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ONTOGENETIC CHANGE IN DENTAL DIMENSIONS OF THE OLIGOCENE (ORELLAN) LEPORID *PALAEOLAGUS* LEIDY (MAMMALIA, LAGOMORPHA) FROM NEBRASKA

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ABSTRACT

A large sample of the fossil leporid *Palaeolagus haydeni* Leidy, 1856 (Mammalia, Lagomorpha, Leporidae) from the early Oligocene (Orellan North American Land Mammal Age) of Nebraska, consisting of over 200 specimens from a single locality was analyzed to compare dental dimensions of the individual cheek teeth at different wear stages (=ontogenetic age) in order to ascertain if there was any change in tooth size or proportions. The greatest change was the increase in length of the anterior premolars (P2, p3) and last lower molar (m3). The more central cheek teeth either had a decrease in length (P4-M2), or remained approximately the same in length (p4-m1). All cheek teeth increased in width with age, ranging from 1% to over 30%. The length of the entire tooth row, both upper and lower, increased slightly in older individuals mainly reflecting the increase in length of the premolars. The length of the molars (M1-M3/m1-m3) however, decreased with wear. This amount of variation in size is reflected in the generally large size range of the cheek teeth in large samples of fossil leporids.

INTRODUCTION

Lagomorphs are a large part of the fauna from the "White River beds" of western North America (see Prothero and Emry, 2007) consisting of thousands of specimens, ranging from the late Eocene (Chadronian North American Land Mammal Age) to the middle Oligocene (Whitneyan NALMA: Leidy, 1856; Wood, 1940; Gawne, 1978; Emry and Gawne, 1986; Storer, 1984; Korth and Hageman, 1988; Dawson, 1958, 2008). The bulk of the recognized species belong to the palaeolagine leporid *Palaeolagus* Leidy, 1856, with six recognized species from this time range (Dawson, 2008). One characteristic of these large samples is the wide range of variation in size of the cheek teeth within a single species (e.g., Gawne, 1978: table 3; Storer, 1984: 5; Korth and Hageman, 1988: tables I, II). It has been noted that the anterior premolar (both upper and lower) increased in length at later wear stages which would increase the size range of these teeth in a fossil population (Gawne, 1978: text-fig. 4; Korth and Hageman, 1988: 147). In this study, a large sample of approximately 200 specimens of maxillae and dentaries of a single species, *P. haydeni* Leidy, 1956, collected and housed by the Field Museum of Natural History (FMNH) from the Orellan (early Oligocene) of Sioux County, Nebraska were examined and measured to determine if any changes in size or proportions of the cheek teeth occurred at the different ontogenetic ages of the individual specimens. The ages of the individual specimens were determined by a sequence of wear patterns, and divided into five age groups in order to determine any patterns of changes.

MATERIALS AND METHODS

Dental Terminology—Dental terminology used follows that of Dawson (1958) and White (1987: fig. 1; 1991: fig. 1). Upper teeth are represented by capital letters, lower teeth by lower-case letters (e.g., P3 or p3).

Measurements—Specimens in the sample were measured by taking photographs using the computer program Photoshop. The program was able to calibrate the number of pixels in a distance to millimeters, and it remained accurate as long as the height of both the compound microscope and the sample remained consistent. Photographs were taken of each specimen and the maximum length and width of each tooth at the occlusal surface of all available teeth on each specimen were measured to the nearest 0.01 mm. Length of the tooth row (p3-m3, P3-M3) and molar row (m1-m3, M1-M3) were taken at the occlusal surface, not at the alveolar margin.

