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Lagomorphs from the Zia Sand Miocene of New Mexico

CONSTANCE ELAINE GAWNE[1]

ABSTRACT

Lagomorphs of ?latest Arikareean-medial Hemingfordian faunas from the Zia Sand include at least two archaeolagine leporids and an ochotonid. The latest Arikareean or earliest Hemingfordian Standing Rock local fauna includes *Archaeolagus* cf. *macrocephalus*, tentatively referred to *A. macrocephalus*, of the early Hemingfordian of South Dakota, on morphology of lower teeth; it resembles *Hypolagus* in size and crenulation of hypostriae, but differs sufficiently in morphology of anterior premolars to make close relationship unlikely. Limb structure, although far advanced over *Palaeolagus*, suggests less cursorial locomotion than *Sylvilagus* or *Oryctolagus*. *Archaeolagus* sp., of the medial Hemingfordian Blick local fauna, appears less advanced than *A.* cf. *macrocephalus* in structure of upper cheek teeth. It is similar to some specimens from medial Hemingfordian rocks of Nebraska, and may also be related to *Panolax* of the early Pliocene of New Mexico. Fragmentary specimens from the Jeep and Mesa Prospect local faunas can be identified only as *Archaeolagus incertae sedis*.

Oreolagus cf. *nebrascensis*, of the Blick local fauna, is represented by a fragmentary lower jaw and associated partial innominate bone. The latter shows some resemblance to *Prolagus* in form of acetabulum and iliac blade, but also resembles *Palaeolagus*, especially in form of the large, high iliac tubercle, suggesting retention of primitive lagomorph morphology and relatively unspecialized mode of locomotion.

INTRODUCTION

The Zia Sand, ?Late Arikareean through medial Hemingfordian deposits exposed in a series of fault blocks north and west of Albuquerque, New Mexico, were distinguished as a formation by Galusha (1966); a history of field work in the area, previous publications on the rocks included, and relationships to other units were included in that paper and discussed further by Galusha and Blick (1971, pp. 38-40). Gawne (MS) studied the faunas, sediments, and paleoecology of the formation; of that study, the rodents have been described (Gawne, 1975). In this paper I present the lagomorphs of the Zia Sand.

The lagomorphs were found in localities discussed by Galusha (1966): Standing Rock Quarry, 60 to 65 feet above the base of the type section of the Zia Sand and of its lower member,

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the Piedra Parada Member; Blick Quarry, 300 feet above the base of the Chamisa Mesa Member, and Cynarctoides Quarry, near the same stratigraphic level; Jeep Quarry, 275 to 300 feet higher in the same section, 75 feet below the base of the Tesuque Formation of the Santa Fe Group; and Mesa Prospect, 15 feet above Jeep Quarry.

Faunal lists of three of the four local faunas recognized were given by Gawne (1975). The Standing Rock local fauna, which includes *Archaeolagus* cf. *macrocephalus*, was assigned a late Arikareean age by Galusha (1966) and an age intermediate between described Arikareen and Hemingfordian faunas by Gawne (MS; 1975). The Blick local fauna, including *Archaeolagus* sp. and *Oreolagus* cf. *nebrascensis*, is of medial Hemingfordian age; the Jeep local fauna, which includes an archaeolagine leporid, is late medial Hemingfordian. The Mesa Prospect local fauna, in addition to the archaeolagine leporid described below, includes an amphicyonid carnivore, a diceratherine rhinoceros, *Parahippus* cf. *tyleri*, cf. *Merychippus*, *Merycodus* cf. *sabulonus*, Pecora *incertae sedis*, *Protolabis* sp., and cf. *Homocamelus*. This local fauna, stratigraphically above the Jeep local fauna, is considered near in age to, but older than, the Sheep Creek local fauna of Nebraska on the basis of the stages of evolution of the horses and merycodont.

ACKNOWLEDGMENTS

I am very grateful to Prof. Malcolm C. McKenna, who supervised this study; and to Messrs. Ted Galusha, Beryl Taylor, and Morris Skinner, and Dr. Richard Tedford for making available specimens from the Frick Collection, unpublished stratigraphic information, and preliminary conclusions of studies in progress, and for numerous invaluable discussions. I thank Mr. Chester Tarka for the photographs, Miss Lorraine Meeker for the drawings, and both for technical advice.

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ABBREVIATIONS

The following abbreviations are used to designate institutional collections:

AMNH, the American Museum of Natural History
CIT, California Institute of Technology collection, Natural History Museum of Los Angeles County
F:AM, Frick American Mammals, the American Museum of Natural History
FMNH, Field Museum of Natural History

ORDER LAGOMORPHA

FAMILY LEPORIDAE

SUBFAMILY ARCHAEOLAGINAE DICE, 1929

ARCHAEOLAGUS DICE, 1917

Archaeolagus cf. *macrocephalus* (Matthew, 1907)

Referred Specimens. F:AM 22276, 22277, and 22292, left maxillae; 22278, 22280, 22283, 22286, and 22287, partial right rami; 22289 and 22291, partial left rami; 22282, left maxilla, right ramus and skeletal elements; 22290, partial left maxilla, upper molariform tooth, and partial left ramus; 22288, partial mandible; 22284 and 22285, partial premaxillae; 22281, right and left P_3, P^2, two upper molariform teeth, and skeletal elements; 22279, tarsus with partial metatarsals; and 25409, nearly complete skeleton with skull and mandible. All from Standing Rock Quarry, Standing Rock local fauna.

Description and Comparisons. I^1 (fig. 1) is divided into two lobes by an open V-shaped groove (wider in an immature specimen) crossing about one-fourth of the occlusal surface. The medial lobe is slightly narrower than the lateral; both have convex anterior surfaces. I^1 of *Archaeolagus ennisianus* (AMNH 7191 a, b) has a narrower groove, flattened lobes, and narrower lingual lobe with a flat anteroexternal surface meeting the medial surface in a 45-degree angle. The occlusal surface of I^2 is a transversely elongate oval.

