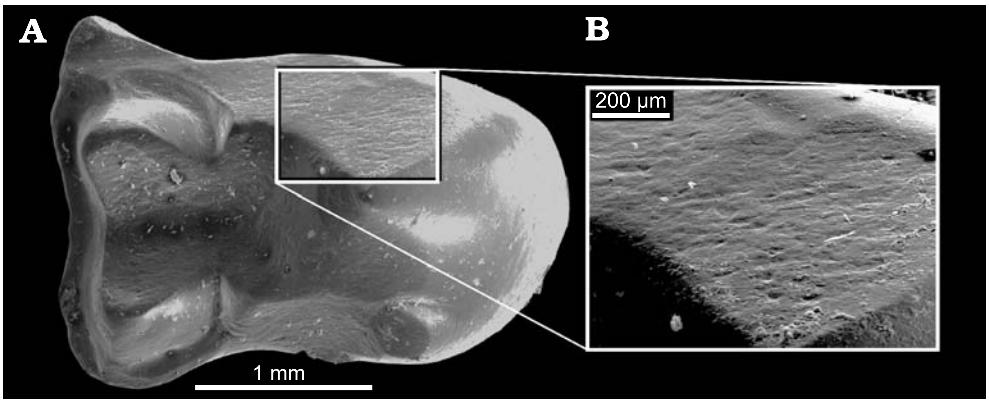

Fig. 5. The hyopsodontid “condylarth” *Chacomylus sladei* gen. et sp. nov., Nacimiento Formation, lower Paleocene (late Puercan; Pu3), San Juan Basin, New Mexico, a cast of the holotype (NMMNH P-41208). **A**. Electron micrograph a right M1, showing details of the 3(5) wear facet following (Hunter and Fortelius 1994) on the mesial face of the protocone (enlarged in **B**).

buccal corner of the tooth. A transverse groove caused by wear separates the stylocone from what may be the parastyle positioned mesial to the paracone. This groove has at least partially obliterated the stylocone and parastyle.

M3.—The M3 (Fig. 3D), represented by NMMNH P-44353, is smaller than both M1 and M2. The width of the M3 is reduced distally and the metacone is much smaller than the paracone. The distal margin of the protocone is expanded. A paraconule is present and positioned close to the paracone. A wear facet on the posterior face of the protocone that extends buccally to the metacone has largely erased evidence for a metaconule.

p3.—NMMNH P-34838 is tentatively identified as a p3 (Fig. 4A). The crown is bulbous and dominated by the protoconid; a preprotocristid descends mesially from the protoconid, terminating above the swollen base of the crown. A paraconid is not present. Distally, the tooth supports a small talonid basin that lacks distinct cuspids. A ridge extends distobuccally from the protoconid to form the buccal margin of this basin. A small talonid basin is bounded buccally, distally, and lingually by a raised ridge.

m2.—The m2 (Fig. 4D) is nearly rectangular in occlusal view. The trigonid is low so that the talonid is about two-thirds its height The protoconid and metaconid are rounded and subequal in size. The paraconid is high (sensu Zack et al. 2005), lingual and closely appressed to the metaconid, with its base fused to that of the metaconid. The distal wall of the trigonid is strongly worn so that it is oriented nearly transverse. However, we suspect that the distal wall of the metaconid was originally more distally positioned than that of the protoconid and some of it has been removed by wear. The talonid is subequal in width to the trigonid. The hypoconid is the largest of the talonid cuspids followed by the entoconid and the hypoconulid. The talonid is closed lingually by an entocristid that terminates mesially at the base of the metaconid. The hypoconulid is positioned lingual to the midline of the tooth, closely coupled with the entoconid. A distinct notch separates the hypoconulid from the hypoconid. The cristid obliqua intersects the trigonid below the protocristid notch. The tooth is exodaenodont, with the buccal sides of both the trigonid and talonid inflated and overhanging the buccal surfaces of the roots. A small precingulid extends buccally from the hypoconulid and terminates below the hypoconid. A lingual cingulid is not present. A small cuspid in the hypoflexid represents a remnant of the ectocingulid. The distal face of the trigonid and the mesial face of the hypoconid, buccal to the cristid obliqua (wear facets 1 and 3, respectively; sensu Crompton and Kielan-Jaworowska 1978), are heavily worn, with the angle formed between these two planar surfaces closely matching the profile of the M1 paracone and protocone as seen in buccal view (Fig. 3G).

m3.—The single known m3 (NMMNH P-55397; Fig. 4C) closely resembles the m2, but is narrower. The talonid is narrower than the trigonid and more elongate. The hypoconulid is relatively larger and extends further distally.