Horizon and Locality—In the FMNH records, the locality and horizon of all specimens discussed

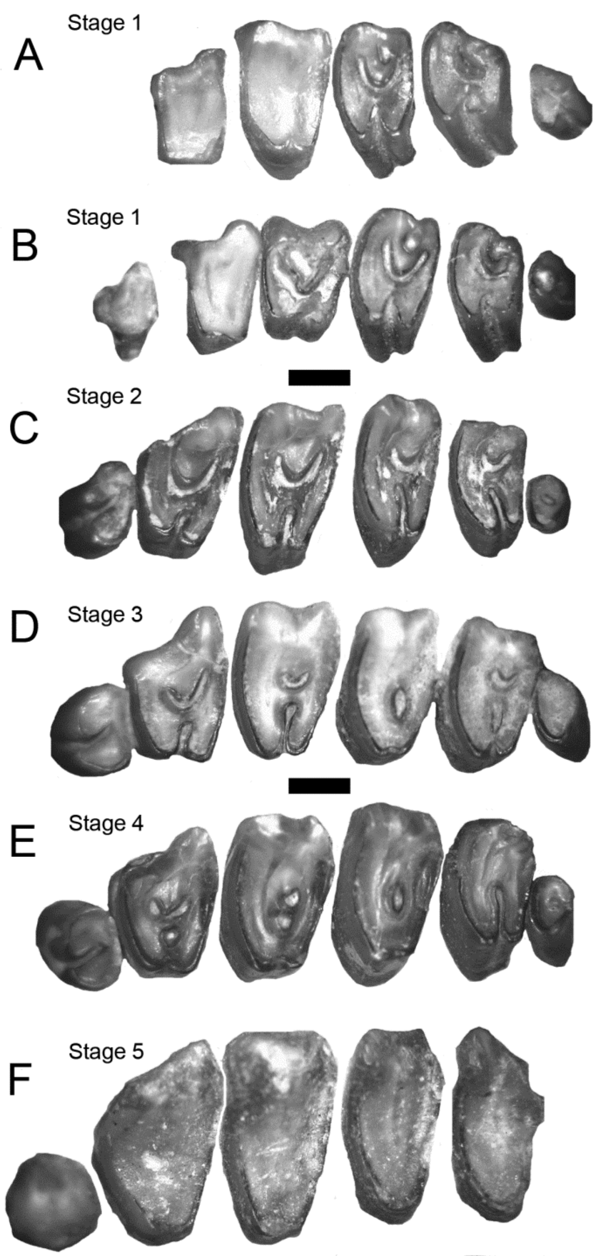


FIGURE 1. Upper dentitions of *Palaeolagus haydeni* from Round Top showing defined wear stages. A, B, Stage 1. A, FMNH PM 2670, left dP3-dP4, M1-M3. B, FMNH PM 2649 left dP2-dP3, P4-M3. C, Stage 2, FMNH PM 2520, right P2-M3 (reversed). D, Stage 3, FMNH PM 2519, right P2-M3 (reversed). E, Stage 4, FMNH PM 2528, right P2-M3 (reversed). F, Stage 5, FMNH PM 2677, left P2-M2. Anterior to left on all figures. Bar scales = 1 mm.