P^2 (fig. 2 a, h) has an anterior, straight-sided,

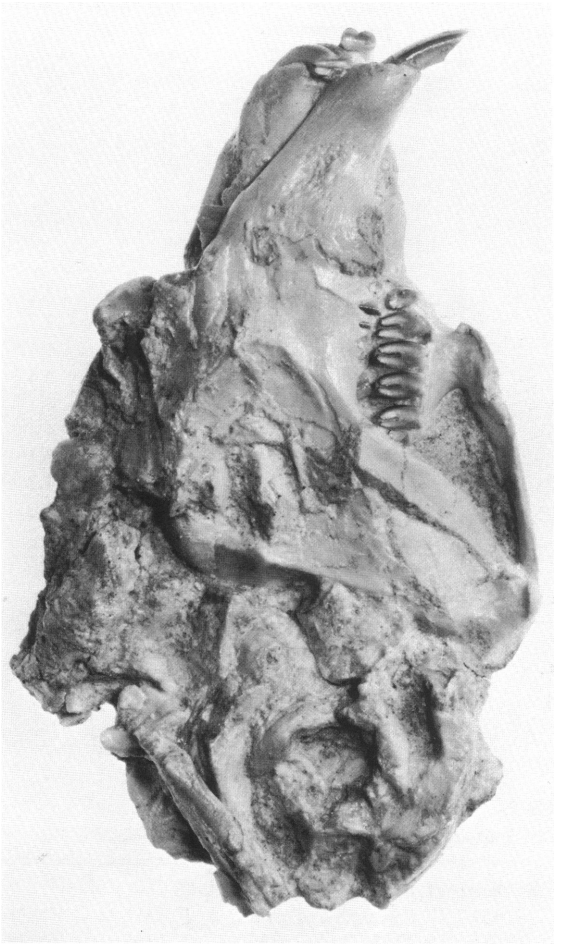

FIG. 1. *Archaeolagus* cf. *macrocephalus*, F:AM 25409, ventral view of skull, with left lower jaw covering palate and proximal end of scapula lying on basicranium.

cement-filled fold extending anterolabially two-fifths to one-half the anteroposterior length of the tooth. Facing anterolingually is a persistent groove, varying from a broad concavity to a sharp right angle, lacking cement. A similar groove is seen in some specimens of *A. ennisianus*, e.g., the holotype, AMNH 7190.[1] No specimen shows the labial groove characteristic of *Hypolagus* (Dawson, 1958, p. 44).

[1]The holotype of *Archaeolagus ennisianus*, AMNH 7190, has recently undergone additional preparation; a supplementary description is given in the Appendix.

Hypostriae on P^3-M^2 (fig. 2 a, i) extend one-third to one-half of the tooth width, longest on M^1 or M^2. The walls are straight-sided to moderately crenulated, with maximum crenulation on M^1 or M^2; folds may be more numerous on either anterior or posterior wall. Although wide variation occurs, the tooth row is most often widest at the posteroloph of P^3, and P^4 is most often longest. M^3 is a simple oval, elongate transversely. Enamel is reduced as in modern leporids. Cement fills P^3-M^2 hypostriae and overlaps slightly onto the lingual walls.

The lower incisor (fig. 1, 2 b, d, e) is nearly triangular in cross-section, with straight anterior and lingual faces, convex posterolabial face, and rounded posterolingual angle. The tooth, nearly as long as wide, is less anteroposteriorly flattened than that of *A. ennisianus*. The posterior end of the shaft lies below the P_3 trigonid or a point immediately in front of it.

P_3 (fig. 2 b, f, g) is long, with a straight labial side indented by the cement-filled posterior reentrant and cementless anterior groove, smoothly convex anterior and lingual margins, and convex to flattened posterior margin. AMNH 12910, holotype of *A. macrocephalus*, has a flattened anterolingual surface and thus a narrower anterior lobe than that in the Standing Rock Quarry sample; the difference, however, is slight. P_3 of *A. ennisianus* is also elongate and variable in shape; however, the anterior lobe of the trigonid projects less far labially, so that the anterior groove faces anterolabially rather than labially.

As in modern leporids, reduction of enamel of P_4-M_2 (fig. 2 b, c) increases with ontogenetic age. Enamel is missing from the anterior face and the lingual bridge, and may also be absent from the posterior and lingual talonid faces and the lingual trigonid face. The two columns of M_3 are persistently separate; enamel is missing from the anterior trigonid face and the lingual faces of both columns.

The sample size of *Archaeolagus* cf. *macrocephalus* is insufficient for statistical analysis; most measurements (tables 1, 2) fall within the lower parts of the observed ranges given by Dawson (1958, p. 51) for *Hypolagus vetus*. M^3 is shorter and M_3 smaller in all dimensions than those of *H. vetus*. Size differences from the holo-

TABLE 1
Measurements (in Millimeters[a]) of Lagomorph Upper Teeth

	Archaeolagus cf. *macrocephalus*						
	F:AM 22276	F:AM 22277	F:AM 22281	F:AM 22282	F:AM 22284	F:AM 22285	F:AM 22290
I^1 Length	–	–	–	–	1.9	1.9	–
I^1 Width	–	–	–	–	2.8	2.9	–
I^2 Length	–	–	–	–	0.9	0.8	–
I^2 Width	–	–	–	–	1.5	1.5	–
P^2 Length	1.6	1.5	1.3	1.6	–	–	–
P^2 Width	3.1	3.4	2.9	3.2	–	–	–
P^3 Length	2.3	2.2	–	2.4	–	–	2.2
P^3 Width Anteroloph	–	–	–	–	–	–	3.7[b]
P^3 Width Posteroloph	–	–	–	–	–	–	4.5[b]
P^4 Length	2.4	2.5	–	2.4	–	–	2.4
P^4 Width Anteroloph	4.6	–	–	–	–	–	4.1[b]
P^4 Width Posteroloph	4.7	–	–	4.4	–	–	4.4[b]
M^1 Length	2.5	2.3	2.2	2.1	–	–	2.1
M^1 Width Anteroloph	4.8	4.6	4.5	4.2	–	–	4.2
M^1 Width Posteroloph	4.6	4.4	4.5	–	–	–	4.3
M^2 Length	2.2	2.1	1.9	–	–	–	–
M^2 Width Anteroloph	4.2	4.3	4.1	–	–	–	–
M^2 Width Posteroloph	4.1	4.0	–	–	–	–	–
M^3 Length	0.8	1.1	–	–	–	–	–
M^3 Width	1.7	2.0	–	–	–	–	–

[a]Measured on occlusal surface unless otherwise indicated.
[b]Estimated.
[c]Measured on column.

TABLE 2
Measurements (in Millimeters[a]) of Lagomorph Lower Teeth

	Archaeolagus cf. *macrocephalus*							
	F:AM 22277	F:AM 22280	F:AM 22281	F:AM 22282	F:AM 22283	F:AM 22286	F:AM 22288	F:AM 22289
I Length	–	2.0	–	–	2.5	–	–	–
I Width	–	2.1	–	–	2.6	–	–	–
P_3 Length	3.4	2.8	3.0	3.1	3.5	–	–	2.9
P_3 Width Trigonid	2.8	2.3	2.5	2.5	2.5	–	–	2.6
P_3 Width Talonid	2.8	2.3	2.5	2.5	3.0	–	–	2.4
P_4 Length	–	2.9	–	–	–	–	2.9	2.5
P_4 Width Trigonid	–	2.9	–	–	–	–	3.1	3.1
P_4 Width Talonid	–	2.1	–	–	–	–	2.4	2.6
M_1 Length	–	–	–	–	–	3.2	2.8	3.1
M_1 Width Trigonid	–	–	–	–	–	3.4	3.0	3.5
M_1 Width Talonid	–	–	–	–	–	–	2.2	2.2
M_2 Length	–	–	–	–	–	3.1	3.1	–
M_2 Width Trigonid	–	–	–	–	–	–	3.0	–
M_2 Width Talonid	–	–	–	–	–	–	2.2	–
M_3 Length	–	–	–	–	–	1.7	–	–
M_3 Width Trigonid	–	–	–	–	–	1.4	–	–
M_3 Width Talonid	–	–	–	–	–	1.1	–	–

[a]Measured on occlusal surface unless otherwise indicated.
[b]Measured on column.