Discussion

Zack et al. (2005) discussed the difficulty in classifying many early Paleocene mammals that are small and have bunodont teeth. Many of these taxa, like *Chacomylus sladei*, are represented only by dental remains. In addition, several clades such as hyopsodontid “condylarths”, erinaceomorph lipotyphlans, and pentacodontid pantolestans converge in dental morphology (see Zack et al. 2005). *C. sladei* shows similarities in dental morphology to both hyopsodontid and apheliscid “condylarths”.

Chacomylus sladei is significantly smaller (Table 1) than any hyopsodontid (sensu Zack et al. 2005) with the exception of the early Paleocene, South American *Tiuclaenus minutus* (Muizon and Cifelli 2000: tables 4, 5) which is only slightly smaller. *T. minutus* is about 97% the size of *C. sladei*, based on length of m2. The upper and lower molars of *C. sladei* fall near or within the size range of the apheliscids *Gingerichia geo-*

doi:10.4202/app.2009.0147

teretes and *Gingerichia hystrix* (Zack et al. 2005). This is about 75% the size of *Promioclaenus acolytus* which is among the smallest of early Paleocene hyopsodontids, and is similar in size to the smallest specimens of the periptychid *Oxyacodon agapetillus*, previously the smallest "condylarth" documented from the Nacimiento Formation of New Mexico (Archibald et al. 1983).