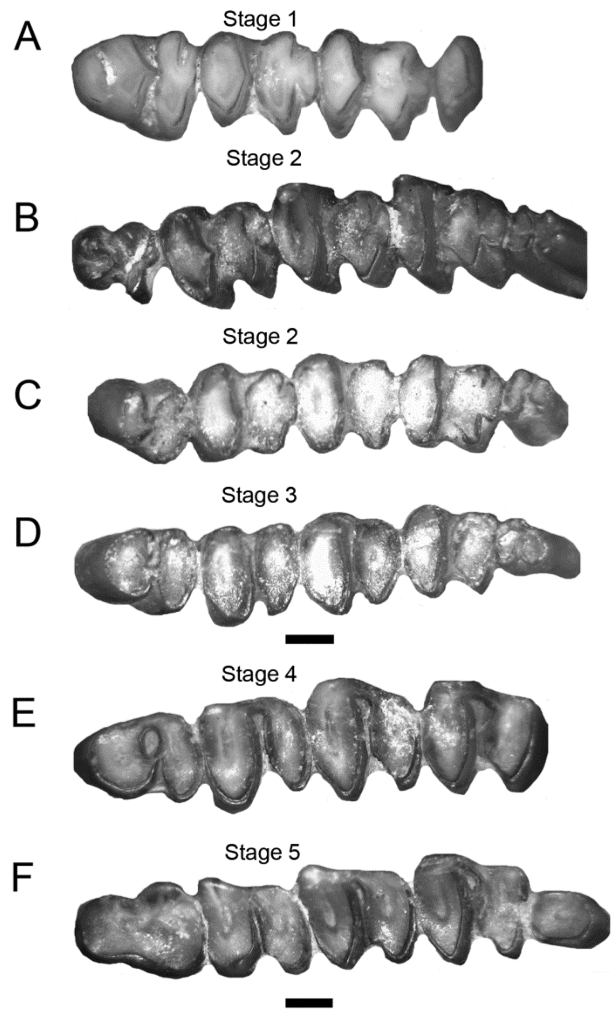


FIGURE 2. Lower dentitions of *Palaeolagus haydeni* from Round Top showing defined wear stages. A, Stage 1, FMNH PM 2792, left dp3-m2(partial). B, C, Stage 2. B, FMNH 2441 left p3-m3. C, FMNH 2390 right p3-m3 (reversed). D, Stage 3, FMNH 2389, right p3-m3 (reversed). E, Stage 4, FMNH 2394, right p3-m2 (reversed). F, Stage 5, FMNH 2442, left p3-m3. Anterior to left on all figures. Bar scales = 1 mm.

herein were from "Round Top, Lower Brule Formation, Sioux County, Nebraska." A composite stratigraphic section of this area was first presented by Darton (1899: fig. 226; =Round Top to Adelia Station). This section included what is currently known as the Chadron, Brule, Gering, and Arikaree Formations, ranging from the late Eocene (Chadronian) to latest Oligocene (Arikareean) in age. Schultz and Stout (1955) named this area as the type section of the Brule Formation, which was divided into the Orella (lower) and Whitney (upper) Members (Schultz and Stout, 1938) on which the provincial Land Mammal Ages Orellan and Whitneyan were defined (Wood et al., 1941: see Emry et al. 1987 for complete historical review). In the figured sections provided by Schultz and Stout (1955: fig. 3, sections 8 and 9), the bulk of the section at Round Top belonged to the Whitney Member, with only the very lowest parts belonging to the upper part of the Orella Member (=Orella D). However, Round Top is in the vicinity of Toadstool

Park where the entire Orella Member type section is present. It is likely that the entire area around Round Top, including Toadstool Park, was the source of this collection. Since the specimens are from the "Lower Brule" they are more likely from the Orella Member (see Schultz and Stout, 1955: fig. 3, sections 4-7) which is generally more fossiliferous than the Whitney member.

Specimens Examined—FMNH PM 2751, 2792, partial dentaries with dp3-m1; FMNH PM 2726, 2768, 3062, 3063, dentary fragments with dp3-dp4; FMNH PM 2064, dentary fragment with dp3; FMNH PM 3061, dentary fragment with dp4; FMNH PM 2386–2391, 2439–2441, 2443, dentaries with p3–m3; FMNH PM 2448, 2392–2399, 2444–2446, 2449, dentaries with p3–m2; FMNH PM 2404, 2457, 2461, 2466, 2405–2409, 2411, 2412, 2452–2460, 2462–2464, 2465, dentaries with p3–m1; FMNH PM 2420– 2427, 2429–2431, 2433– 2436, 2477, 2478–2507, 2509, dentaries with p3–p4; FMNH PM 2447, 2400–2402, 2450, 2451, 2469, 2474, dentaries with p4–m3; FMNH PM 2403, 2413–2418, 2467, 2468, 2471–2473, dentaries with m1-m3; FMNH PM 2437, 2438, 2508, 2510, 2511, dentaries with m2–m3. FMNH PM 2537, 2649, maxillae with dP2-M3; FMNH PM 2538, 2637, maxillae with dP2-M2; FMNH PM 2663, maxilla with dP2-M1; FMNH PM 2670, maxilla with dP3–M3; FMNH PM 2671, maxilla with dP3-M2; FMNH PM 2519–2536, 2631–2636, 2639, 2647, maxillae with P2-M3; FMNH PM 2638, 2640–2646, 2648, 2662, 2665, 2667, 2672, maxillae with P2-M2; FMNH PM 2664, 2666, maxillae with P2-M1; FMNH PM 2650–2661, maxillae with P3-M3; FMNH PM 2668, 2669, 2673–2678, maxillae with P3-M2.

