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Lagomorphs (Mammalia) from the Oligocene (Orellan and Whitneyan) Brule Formation, Nebraska

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LAGOMORPHS (MAMMALIA) FROM THE OLIGOCENE (ORELLAN AND WHITNEYAN) BRULE FORMATION, NEBRASKA

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Analysis of a stratigraphically-controlled sample of over 2,000 lagomorph specimens in the University of Nebraska State Museum, collected from sediments in the Brule Formation (Oligocene) of Sioux and Scotts Bluff Counties, Nebraska, indicates biostratigraphic and evolutionary changes in the lagomorph fauna throughout the Orellan of Nebraska.

A new species, *Palaeolagus hemirhizis*, described from the Orella A horizon, is intermediate between the typical Orellan species *P. haydeni* and the Chadronian species *P. temnodon* from Montana, Wyoming, and Saskatchewan. *Palaeolagus haydeni* and *P. burkei* show almost complete overlap in size range of cheek teeth, with the means of the measurements for *P. burkei* being slightly smaller than those of *P. haydeni*. *Palaeolagus haydeni* is known from Orella B through D, *P. burkei* from Orella C and D, and *P. intermedius* is known only from Orella D. Only *Megalagus turgidus* is known from all horizons of the Orella Member. Size change through the Orellan is demonstrated for *P. burkei*, *P. haydeni* and *M. turgidus*. Specimens of *P. haydeni*, *P. burkei*, *P. intermedius*, and *M. turgidus* are also known from the Lower Whitney Member (Whitneyan).

† † †

INTRODUCTION

The first lagomorph described from the Oligocene of the Great Plains was *Palaeolagus haydeni* by Leidy (1856). The last species was named over eighty years later by Wood (1940) — *P. burkei*. The most recent review of Oligocene lagomorphs of North America was by Dawson (1958), who identified five species from the Orellan and Whitneyan of the Great Plains — *P. haydeni*, *P. burkei*, *P. intermedius*, *Desmatolagus*? *gazini*, and *Megalagus turgidus*. All authors since Wood (1940) have considered that all Orellan species occurred throughout the Orellan, and many extended into the Whitneyan with no morphologic change. Most recently, Prothero (1985) discussed the biostratigraphy of the entire Oligocene fauna and showed the same lagomorphs occurring through the Orellan or Whitneyan (though he worked only on the generic level).

During the 1930's a large collection of vertebrate fossils was amassed by the University of Nebraska State Museum from the White River Group in western Nebraska. Among the fossils collected were over 2,000 lagomorph specimens, predominately mandibles and maxillae, from Sioux and Scotts Bluff counties. This excellent stratigraphically-controlled sample has allowed for the examination of change, both morphologic and biostratigraphic, in the lagomorphs of the Orellan and early Whitneyan of Nebraska.

All collecting localities cited below are referred to by their University of Nebraska State Museum designations. Precise locality data are available through the files of that institution. All dental measurements were taken at the occlusal surface.

Abbreviations used: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CM, Carnegie Museum of Natural History, Pittsburgh; UNSM, University of Nebraska State Museum, Lincoln. The dental terminology used below is that of Wood (1940) and Dawson (1958).

SYSTEMATIC PALEONTOLOGY

Order LAGOMORPHA Gidley, 1912

Family LEPORIDAE Gray, 1821

Subfamily PALAEOLAGINAE Dice, 1929

Procaprolagus Gureev, 1960

Procaprolagus gazini (Burke, 1936)

(Fig. 1)

Desmatolagus gazini Burke, 1936
Desmatolagus? *gazini* Burke, Dawson, 1958
Procaprolagus gazini (Burke) Storer, 1984

Type specimen. CM 37, maxilla with LP^3-M^2.

Horizon and locality. Type from "Badland Creek," Orella Member, Brule Formation, Nebraska. Referred specimen from UNSM locality Sx-14, Orella Member (level uncertain), Burle Formation, Sioux County, Nebraska.

Age. Orellan (middle Oligocene).

Referred specimen. UNSM 81083, RP^3.

Discussion. Burke (1936) first described this species and referred it to the Asian Oligocene genus *Desmatolagus* Matthew and Granger (1923). Later, Dawson (1958) stated that *D. gazini* represented a genus distinct from all known Oligocene North American lagomorphs but questioned its allocation to *Desmatolagus* and retained it in only questionably. Storer (1984) referred *D. gazini* to another Asian genus, *Procaprolagus* Gureev (1960), based on Sych's (1975) review of the Asian Oligocene genera of lagomorphs. This species is here retained in *Procaprolagus* based on Storer's arguments and the lack of any contradictory information observed on the referred specimen.

