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AN IRVINGTONIAN SPECIES OF *BRACHYLAGUS* (MAMMALIA: LAGOMORPHA) FROM PORCUPINE CAVE, PARK COUNTY, COLORADO

Colleen N. Ramos[1]

ABSTRACT.—*Brachylagus* is currently a monotypic genus of uncertain origins and known only from Holocene and late Rancholabrean. A new species of leporid is described from the early and middle Pleistocene (Irvingtonian) deposits of Porcupine Cave, Park County, Colorado. Stratified deposits of the Pit and the Velvet Room, 2 localities within Porcupine Cave, have been dated biochronologically and paleomagnetically from the middle Irvingtonian and early to middle Irvingtonian, respectively. *Brachylagus coloradoensis,* sp. nov., is characterized by its conserved p3 enamel patterns which are intermediate between *B. idahoensis* and *Hypolagus,* and its size which is slightly larger than that of *B. idahoensis.* This suggests a possible ancestral relationship between *Hypolagus* and *Brachylagus.*

Key words: Brachylagus, *Irvingtonian,* Brachylagus idahoensis, *pygmy rabbit, Leporidae, Lagomorpha, Pleistocene.*

Brachylagus idahoensis (pygmy rabbit), the sole living species of *Brachylagus,* is a small rabbit that is restricted to dense stands of sagebrush (*Artemisia* spp.) in the Great Basin. An isolated population also survives in eastern Washington and is currently the subject of attention by conservationists. Because of its highly specific habitat needs (as reviewed by Dobler and Dixon 1990), the species is vulnerable to local extirpation as its natural habitat is modified and/or destroyed by agriculture and cattle grazing. The species has apparently existed in the Great Basin area for much of its evolutionary history as only a single paleontological site is known from outside its current range (Walker 1987).

The genus has a long history of taxonomic uncertainty but is now generally considered to be valid. The species now known as *B. idahoensis* was first described by Merriam (1891) but ascribed to the genus *Lepus.* Miller (1900) formally proposed the subgenus *Brachylagus,* which Lyon (1904) elevated to full generic status, a usage maintained by Nelson (1909). Later authors placed the species in the genus of *Sylvilagus* (Grinnell et al. 1930, Orr 1940, Durrant 1952). More recent morphological work has supported the generic status of *Brachylagus* (Kenner 1965), with recent genetic work (reviewed by Chapman and Ceballos 1990) further substantiating this.

Brachylagus idahoensis, being the smallest leporid in North America, is easily identified by its unique p3 enamel patterns and its small size. Even so, few paleontological sites include this species in their faunal lists; thus, it has a limited fossil record that extends only to the late Rancholabrean (Kurtén and Anderson 1980). However, material from Cathedral Cave, an Irvingtonian site in eastern Nevada, has yielded isolated teeth easily referable to *B. idahoensis* (C.J. Bell personal communication). Despite its limited geologic presence, this genus has been hypothesized to have originated either in the Miocene and descended from the genus *Alilepus* (Hibbard 1963), or later in the Pliocene and again derived from *Alilepus* (White 1991b). These hypothetical ancestries are based upon formation of the p3 enamel pattern found in *Brachylagus,* which is completely distinct from other North American leporids. Given the limited fossil record of *Brachylagus* and extensive radiation of the genus *Hypolagus* during the Pliocene, a reasonable, alternative hypothesis is that *Brachylagus* arose directly from *Hypolagus* in the late Blancan or early Irvingtonian. These hypotheses are summarized in Figure 1 and evaluated below.

The species described here occurs in the Irvingtonian deposits of Porcupine Cave, Park County, Colorado. The cave contains several