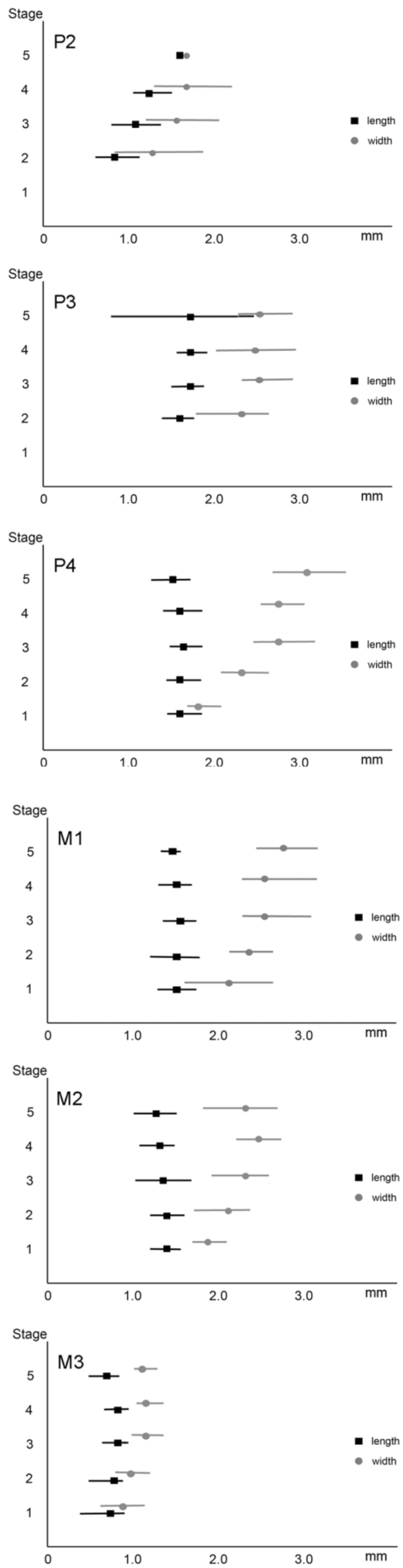
Species Identification—All specimens included were identified as *Palaeolagus haydeni* Leidy, 1856, following the diagnoses presented by Wood (1940) and Dawson (1958). This species differs from the contemporaneous *P. burkei* Wood, 1940, in being slightly larger (Tables 1, 2), and having a less persistent main anterior reentrant on P3 and posterior internal reentrant on p3 and the having the lingual bridge between the talonid and trigonid on the lower cheek teeth form at an earlier stage of wear. The sample differs from the Chadronian species *P. primus* Emry and Gawne, 1986, and *P. temnodon* Douglass, 1901, in being slightly smaller (see appropriate tables in Wood, 1940; Dawson, 1958; Gawne, 1978; Storer, 1981; Emry and Gawne, 1986), and lacking persistent buccal roots on the upper premolars. The specimens differ from the Oligocene *P. intermedius* Matthew, 1899, by their much smaller size and from the Arikareean species of the genus by having lower-crowned cheek teeth with more persistent crescents on the upper cheek teeth (see Schlaikjer, 1935; Dawson, 1958).

TABLE 1.—Wear Stages (=ontogenetic age) as determined by wear patterns for p3 and P3.

Upper P3	
Stage 1	Deciduous premolars present (Figures 1A, B).
Stage 2	P3 present, may not be fully erupted, only slightly worn, all re-entrants open (Figure 1C).
Stage 3	Anterior reentrant remains open; hypostria open lingually (Figure 1D).
Stage 4	Crescent formed (anterior re-entrant closed anteriorly), hypostria closed, fossette formed (Figure 1E).
Stage 5	Completely worn, occlusal surface consists of entirely dentine; enamel limited to outline of the tooth (Figure 1F).
Lower p3	
Stage 1	dp3 present (Figure 2A).
Stage 2	p3 present, may not be fully erupted or in early stages of wear (complex occlusal pattern retained; Figures 2B, C).
Stage 3	Only posterior buccal and posterior lingual reentrants remain open (Figure 2D).
Stage 4	Posterior lingual re-entrant closed; circular fossettid formed; posterior buccal re-entrant open (Figure 2E).
Stage 5	Completely worn, occlusal surface consists of entirely dentine; enamel limited to outline of the tooth (Figure 2F).