TABLE 1 – (*Continued*)

(*A.* cf. *macrocephalus*)			*Archaeolagus* sp.		*Archaeolagus ennisianus*	
F:AM 22292	F:AM 25409	Observed Range	F:AM 25410	F:AM 25411	F:AM 25412	AMNH 7190
–	1.6	1.6-1.9	–	–	–	–
–	2.8	2.8-2.9	–	–	–	–
–	–	0.8-0.9	–	–	–	–
–	1.2	1.2-1.5	–	–	–	–
1.5	1.5	1.3-1.6	–	1.2[c]	–	1.3
3.1	2.9	2.9-3.4	–	2.6[c]	–	2.3
2.4	2.3	2.2-2.4	1.9[c]	2.1[c]	–	1.8
4.1	3.6	3.6-4.1	3.6	2.7[c]	–	2.9
4.8	4.5	4.5-4.8	4.0	3.8[c]	–	3.6
2.4	2.3	2.3-2.5	–	2.1[c]	2.1[c]	1.8
4.2	4.6	4.1-4.6	–	4.3[c]	3.9[c]	3.4
4.6	4.5	4.4-4.7	–	4.3[c]	3.9[c]	3.5
2.4	2.3	2.1-2.5	–	2.0[c]	1.9	1.8
4.1	4.2	4.1-4.8	–	3.8[c]	3.9	3.2
4.1	4.1	4.1-4.6	–	3.8[c]	3.9	3.3
2.3	2.0	1.9-2.3	–	1.9[c]	1.7	1.6
3.4	3.9	3.4-4.3	–	–	3.6	3.1
3.3	3.5	3.3-4.1	–	3.5[c]	3.2	2.8
0.6	0.9	0.6-1.1	–	–	0.7	0.9
2.1	1.7	1.7-2.1	–	–	1.5	1.6

TABLE 2 – (*Continued*)

	(*Archaeolagus* cf. *macrocephalus*)				*Archaeolagus macrocephalus*	*Archae-olaginae* sp.	*Archaeolagus ennisianus*	*Oreolagus* cf. *nebrascensis*
F:AM 22290	F:AM 22291	F:AM 22292	F:AM 25409	Observed Range	AMNH 12910	F:AM 25413	AMNH 7190	F:AM 25415
–	–	–	2.3	2.0-2.5	2.2	2.2	–	1.5
–	–	–	2.5	2.1-2.6	2.6	2.4	–	1.3
–	–	–	–	2.8-3.5	3.1	–	2.5	–
–	–	–	–	2.3-2.9	2.6	–	2.1	–
–	–	–	–	2.3-3.0	2.7	–	2.2	–
–	–	3.0	3.4	2.5-3.4	2.9	2.8	2.3	1.7[b]
–	–	–	3.3	2.9-3.3	3.2	3.3	2.6	1.8[b]
–	–	2.6	3.0	2.1-3.0	2.5	2.8	1.6	1.6[b]
3.1	3.0	–	–	2.8-3.2	3.1	2.8	2.4	1.7[b]
3.6	3.6	–	–	3.0-3.6	3.4	3.2	2.5	2.0[b]
2.4	2.4	–	–	2.2-2.4	2.6	2.5	1.9	1.6[b]
3.1	3.0	–	–	3.0-3.1	3.2	–	2.5	–
3.3	2.9	–	–	2.9-3.3	3.2	–	2.3	–
2.2	2.4	–	–	2.2-2.4	2.4	–	1.9	–
1.6	1.5	–	1.9	1.5-1.9	1.9	–	1.5	–
1.6	1.5	–	–	1.4-1.6	1.7	–	1.3	–
1.0	0.9	–	–	0.1-1.1	1.0	–	0.8	–