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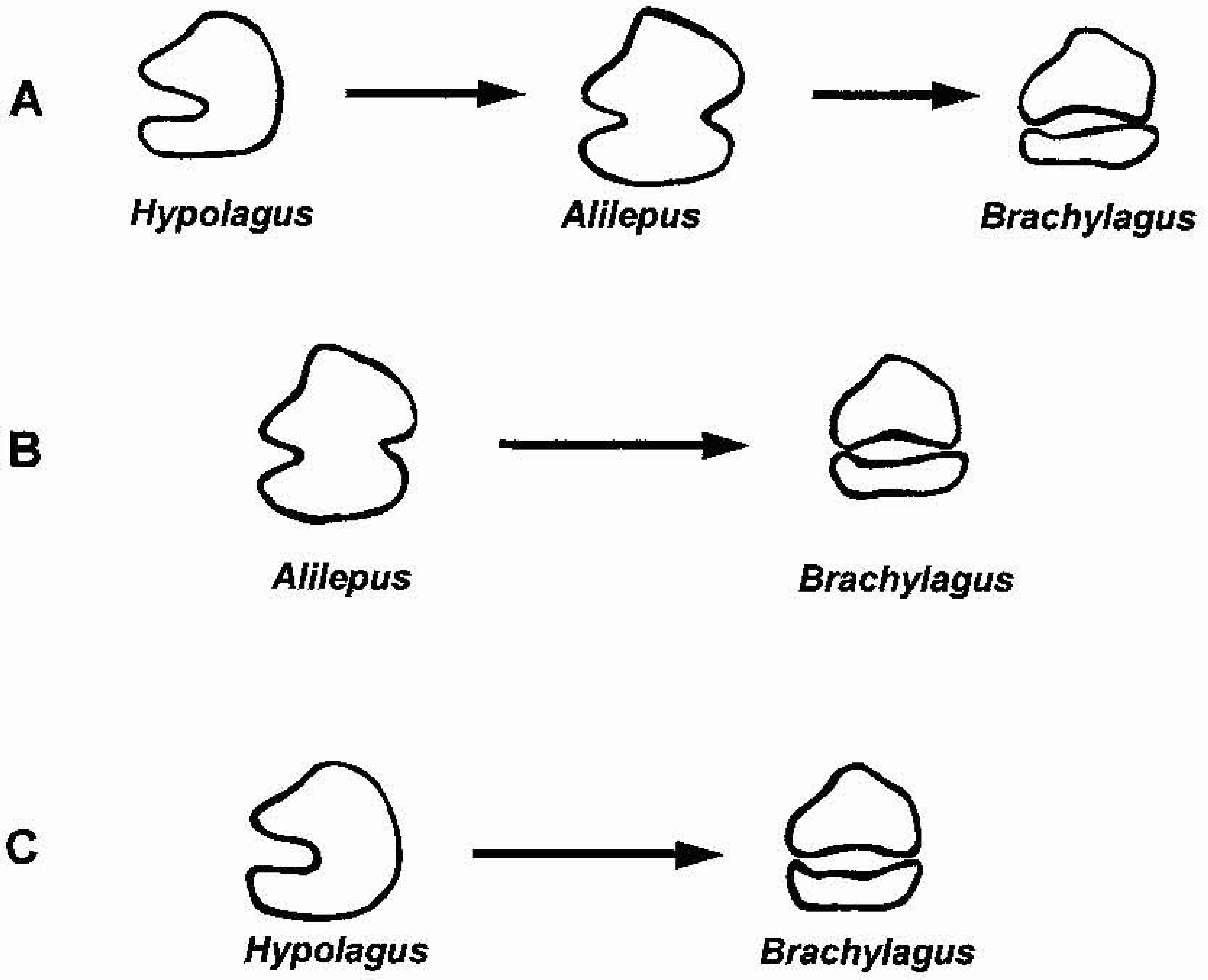

Fig. 1. Summary of hypotheses concerning evolution of p3 form seen in *Brachylagus*: A, *Brachylagus* descending from *Alilepus*, posterior-external reentrant (PER) fuses with posterior internal reentrant to form separate lobes as seen in *Brachylagus* (summarized from Hibbard 1963); B, *Brachylagus* descending from *Alilepus* (which arose from *Hypolagus*) during late Pliocene or early Pleistocene (after White 1991b); and C, *Brachylagus* descending directly from *Hypolagus*, PER eventually extends completely across width of the tooth to separate the trigonid from the talonid.

rooms from which fossils have been collected (Barnosky and Rasmussen 1988, Wood and Barnosky 1994, Anderson 1995). These rooms and areas represent localities within Porcupine Cave and include the Pit, Velvet Room, and Mark's Sink. Fossil deposits range in age from early to late Irvingtonian. The Pit, a small room in the cave, was excavated by the Carnegie Museum (CM) in the 1980s and was originally thought to date between approximately 0.38 my to roughly 0.8 my (Barnosky and Rasmussen 1988, Wood and Barnosky 1994). More recent analyses date the majority of the Pit around 850,000 y.b.p. (Barnosky personal communication). Paleomagnetic studies of the Velvet Room have found that the upper 5 levels correlate to the present normal polarity while the majority of the lower levels were deposited during the Matuyama reversed polarity chron (B. Raynolds and J. Friedman personal communication) and are therefore at least 0.78 million years in age. Mark's Sink, an isolated section of the Velvet Room, contains bioturbated material in its upper sections, while its lower portions are stratified and apparently undisturbed. These lower levels are also yielding mammal species, such as *Hypolagus*, that are older than those found anywhere else in the cave. Although other rooms with fossilized remains exist and have been sampled, the 3 rooms described above have produced most fossil specimens to date and may, collectively, span more than one million years.