Chacomylus sladei possesses a unique combination of dental characters that clearly distinguish it from other mammals. It is grossly similar to a number of approximately contemporaneous hyopsodontid and apheliscid "condylarths" (sensu Zack et al. 2005). However there are a number of significant differences. For example, the P4 lacks a parastyle, a condition that is not known for any hyopsodontid (the P4 is not known for a number of hyopsodontid taxa including *Oxytomodon*, *Tiznatzinia*, *Litomylus orthronepius*, and *Bubogonia saskia*), but it is relatively small in *Choeroclaenus*. *Chacomylus* lacks the relatively large size and inflation of the P4 found in a number of hyopsodontids and apheliscids (e.g., *Choeroclaenus*, *Mioclaenus*, *Gingerichia*, *Phenacodaptes*). In these taxa, the enlarged and swollen P4 is consistently associated with a relatively large and inflated p4. Therefore, we predict that the p4 of *Chacomylus* is relatively small, probably smaller than the m1. The upper molars of *Chacomylus* have a narrow stylar shelf consisting of an ectocingulum similar to that of other Puercan hyopsodontids such as *Valenia*. It is distinctly narrower than that of *Litomylus orthronepius*. The paracone and metacone are subequal and spaced close together so that their bases are partly conjoined. This is different than is seen in other hyopsodontid or apheliscid "condylarths" in which the bases of the paracone and metacone are usually separated by a cleft lingual and buccal to the centrocrista. Extensive wear over this area of the upper molars of *Chacomylus* make examination of the centrocrista impossible, however in buccal view (Fig. $3B_2$) the paracone and metacone are clearly merged significantly above the level of the ectocingulum. Both the M1 and partial M2 of *Chacomylus* show heavy wear that has obliterated much of the details of the conular region. The M1 and M2 bear large protocones that are broadly expanded lingually so that the tooth maintains a near constant mesiodistal length from a position below the protocone apex to a position at the lingual bases of the para- and metacone. Most hyopsodontids and apheliscids widen buccally, giving the teeth a more triangular shape in occlusal view, or much of the lingual expansion of the tooth is due to the linguodistal expansion of the postcingulum and hypocone rather than the protocone itself. The relative sizes of the molar protocones are similar to that of *Litaletes*, but the upper molars of *Chacomylus* are more transverse. The anterior cingulum, only visible on the partial M2 in *Chacomylus*, resembles that of hyopsodontids in being lower than the postcingulum rather than rising from the same level on the base of the protocone as in apheliscids. The M3 of *Chacomylus* is about two-thirds the size of the M1 and similar in relative size to that of the hyopsodontid *Promioclaenus.* The p3 of *Chacomylus*, if the referral of NMMNH P-44345 is correct, differs from *Bomburia*, *Valenia* and *Choeroclaenus* (the p3 is unknown for *Tiznatzinia*) in lacking a paraconid and in having a featureless talonid, lacking a medial ridge. The lower molars show a similar relative size of m3 and m2 (m3 L/m2 L of *Promioclaenus lemuroides* is 0.98; TEW unpublished data), but the m3 of *Chacomylus* is slightly larger, with a length that exceeds that of m2 (m3 L/m2 L of *Chacomylus* is 1.08; Table 1). The p3 is similar in shape and in size relative to the m2 as that of the hyopsodontid *Litaletes*, but differs in being more basally inflated, and in lacking a paraconid and talonid cusps. The lower molars of *Chacomylus* are strikingly similar to those of *Haplaletes disceptatrix*. They are similar in length and width, show similar relative height and width of the trigonids and talonids, and similar size and position of most of the cusps. In addition, the distal wall of the trigonid shows a similar nearly transverse orientation and inclination. The talonid is also similar, except that the hypoconulid and entoconulid of *Chacomylus* are more confluent and are not separated by a distinct notch (see Zack et al. 2005: fig. 7). The entocristid is similar in that it extends mesially to the base of the metaconid to close off the lingual margin of the talonid basin. This is in contrast to the condition seen in most hyopsodontids (*Mioclaenus* is an exception) in which the entocristid terminates distal to the base of the metaconid, leaving a narrow, V-shaped opening in lingual view. Lower molars are also similar in the degree of distension of buccal enamel. However, the lower molars of *Chacomylus* differ from those of *H. disceptatrix* in several important ways; as in other aphelsicids, *H. disceptatrix* lacks a lingually positioned paraconid perched high on the mesial edge of the metaconid, and it bears strong ectocingulids that extend completely across the buccal margins of the lower molars. The poorly known *Oxytomodon perissum* is also similar to *Chacomylus* and possesses a similar degree of exodaenodonty, but differs in the more oblique orientation of the distal wall of the trigonid, and in the shape and orientation of the entocristid which extends mesially to a position near the lingual base of the metaconid rather than directly to its distal base.

Phylogenetic analysis

Zack et al. (2005) revised the Hyopsodontidae and Apheliscidae based on the results of a phylogenetic analysis of 27 small-bodied "condylarths" from the Paleogene of western North America and Europe using a combination of 59 dental and postcranial (mostly tarsal) characters (Zack et al. 2005: appendix 3). Based on this analysis, Zack et al. (2005) identified several phylogenetically informative dental features in both the Apheliscidae and Hyopsodontidae.

As a preliminary examination of the phylogenetic relationship of *Chacomylus* and in order to test for its relationship with the Apheliscidae and Hyopsodontidae, we scored *Chacomylus sladei* for the character states provided in Zack et al. (2005: appendix 2). *Chacomylus sladei* was not scored for the lower premolars because of uncertainty regarding the identification and loci of the single lower premolar tentatively referred to this taxon. In addition, we included two small Puercan (early Paleocene) hyopsodontid or apheliscid taxa, *Litomylus orthronepius*, from the Rav W-1 locality of southern Saskatchewan and *Valenia wilsoni*, a hyopsodontid from New Mexico and Wyoming. The scorings of these taxa are provided in Appendix 1.

