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New perspectives on lagomorph and rodent biochronology in the Anza-Borrego Desert of southern California, USA

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ABSTRACT

Faunal compilations and biochronologies of the late Pliocene to early Pleistocene often include some or all of the Anza-Borrego Desert records of *Lepus*, *Microtus* with five closed triangles, *Microtus meadensis*, and *Lasiopodomys*, especially because they are among the oldest, if not the oldest, reported records for those taxa in North America. The purported *Lepus* specimens are represented by three partial dentaries with incomplete dentitions, each retaining the third premolar, one of which is incomplete. The arvicoline specimens include one edentulous dentary and three isolated lower first molars, one of which is incomplete. We provide a detailed review of background documentation and identify inaccuracies in taxonomic assignment, stratigraphic origin, and general curatorial documentation that affect the identity and reliability of the individual specimens and have important ramifications for Pliocene-Pleistocene biochronology. As a result of our review, we reassign all *Lepus* records to Leporinae, genus and species indeterminate. The specimen of *Microtus* with five closed triangles cannot be placed in a reliable stratigraphic context, and the edentulous jaw is diagnosable only to Arvicolinae, genus and species indeterminate. The locality that produced the *Microtus meadensis* specimen is stratigraphically higher and in a different section of the Anza-Borrego Desert than previously reported, lowering the age of the specimen by nearly a million years. We retain the *Lasiopodomys* designation although we are hesitant to accept '*Lasiopodomys*' as a higher order taxon; the specimen is from reversed polarity sediments dating to between 1.77 and 1.07 Ma, making it the oldest reported specimen of the *Lasiopodomys* morphotype.

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KEY WORDS: Vallecito Creek - Fish Creek; *Microtus californicus*?; *Microtus* (= *Terricola*) *meadensis*; *Lasiopodomys* morphotype; *Lepus* cf. *callotis*

INTRODUCTION

The Anza-Borrego Desert (ABD) constitutes the northwestern portion of the Colorado Desert, which extends from the eastern slope of the Peninsular Ranges to the Colorado River, and from San Gorgonio Pass in the north to Baja California Norte. Anza-Borrego Desert State Park (ABDSP) is one of five parks within the Colorado Desert District of the California Department of Parks and Recreation and encloses the Anza-Borrego Desert. Extensive exposures of late Miocene through Pleistocene fossiliferous sediments have yielded important collections of vertebrate fossils, beginning in the 1930s and 1950s (e.g., Frick 1937; Downs 1957, 1967; Brattstrom 1961; White and Downs 1961, 1965; Downs and Woodard 1962; Howard 1963; White 1965, 1968, 1969; Downs and White 1965, 1966, 1968; Hibbard et al. 1965). These fossils, especially those from the Vallecito Creek – Fish Creek sequence, played a role in the development of biostratigraphic correlations and biochronologic interpretations across western North America, and continue to figure prominently in late Pliocene to early Pleistocene paleontological investigations. The stratigraphic and chronologic significance of the ABD faunas is highlighted by the fact that several ABD specimens were reported previously as either the earliest or latest known records of mammalian taxa in North America. Purported earliest occurrences include *Microtus* cf. *M. californicus*, *Equus* (*Equus*), *Euceratherium*, *Nothrotheriops*, and *Sylvilagus*; purported latest occurrences include *Borophagus diversidens*, and cf. *Dinohippus* sp. (Lundelius et al. 1987; Repenning 1987, 1992; Cassiliano 1999; Bell et al. 2004b). Interpretations of the stratigraphic and chronologic placement of these and other taxa helped to shape discussions of the absolute age of the local boundary between the Blancan and Irvingtonian mammal ages (e.g., Opdyke et al. 1977; Cassiliano 1999), and were important in secondary syntheses of local to continental and global-scale concepts of taxonomic relationships, biochronology, and environmental change (e.g., Opdyke et al. 1977; Lundelius et al. 1987; Lindsay et al. 1990; Martin et al. 2003; Bell et al. 2004b).

Some previous authors noted difficulties in their attempts to reconcile taxonomic identifications and ages of ABD specimens with the known biochronologic and biogeographic distribution of Blancan and Irvingtonian mammals elsewhere (Zakrzewski 1972; Repenning 1992; Repenning et al. 1995; Cassiliano 1999; Bell et al. 2004b). Our examinations of ABD leporid and arvicoline rodent specimens and the documents associated with their collection and curation revealed important inconsistencies among published information, database records, catalogued specimens, and data recorded in field notes. Most of these inconsistencies originated in the complex curatorial history of the ABD collections, but they have important ramifications for biochronologic interpretations within the Anza-Borrego Desert and throughout western North America.

MATERIALS AND METHODS

We examined ABD specimens and associated primary and published documents of specimens that were previously referred to the lagomorph *Lepus* and the arvicoline taxa *Lasiopodomys*, *Microtus*, and *Terricola*. Data inconsistencies and their consequences are discussed below.

Institution and Field Collection Notation

Fossil specimens collected from the Anza-Borrego Desert and now curated at the Colorado Desert District Stout Research Center (SRC) comprise collections obtained under state permit by the Natural History Museum of Los Angeles County (LACM), the Imperial Valley College Museum (IVCM), and SRC staff and ABDSP Paleontology Society volunteers. All locality and specimen numbers originally assigned by those institutions are retained in the current ABDSP collection database, along with the parenthetical acronym for the collecting institution. The Park acronym is prefixed to the original collecting institution acronym for both the locality and specimen numbers, e.g., ABDSP(LACM), ABDSP(IVCM). The letter 'V' (signifying 'vertebrate fossil') is prefixed to the specimen number, to distinguish it from the locality number and from non-vertebrate fossils within the ABDSP system. Locality and specimen numbers separated by a forward slash, e.g., ABDSP(IVCM) 68123/V24828, indicate the association between a specimen and the locality where it was found. Specimen numbers published prior to consolidation

of the collections appeared in the cited publications without 'ABDSP' or 'V' appended.

In our stratigraphic terminology 'VCFC section' refers to the sediments of the Vallecito Creek-Fish Creek Badlands in the southern part of the Park; 'Borrego Badlands section' refers to the sediments within the Borrego Badlands in the northern part of the Park; 'Anza-Borrego Desert' refers to the fossiliferous sediments of the entire Park, including the VCFC, Borrego Badlands, and other sections.