In the 1980s certain specimens from the Pit were identified as *Brachylagus idahoensis* by Barnosky and Rasmussen (1988). While analyzing the leporid remains from the Velvet Room and Mark's Sink, I discovered several teeth and mandibles similar in size to those of *B. idahoensis* but lacking the diagnostic p3 enamel pattern of this species. When I reexamined the Pit specimens, I found that they too lacked the *B. idahoensis* form of p3. Previous morphometric work (Ramos in press) provided a large sample of extant *B. idahoensis* ($n = 85$) as well as an understanding of variation in dental characters for this species. When used for comparison with the Porcupine Cave fossils, these data demonstrated that although the fossils were similar in several ways to *B.*

idahoensis, distinct differences indicated a new species of *Brachylagus*.

METHODS

Porcupine Cave is located at 2900 m in the NW1/4 of SW1/4 Sec. 23, T15S, R76W in Park County, Colorado. Fossil material was collected by Denver Museum of Natural History (DMNH) crews using 0.64-m^2 grid excavated in 2-cm levels for the stratified deposits of the Velvet Room. The upper region of Mark's Sink is unstratified and the grid system was not applied; however, the lower sections separate into strata that have been carefully excavated utilizing the grid and level system described above. Material was screened and washed, then brought to DMNH for identification and cataloging. Material from the Pit was excavated using different methodology (see Barnosky and Rasmussen 1988) and much of that material is housed in CM.

Using Mitutoyu calipers calibrated to 0.02 mm, I measured the fossil material as well as 85 recent skulls of *Brachylagus idahoensis* for comparison. Measurements followed previously published conventions (Bensley 1926, Findley et al. 1975, White 1987) and are as follows: (1) depth of mandible at anterior alveolus of p4, (2) length of alveolar tooth row of mandible, (3) length of p3, (4) width of p3, (5) width of p4, (6) width of m1, (7) width of m2, (8) width of m3, (9) length of diastema, (10) length of maxillary alveolar tooth row, (11) depth of anterior zygomatic process, (12) width of P2, (13) width of P3, (14) width of P4, (15) width of M1, (16) width of M2, (17) width of M3. Diastemata of maxillae are rarely preserved and were not included in the analysis. Enamel pattern terminology follows White (1987, fig. 3).

The data were then subjected to descriptive statistics using Microsoft Excel. In addition, a 2-sample t test was performed upon widths and lengths of p3 between the 2 species. Only adult specimens of both the recent and fossil material were used. Fossil specimens were determined to be adult if the cheek teeth showed no alteration in size and enamel pattern from their base to their occlusal surface, sutures were well knit, and the bone was not highly porous. Specimens were determined to be immature and excluded from the analysis if any of the above conditions were not met.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE
Fischer de Waldheim, 1817
Genus *Brachylagus* Miller, 1900
Brachylagus coloradoensis,
new species

HOLOTYPE.—DMNH #33261, incomplete right dentary with p3; lacking incisor, p4, m1, m2, and m3, coronoid process, condyloid process, and angle of mandible (Fig. 2).