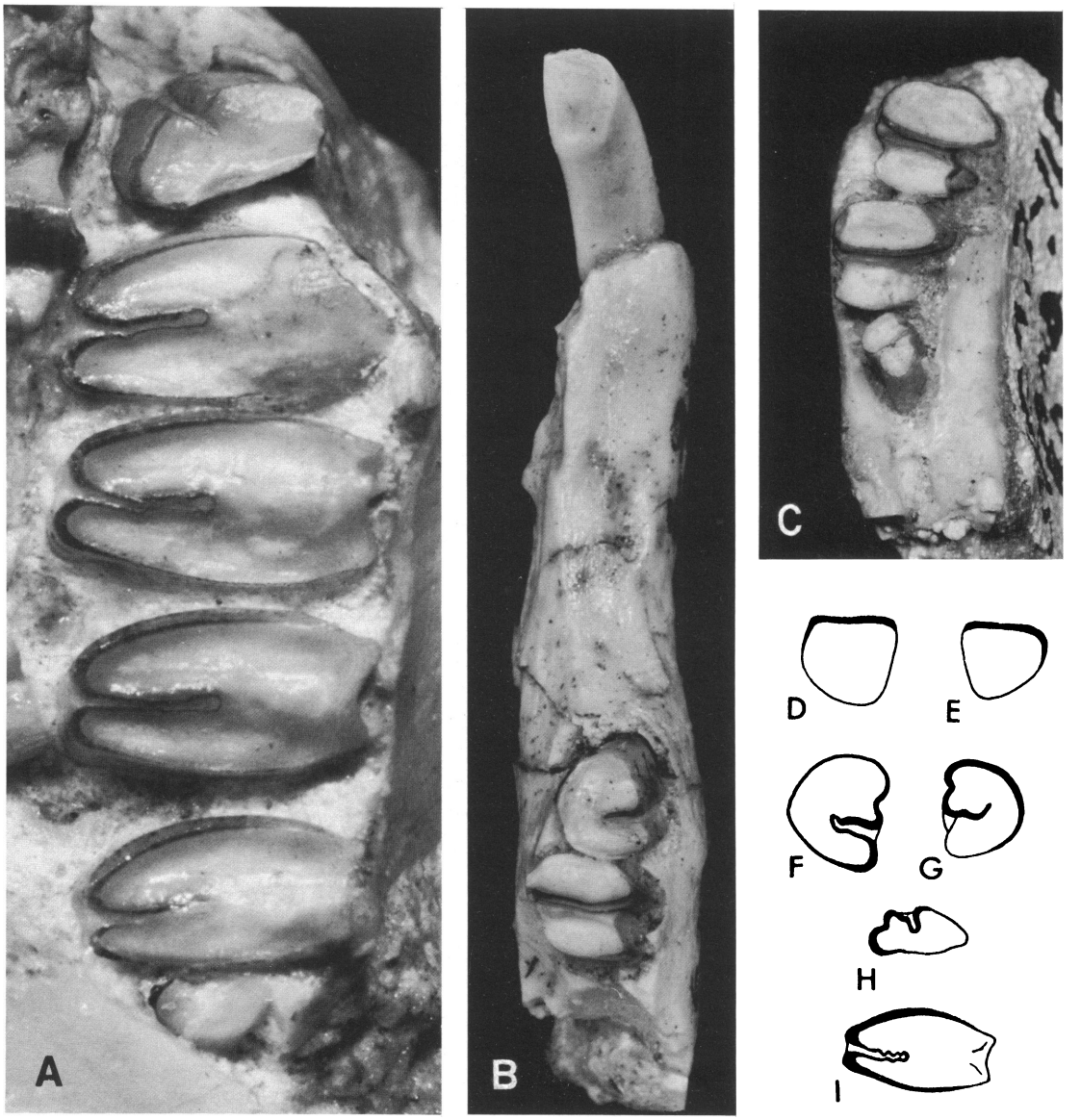

FIG. 2. Dentition of *Archaeolagus* cf. *macrocephalus*. A. F:AM 25409, left upper cheek teeth, ×10. B. F:AM 22288, anterior half of horizontal ramus with I-P_4, ×5. C. F:AM 22286, posterior half of horizontal ramus with M_{1-3}, ×5. D. F:AM 22283, cross-section of incisor, ×4. E. F:AM 25409, cross-section of incisor, ×4. F. F:AM 22283, P_3, ×4. G. F:AM 22281, P_3, ×4. H. F:AM 22292, P^2, ×4. I. F:AM 22277, M^1, ×4.

type of *A. macrocephalus* are insignificant. *A. ennisianus* is smaller; observed ranges do not overlap.

Compared with upper teeth assigned to *A.* cf. *macrocephalus* by Green (1972, pp. 382-383, fig. 1 W-Z, table 5) from Black Bear Quarry II (Rosebud Formation of Macdonald, 1963, 1970), the Standing Rock Quarry specimens tend to be larger with more complicated hypostriae. Reference of the Black Bear Quarry II specimens to *A.*

macrocephalus is tentative because no lower dentitions are associated with them.

The skull of F:AM 25409 is complete but strongly compressed dorsoventrally, and the palate is covered by the left dentary (fig. 1). The premaxilla-occipital crest length, as preserved, is 73 mm. The zygomatic arch is as deep as that of *Lepus* or *Oryctolagus*, exceeding that of *Sylvilagus* (Lyon, 1903, pp. 345); that of *Hypolagus* is also deep (Hibbard, 1969, fig. 3 F; Sych, 1965, p. 17). The zygomatic process of the squamosal is long, as in *Oryctolagus*, *Caprolagus*, and *Pentalagus*, and unlike that of *Lepus*, *Sylvilagus*, and *Romerolagus*. The anteroinferior angle of the zygoma is slightly more expanded than in *A. ennisianus*, but less so than that of *Lepus*, least expanded among modern leporids (Lyon, 1903, pp. 345-346). The anterior root of the arch lies between the middle of P^3 and the middle of M^1; that of *A. ennisianus* is more anterior, its front margin opposite P^2 and its posterior opposite the back of P_4. The difference in anterior extent is due largely to the different form of the anterior surface of the zygoma root. The anterior margin of the root in *A. macrocephalus* corresponds to a similarly placed ventral ridge in *A. ennisianus* (Dawson, 1958, p. 43), but in the latter the anterodorsal surface of the root extends forward to the level of P^2 in a low ridge that also encloses the anterior concavity of the arch root dorsally. This shallow concavity is open dorsally in *A.* cf. *macrocephalus*, which lacks the buttress-like anterodorsal projection of the arch base.

On the palate, the incisive foramina extend posteriorly to a level opposite the front or middle of P^3, and are separated posteriorly by a narrow medial projection of the maxillae as in *Lepus*. The anterior limit of the internal nares lies opposite M^1. The palatine suture extends forward to a point opposite the posterior half of P^4; the palatine component of the bony bridge is short. The palatine foramen is opposite a point between P^4 and M^1, usually separated from the palatine suture by a thin lamina of the palatine. A second palatine foramen lies behind the principal foramen; two or three secondary foramina are present in the holotype of *A. ennisianus*. An anterior foramen is present in the maxilla just lingual to P^3; a similar foramen lies between P^3 and P^4 in the holotype of *A. ennisianus*. This foramen has not been reported in leporids; it occupies the same position as the foramen premolare of ochotonids (Bohlin, 1942, pp. 59-60).

The diastema of the dentary (fig. 1, 2 b) is short, 25 percent of the length of the dentary, compared with *A. ennisianus* (28 percent), *Hypolagus* sp. aff. *H. vetus* (28 percent; from Hibbard, 1969, p. 86-87, table 1) and modern leporids (*Lepus*, 31 percent, and *Sylvilagus*, 29 percent, in representative specimens), though longer than *Palaeolagus haydeni* (22 percent). The alveolar length of the tooth row is 33 percent of dentary length, as long as that of *P. haydeni* and longer than the other taxa measured (*A. ennisianus*, 30 percent; *Hypolagus* sp. aff. *H. vetus*, 27 percent; *Sylvilagus*, 29 percent; and *Lepus*, 28 percent). Comparison of these proportions indicates that most of the lengthening of the diastema in leporids has been at the expense of the tooth row rather than by lengthening of the horizontal ramus.

The ventral margin of the horizontal ramus is smoothly convex, whereas that of the holotype of *A. macrocephalus* is straight below the posterior cheek teeth. The anterior margin of the ascending ramus is more vertical than that of *Lepus* or *Sylvilagus*, less than that of *Romerolagus*, and similar to that of *Palaeolagus haydeni* (AMNH 38948). The vestigial coronoid process is as large as that of *P. haydeni*. A single large mental foramen lies anterior to P^3; a cluster of small foramina lies below P_3. The masseteric fossa is limited anteriorly by a distinct ridge below the M_2 talonid, and posteriorly by a straight vertical ridge traceable to near the top of the ascending ramus, on which the masseteric tubercle forms a small eminence (fig. 1). Such a posterior ridge is occasionally approached in *Oryctolagus* and *Pronolagus*, but in these genera is very weak and situated farther posteriorly.

Of the badly crushed vertebrae of F:AM 25409 (fig. 3) a lumbar retains a straight transverse process arising abruptly from the anterior half of the vertebral body, in these characters and in length resembling those of *Lepus*. The posterior ribs are expanded as in *Lepus* (fig. 3 a, left of scapula).