The referred specimen, UNSM 81083, differs from the P^3 of the holotype only in having a more flattened lingual margin and in being slightly different in size (a-p, 2.13 mm; tr, 3.87 mm; see Table I for abbreviations). The exact horizon of the specimens of *P. gazini* is not known. The locality and horizon information recorded with the holotype is simply "*Oreodon* beds, Badland Creek, Sioux County, Nebraska." The difficulty with this is that the exact location of Badland Creek is not known. There is no Badland Creek on any of the available maps of Sioux County, Nebraska, dating from 1909 to the present. It is evident from the field notes of the Carnegie Museum parties around the turn of the century (when the specimen was recovered) that Badland Creek is a small creek north of Harrison, Nebraska. Several other creeks (such as Warbonnet Creek, Cottonwood Creek) referred to in the CM field notes can be located. It is quite possible that the name Badland Creek was not a local term but one adopted by the CM field parties for an unnamed creek in Sioux County.

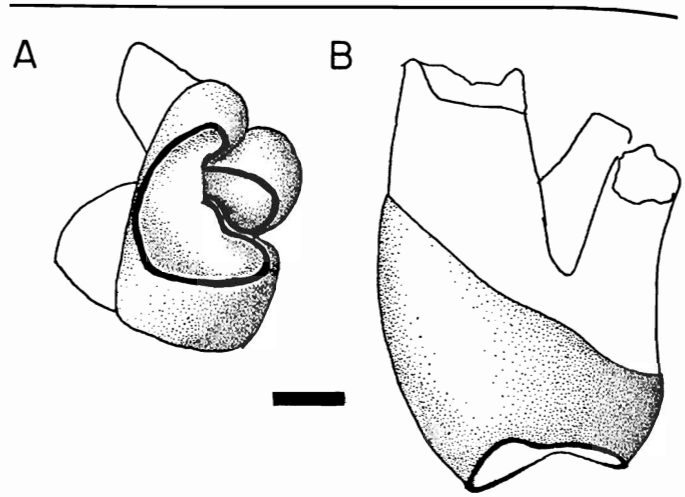

FIGURE 1. *Procaprolagus gazini*, UNSM 81083, RP^3. **A,** occlusal view. **B,** posterior view. Bar scale = 1 mm.

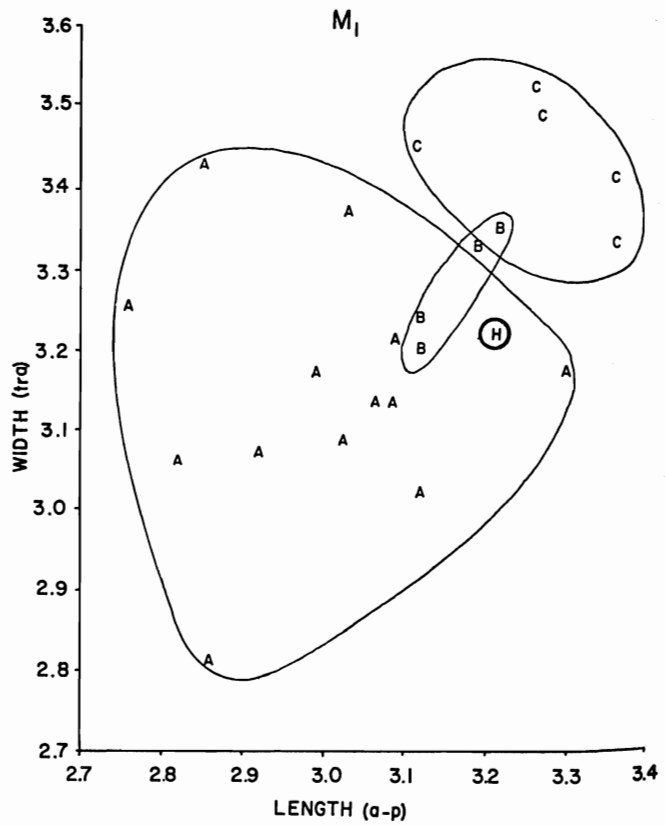

FIGURE 2. Graph of length versus width of M_1 of *Megalagus turgidus* from Brule Formation, Nebraska. Capital letters indicate horizon of Orella Member from which each specimen was recovered. **H.** indicates holotype of *M. turgidus*, AMNH 5635, from Colorado. Both axes in millimeters.

The referred specimen of *P. gazini* was collected from UNSM locality Sx-14. The recorded horizon in the UNSM field notes of 1932 (when the fossil was collected) is "lower Orella" which is equivalent to either Orella A or B. It is not surprising that this primitive species is from the lower part of the Orella Member.

Megalagus Walker, 1931

Megalagus turgidus (Cope, 1873)

(Table I)

Type specimen. AMNH 5635, mandible with LP_3-M_3.