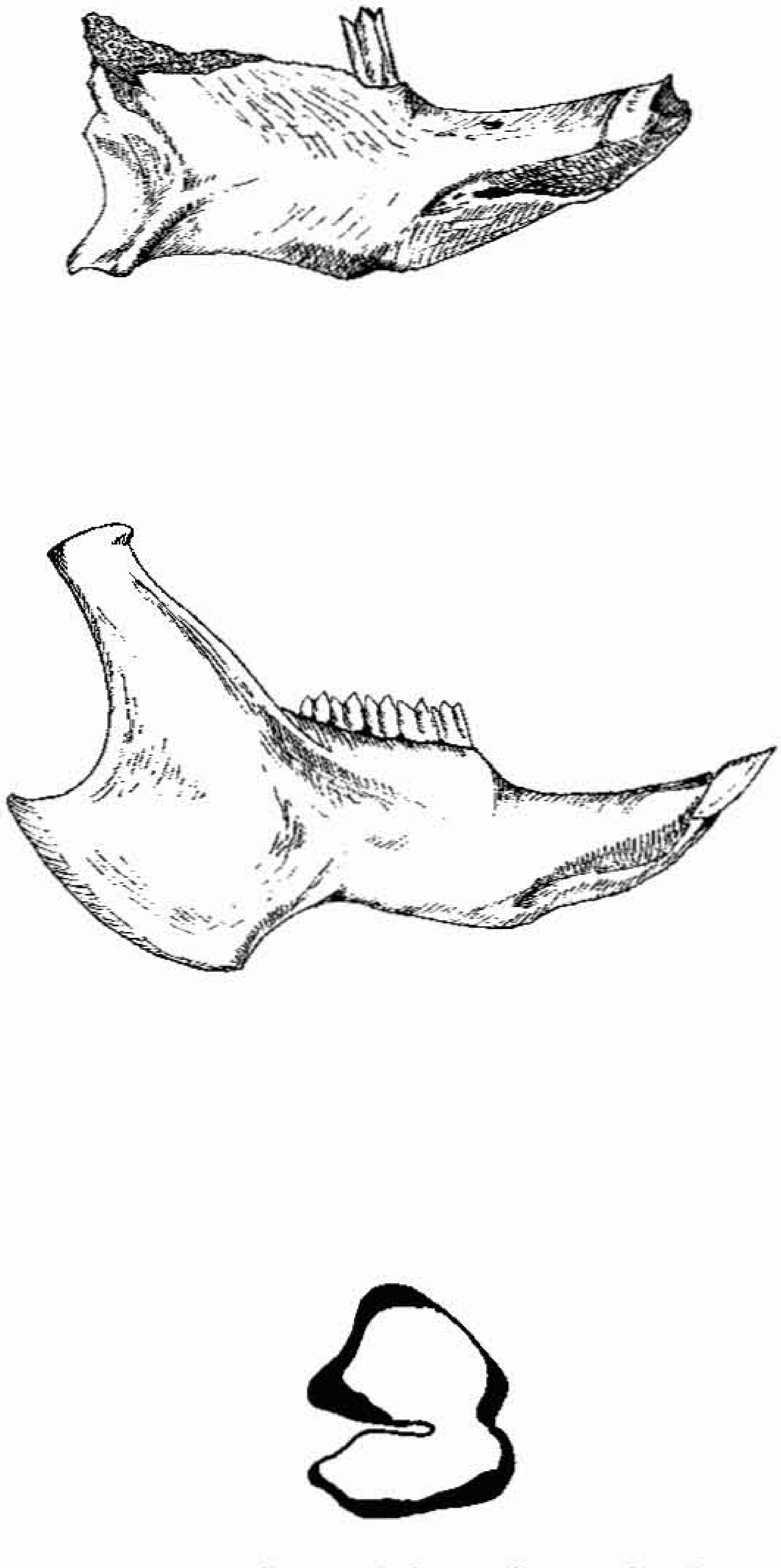

Fig. 2. DMNH #33261, holotype for *B. coloradoensis* (top), and mandible of *Brachylagus idahoensis* (UCM #5840), both shown from labial view. Camera lucida drawing of p3 from holotype; labial is to left, lingual to the right, top is anterior, bottom is posterior.

HYPODIGM.—Pit: CM #66408–66409, p3; CM #66431, edentulous right maxilla; CM #66432, edentulous left maxilla; CM #65486, left dentary with p4–m2; CM #66604, p3; CM #65607, p3. Velvet Room: DMNH #28901, 33250, 33255, p3. Mark's Sink: DMNH #28902, left humerus; DMNH #33257, left dentary with p3–p4; DMNH #33260, three isolated p3s; DMNH #33272, four isolated p3s; DMNH #33271, left dentary with p3–m2; DMNH #33270, left dentary with p3–m1.

TYPE LOCALITY AND AGE.—Middle Pleistocene, early to middle Irvingtonian, DMNH Locality No. 1349, Porcupine Cave, 2900 m, Park Co., Colorado (NW1/4 of SW1/4 Sec. 23, T15S, R76W, Lat. 38°43′45″N, Long. 105° 51′41″W, Gribbles Park 7.5′ Quad).

ETYMOLOGY.—Named for the locality and following the precedent set in this genus. At present, this species is known only from a single site in Colorado.

DIAGNOSIS.—The enamel pattern of the p3 is distinct from that of *B. idahoensis* in having a posteroexternal reentrant (PER) that extends between 1/3 and 2/3 the width of the tooth (Fig. 3). The posterointernal reentrant (PIR), when present, is only a slight indentation. Dimensions of postcranial material strongly resemble those of modern *B. idahoensis* but are slightly more robust.