Zack et al. (2005) performed their parsimony analysis using NONA v2.0 (Goloboff 1999). We ran the same analysis (including the pentacodontid *Aphronorus* spp.; characters unordered; Zhelestidae was used as the outgroup taxon) using TNT (Goloboff et al. 2008), using first a new technology search (using sectorial search, rachet, drift, and tree fusing) as a driven search, finding the minimum length ten times. Maximum trees was set at 50,000. This was followed by a traditional search of the resulting starting trees from RAM using a tree bisection reconnection (TBR) swapping algorithm. This resulted in two most parsimonius trees, five fewer than obtained by Zack et al. (2005), with a minimum length of 197 (CI: 0.391; RI: 0.632), one step longer than the shortest trees obtained by Zack et al. (2005) with similar CI and RI values. The resulting consensus tree is similar to that obtained by Zack et al. (2005: fig. 8A), but *Aphronorus* spp. is basal to *Protungulatum*.

We then revised the scoring of one taxon from the original Zack et al. (2005) character-taxon matrix, finding that the apheliscid *Litomylus dissentaneous* has “weak” (1) distention of the enamel on buccal side of lower molars (character 8) rather than “absent” (0) exodaenodonty. The results of our analysis with the revised character-taxon matrix resulted in two trees with a minimum length of 207 and significantly higher CI (0.786) and RI (0.936) values. However, the topology of the strict consensus tree is the same.

With the addition of *Chacomylus*, *Litomylus orthronepius*, and *Valenia wilsoni* two most parsimonious trees were found with a minimum length of 207 (CI: 0.372; RI: 0.601). The strict consensus tree (Fig. 6) resembles that of Zack et al. (2005: fig. 8A), with *Chacomylus*, *Litomylus orthronepius*, and *Valenia wilsoni* occupying a position as the sister to *Molinodus*, near the base of the Hyopsodontidae.

This phylogenetic analysis upholds a monophyletic Hyopsodontidae and Apheliscidae as revised by Zack et al. (2005). However, we find that these nodes are poorly supported (Bremer values of 1; Fig. 6). We also conclude that *Chacomylus sladei* is a hyopsodontid near the poorly known *Litomylus orthronepius*. Two of the three characters that are synapomorphies uniting the Hyopsodontidae (Fig. 6, node B) are tarsal characters (characters 51 and 58; Appendix 2) that are unknown for *Valenia wilsoni*, *Litomylus orthronepius*, and *C. sladei*. In addition, the single character that unites *Molinodus* and *Valenia* + (*L. orthronepius* + *Chacomylus sladei*) is unknown for *L. orthronepius* + *Chacomylus sladei*. Therefore, we consider these results to be tentative.