Ontogenetic Age Determination—Previously, ontogenetic age determination of fossil small mammals was done by the crown-height measurement of the cheek teeth of brachydont species (Korth and Evander, 1986; Korth, et al., 2015; Czaplewski, 2011). However, the change in occlusal pattern of the cheek teeth has been used for larger mammals with hypsodont cheek teeth (Kurten, 1953; Van Valen, 1964; Voorhies, 1969; Shipman, 1981). Czaplewski (2011: fig. 7) attempted to use occlusal pattern on a hypsodont Pliocene rodent but found the results were ambiguous. In this study, the occlusal pattern of cheek teeth of the subhypsodont lagomorph *Palaeolagus* was used.

Because of the minimal amount of change due to wear on P4/p4 and the molars of *Palaeolagus* (only very young and very old can be distinguished) the ontogenetic age of each specimen was determined by examining the wear pattern on the occlusal surface of P3 and p3 only. Five stages of wear were defined (Table 1; Figures 1, 2). The ages of the specimens that did not have P3/p3 intact were not assessed.



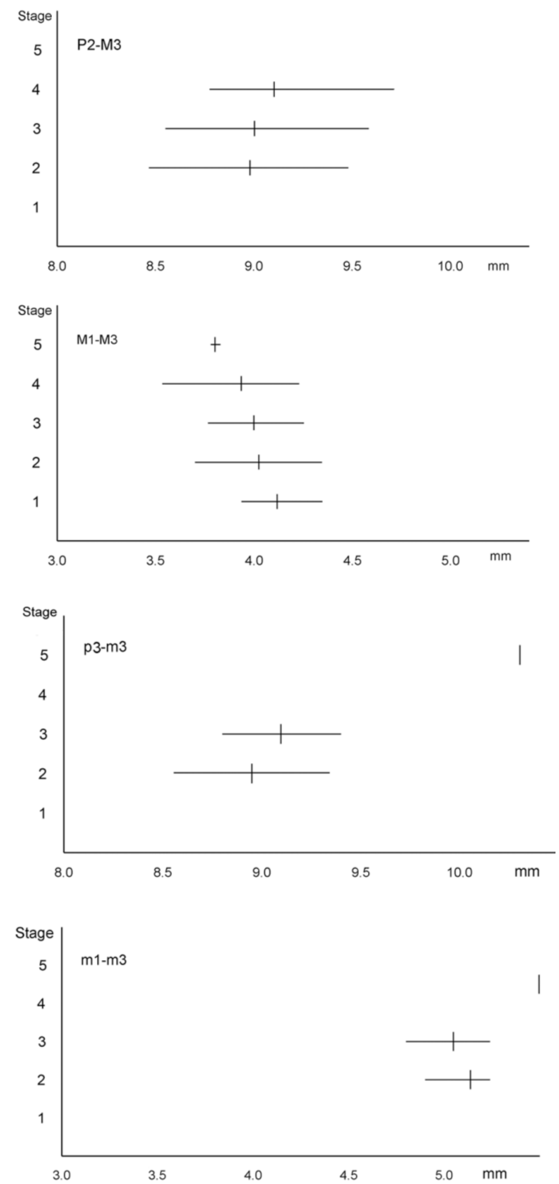


FIGURE 3 (left). Length and width of individual upper cheek teeth of *Palaeolagus haydeni* from Round Top for each Wear Stage. Vertical axis = Wear Stage; horizontal axis = mm. Black squares = mean length, gray circles = mean width. Horizontal bars = +/- one standard deviation.

FIGURE 4 (above). Length of upper and lower tooth rows of *Palaeolagus haydeni* from Round Top. Axes as in Figure 3. Vertical bar = mean; horizontal bar = +/- one standard deviation.