Additional institution and field collection abbreviations include GJM = George J. Miller field number; HJG = Harley J. Garbani field number; UADZ= Department of Zoology, University of Arizona (as published by White 1984); UF = Florida Museum of Natural History, Vertebrate Paleontology (as published by White 1991b).

Documentation Resources

Primary documentation for the specimens reviewed here is on file at the Paleontology Section, SRC at ABDSP. Documents are either originals produced at IVCM and ABDSP or photocopies of original documents on file at LACM. Primary documents include field notebooks, field and master aerial photographs with localities pinpointed and labeled, locality catalogue cards, specimen catalogue cards, specimen tray labels, locality and specimen notes produced during the ongoing process of curation, letters of correspondence and database records for localities and specimens, including an unaltered 1994 copy of the LACM Anza-Borrego Desert specimen database records (1994 LACM database) obtained prior to the transfer of specimens to ABDSP.

Measurements

The anteroposterior lengths of leporine p3s were measured using the orientation of White's (1991a:68) figure 2. Arvicoline m1s were measured along the occlusal surface, from the anterior to posterior edge. Tooth measurements were made through a dissecting microscope with a graduated reticle calibrated to 0.01 mm, and the tooth occlusal surface aligned parallel with the plane of the objective lens. The length of the leporine i–p3 diastema was measured with a 150 mm dial caliper calibrated to 0.01 mm.

Figures

All tooth images were drawn in Adobe Illustrator over digital photographs of the specimens. The accuracy of the outlines of the enamel, dentine, and cement features was verified by continuous comparison of the drawing, image, and direct observation of each specimen through the dissecting microscope. Examples of terms used in the text to describe leporine tooth morphology are illustrated in Figure 1.

RESULTS

Leporidae (*Lepus*)

Published Reports and Identification Criteria. Early publications of the vertebrate fauna of the Anza-Borrego Desert listed *Lepus* and/or cf. *Lepus* without reference to particular specimens or localities (Downs and Woodard 1962; Downs and White 1968; Kurtén and Anderson 1980). In the first published study of the Anza-Borrego Desert fossil leporids, White (1984) listed no specimens definitively as '*Lepus*', but identified three specimens as 'Leporinae, genus, and species indeterminate' because they could represent either *Lepus* or *Sylvilagus*.

Subsequent statements attributed generic and tentative specific allocations to personal communications from John White. For example, Lundelius et al. (1987, p. 214) listed *Lepus* in the Anza-Borrego Desert at "about 2.0 Ma (White, personal commun., 1985)", and subsequently stated (page 220) "In the Vallecito Creek Local Fauna in the Anza-Borrego sequence . . . *Lepus* cf. *callotis* occurs at the base of the Olduvai subchron at about 1.9 Ma (White, personal commun., 1985)." In his major review paper on Miocene and Pliocene leporines, White (1991a:78) listed only two Blancan locality records for *Lepus* (Borchers in Kansas and Big Springs in Nebraska). A *Lepus* record at Anita, Arizona, indicated on White's (1991a:87) figure 14, was plotted in the transition zone between Blancan and Irvingtonian ages. The Anita fauna may be much older, is taxonomically and stratigraphically problematic, and needs full reexamination (Morgan and White 2005). White (1991a:87 figure 14) plotted two *Lepus* records as Irvingtonian (sensu Lundelius et al. 1987) in age, one from Inglis 1A in Florida, and another from the Anza-Borrego Desert, California. Our interpretation of the latest *Lepus* record in that figure is based on the caption statement, "The small horizontal lines indicate stratigraphic level in the Anza-Borrego Desert Section;" one such line appears at the top of the *Lepus* stratigraphic occurrence bar. However, the symbology is inconsistent elsewhere within the figure (e.g., the *Aztlanolagus* occurrence bar mistakenly includes a reference to the Anza-Borrego Desert Section). The 'ABD *Lepus*' mark is placed