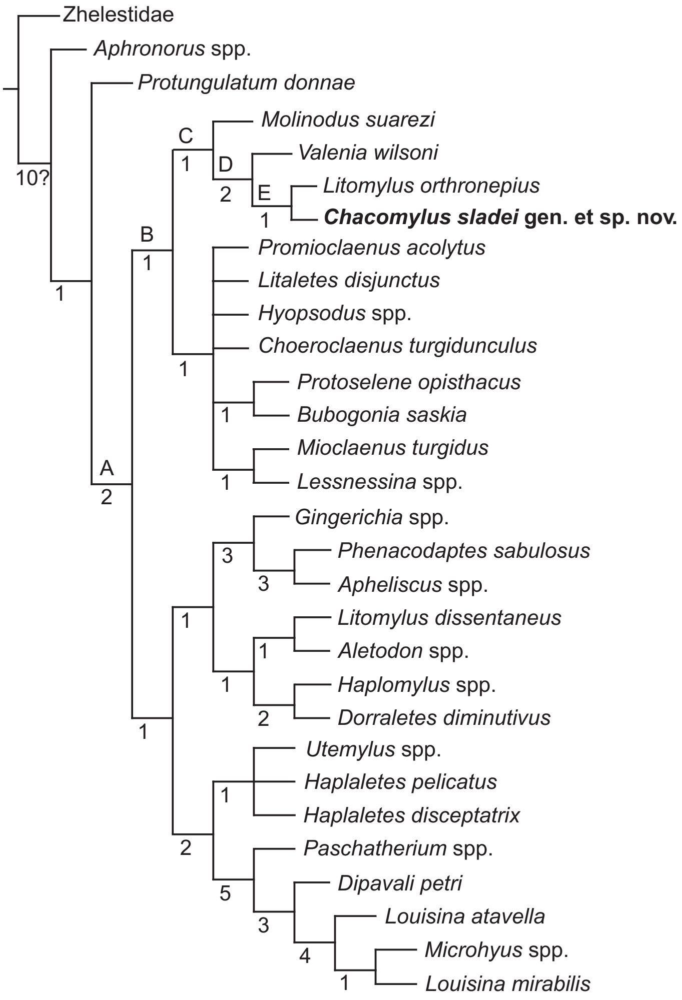

Fig. 6. Strict consensus tree derived from parsimony analysis of data in Zack et al. (2005) with the addition of *Chacomylus sladei*, *Valenia wilsoni*, and *Litomylus orthronepius* (see text and Appendix 1). List of common synapomorphies for selected nodes (labeled A–G) are listed in Appendix 2. Numbers below nodes indicate Bremer branch support calculated from a pool of 50,000 suboptimal trees of up to 10 steps longer than the shortest trees obtained.

Dental function

Chacomylus sladei has unusual morphology and occlusal wear compared to other Puercan mammals. Puercan faunas are dominated by middle sized peryptichid, arctocyonid, and hyopsodontid “condylarths” that emphasize tip-crushing wear that results in the abrasion of enamel from cusp apices (Dewar 2003). In contrast, *C. sladei* exhibits little or no cusp tip wear. It is instead characterized by the conspicuous development of broad shearing surfaces. Following the terminology of Hunter and Fortelius (1994), upper and lower molars of *C. sladei* especially emphasize facets 2(1) and 6(3). Facet 2(1) is expanded on the lower molar to involve the entire postvallid wall and the sides of the protoconid and metaconid, and is confluent with facet 3(5). On the upper molar, facet 2(1) occupies most of the mesial sur-

doi:10.4202/app.2009.0147

face of the tooth, and is confluent with 3(5). Facet 6(3) on the lower molar extends the length of the cristid obliqua superiorly and extends inferiorly to the hypoflexid. On the upper molar, facets 6(3) and 7(4) occupy the entire distal side of the paracone and mesial side of the metacone, respectively. They extend to the cusp tips but there is no wear of the cusp tips. *Chacomylus sladei* also exhibits development of facets 9(6) and 4(7n). These are small on the lower molars, near the tips of the entoconid and hypoconulid respectively, but they are prominent, expanded, and confluent on P-41208, an upper molar.

The presence of exodaenodonty on the lower molars is unique among hyopsodontine "condylarths" and is probably related to the strong emphasis on shearing and resultant high rate of wear experienced by this animal. Given the small size of *C. sladei* and that its chewing adaptations are unique among its contemporaries, we infer that it had a specialized diet compared to other Puercan "condylarths." A similar niche was apparently adapted by the late Paleocene by some apheliscids in the northern Rocky Mountain Region, such as *Gingerichia*, that are convergent on some of the dental features of *Chacomylus*.

Conclusion

Williamson (1996) argued that the lower diversity of mammals in late Puercan (Pu3) faunas of New Mexico was largely explained by collecting biases. Screenwashing techniques had been employed to recover small middle Puercan (Pu2) mammal taxa that were not recoverable from concreted Pu3 sites. This resulted in some apparent faunal differences and an apparently lower diversity for the late Puercan. The recovery of a new hyopsodontine "condylarth," as well as other small mammals (Williamson and Weil 2002; Williamson et al. in press), from a new, late Puercan microvertebrate locality addresses some of the previous collecting bias. The absence of *Chacomylus sladei* from older, Pu2 microvertebrate localities, despite the more intensive microvertebrate sampling efforts, suggests that it is absent from older faunas of the Nacimiento Formation. We therefore conclude that it represents a potential Pu3 index taxon.