COMPARISONS.—*Brachylagus coloradoensis* may be distinguished from *Hypolagus* species by its smaller size. Also, the PER of *B. coloradoensis* p3 extends farther across the tooth width, generally greater than 1/2 the distance (Fig. 3). Although *B. idahoensis* is of similar size, *B. coloradoensis*, sp. nov., is generally more robust. In comparing the size of p3, *B. coloradoensis* is approximately 12–15% larger than the average *B. idahoensis* although some specimens fall within the range of individual variation for *B. idahoensis* (Tables 1, 2). Results of the 2-sample t test indicate that p3 of *B. idahoensis* and p3 of *B. coloradoensis* differ in length ($F_{81,19} = 4.5$, $P < 0.0001$) and width ($F_{81,19} = 2.66$, $P < 0.001$). These results, and the differences between enamel patterns, indicate that the 2 samples are not drawn from the same population and support the designation of *B. coloradoensis* as a species separate from *B. idahoensis*. The PER of *B. coloradoensis* does not extend completely across the tooth width as in *B. idahoensis*. No complete skulls of *B. coloradoensis* are known from this site; however, portions of dentaries and edentulous maxillae are present. Disarticulated postcranial material has been tentatively assigned to this species due to the unusually small size which allows no other confident identification within the Leporidae. Several uncataloged humeri, ulnae, and podial remains have thus been identified to *B. coloradoensis* and are similar in size to corresponding elements of *B. idahoensis*.

DISCUSSION

Brachylagus coloradoensis, sp. nov., shows some affinity to the extinct genus *Hypolagus* that radiated profusely in the Pliocene (Fig. 3). Although some p3s of *B. coloradoensis* display patterns with clear PIRs as seen in *Alilepus*, none of the upper molars found and ascribed to *B. coloradoensis* display the characteristic enamel lake found in *Alilepus*. This lake is also absent in *Hypolagus*. *Hypolagus* is easily distinguished by its simpler p3 enamel patterns and larger size.

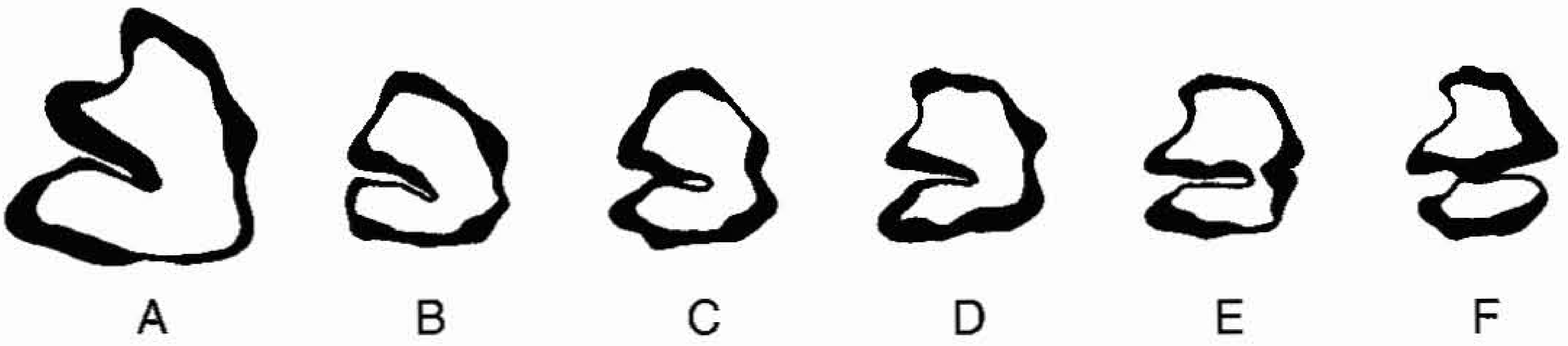

Fig. 3. Comparison of p3 enamel patterns for *Hypolagus*, *B. coloradoensis*, and *B. idahoensis*. A is *Hypolagus* (redrawn from White 1987:439), B–E (DMNH # unknown, DMNH #33257, DMNH #33255, and DMNH #33260) represent the range of variation seen in specimens of *B. coloradoensis*. B predominates slightly in earlier sediments whereas C becomes somewhat more plentiful in younger sediments at Porcupine Cave. F is that of *B. idahoensis* (UCM #5840). Note also that some specimens of *B. coloradoensis* have a slight posterior-internal reentrant (PIR).