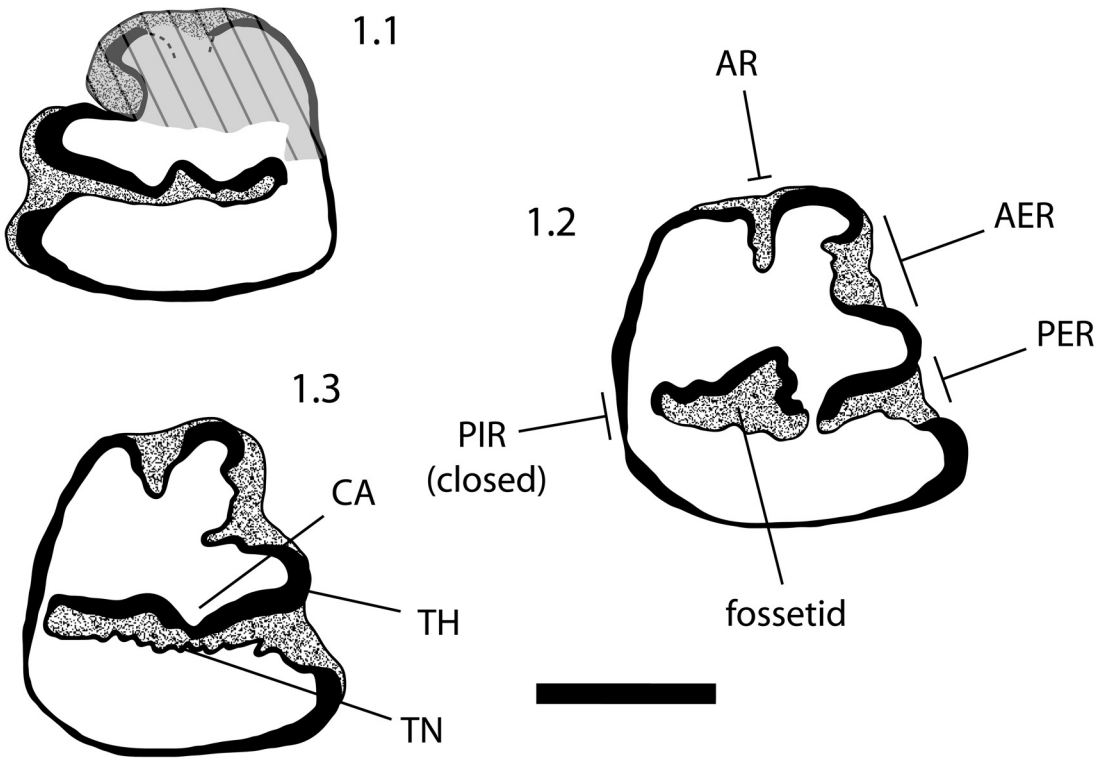

FIGURE 1. Occlusal view of lower third premolar of indeterminate leporine lagomorphs from Anza-Borrego Desert State Park. The top of the figure is anterior. **1.1**, ABDSP (IVCM) 113/V413, left p3; **1.2**, ABDSP(IVCM) 113/V1275, right p3; **1.3**, ABDSP(LACM) 1906/V24889, right p3. Gray lined area is broken and at a lower level than the rest of the illustrated surface. Dashed lines indicate indeterminate trace of enamel. AR = anterior reentrant, AER = anterior external reentrant, CA = central angle, Fossetid = cement filled enamel lake, PER = posterior external reentrant, PIR = posterior internal reentrant, TH = thick enamel, TN = thin enamel. Scale equals 2 mm.

opposite the Coleman 2A (Florida) label and might also be interpreted as indicating the *Lepus* reported from there by Martin (1974). White did not discuss individual specimens in his (1991a) review.

A total of four specimens from ABD were, at some time, referred in publication at least tentatively to *Lepus*. The documentary history, taxonomic, and stratigraphic complications of those specimens are discussed individually below. Taxonomic determination of isolated partial dentaries and teeth of North American leporines can be difficult or impossible. The enamel pattern and degree of enamel folding of the lower premolar (p3), the anteroposterior length of the tooth, and the i–p3 diastema length are the only characters suggested to permit differentiation of *Nekrolagus progressus*, some species of *Lepus*, and some species of *Sylvilagus* (e.g., Hibbard 1963; Dalquest 1979; White 1984, 1991a, 1991b; Dalquest et al. 1989).

In the paedomorphic pattern of leporines, the posterior internal reentrant (PIR) is open lingually. Adult specimens of *Nekrolagus*, *Lepus*, and *Sylvilagus* typically have an enamel band along the lingual edge, closing the PIR. If the cement in the PIR is not continuous with that in the posterior external reentrant, a cement filled enamel lake or fossetid (Dalquest et al. 1989) is created, designated the '*Nekrolagus*-pattern' (figure 1a); otherwise the PIR is continuous with the PER, resulting in the '*Lepus*-pattern' (Hibbard 1963, figure 1b). Both patterns occur variously in *Nekrolagus*, *Lepus*, and *Sylvilagus*. The *Nekrolagus*-pattern was recorded in 88% (156 of 178 specimens) of *N. progressus* (Hibbard 1963), three of 22 specimens of *S. webbi* (White 1991b), one of 21 specimens of *S. hibbardi* (White 1984, 1991a), and one of four specimens of *Lepus* from Big Springs, Nebraska (White 1991a, figure 9). It is otherwise rare in *Lepus* and other *Sylvilagus* (Hibbard 1963).

Specimen Descriptions and Provenience. ABDSP(IVCM) 113/V413 is a partial left dentary with p3 (Figure 1.1) and p4. Approximately 90% of the p3 occlusal surface is broken and missing although most of the enamel pattern in the cross-section of the broken area is visible. The anterior third of the tooth is broken below the alveolar rim,

leaving the outline of the tooth enamel partially obscured, and the anterior reentrant ill defined. The anteroposterior length of the tooth is 3.7 mm. The i–p3 diastema length is 18.3 mm, although the anterior margin is incomplete. The bone appears to be diagenetically unaltered with no matrix attached to the bone and no visible permineralization or internal encrustation of gypsum or calcite crystals. Foramina and vacuities in the bone are partially filled with unconsolidated sand grains.

The identification of specimen 113/V413 was given as "*Lepus* sp. cf. *L. callotis*" by Cassiliano (1994, p. 147). Specimen V413 shows none of the characteristics of preservation through protracted burial and permineralization as seen in specimens V1275 and V24889. Although this does not prove specimen V413 is not a fossil, it does leave open the possibility that it may be a modern specimen. Leporine bones are among the most abundant of recently deposited bones found on and in the surface sediments in ABD, and sometimes they are collected mistakenly as fossils. Once returned to the laboratory they can be difficult to separate from fossil specimens without detailed provenience information. Field notes are not known for most of the IVCM localities, so written and dated records of the circumstances of collection are not available for V413.

ABDSP(IVCM) 113/V1275 is a partial right dentary with p3 (Figure 1.2), p4, m1, m2, and m3. The anteroposterior length of the p3 is 4.0 mm. The i–p3 diastema is missing. The specimen appears to be diagenetically altered and is encrusted with matrix. All openings are either permineralized or filled with cemented matrix. Field notes and written record of collection circumstances are unavailable for this specimen.

Primary documentation (specimen catalogue cards) for ABDSP(IVCM) 113/V1275 includes two different field numbers, GJM 947 = (IVCM) Locality 27, and GJM 1024 = (IVCM) Locality 113; the two localities are physically separated by about 20 m. The date of collection, '26 April 1978', is consistent on all documents for this specimen, however, no other specimen in the current ABDSP database is listed with that date. All other specimens from locality 113 were collected on 24 November 1974. Locality 27 lists several dates of collection for the specimens, indicating separate survey and collecting events. The majority of the specimens from locality 27 are from disaggregated coprolites. Whether or not V1275 was recovered from a coprolite is unclear. Cassiliano (1994, p. 147) reported this specimen as '*Lepus callotis*' under catalogue number 113/V4812 (=V1275, L.K. Murray specimen notes, 23 May 1996, on file at SRC).