Chacomylus sladei exhibits a number of unique features compared to its contemporary hyopsodontids including small size, enlarged upper molar protocones, and exodaenodonty of the lower molars. The small size, lower molar exodaenodonty, and attritional wear indicating emphasis on transverse chewing, are unusual for a Puercan "condylarth" and suggest that *Chacomylus sladei* had a different diet than other hyopsodontines. Indeed, it may have had a specialized diet compared to other contemporary therian mammals. It ignificantly increases the known morphological, and probably ecological, diversity for late Puercan mammalian faunas.

Acknowledgements

We express gratitude to Pat Hester and Sherri Landon (Bureau of Land Management, Albuquerque, USA) for providing permitting and field assistance. We thank numerous individuals for assistance in the field and for microvertebrate recovery using underwater screening methods including Lavina Becenti, Jimmy Benally, Garrett Briggs, Chris Hughes, Warren Slade, and Will Tsosie (New Mexico Museum of Natural History & Science, Albuquerque, USA) and Kent Smith (Oklahoma State University, Tulsa, USA). We are appreciative of the constructive reviews by David Archibald (San Diego State University, San Diego, USA), Craig Scott (Royal Tyrrell Museum of Palaeontology, Drumheller, Canada), and an anonymous reviewer that led to an improved manuscript. This work was supported by the National Science Foundation (EAR 0207750 to TEW and EAR 0207732/EAR 0654096 to AW).

References

Archibald, J.D. 1998. Archaic ungulates ("Condylarthra"). *In*: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America. Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*, 247–259. Cambridge University Press, Cambridge.

Archibald, J.D., Rigby, J.K. Jr., and Robison, S.F. 1983. Systematic revision of *Oxyacodon* (Condylarthra, Periptychidae) and a description of *O. ferronensis* n. sp. *Journal of Paleontology* 57: 53–72.

Cope, E.D. 1881. Mammalia of the lowest Eocene. *American Naturalist* 15: 829–831.

Crompton, A.W. and Kielan-Jaworowska, Z. 1978. Molar structure and occlusion in Cretaceous therian mammals. *In*: P.M. Butler and K.A. Joysey (eds.), *Studies in the Development, Function and Evolution of Teeth*, 249–289. Academic Press, London.

Dewar, E.W. 2003. Functional diversity of dental function within the Littleton fauna (early Paleocene), Colorado: Evidence from body mass, tooth structure, and tooth wear. *Paleobios* 23: 1–19.

Goloboff, P.A. 1999. NONA, Version 2.0. Goloboff, P.A., Tucuman, Argentina.

Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Hunter, J.P. and Fortelius, M. 1994. Comparative dental occlusal morphology, facet development, and microwear in two sympatric species of *Listriodon* (Mammalia: Suidae) from the middle Miocene of Western Anatolia (Turkey). *Journal of Vertebrate Paleontology* 14: 105–126.

Johnston, P.A. and Fox, R.C. 1984. Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. *Palaeontographica Abteilung A: Palaeozoologie Stratigraphie* 186: 1–6.

Lucas, S.G. 1984. Early Paleocene vertebrates, stratigraphy and biostratigraphy, West Fork of Gallegos Canyon, San Juan Basin, New Mexico. *New Mexico Geology* 6: 56–60.

Muizon, C., de and Cifelli, R.L. 2000. The "condylarths" (archaic Ungulata, Mammalia) from the early Palaeocene of Tiupampa (Bolivia); implications on the origin of the South American ungulates. *Geodiversitas* 22: 47–150.

Szalay, F.S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. *Bulletin of the American Museum of Natural History* 140: 193–330.

Trouessart, E.L. 1879. Catalogue des mammifères vivants et fossiles. Insectivores. *Revue et Magain de Zoologie Puere et Appliquée, Paris* 3, 7: 219–285.

Van Valen, L. 1978. The beginning of the age of Mammals. *Evolutionary Theory* 4: 46–80.

Van Valen, L. 1988. Paleocene dinosaurs or Cretaceous ungulates in South America? *Evolutionary Monographs* 10: 79.

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: 1–140.

Williamson, T.E. and Carr, T.D. 2007. *Bomburia* and *Ellipsodon* (Mammalia: Mioclaenidae) from the Early Paleocene of New Mexico. *Journal of Paleontology* 81: 966–985.