TABLE 1. Dimensions and descriptive statistics of dentary and lower dentition of *Brachylagus coloradoensis* and *B. idahoensis* (in parentheses). Values for *B. idahoensis* are for left measurements only.

Measurement	$\bar{x} \pm s$	Range	*n*
Alveolar length of toothrow	10.48 (n/a) (9.1 ± 0.34)	n/a (8.24–10.26)	2 (85)
Length of diastema	10.9 (n/a) (9.0 ± 0.43)	n/a (8.46–11.92)	1 (85)
Depth of dentary at p4	8.86 ± 0.30 (7.54 ± 0.42)	7.74–9.56 (6.60–8.26)	4 (85)
Length of p3	2.02 ± 0.28 (1.78 ± 0.11)	1.74–2.56 (1.62–2.28)	19 (85)
Width of p3	1.80 ± 0.22 (1.6 ± 0.11)	1.40–2.12 (1.42–2.18)	19 (85)
Width of p4	2.34 ± 0.12 (1.96 ± 0.1)	2.12–2.54 (1.68–2.22)	5 (85)
Width of m1	2.35 ± 0.12 (1.98 ± 0.1)	2.24–2.46 (1.78–2.26)	4 (85)
Width of m2	2.22 ± 0.16 (1.94 ± 0.1)	2.08–2.40 (1.74–2.20)	3 (85)
Width of m3	1.70 (n/a) (1.02 ± 0.09)	n/a (0.82–1.30)	2 (85)

TABLE 2. Dimensions and descriptive statistics of maxilla and upper dentition of *Brachylagus coloradoensis* and *B. idahoensis* (in parentheses). Values for *B. idahoensis* are for left measurements only.

Measurement	$\bar{x} \pm s$	Range	*n*
Alveolar length of toothrow	10.08 (n/a) (9.13 ± 0.35)	n/a (8.32–10.1)	2 (85)
Depth of zygomatic process	3.49 (n/a) (3.49 ± 0.31)	n/a (2.88–4.24)	2 (85)
Width of P2	2.09 (n/a) (1.73 ± 0.14)	n/a (1.52–2.36)	2 (85)
Width of P3	3.19 (n/a) (2.96 ± 0.2)	n/a (2.58–3.38)	2 (85)
Width of P4	3.19 (n/a) (2.98 ± 0.17)	n/a (2.52–3.64)	2 (85)
Width of M1	3.05 (n/a) (2.87 ± 0.18)	n/a (2.36–3.26)	2 (85)
Width of M2	2.6 (n/a) (2.6 ± 0.15)	n/a (2.32–2.96)	2 (85)
Width of M3	1.15 (n/a) (1.07 ± 0.18)	n/a (0.6–1.84)	2 (85)

The lower third premolar (p3) is considered somewhat diagnostic among leporids and has been used in numerous species descriptions, especially of extinct leporids (White 1984, 1987, 1991a, 1991b, Hibbard 1963). In *B. coloradoensis* there is some variation in this character which, based upon the limited number of specimens available, seems to be present regardless of geologic age. In short, no particular evolutionary trend is seen in this character. Although the simplest form is slightly more prevalent in older strata and the more derived form seems more prevalent in later strata, both extremes of the continuum are present in oldest and youngest strata. The range of variation in the p3 enamel pattern of *B. coloradoensis* is depicted in Figure 3. The P2 contains a single anterior reentrant as in *B. idahoensis* and *Hypolagus*.

The size of the Mark's Sink *B. coloradoensis*, which is presumably the oldest in the cave, is somewhat larger than that of either the Velvet Room or Pit specimens of *B. coloradoensis* (Fig. 4) while retaining more conservative p3 enamel patterns. This is an intriguing trend and may indicate a time frame for the cladogenic event that gave rise to the genus *Brachylagus*. Unfortunately, the strata from which these earliest specimens come are bracketed only with upper and lower time limits and there is little refinement in the age estimates of the levels themselves. Therefore, a more accurate picture of the rate at which the variation narrowed is not possible at this time.

However, the wide range of size variation noted for specimens of *B. coloradoensis* in the early Irvingtonian of Porcupine Cave (Fig. 4) may indicate that the cladogenetic event occurred shortly (in geologic terms) before the Porcupine Cave record. At least 2 species of *Hypolagus*, as yet unidentified, are present in the older sections of Mark's Sink with the *B. coloradoensis* material. One of these species is very small, though still somewhat larger than the largest specimens of *B. coloradoensis*. The relationship between *B. coloradoensis* and this small *Hypolagus* is unclear at present. A more detailed phylogenetic analysis utilizing several characters is currently in progress and should provide stronger evidence concerning the origins of *Brachylagus* and its relationships to extinct and extant genera (C.N. Ramos in preparation).