ABDSP(LACM) 1906/V24889 is a partial right dentary with p3 (Figure 1.3), p4, m1, and m2. The anteroposterior length of the p3 is 3.8 mm. The i–p3 diastema length is 17.3 mm, although the anterior bone margin is incomplete. The specimen appears diagenetically altered with matrix attached, permineralization, and crystalline growth present as on specimen V1275.

The catalogue number of ABDSP(LACM) 1906/V24889 was misprinted in the caption of Figure 6 (White 1984, p. 46) as "LACM 24839." The undated label in the specimen tray for this fossil has the words '*Lepus*' and 'cf. *L. callotis*' printed on the taxon name line by two different hands with 'JAW' (J. White's initials, in his handwriting) on the same line. This fossil is the only ABD specimen with direct indication of identification to '*Lepus*' by White. Although it is unclear to which identification the signature refers, either indicates that White at some time considered the specimen to be *Lepus*.

ABDSP(IVCM) 110/V407 is a partial right dentary with p3, p4, and m1, and was reported as "*Lepus* sp." by Cassiliano (1994, p. 147). The specimen is no longer available for study. It was reinterpreted to be a modern specimen by the ABDSP curatorial staff, and according to the ABDSP database was removed from the collection and discarded. This removal occurred before the curatorial staff was aware that the specimen was included in Cassiliano's dissertation (1994). ABDSP documents indicate that specimen V407 was among the leporid specimens loaned to John White in 1979, although he did not include it in any of his publications. Subsequent publications by Cassiliano (1997, 1999) listed leporid specimens by taxonomic designation ('*Lepus callotis*', '*Lepus* sp. cf. *L. callotis*', and '*Lepus* sp.') but not by specimen number.

Taxonomic Allocation. In the original description of the three fossil specimens under discussion, White (1984, p. 53) stated that the fossils were comparable to the mandibles of *Lepus townsendii* and *Sylvilagus cunicularius* and, "In enamel patterns of cheek teeth, specimens of *S. cunicularius* are indistinguishable from any North American species of *Lepus* or *Sylvilagus*. Thus if the only available characters to identify a specimen are size and enamel patterns on p3, the specimen cannot be referred with certainty to either *Lepus* or *Sylvilagus*." Using these criteria he concluded that the specimens were identifiable only to "Leporinae, genus, and species indeterminate." Subsequently,

White (1991a:78) indicated that "larger size and the presence of folding of TN in PER [thin enamel on the posterior margin of the posterior external reentrant] could be used to diagnose *S. cunicularius*," and that mandibles could be identified as *Lepus* if the [i–p3] “diastema [is] 21 mm in length or longer," or if the p3 has the combination of "an anteroposterior length of 3.7 mm or larger" and enamel pattern similar to the predominant patterns of "*L. californicus* and *L. townsendii*, as shown in {f}igure 10."

All three of the ABD fossil p3s have an anteroposterior length of 3.7 mm or greater. The two specimens with measurable (although incomplete) i–p3 diastemas each have a diastema length of less than 21.0 mm. Specimen V1275 has a cement-filled enamel lake (fossettid) separated from the PER by a dentine isthmus. Folding of thick enamel in PER (TH) of the three ABD p3s is 'simple'—"one small or shallow loop at the lingual margin of the central angle and/or a loop at the extreme lingual end of the re-entrant" to 'moderate'—"as in simple but with one or two additional small loops" (Dalquest et al. 1989, p. 299), while folding of TN is 'none' or 'simple'.

Based solely on the criteria of White (1991a; enamel pattern on p3 similar to the predominant enamel patterns of *L. townsendii* and *L. californicus* as in his figure 10 and anteroposterior length of 3.7 mm or greater) the two specimens V413 and V24889 might be considered to be *Lepus*. However, V413 shares similar enamel characters (TH and TN in PER) with *Nekrolagus progressus* specimens reported by Hibbard (1963, p. 3, figures 1f, g, h, i), and falls within the size range of *N. progressus* (anteroposterior length of p3 = 2.7–3.8 mm, N = 38 specimens; White 1991a, table 3). Specimen V24889 shares similar enamel characters with *Sylvilagus webbi*. The p3 falls within the size range of *S. webbi* (anteroposterior length of p3 = 3.0–4.3 mm, N = 22 specimens; White 1991b, table 1); and its enamel pattern is similar to at least two *S. webbi* specimens (UF49841 and UF49847 in White 1991b figure 1). The enamel lake in specimen V1275 makes it a likely candidate for *Nekrolagus* (White 1991a) but an enamel lake is also found in some specimens of *Lepus* and *Sylvilagus* (Hibbard 1963; White 1991b). The incomplete diastema lengths of specimens V24889 and V413 approach 21 mm, one of White's (1991a) criteria separating *Lepus* from *Sylvilagus*. The two specimens also fall near the high end of the ranges of *Nekrolagus progressus* as well as *S. webbi* specimens from chronologically similar (Blancan) Florida sites; the diastema length range of *Nekrolagus progressus* is 16.8–18.5 mm (N = 3 specimens; White 1991a); and the diastema length range of *S. webbi* is 14.3–18.8 mm, (N = 7 specimens; White 1991b). All three ABD p3 specimens also appear to be similar in size and/or enamel pattern to the modern *S. cunicularius* specimen, UADZ5133 of White's (1984, p. 46) figure 6.

Locality (IVCM) 113 is located stratigraphically near the base (1.95 Ma) of the Olduvai magnetic polarity chron C2n while locality (LACM) 1906 is above the top (1.77 Ma) of the Olduvai. The oldest age estimate that can be applied to locality (IVCM) 113 is between about 1.9 and 2.0 Ma, and for locality (LACM) 1906 between about 1.3 and 1.4 Ma. These two localities lie in the middle of the geographic and stratigraphic distribution of *Sylvilagus hibbardi* in the VCFC section, along with multiple sites listed on the database as containing elements diagnosable only to '*Sylvilagus* or *Lepus*'. The estimated age of locality 113 reveals that specimens V413 and V1275 are those referred to by Lundelius et al. (1987, p. 214, 220; see above) as either "*Lepus*" or "*Lepus* cf. *L. callotis*." However, none of the ABD specimens has an enamel pattern remotely similar to the predominant enamel pattern for *L. callotis* as illustrated by White (1991a, figure 10), which shows a strong (sensu Dalquest et al. 1989) folding pattern of the TH enamel and moderate to strong folding of the TN enamel.