The scapula (fig. 3 a, b) lacks the acromion and metacromion processes and most of the infraspinous fossa with the lateral angle. Measurements are given in table 3. The lower one-half of the axillary border is straight. The straight verte-

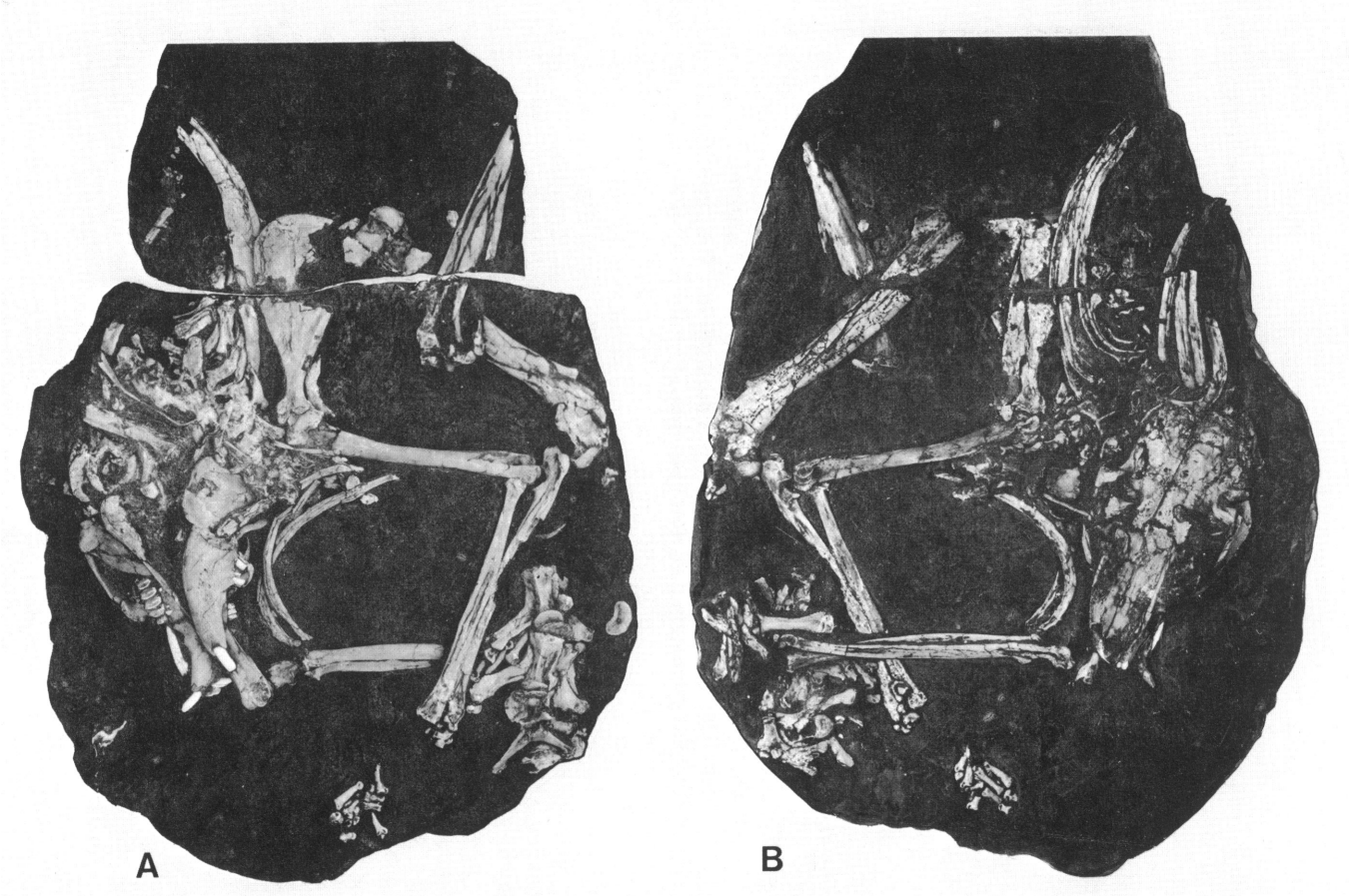

FIG. 3. *Archaeolagus* cf. *macrocephalus*, F:AM 25409, partially articulated skeleton. Larger of two blocks, photographed in ultraviolet light, ×0.5. A. Upper surface. B. Lower surface, after removal of matrix.