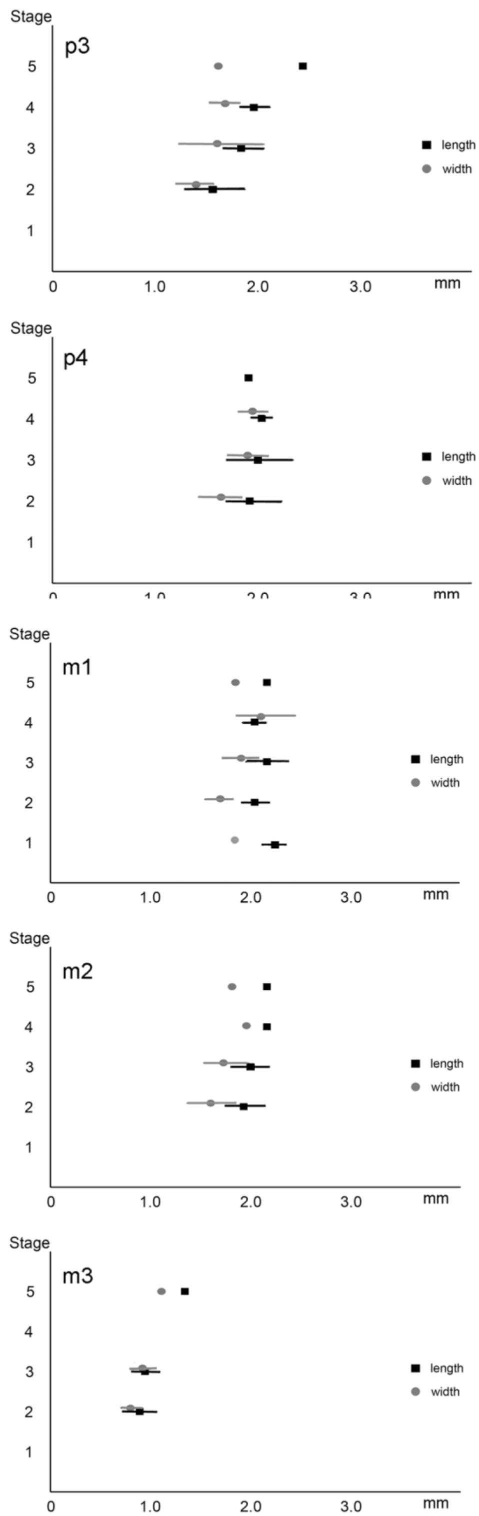


FIGURE 5. Length and width of individual lower cheek teeth of *Palaeolagus haydeni* from Round Top for each Wear Stage. (see Figure 2 for explanation of axes and symbols).

RESULTS

Upper Cheek Teeth—The width of all upper cheek teeth increased with wear stage, ranging from a 12% increase in P3 from Stages 2 to 5 to a 38% increase in the width of P4 from Stages 2 to 5 (Figures 1, 3, 4; Table 2). The upper molars averaged an approximate 20% increase in width from Stage 1 to 5. The changes in length varied greatly. P2 and P3 increased in length from 6% in P3 to 40% in P2. P4, M1, and M2 decreased in length from 5 to 9%. The length of M3 decreased slightly. The length of the entire tooth row, P2-M3, increased slightly due to the greater increase in length of the premolars, even though there was a decrease of approximately 7% in the length of M1-M3 (Table 2; Figure 4).

Lower Cheek Teeth—Unfortunately, there was only one specimen of lower cheek teeth from Wear Stage 5 and no Stage 1 or Stage 4 specimens had any molars posterior to m1, so the results are not as definite as for the uppers (Figure 5; Tables 1, 3). However, the results are not markedly different from those of the upper cheek teeth. The lowers generally showed an increase in width with wear ranging from a 13% increase in the width of m2 to a 27% increase in m3. The width of m1 was virtually unchanged from Stage 1 to Stage 5. The p3 had an increase in width of 35% from Stage 2 to 5, reflecting the similar amount if increase in P2. The length of p4, m1 and m2 either remained the same length or increased slightly (less than 10%). The m3 showed an increase in length equivalent to that of p3 (36%) unlike M3 which had a decrease in length. Although not as well supported, the complete lower tooth row (p3-m3) increased in length (approximately 10%), reflecting the increase in length of the premolars and m3 (Figure 4). The change in length of m1-m3 appears to be the same as for M1-M3 for Stages 2 and 3, but the single specimen of lower molars from Stage 5 is markedly larger and does not follow the decreasing trend in length of M1-M3 and no specimens from Stages 1 or 4 had the complete set of molars for comparison.