The three fossil specimens discussed herein appear significantly larger than *S. hibbardi*, also reported from the associated strata, and may represent one or more different taxa. Based on criteria developed in previous discussions (e.g., Hibbard 1963; Dalquest 1979; White 1984, 1991a, 1991b; Dalquest et al. 1989), specimen V1275 appears similar to *Nekrolagus*, and specimens V413 and V24889 appear similar to *Lepus* and some large *Sylvilagus*. However, specimen V413 also appears to be a modern specimen while specimen V1275 suffers from imprecise provenience data. All three specimens lack sufficient diagnostic characters for incontestable designation as *Nekrolagus*, *Lepus*, or *Sylvilagus*. Well supported taxonomic identity and stratigraphic position are paramount for establishment of early records for these taxa. We therefore reaffirm White's original (1984) referral of these three specimens to 'Leporinae, genus and species indeterminate.' We searched the ABDSP fossil collection for other specimens possibly referable to *Lepus*, but found none with sufficient diagnostic characters for reference to that genus.

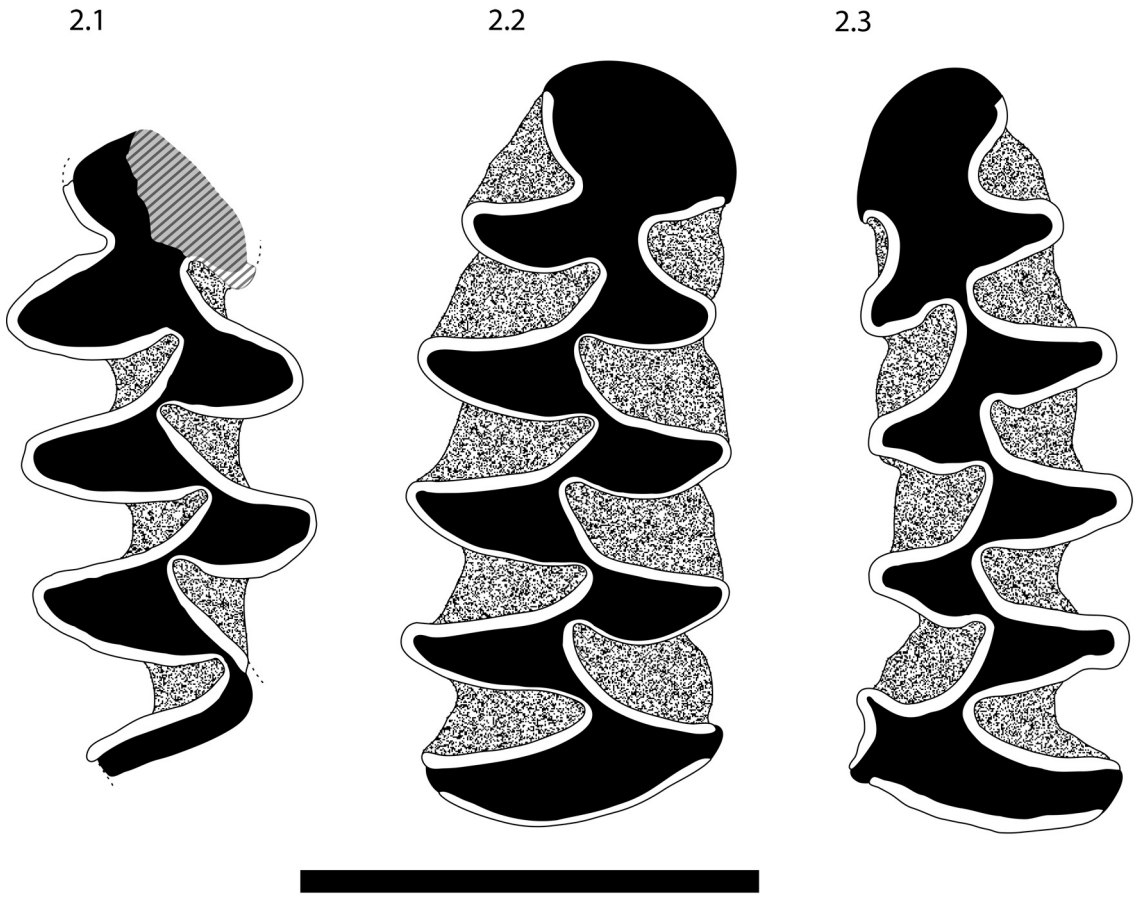

FIGURE 2. Occlusal view of lower first molar of arvicoline rodents from Anza-Borrego Desert State Park. The top of the figure is anterior. **2.1**, ABDSP(LACM 1942/V8252, right m1, *Lasiopodomys* morphotype; **2.2**, ABDSP(LACM) locality indeterminate/V24540, right m1, *Microtus* sp. with 5 closed triangles; **2.3**, ABDSP(LACM) 68123/V24828, left m1, *Microtus* (=*Terricola*) *meadensis*. Gray lined area is broken and at a lower level than the rest of the illustrated surface. Dashed lines indicate indeterminate trace of enamel. Scale equals 2 mm.

Arvicolinae

Published Reports and Identification Criteria. Fossil specimens from ABD were referred previously to several arvicoline taxa including *Ondatra idahoensis*, *Ophiomys parvus*, *Mictomys anzaensis*, *Lasiopodomys* sp., *Microtus* (sometimes as *M. californicus*, sometimes with questionable allocation to that species, sometimes simply as '*Microtus* sp.'), and *Microtus* (or *Terricola*) *meadensis* (Zakrzewski 1972; Repenning 1992; Repenning et al. 1995; Bell et al. 2004a). Only the *Microtus* and *Lasiopodomys* specimens are reviewed here.