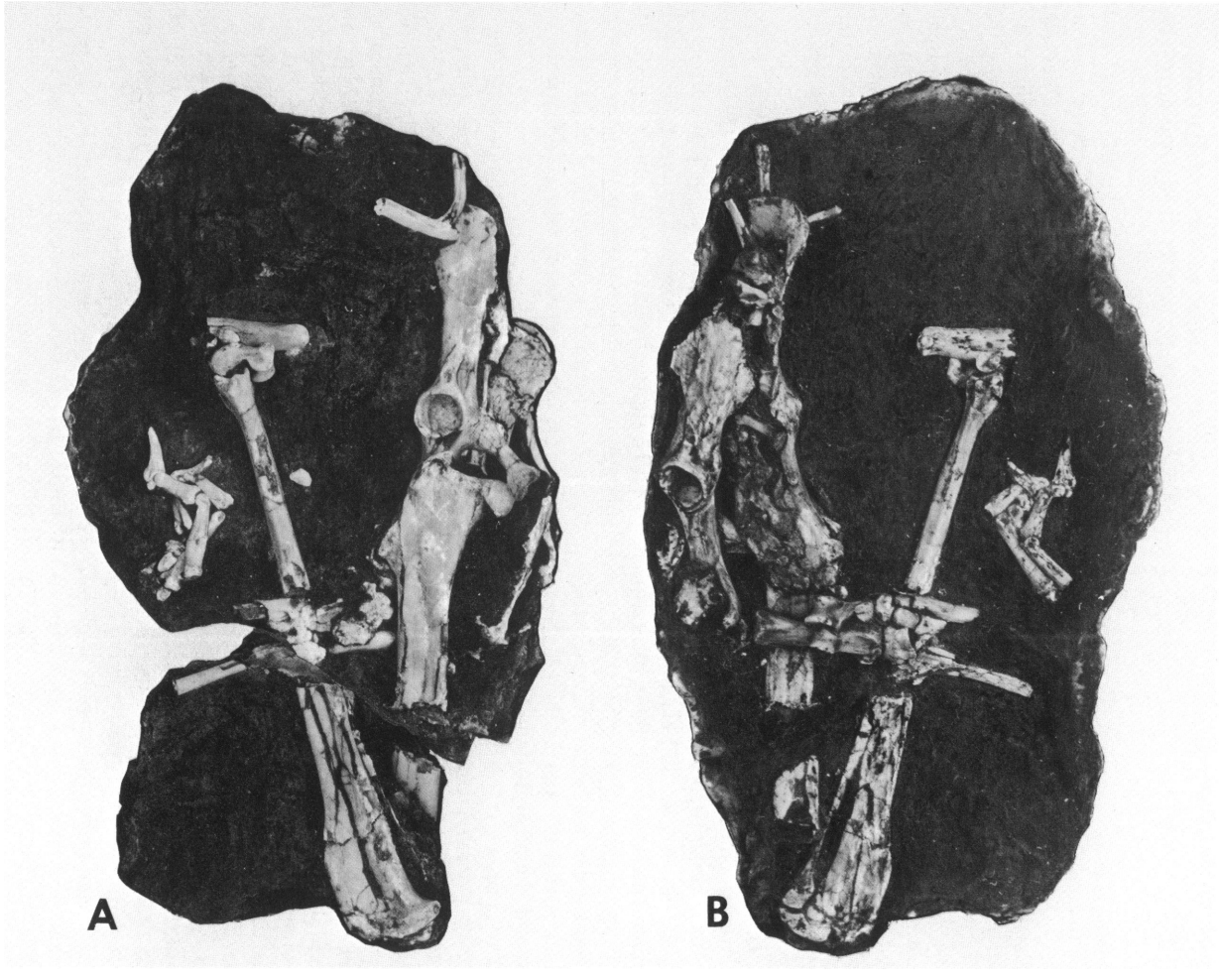

FIG. 4. *Archaeolagus* cf. *macrocephalus*, F:AM 25409. Smaller of two blocks, photographed in ultraviolet light, ×0.75. A. Upper surface. B. Lower surface, after removal of matrix.

TABLE 3
Dimensions in Millimeters of Skeletal Elements of *Archaeolagus cf. macrocephalus*. F:AM 25409

Height of scapula	53
Width of scapula at mid-height	17
Length of humerus	69
Length of ulna	80
Length of radius	70
Length of innominate bone	67
Length of ilium (from center of acetabulum	39
Length of acetabulum	8
Length of obturator foramen	14
Length from acetabulum to iliac tubercle	4
Length of iliac tubercle	5
Length of femur	91
Length of tibiofibula	105-107
Length of calcaneum	23

bral border is oriented at right angles to the spine; anteriorly it curves gently downward to meet the convex superior border in a rounded medial "angle." In *Lepus* and *Sylvilagus* the vertebral border anterior to the spine meets the spine at an acute angle and joins the straight or convex superior border in a better defined medial angle. The neck is slightly shorter than in *Lepus* or *Sylvilagus*, and the angle formed by the superior and axillary borders is near 48 degrees, like that of *Hypolagus brachygnathus* and exceeding those of *Lepus* (43 ± 3 degrees) and *Oryctolagus* (35 ± 3 degrees) (Sych, 1965, p. 48); this delimits the neck more clearly than in modern leporids. The maximum breadth of the infraspinous fossa is unknown; the supraspinous fossa is relatively wider than those of most or all specimens of *Lepus californicus* and *L. europais* examined. Because of the shape of the supraspinous fossa its area is even greater relative to those of modern genera. Sych's figure (1965, pl. 5, fig. 1) of the scapula of *H. brachygnathus* suggests that the maximum width of the fossa is similar, but its area is less. In summary, the scapula is closer in shape to that of *Lepus* or *Sylvilagus* than to that of *Palaeolagus* (Dice, 1933, p. 305, fig. 10) and *Litolagus* (Dawson, 1958, p. 34) but is less advanced than modern genera in its short, broad form, short neck and relatively large supraspinous fossa. It also seems less advanced than that of *Hypolagus brachygnathus* in its more convex superior border. The specimens of *H. vetus*, *H.* sp. aff. *H. vetus*, and *Pratilepus vagus* (Campbell, 1969) are too fragmentary for comparison.

The distal keels of the humerus (fig. 3 a, b) are as sharply ridged as those of *Sylvilagus*. The medial condyle is smaller than that of *H. vetus* (Dawson, 1958, fig. 30 c); the deltoid crest extends more than half the length of the shaft. The posterior margin of the olecranon lies on a line with the posterior margin of the ulnar shaft as in *Lepus*, rather than inclining anteriorly as in *Sylvilagus*. The semilunar notch is shallower than in either genus. The lateral articular facet for the head of the radius is small and placed unusually far posteriorly and distally. Much as in *Sylvilagus*, the anteromedial half of the distal end consists of a concave facet, and the posterolateral half of a knoblike styloid process projecting about 1.5 mm. farther distally.

The radius is like that of *Sylvilagus*, with a deep groove for articulation with the humerus. The carpals are fragmentary; the metacarpals and phalanges are like those of *Sylvilagus*, but may be slightly shorter relative to the ulnar length. The metapodials and phalanges of *A. macrocephalus* were described by Matthew (1907, p. 215); those of *A.* cf. *macrocephalus*, where comparable, are similar.

Measurements of the innominate bone (fig. 5) are given in table 3. The ilium is longer relative to total length than that of *Sylvilagus*, *Lepus*, or *Hypolagus vetus* (Dawson, 1958, fig. 28). The angle between superior and inferior fossae of the ilium appears smaller than in *Sylvilagus*, and much smaller than in *Lepus*. The iliac tubercle is more elevated (nearly 3 mm. above the iliac spine) than in any modern leporid examined, and is joined to the acetabulum by a more pronounced ridge, the rugose surface of which indicates a muscle attachment. The apex of the tubercle bears a concavity with a triangular rim. The damaged ischial tuberosity appears to have been less massive and expanded less far posteriorly than in *Lepus*, but can be matched in some specimens of *Sylvilagus*. The lateral process of the ischial tuberosity is shorter-based than in *Lepus* or *Sylvilagus*, at least partly due to the lesser expansion of the tuberosity, but projects laterally as in *Lepus*.

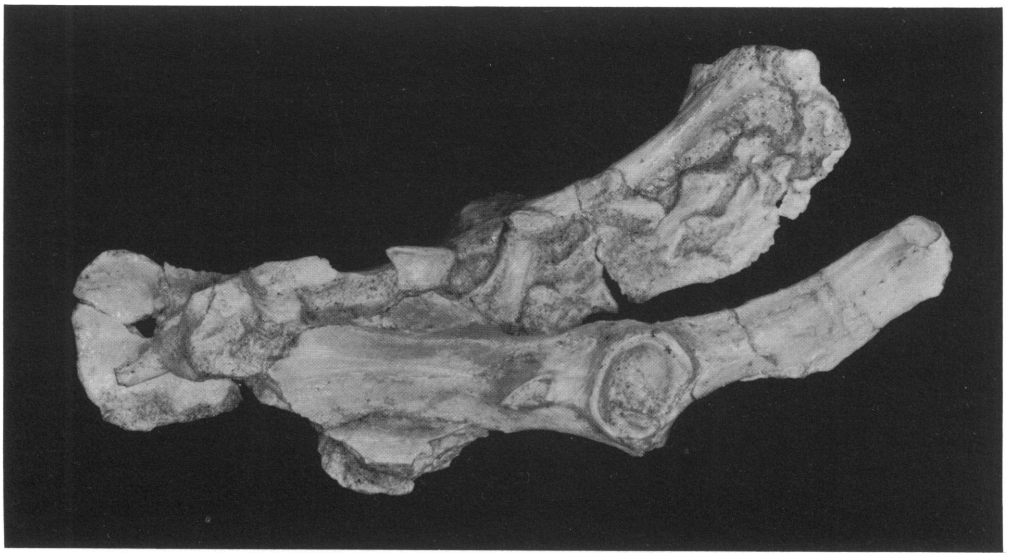

FIG. 5. *Archaeolagus* cf. *macrocephalus*, F:AM 25409. Pelvis, ×1.5.