CONCLUSIONS

Large samples of late Paleogene lagomorphs are characterized by having large ranges of size of the cheek teeth; more than is generally accepted typically for fossil mammals (see Introduction for citations). The sample of *Palaeolagus* from Sioux County, Nebraska discussed here demonstrates that these wide ranges of variation are, at least in part, due to the change in shape of the individual cheek teeth as they wear.

The most significant changes with wear are in the lengths of the anterior premolars (P2/p3) and m3 which increase in length over 30% from the earliest wear stages to the latest. The central cheek teeth (P4-M2/ p4-m2) either retain the same length (lowers) or are slightly shortened (uppers) with wear. All cheek teeth increase in width with wear. The change in dimensions of the cheek teeth through the life of these animals is significant enough to accommodate much of the great variation in size of species of fossil leporids and should be considered when identifying species.

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TABLE 2.—Dental measurements of upper dentitions of *Palaeolagus haydeni* from Round Top. Abbreviations: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; Min, minimum measurement; Max, maximum measurement; SD, standard deviation. Measurements in mm.

	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P2-M3	M1-M3
Complete sample														
N	42	42	63	63	66	66	70	70	64	64	44	44	30	41
M	1.08	1.57	1.66	2.44	1.69	2.65	1.47	2.50	1.39	2.21	0.70	1.03	9.10	3.99
Min	0.58	0.89	1.26	1.26	1.34	1.64	0.74	1.55	0.80	1.63	0.30	0.67	7.78	3.37
Max	1.76	3.33	2.13	3.31	2.09	3.49	1.88	3.44	1.89	3.39	1.16	1.39	10.20	4.81
SD	0.28	0.57	0.18	0.43	0.16	0.43	0.20	0.43	0.17	0.35	0.15	0.17	0.52	0.28
Stage 1														
N					3	3	7	7	6	6	3	3	2	2
M					1.69	1.91	1.47	2.14	1.43	1.93	0.65	0.83	9.60	4.12
Min					1.56	1.78	1.09	1.58	1.32	1.76	0.46	0.67	9.24	3.97
Max					1.79	2.06	1.66	2.36	1.59	2.08	0.96	1.13	9.96	4.26
SD					0.12	0.14	0.19	0.26	0.10	0.11	0.27	0.26	0.51	0.20
Stage 2														
N	18	18	23	23	23	23	23	23	21	21	17	17	12	16
M	0.94	1.34	1.60	2.25	1.69	2.37	1.47	2.30	1.43	2.07	0.69	0.98	8.98	4.02
Min	0.58	0.72	1.26	1.26	1.40	1.64	0.74	1.55	1.22	1.66	0.30	0.72	7.78	3.37
Max	1.57	2.87	1.86	3.18	1.89	2.80	1.79	2.70	1.89	2.58	1.16	1.20	9.68	4.81
SD	0.25	0.56	0.17	0.40	0.13	0.30	0.22	0.28	0.14	0.25	0.19	0.16	0.50	0.32
Stage 3														
N	13	13	22	22	22	22	22	22	21	21	14	14	10	14
M	1.08	1.58	1.70	2.58	1.73	2.83	1.51	2.65	1.37	2.26	0.72	1.09	9.03	4.01
Min	0.80	1.24	1.36	1.88	1.37	2.24	1.02	1.67	0.80	1.63	0.59	0.95	8.59	3.72
Max	1.76	2.96	1.97	3.21	2.09	3.49	1.88	3.44	1.79	2.95	0.88	1.27	10.20	4.43
SD	0.24	0.45	0.15	0.39	0.16	0.37	0.18	0.41	0.22	0.36	0.08	0.10	0.51	0.23
Stage 4	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P2-M3	M1-M3
N	10	10	12	12	12	12	12	12	10	10	7	7	6	7
M	1.28	1.69	1.74	2.52	1.69	2.84	1.43	2.61	1.33	2.44	0.74	1.10	9.29	3.87
Min	1.02	1.34	1.45	1.84	1.39	2.31	1.02	1.66	1.18	1.90	0.60	0.98	8.63	3.57
Max	1.56	3.02	1.95	3.31	1.95	3.25	1.77	3.17	1.55	2.75	0.96	1.26	10.09	4.39
SD	0.19	0.49	0.17	0.47	0.20	0.27	0.20	0.50	0.11	0.25	0.13	0.09	0.56	0.35
Stage 5														
N	1	1	4	4	4	4	4	4	4	4	2	2		2
M	1.59	1.68	1.71	2.57	1.57	3.06	1.39	2.78	1.30	2.26	0.64	1.04		3.82
Min			1.33	2.24	1.34	2.48	1.27	2.38	1.11	1.91	0.56	0.68		3.80
Max			2.13	3.01	1.70	3.42	1.50	3.28	1.39	2.74	0.72	1.39		3.83
SD			0.36	0.33	0.17	0.43	0.11	0.37	0.13	0.38	0.11	0.50		0.02