Williamson, T.E. and Weil, A. 2002. A late Puercan (Pu3) microfauna from the San Juan Basin, New Mexico. *Journal of Vertebrate Paleontology* 22: 119–120.

Williamson, T.E., Weil, A., and Standhardt, B.R. 2011. Cimolestids (Mammalia) from the early Paleocene (Puercan) of New Mexico. *Journal of Vertebrate Paleontology* 31: 162–180.

Zack, S.P., Penkrot, T., Krause, D.W., and Maas, M.C. 2005. A new apheliscine “condylarth” mammal from the late Paleocene of Montana and Alberta and the phylogeny of “hyopsodontids”. *Acta Palaeontologica Polonica* 50: 809–830.

Appendix 1

Scoring of *Chacomylus sladei*, *Litomylus orthronepius*, and *Valenia wilsoni* to the character states provided by Zack et al. (2005). Scoring for *L. orthronepius* is based on examination of UALP 15121, 15122 (holotype), 15123, 16033–16035, and 16038 and descriptions and illustrations in Johnston and Fox (1984). Scoring for *V. wilsoni* is based on examination of KU 9446 (holotype), AMNH 23157, 59788, 59904, and NMMNH P-15212 and descriptions in Van Valen (1978, 1988) and Muizon and Cifelli (2000).

	10	20	30	40	50	60
Chacomylus sladei	???????110	1010001001	1021100110	0?000??001	01101?????	?????????
Litomylus orthronepius	???????110	1010001011	1021100???	???0000001	01100?????	?????????
Valenia wilsoni	0200000010	1010001011	1021100011	0000000001	01000?????	?????????

Appendix 2

List of characters in common on the most parsimonious trees diagnosing the selected nodes on the strict consensus tree in Fig. 6. Characters are from Zack et al. (2005: appendix 2).

A. (Hyopdosodontidae + Apheliscidae)

Character 9. Lower molar trigonids much higher than talonids (0), somewhat higher than talonids (1), or trigonids and talonids subequal in height (2): 0 → 1

Character 19. Hypoconulid on m1–2 on lingual side of talonid, twinned with entoconid (0), in a median position, separate from hypoconid and entoconid (1), or shifted buccally and twinned with hypoconid (2): 1 → 0

Character 25. m3 trigonid width subequal to or slightly wider than m2 trigonid width (0), somewhat narrower than m2 trigonid width (1), or much narrower than m2 trigonid width (2): 0 → 1

B. (Hyopsodontidae)

Character 13. m2–3 paraconid distinctly separated from metaconid (0) or partially to completely fused to metaconid at base (1): 0 → 1

Character 51. Medial trochlear ridge of astragalus absent such that medial portion of trochlea faces dorsomedially (0) or present such that medial portion faces medially (1): 1 → 0

Character 58. Posteromedial projection of astragalar body absent (0) or present (1): 0 → 1

C. *Molinodus suarezi* + (*Valenia wilsoni* + [*Litomylus orthronepius* + *Chacomylus sladei*])

Character 2. p4 paraconid better developed than metaconid (0), as developed as metaconid (1), or weaker than metaconid (2):1 → 2

D. (*Valenia wilsoni* + [*Litomylus orthronepius* + *Chacomylus sladei*])

Character 29. P4 metacone absent (0), weakly developed (1), or well developed and well separated from paracone (2): 0 → 1

Character 34. M1–2 paracone subequal in size to metacone (0) or larger than metacone (1): 1 → 0

Character 42. M1–2 postprotocingulum absent (0) or present (1): 0 → 1

E. *Litomylus orthronepius* + *Chacomylus sladei*

Character 8. Distention of enamel on buccal side of lower molars absent (0), weak (1), or strong (2): 0 → 1

Character 43. M1–2 hypocone small to absent (0), well developed but smaller than protocone (1), or subequal in size to protocone (2): 0 → 1

F. *Chacomylus sladei*

Character 45. M1–2 postcingulum arises from same level on protocone as anterior cingulum (0) or arises higher on protocone than anterior cingulum (1): 0 → 1

doi:10.4202/app.2009.0147