The greater trochanter of the femur (fig. 4 a) is oriented as in *Sylvilagus*; that of *Lepus* projects farther proximally. The lesser trochanter is shorter-based than in the modern genera; its apex is similarly placed, but the ridge forming its distal margin turns abruptly laterad, nearly at right angles to the long axis of the bone. The third trochanter is placed more distally than in the modern genera, but much more proximally than in *Palaeolagus*.

The left tibiofibula is incomplete, but the missing part can be reconstructed from its impression in the matrix (fig. 4). The fibula is separate for less of its length than that of *Lepus* or *Sylvilagus*. The shaft is more slender than that of an equally long tibiofibula of *Lepus*. The distal end of the bone is narrower than in *Lepus*, but the articular facets are similar.

The tarsus is approximately as advanced as that of *Hypolagus vetus* (Dawson, 1958, fig. 33; p. 56); the distal part of the calcaneum and the navicular are relatively shorter than those of *Lepus* and *Sylvilagus*, as is the contact between the two bones. Compared with modern genera, the end of the tuber calcanei and the articular facet for the tibia are less deeply grooved, and the process projecting laterally from the disto-dorsal margin of the calcaneum is larger. The calcaneum and astragalus of the holotype of *Archaeolagus macrocephalus* cannot be distinguished from the Standing Rock Quarry specimen. *H.* sp. aff. *H. vetus* (Campbell, 1969, pl. 2, fig. 9-10) appears slightly more advanced in proportions and in depths of grooves than *A. macrocephalus* or *H. vetus*.

Comparison of limb proportions with data given by Campbell (1969, table 2) and additional measurements of modern leporids indicates an over-all resemblance to *Oryctolagus cuniculus* and *Sylvilagus floridanus*, from which it differs only in the lower ratio of femur to tibia. In the latter ratio it is intermediate between *S. floridanus*, *Lepus californicus*, and *Hypolagus* sp. aff. *H. vetus*. The last species has a longer forelimb than that of *A.* cf. *macrocephalus*, though proportions within the limbs are similar.

Discussion. The leporids from Standing Rock Quarry belong to a single species that cannot be separated on present evidence from *Archaeolagus macrocephalus* of the "Upper Rosebud" of South Dakota.[1] The upper dentition of *A. macrocephalus* is unknown. The specific characters

[1]From AMNH "Rosebud" locality 17, Rosebud Formation (Macdonald, 1970, p. 15); Rosebud or Harrison Formation (Macdonald, 1963, p. 155); Lower Marsland Formation (Schultz and Falkenbach, 1947, p. 222); equivalent of Upper Harrison Formation of Peterson (1907, p. 23).

TABLE 4
Proportions of Lengths of Limb Elements of *Archaeolagus* cf. *macrocephalus*, F:AM 25409

Humerus / Ulna	0.86
Humerus / Femur	0.76
Ulna / Tibiofibula	0.75
Femur / Tibiofibula	0.85-0.87
Humerus + Ulna / Femur + Tibiofibula	0.75

given by Dawson (1958, p. 44) for *A. macrocephalus* apply to *A.* cf. *macrocephalus* from Standing Rock Quarry: "Size larger than other known species of *Archaeolagus*. P_3 elongate anteroposteriorly, having on trigonid shallow anteroexternal groove that seems to lack cement and faces mostly externally. On medial surface of jaw, posterior end of swelling over incisor is situated in a line below middle of P_3 and slightly above mid-depth of jaw." Additional characters of the Standing Rock Quarry sample include: Hypostriae of upper molariform teeth crenulated on most but not all specimens. Distinguished from *Hypolagus* by shortness of hypostriae, which extend one-third to one-half the width of the tooth; and by lack of a buccal fold, and presence of a lingual groove, on P^2.

To determine if *A.* cf. *macrocephalus* from Standing Rock Quarry is conspecific with *A. macrocephalus* and/or *A.* cf. *macrocephalus* from Black Bear Quarry II, larger samples with associated upper and lower dentitions are needed from both South Dakota localities. The Frick Collection includes lower dentitions like those of *A. macrocephalus* and the Standing Rock Quarry specimens, and an upper dentition like those from Standing Rock Quarry except for slightly greater crenulation of hypostriae, from seperate localities in lower Hemingfordian localities in eastern Wyoming. These specimens, though not proved to belong to the same species, support an early Hemingfordian age for Standing Rock Quarry, and cast some doubt on the identification of the Black Bear Quarry II sample.

Archaeolagus cf. *macrocephalus*, like *A. macrocephalus* (Dawson, 1958, p. 38), is clearly closer to *A. ennisianus* from the John Day Formation of Oregon than to other species of the genus. *Archaeolagus* cf. *macrocephalus* approaches *Hypolagus* more closely in complication of upper teeth and in osteology than do other described species of the genus. However, the lingual groove on P^2 makes *A. macrocephalus* a less likely ancestor for *Hypolagus* than *A. primigenius* or *A. acaricolus*. Ecologically *A.* cf. *macrocephalus* seems to have been a "rabbit" rather than a "hare." Articular surfaces of limb bones, and therefore directions and limitations of joint motion, were generally similar to those of *Sylvilagus* and far advanced over those of *Palaeolagus*. The relatively short foreleg with its short ulna is comparable with the less cursorial modern forms, and the primitive scapula and innominate bone suggest less cursorial locomotion than that of *Oryctolagus*, the European rabbit, though the relatively long tibiofibula suggests speed (cf. Smith and Savage, 1956, pp. 607-609; Camp and Borell, 1937; and Dawson, 1958, pp. 67-69).

Arachaeolagus sp.

Referred Specimens. F:AM 25411 and 25412, partial maxillae, from Cynarctoides Quarry, and 25410, P^4, from Blick Quarry, both Blick local fauna.

Description and Comparisons. P^2 (fig. 6) has an anterior, cement-filled, posterolabially directed fold extending across two-fifths of the anteroposterior length of the tooth. It has neither a lingual nor a labial groove. In all these characters it resembles *Archaeolagus ennisianus*; the labial lobe is, however, narrower, and trapezoidal rather than triangular.

The hypostriae of P^3-M^2 extend one-fifth to two-fifths of the widths of the occlusal surfaces, longest on P^4 or M^1; the walls are not crenulated. In these characters and in length the molariform teeth resemble those of *A. ennisianus*; they are, however, wider, and M^3 is smaller (table 1).

The anterior root of the zygoma extends from the front of P^3 to the middle of P^4, shorter than

FIG. 6. *Archaeolagus* sp., F:AM 25411, P^2-M^2, ×4.

in *A. ennisianus*, and deeper. The concavity anterior to it is shallow, and its dorsal limit is less distinct than in *A. ennisianus*. The palatine foramen lies opposite the front of M^1, separated from the palatine suture by a thin lamina of the palatine; a small foramen lies posteromedial to it. The palate lateral to the internal nares is as wide as in *A. ennisianus*.