TABLE 3.—Dental measurements of lower dentitions of *Palaeolagus haydeni* from Round Top. Abbreviations as in Table 2. Measurements in mm.

Complete sample

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p3-m3	m1-m3
N	97	97	105	105	71	70	52	52	37	37	11	32
M	1.79	1.55	1.97	1.79	2.08	1.82	1.97	1.74	0.99	0.91	8.97	5.12
Min	0.82	1.09	1.35	1.18	1.59	1.43	1.57	1.02	0.69	0.55	8.29	4.25
Max	2.42	1.94	2.35	2.38	2.37	2.20	2.23	2.20	1.35	1.21	10.04	5.61
SD	0.29	0.18	0.18	0.23	0.19	0.20	0.17	0.22	0.17	0.14	0.48	0.37

Stage 1

	m1L	m1W
N	2	2
M	2.26	1.78
Min	2.20	1.78
Max	2.32	1.78

Stage 2

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p3-m3	m1-m3
N	30	30	31	31	14	14	9	9	6	6	6	6
M	1.57	1.41	1.93	1.63	2.03	1.67	1.94	1.59	0.86	0.80	8.94	5.12
Min	1.00	1.09	1.35	1.18	1.59	1.45	1.57	1.02	0.69	0.71	8.57	4.92
Max	2.24	1.79	2.24	2.11	2.24	1.84	2.16	1.78	1.04	0.90	9.60	5.25
SD	0.32	0.17	0.19	0.22	0.17	0.12	0.22	0.24	0.12	0.09	0.38	0.11

Stage 3

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p3-m3	m1-m3
N	54	54	54	54	30	30	14	14	4	4	4	4
M	1.85	1.60	2.00	1.87	2.14	1.88	1.99	1.77	0.95	0.95	9.09	5.06
Min	1.37	1.29	1.45	1.29	1.63	1.58	1.61	1.30	0.79	0.87	8.81	4.76
Max	2.23	1.94	2.35	2.38	2.37	2.20	2.23	1.86	1.17	1.00	9.50	5.31
SD	0.18	0.14	0.18	0.19	0.18	0.17	0.19	0.22	0.16	0.07	0.30	0.27

Stage 4

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W
N	12	12	12	12	4	4	1	1
M	2.05	1.68	2.04	1.93	2.04	2.14	2.16	1.94
Min	1.59	1.30	1.90	1.70	1.89	1.74		
Max	2.39	1.92	2.22	2.18	2.13	2.51		
SD	0.22	0.17	0.10	0.15	0.11	0.31		

Stage 5

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p3-m3	m1-m3
N	1	1	1	1	1	1	1	1	1	1	1	1
M	2.42	1.66	1.91	1.65	2.14	1.83	2.16	1.83	1.35	1.10	10.04	5.61