Of the hypotheses concerning the ancestral stock of this genus (Fig. 1), it appears just as likely that *Brachylagus* arose directly from *Hypolagus* as from *Alilepus*. Although *B. coloradoensis* exhibits p3s of both *Hypolagus* and *Alilepus* form, there are no enamel lakes present in any of the upper molars examined. Enamel lakes in upper cheek teeth are absent in *Hypolagus*, but present in P3 of *Alilepus*, and may represent plesiomorphic characters retained from Paleolaginae from which Archaeolaginae arose. Also, the time frames hypothesized by Hibbard (1963) and White (1991a) are unsubstantiated by the fossil record as there is no evidence that *Brachylagus* existed earlier than the very latest Blancan to earliest Irvingtonian.

Genera such as *Lepus* and *Sylvilagus* are not considered to have originated directly from *Hypolagus*. One or more potential intermediates have been hypothesized over the years, including *Alilepus*, *Serengetilagus (Pliopentalagus)*, and others (Hibbard 1963, White 1991b), and fossil evidence does not dispute these hypotheses. However, *B. coloradoensis* appears to indicate a more direct transition from *Hypolagus* to *Brachylagus*. Thus, the living pygmy rabbit may be the only direct descendent of an extinct genus and may be more distantly related to *Sylvilagus* than previously thought. Although Halanych and Robinson (1997) found some molecular evidence placing *Brachylagus* as sister taxon to *Sylvilagus* based upon mitochondrial 12S rDNA data, other aspects of their analysis did not support this strongly. I find that the high degree of morphological differences between *Brachylagus* and *Sylvilagus*, as well as the paleontological evidence described above, present a strong case against a close relationship between them (see also Kenner 1965, Green and Flinders 1980).

Given the high degree of habitat specificity exhibited by the extant species of *Brachylagus*, it would be interesting to determine whether its extinct species was also highly habitat specific. Unfortunately, paleoecological evidence at Porcupine Cave is scanty and restricted mostly to faunal remains. Such postcranial remains as have been assigned to *B. coloradoensis* resemble *B. idahoensis* in almost all details. This indicates a similar degree of locomotor adaptation as seen in the extant species. *Brachylagus coloradoensis* was probably also closely