These specimens represent a persistently primitive leporid distinguished from *Archaeolagus ennisianus* by its broader cheek teeth and more posterior position of the anterior zygoma root, and possibly by a difference in the shape of P^2. *Archaeolagus acaricolus* (Dawson, 1958, pp. 39-41) is smaller, with narrow cheek teeth. The specimen from Split Rock, Wyoming, reported by Dawson (1965, p. 14) as Leporidae sp. is also narrower than those from the Blick local fauna. The lack of P_3 prevents assignment of these specimens to one of the two lineages of *Archaeolagus* recognized by Dawson (1958, p. 38). Dawson cited several specimens from middle Hemingfordian deposits possibly intermediate between described *Archaeolagus* species and *Hypolagus* (1958, pp. 44-45). The Frick Collection includes several more, from localities in the Runningwater Formation of Nebraska. These middle Hemingfordian archaeolagines may include more than one species, and associated upper and lower dentitions are not known; at least one specimen resembles those of the Blick local fauna. It appears unwise to give a species name to the Blick *Archaeolagus* until study of the specimens from Nebraska is completed.

The Blick local fauna form could also represent a link between *A. ennisianus* or *A. acaricolus* and *Panolax sactafidae*, a large leporid with persistently primitive cheek teeth described by Cope (1874, p. 151) from the "Santa Fe Marls" of New Mexico (Galusha and Blick, 1971, listed the holotype of this species as from the mainly early Pliocene Pojoaque Member of the Tesuque Formation, Santa Fe Group). Dawson (1965, p. 14) noted other leporid specimens of primitive aspect contemporaneous with *Hypolagus*.

ARCHAEOLAGINAE *INCERTAE SEDIS*

Referred Specimens. F:AM 25413, partial left ramus with broken incisor and P_4-M_1, from the green zone 18 feet above Jeep Quarry, Mesa Prospect local fauna; and 25414, distal end of a left humerus, from Jeep Quarry, Jeep local fauna.

Description and Comparisons. The incisor of F:AM 25413 is slightly wider than long in cross-section, nearly trapezoidal in outline, and widest anteriorly; anterior and medial faces are flat, and lateral and posterior faces convex. The posterior end of the shaft lies below the front of the P_3 alveolus, which is 3.1 mm. long. Enamel of P_4 and M_1 is reduced as in modern leporids; measurements are given in table 2.

The diastema is about 14 mm. long. The anterior mental foramen lies 2.8 mm. anterior to the P_3 alveolus, and a cluster of small foramina below P_3.

F:AM 25414 is the damaged distal end of a left humerus. The keels appear as well developed as in *Sylvilagus*.

These specimens represent one or two archaeolagines of the size of *A. macrocephalus* or *H. vetus*; they are inadequate for generic assignment.

FAMILY OCHOTONIDAE

OREOLAGUS DICE, 1917

Oreolagus cf. *nebrascensis* McGrew, 1941

Referred Specimen. F:AM 25415, fragmentary right ramus with incisor and P_4-M_1, and associated innominate bone, from Blick Quarry, Blick local fauna.

Description and Comparisons. This specimen is tentatively assigned to *Oreolagus nebrascensis* because of similarity of dental proportions (table 2); only in *O. nebrascensis*, of the four described species of the genus, do P_4-M_2 tend to be shorter than wide (Dawson, 1965, p. 31). P_4 and M_1 closely resemble those of the holotype, FMNH P26280, though the trigonid of P_4 has a more pronounced anterolabial concavity. The incisor, in cross-section, approaches a 45-degree right triangle with an anteromedial right angle and a rounded posteromedial angle.

The partial innominate bone (fig. 7) includes the acetabulum, most of the iliac blade, and the upper half of the pubis. The acetabulum is widely open posteroventrally as in *Ochotona* and *Prolagus* (Dawson, 1969, fig. 27). The angle between pubis and ischium is less acute than in

FIG. 7. *Oreolagus* cf. *nebrascensis*, F:AM 25415, partial innominate bone, ×3. A. Dorsal view, iliac blade at top, iliac tubercle projecting toward left. B. Lateral view, iliac blade at top, pubis projecting to left, acetabulum at bottom.

either genus; it may, however, be distorted. The iliac tubercle is high and bladelike as in *Palaeolagus haydeni* (e.g., AMNH 5690), its profile like that of *Prolagus*. As in *Prolagus*, the iliac blade consists of three surfaces. The ventrolateral and dorsolateral surfaces are subequal in area and concave. The ridge separating them passes dorsal to the iliac tubercle and turns outward to merge with the mid-dorsal rim of the acetabulum. The iliac tubercle thus projects from the ventrolateral surface, but is joined to the ridge anteriorly by a low crest. A similar condition is seen in some specimens of *Palaeolagus haydeni*. The dorsal surface of the iliac blade is narrow and less clearly differentiated than in *Prolagus*.

This innominate bone is ochotonid in its expansion of the ventrolateral surface of the iliac blade, orientation of the iliac tubercle, and broad posteroventral opening of the acetabulum, but resembles *Palaeolagus haydeni* in the orientation of the pubis and of the ridge separating the ventrolateral and dorsolateral iliac surfaces, which may be interpreted as conditions retained from primitive lagomorphs.

APPENDIX

Supplementary description of the holotype of:

Archaeolagus ennisianus

The holotype of *Archaeolagus ennisianus* (Cope, 1881, pp. 835-836) has only recently been freed of matrix. It is the skull, jaws, atlas, and partial axis of a young animal, as shown by unfused sutures. P^4-M^2 show darkened areas in the dentine labial to the hypostriae as described by Dawson (1958, p. 42) in AMNH 7210. P^2 has a small, persistent, V-shaped lingual groove in addition to its cement-filled anterior reentrant; this lingual groove appears in some other specimens of *A. ennisianus*. Dental characters are otherwise as described by Dawson from referred specimens (1958, pp. 42-43).

The palatine suture extends anteriorly to a point opposite the front of P^4. The largest palatine foramen lies at the palatine suture, separated from it by a thin lamina of the palatine; three smaller foramina lie behind it, medial to M^1. A small foramen lies in the palatine medial to M^3, and another in the maxilla just posterolingual to P^3. The tooth rows are 9 mm. apart both anteriorly and posteriorly. The internal nares are 4 mm. wide between the second molars, slightly narrower than those of CIT 5181, referred to *A. ennisianus* (Dawson, 1958, fig. 22 a), but wider than those of *Palaeolagus haydeni*. The incisive foramina are 5.3 mm. wide between the anterior ends of the second premolars; they are likewise intermediate between those of CIT 5181 and *P. haydeni*. Other osteological features, including the form and position of the anterior zygoma root, agree with CIT 5181 and other referred specimens of *A. ennisianus*.

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