The recognized North American arvicoline fossil record consists predominantly of isolated teeth and partial tooth rows preserved in fragmentary (or, rarely, intact) lower jaws and maxillae. The lower first molar (m1) has long been recognized as the most useful tooth for determining taxonomic affinity in North American arvicolines. For some taxa the upper second and/or third molars (M2, M3) may also help to refine taxonomic allocation. Relatively few discrete morphological characters are preserved on isolated m1s, but systematically informative features include the presence or absence of roots, presence or absence of cementum in reentrant angles, the number of alternating triangles, differentiation in thickness of enamel on the anterior and posterior edges of triangles, and the relative closure of triangles with respect to each other and with other dentine fields on the tooth (posterior loop, anterior loop).

Specimen Descriptions and Provenience. ABDSP(LACM) 1942/V8252 is a poorly preserved, isolated, right m1 (Figure 2.1). The specimen is broken and partially encased in matrix. The original occlusal surface appears to be entirely broken away. The posterior loop is represented only by the

leading edge of the enamel and a portion of the dentine field. The first four triangles (counting from the posterior end of the tooth) are completely closed off from one another, although the fourth is somewhat confluent with the fifth. The first and third are more expanded labiolingually than are the second and fourth. The fifth is broken near the point where it meets the anterior cap. The breakage obscures some of the detail, but it appears that the fifth triangle was confluent with the anterior cap. There is no obvious development of a sixth triangle. Cement is present in most reentrant angles, but is lacking on the most anterolingual reentrant. There is little or no enamel thickness differentiation between the leading and trailing edges of the triangles. The locality designation for the specimen, and its stratigraphic placement, are undisputed and appear to be correct. Locality 1942 is stratigraphically above the Olduvai Chron (C2n) and below the Jaramillo (C1r.1n), and is therefore between 1.77 Ma and 1.07 Ma in age.

ABDSP(LACM) V24540 is an isolated, unrooted, right m1 (Figure 2.2); intact posterior loop with five closed triangles; sixth and seventh triangles are well-developed and confluent with each other and with the rounded anterior cap of the tooth. Enamel thickness is strongly differentiated on all triangles, with trailing edge enamel on each triangle thinner than that on the leading edge. Extensive cement is present in all reentrant angles. The anteroposterior length of the m1 is 3.4 mm.

ABDSP(LACM) V24540 was originally published under locality '6814' (Zakrzewski 1972). Subsequent publications listed the specimen locality as '6683' (Repenning 1992) and '6686' (Repenning 1998). The primary data for this specimen are inconsistent. The specimen label, vial cork, gelatin capsule, and 1994 LACM database all have ‘LACM 24540’ and locality ‘6814’ printed on them, as published originally by Zakrzewski (1972). The field notes, dated 22 January 1968, for locality 6814 (= Field Number HJG446) list "–fox lower jaw frag.–small pellet–rabbit skeleton?—Possible 2 rabbit skeletons or at least parts, as another cranium was close by & enclosed in jacket." The date of collection on the database catalogue for most specimens (including V24540) from locality 6814 is given as '13 April 1968', three months later than the date given in the field notes. When Charles Repenning began working on the ABD arvicolines in 1990, LACM curatorial staff discovered the date discrepancy for specimen V24540. In correspondence to Repenning LACM staff noted that the tooth was clean of attached matrix, implying it was a screen-washed specimen rather than an *in situ* discovery, and therefore probably was not from locality 6814. Multiple ABDSP(LACM) localities were screen-washed around 13 April 1968, including localities 1357 and 6683, and these were suggested to Repenning as possible sources of V24540. Locality 6683 is the site from which an edentulous jaw, V24649, referred to ‘*Microtus californicus*?’ by Zakrzewski (1972) was recovered (see below), so at least one other arvicoline specimen is known from that locality. Other localities (besides 6683 and 1357) also produced matrix for screenwashing around the same time and may be the source of V24540 (written correspondence between C. Repenning and LACM, 09 May 1990 to 22 June 1990). The locality and stratigraphic data for this specimen are seriously compromised. The specimen cannot, therefore, be considered in evaluations of the temporal range of arvicolines within ABDSP.

The referral of specimen V24540 to locality '6686' (Repenning 1998, p. 52, footnote 9) is apparently a misprint of '6683'. Locality LACM 6686 is not an ABD locality. That locality number does not appear in any of the 1990 'arvicoline' correspondence between Repenning and LACM.

ABDSP(LACM) 6683/V24649 is an edentulous left dentary. The specimen clearly represents an arvicoline rodent with ever-growing teeth (there are no root sockets). The approximate outline of the m1 is still discernible and indicates that there were likely five lingual and four labial reentrant angles. Locality and stratigraphic provenience data are not disputed.

ABDSP(LACM) 68123/V24828 is an isolated, unrooted left m1 (Figure 2.3) with an intact posterior loop with three closed triangles; the fourth and fifth triangles are confluent with one another in a rhombus, but are closed from the anterior dentine fields. The sixth and seventh triangles also are well-developed, and broadly confluent with each other and with the rounded anterior cap. Cement is present in all reentrant angles. The trailing enamel is only slightly thinner than the enamel on the leading edge on each triangle. The anteroposterior length of the m1 is 3.55 mm.

The locality for this specimen (locality 68123) is recorded in the 1994 LACM database, on field aerial photographs, and on a handwritten note (T. Downs, 29 August 1990) as being in the Borrego Badlands. The field notes (field number HJG487, recorded 06 February 1968) placed it in Beckman Wash, Borrego Badlands. Fossils from the site included "horse limb elements—rodent deposit—

Neotoma." At least two sacks of matrix were collected on 08 February 1968 for screenwashing. Downs (handwritten note 29 August 1990) gave an estimated age for this locality as "0.5 Ma or later." An erroneous report that the specimen was from the "Vallecito Creek fauna" (Repenning 1992, p. 50) was apparently based on a written communication from J. White in 1990. We were not able to locate this correspondence, but all other sources of information regarding the position of this locality within ABD indicate it is in the top of the Borrego Badlands, approximately 80 km north of VCFC, in significantly younger sediments. There does not appear to be any major discrepancy in other primary data, therefore the specimen is still valid for biostratigraphic consideration, however, it was not recovered from within the VCFC.