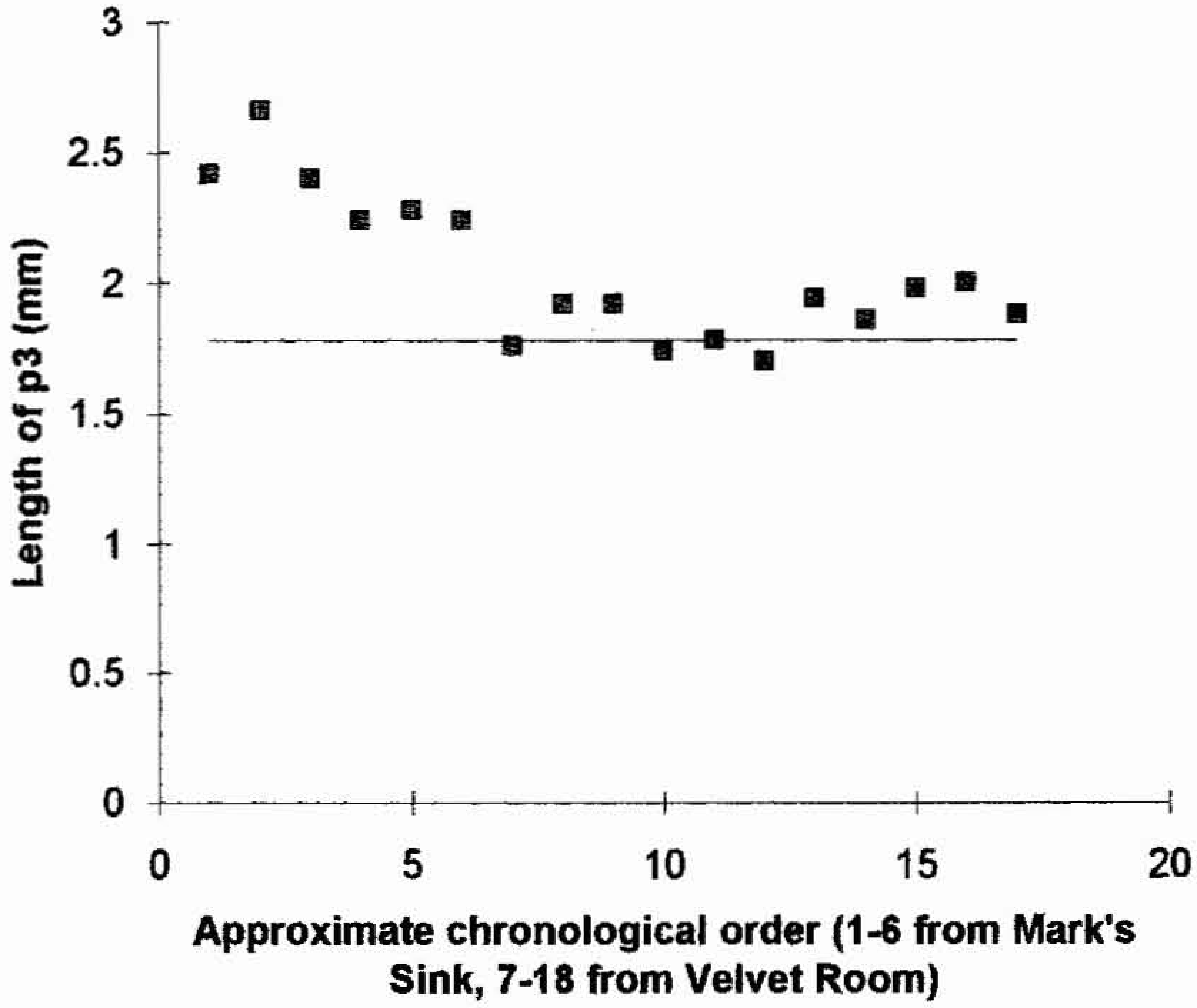

Fig. 4. Change in p3 length over time. Size data plotted over time for the different rooms in Porcupine Cave. Length of p3 has been used to illustrate the general trend, that of wide size range in older sediments, then loss of upper size limits and closer approximation to size range of *B. idahoensis.* Line indicates average p3 length for *B. idahoensis.*

allied to brush and dense cover and avoided open areas, although the plant biota comprising its habitat is impossible to ascertain at this time. However, Barnosky and Rasmussen (1988) reported the consistent concurrence of sage vole (*Lagurus curtatus*) with *B. coloradoensis* (reported as *Sylvilagus idahoensis*). This arvicoline rodent is generally found in stands of *Artemisia* (Armstrong 1972) and currently has a distribution overlapping that of *B. idahoensis.* Both mammal species are absent from the Wyoming Basin, as is *B. idahoensis,* despite the apparent presence of suitable habitat (Walker 1987). The presence of an Irvingtonian species of *Brachylagus* on the eastern side of the Continental Divide and the persistence of extant *Brachylagus* in the Great Basin may indicate that the 2 populations became isolated on opposite sides of the Rocky Mountains after dispersing through the Wyoming Basin. Where the genus originated is unclear; and although I find the presence of a small *Hypolagus* associated with *B. coloradoensis* in the older strata of Mark's Sink to be suggestive, it certainly is not conclusive.

Although complete species associations cannot be reconstructed at this time for Porcupine Cave, it is notable that this new species of leporid was associated with extinct leporids such as *Aztlanolagus* and *Hypolagus* in the oldest sections of Porcupine Cave, yet found with extant species such as *Lepus townsendii* and *Sylvilagus audubonii* in younger sediments at this site (Ramos 1998). These associations do not necessarily indicate sympatry but do indicate a temporal coexistence. Sympatry is rare among species of rabbits and hares, and the remains at Porcupine Cave are the result of predation by raptors and mammals, some of which have large ranges. Prey remains are thus sampled from a potentially wide radius and do not represent close species associations. It is still intriguing to find that this little leporid was able to survive while other leporid species, even genera, were going extinct. Unfortunately, the fossil record at Porcupine Cave truncates several hundred thousand years ago and we cannot know, at this time, how long *B. coloradoensis* survived in association with modern fauna.

Porcupine Cave is continuing to be excavated and specimens of this new species are being added to the collections at DMNH. In addition, temporal limits of localities within the cave are being clarified, which will allow more refined analysis of morphological change, speciation rate, and faunal associations. As further analysis of this important Irvingtonian site continues, our understanding of this extinct species will continue to grow, hopefully providing new insights into the evolutionary history of the single living species of *Brachylagus*.

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