Taxonomic allocation. ABDSP(LACM) 1942/V8252 was originally identified as *Microtus californicus*? (Zakrzewski 1972), but was subsequently transferred to *Lasiopodomys* sp. (Repenning 1992). Specimens that conform to Repenning's morphological concept of *Lasiopodomys* in North America are significantly different in morphology of the m1 from the living representatives in Mongolia and Korea (see Repenning 1992 figure 11, and his discussion on pp. 46–48). The m1s of extant species of *Lasiopodomys* resemble those of many extant species of *Microtus* with five closed triangles. Recent molecular data also nest extant *Lasiopodomys* within crown-group *Microtus* (Galewski et al. 2006), supporting an argument for subsuming at least extant species of *Lasiopodomys* under the name *Microtus*. The extinct '*Lasiopodomys' deceitensis* from North America is distinct (in morphology of m1) from other North American arvicolines, but was originally placed in the genus *Microtus* (Guthrie and Matthews 1971). Such placement may be justified, but the taxonomic affiliations of *deceitensis* are currently based only on molar morphology. Recent molecular analyses show at least weak support for a monophyletic clade of endemic extant North American *Microtus* (e.g., Conroy and Cook [2000] and Galewski et al. [2006]; but see Jaarola et al. [2004]). Based on ingroup commonality and outgroup assessment from those trees, the primitive morphology for m1 in North American *Microtus* was five closed triangles (unambiguous from the Conroy and Cook [2000] analysis; ambiguous in the Galewski et al. [2006] trees). In light of these data, the higher-level taxonomic affinity of '*Lasiopodomys' deceitensis* remains uncertain (Bell et al. 2004a; Bell and Bever 2006). The morphology of ABDSP(LACM) 1942/V8252 is consistent with that of '*Lasiopodomys' deceitensis* from various other localities in North America (reviewed by Repenning 1992) and was placed in taxonomic association with those specimens by Repenning (1992). Our illustration differs in detail from that provided by Repenning (1992, figure 11A), but we accept his identification of the specimen as a *Lasiopodomys*-like morphotype, and hesitatingly retain the use of '*Lasiopodomys'* as a higher-order taxonomic name for specimens with that general morphology. In many North American faunas, this morphotype occurs in such low abundance that it likely represents atypical morphologies of other species (e.g., *Microtus paroperarius*; Bell et al. 2004a). Although *Microtus paroperarius* is not recorded from the Anza-Borrego Desert, the single specimen with a *Lasiopodomys* morphotype probably does not warrant formal taxonomic recognition at this time.

The taxonomic assignments of ABDSP(LACM) V24540 have always implied close affinity with the extant California species, *Microtus californicus*. It was questionably referred to that species by Zakrzewski (1972). The questionable status was dropped by Repenning (1992) who provided a definitive referral to species. The question mark was returned by Repenning et al. (1995), and the specimen was listed as *Microtus* sp. cf. *M. californicus* by Repenning (1998). There are no fewer than 12 recognized extant North American *Microtus* species that share the general m1 morphology seen in extant *M. californicus* (Bell and Barnosky 2000). Without using modern biogeography as a tool to refine taxonomic allocation, there are no known morphologic features of this specimen that permit definitive species allocation. The broader complication of identification of isolated molars of *Microtus* species were discussed by Bell and Repenning (1999), Bell and Barnosky (2000), Bell et al. (2004a), and Bell and Bever (2006). The specimen is best referred to as a member of *Microtus* with five closed triangles on m1.

ABDSP(LACM) 6683/V24649 is an edentulous dentary fragment. The taxonomic affinity of the specimen is poorly resolved. The original description (Zakrzewski 1972) identified it as '*Microtus californicus*?' because the alveolus indicated an unrooted tooth, with reentrant and salient angles consistent with referral to *Microtus*. The argument was supported by the observation that the alveolus morphology was inconsistent with *Mictomys*, the only other arvicoline known at that time from ABD. The fact that the specimen could represent a different genus or species was noted in the original description (Zakrzewski 1972). The last three

decades have seen an increase in the known diversity of arvicolines from ABD (Repenning 1992; Repenning et al. 1995), as well as western range extensions for taxa not previously thought to have occurred west of the Great Plains (e.g., *Microtus paroperarius*, *Allophaiomys pliocaenicus*; Gillette et al. 1999; Bell et al. 2004a, 2004b). These developments, combined with an increasing preference for reliance on diagnostic features of the fossils themselves, lead us to conclude that the most defensible identification for specimen V24649 is 'Arvicolinae.'

ABDSP(LACM) 68123/V24828 was identified as *Terricola meadensis* by Repenning (1992). The morphology of the specimen is certainly consistent with the type population of '*Pitymys' meadensis* from the Cudahy fauna in Kansas (Hibbard 1944; Paulson 1961), and we agree that the species assignation is correct. Higher-level taxonomy for *meadensis* has been a source of confusion and contention for decades. Recognition of distinct 'pitymyine' species groups (variously placed in the genera or subgenera *Pitymys*, *Pedomys*, *Terricola*) was commonplace until the emergence of molecular data that universally found these groups to be polyphyletic (e.g., Moore and Janecek 1990; Conroy and Cook 2000). Based on all available data, the specimen is best considered *Microtus meadensis* (see discussion in Bell et al. 2004a).

DISCUSSION

Lepus is one of several taxa suggested as stratigraphic markers signaling the beginning of the Irvingtonian land mammal age (Lundelius et al. 1987), especially in faunas where other, more preferable marker taxa (e.g., *Mammuthus*, *Microtus*) are unavailable. In his review of the Blancan-Irvingtonian boundary at ABD, Cassiliano (1999, p. 183) concluded that "the use of *Lepus* to define the boundary may be unreliable (Lindsay 1995), but, at present, is the best choice in the FCVC [VCFC] section."

Based on our reanalysis of the ABD leporines there are currently no specimens in the fossil collection that can be diagnosed unequivocally as *Lepus*. This is not to say *Lepus* is not present in the ABD fossiliferous sediments, but with the fossil material currently available its presence is not verifiable. The best course of action at present is to remove *Lepus* from the ABD faunal list and eliminate the purported ABD records from discussions of biochronology. Further work on leporines in the VCFC section is needed.

A similar re-evaluation and removal of '*Lepus*' from the Curtis Ranch and 111 Ranch faunas (Galusha et al. 1984; Lindsay et al. 1990; White 1991a) resulted in the emendation of southern Arizona Pliocene-Pleistocene biochronology and the stratigraphic repositioning of the local Blancan-Irvingtonian boundary. Our study further reduces the number of localities recording the early presence of *Lepus* and increases the importance of the remaining early *Lepus* localities, Big Springs and Borchers, as well as the recently published Blancan records of *Lepus* from Bear Springs, Anita, and San Simon faunas in Arizona (Morgan and White 2005). It also places greater emphasis (Lundelius et al. 1987; Martin et al. 2003) on the caveats regarding the difficulty in diagnosing leporine fossils based on the enamel pattern and size of p3 alone (White 1984, 1991a).

The isolated arvicoline tooth ABDSP(LACM) V24540 was one of the most important specimens reported from ABD. For years it was accepted as the oldest known *Microtus* with five closed triangles in North America, and because of its advanced morphology (five well-developed and fully closed triangles) it became central to hypotheses about arvicoline evolution, phylogeny, dispersal, and biochronology.

The three localities published or proposed for V24540 are of different ages spanning about 1.75 million years. Locality ABDSP(LACM) 6814 lies within the lower normally-magnetized portion of the Gauss (chron C2An3n) between 3.33 and 3.58 Ma. Locality ABDSP(LACM) 6683 is in part of the section currently uncorrelated to the paleomagnetic stratigraphy and may be anywhere from just above the top of the Olduvai (chron C2n; slightly younger than 1.77 Ma) to below the base of the Olduvai, about 2.0 Ma (future magnetic polarity and stratigraphic research in the section may resolve this issue). Locality ABDSP(LACM) 1357 lies stratigraphically below locality 6683 in the same uncorrelated area. Other potential localities from which the specimen might have been collected span almost the entire range of ages in ABD, so any speculation about actual provenience is unwarranted, and will not remove the taint of bad data associated with the specimen.

Microtus (sensu Repenning 1992) was used by Repenning to mark the beginning of his Irvingtonian I division in the southern portion of the United States west of the Rocky Mountains. The earliest appearance of *Microtus* with five closed triangles was placed variously at 1.4 Ma (Repenning 1992, pp. 38, 80), 1.6 Ma (Repenning et al. 1995, pp. 29–

31), and 1.7 Ma (Repenning 1998, p. 52). All of those age assessments were based on the single isolated tooth ABDSP(LACM) V24540 and now must be disregarded. Other early occurrences were summarized by Bell et al. (2004b), and greater attention now needs to be given to those records (Bell and Bever 2006).

The stratigraphic position of the '*Lasiopodomys'* specimen, in reversed polarity sediments dating to between 1.07 and 1.77 Ma, makes it the oldest record of that morphotype in North America (Repenning 1992). It is one of only a few specimens showing a *'Lasiopodomys'* morphotype from west of the Rocky Mountains (Repenning 1992; Bell et al. 2004a). Elsewhere in North America, *Lasiopodomys* morphotypes are known from faunas younger than 850,000 years old (Repenning 1992).

The reported specimen of *Microtus* (=*Terricola*) *meadensis* from ABD is from the top of the Borrego Badlands section, not VCFC. The specimen locality is stratigraphically above the Bishop Ash (average age 758.9 ± 1.8 ka; Sarna-Wojcicki et al. 2000); a stratigraphic change equivalent to an age reduction of at least 1 million years. Repenning's attribution of this specimen to the VCFC formed the basis for his reinterpretation of the geomagnetic polarity stratigraphy in the upper part of that sequence (Repenning 1992; Bell et al. 2004b), an assessment that now must be disregarded.

CONCLUSIONS

The lagomorph specimens from the ABD section that are nearest to *Lepus* in size and morphology can not be identified definitively to the genus *Lepus*. Of the four specimens variously referred to '*Lepus*' ABDSP(IVCM) 113/V413 is the nearest in overall appearance to *Lepus* but only meets the minimum size criterion for p3 of White (1991a). It displays characters also found in specimens of *Nekrolagus* and *Sylvilagus*, and may be a modern specimen. ABDSP(IVCM) 113/V1275 has possible problems with locality provenience and may represent *Nekrolagus progressus*, although more comprehensive work on the collection is required; it is best referred to Leporinae, genus and species indeterminate. ABDSP(LACM) 1906/V24889 is similar to both medium-size *Lepus* and large *Sylvilagus* but is undiagnostic beyond Leporinae, genus and species indeterminate. ABDSP(IVCM) 110/V407 was determined to be a specimen from a modern leporine, was discarded prior to this review, and is unavailable for further study. Based on fossil material currently in the collection *Lepus* does not demonstrably occur in the ABD faunas.

Of the ABD specimens originally published as *Microtus californicus?* (Zakrzewski 1972) ABDSP(LACM) 1942/V8252 appears consistent with Repenning's (1992) taxonomic reassignment of the specimen to '*Lasiopodomys*,' and represents the oldest known *Lasiopodomys* morphotype in North America. ABDSP(LACM)?/V24540 is most accurately identified as *Microtus* sp. with five closed triangles, but lacks locality data. ABDSP(LACM) 6683/V24649 is diagnostic only to Arvicolinae. The specimen of *Microtus meadensis,* ABDSP(LACM) 68123/V24828, is not from VCFC (contra Repenning 1992, 1998) but from the Borrego Badlands, stratigraphically above the Bishop Ash. This is within the known temporal extent of the species elsewhere in North America (Repenning 1987, 1992; Bell et al. 2004a).

The Anza-Borrego Desert specimens from the VCFC sequence no longer contribute to discussions of the early appearance of *Lepus* or the earliest five-triangle *Microtus* in North America. The Blancan-Irvingtonian boundary in the ABD is currently undefined, and its recognition is complicated by uncertain taxonomic affinities and inconsistent primary data associated with many relevant specimens. The VCFC section still represents one of the most important fossil sequences for Blancan and Irvingtonian land mammal ages and the transition between them. Further assessment will improve the understanding of its relevance to local, regional, and continental biochronology, as well as to a general understanding of the evolution of the vertebrate biota in western North America during a dynamic interval of time.

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