Horizon and locality. Type from Cedar Creek Beds, White River Formation, Colorado. Referred specimens from UNSM localities Sx-2 (Orella C), Sx-4 (Orella B), Sx-5 (Orella A), Sx-6 (Orella B, C), Sx-13 (Orella A), Sx-14 (Orella A, D), Sx-17 (Orella D), Sx-18 (Orella A), Sx-19 (Orella C), Sx-24 (Orella B), Sx-25 (Orella A), and Sx-26 (Orella A), Orella Member, Brule Formation, Sioux County, Nebraska; and Sx-23 (Whitney A), Whitney Member, Brule Formation, Sioux County, Nebraska.

Age. Orellan and early Whitneyan (middle to early late Oligocene).

Referred specimens. UNSM 15124, 15601, 15669, 16171, 17094, 17234, 17316, 17361 (all maxillae with upper cheek teeth); and UNSM 15042, 15053, 15083, 15084, 15105, 15126, 15127, 15231, 15236, 15256, 15273, 15373, 15423, 15443, 15458, 15473, 15524, 15526, 15638, 16141, 16171, 16173, 16242, 16258, 16779, 16857, 16975, 17045, 17094, 17234, 17316, 17361, 17489, 17697 (mandibles with lower cheek teeth).

TABLE I. Dental measurements (mm) of *Megalagus turgidus* from Brule Formation, Nebraska. Abbreviations: a-p, anteroposterior length; tr, transverse width; tra, anterior transverse width (trigonid); trp, posterior transverse width (talonid); **N,** number of specimens; **M,** mean; **OR,** size range.

		ORELLA A			ORELLA B			ORELLA C			ORELLA D		
		N	**M**	**OR**	**N**	**M**	**OR**	**N**	**M**	**OR**	**N**	**M**	**OR**
P^2	a-p										2	1.52	1.45-1.59
	tr										2	2.49	2.41-2.57
P^3	a-p	1	2.61	—				2	2.97	2.81-3.13	3	2.95	2.82-3.10
	tr	1	4.00	—				1	5.01	—	2	5.20	5.08-5.32
P^4	a-p	3	2.78	2.49-3.11	1	2.82	—	2	2.93	2.88-2.98	3	2.82	2.71-2.95
	tr	3	3.98	3.45-4.40	1	4.53	—	2	5.15	5.07-5.23	3	5.27	4.63-5.99
M^1	a-p	3	2.28	1.96-2.61	1	2.11	—	2	2.72	2.45-2.98	3	2.65	2.49-2.94
	tr	3	3.89	3.80-4.03	1	4.35	—	2	4.82	4.63-5.00	3	4.86	4.69-5.01
M^2	a-p	1	2.27	—	1	2.38	—	2	2.53	2.29-2.77	3	2.47	2.37-2.57
	tr	-	—	—	1	4.09	—	2	4.48	4.24-4.71	3	4.66	4.42-4.93
M^3	a-p	1	1.45	—				2	1.48	1.37-1.58	2	1.21	1.18-1.24
	tr	1	1.83	—				2	2.20	2.04-2.75	2	2.26	1.83-2.70
P_3	a-p	8	2.57	2.01-2.92	3	2.38	2.24-2.50	2	2.74	2.71-2.76			
	tra	7	2.09	1.77-2.50	3	2.09	1.78-2.24	2	2.28	2.15-2.41			
	trp	6	2.66	2.40-2.96	3	2.82	2.75-2.87	2	2.96	2.84-3.07			
P_4	a-p	17	3.19	2.83-3.63	4	3.30	3.19-3.38	2	3.23	3.06-3.40			
	tra	16	3.28	2.60-3.72	4	3.39	3.28-3.48	2	3.63	3.60-3.65			
	trp	17	2.59	2.01-2.94	4	2.57	2.53-2.60	2	2.62	2.57-2.68			
M_1	a-p	15	2.99	2.76-3.30	4	3.16	3.12-3.22	5	3.27	3.11-3.36			
	tra	14	3.16	2.81-3.43	4	3.28	3.18-3.35	5	3.44	3.33-3.52			
	trp	15	2.54	2.40-2.87	4	2.53	2.49-2.56	5	2.56	2.36-2.78			
M_2	a-p	10	3.09	2.87-3.45	4	3.03	2.85-3.20	4	3.23	2.99-3.43			
	tra	10	3.27	2.99-3.51	4	3.34	3.19-3.44	4	3.31	3.22-3.41			
	trp	10	2.64	2.43-2.96	4	2.45	2.29-2.58	4	2.65	2.60-2.75			
M_3	a-p	3	1.62	1.43-1.78	3	1.75	1.71-1.82	2	1.82	1.76-1.89			
	tra	3	1.83	1.76-1.89	3	1.89	1.86-1.90	2	1.92	1.89-1.94			
	trp	3	1.34	1.11-1.55	3	1.29	1.24-1.35	2	1.40	1.31-1.49			

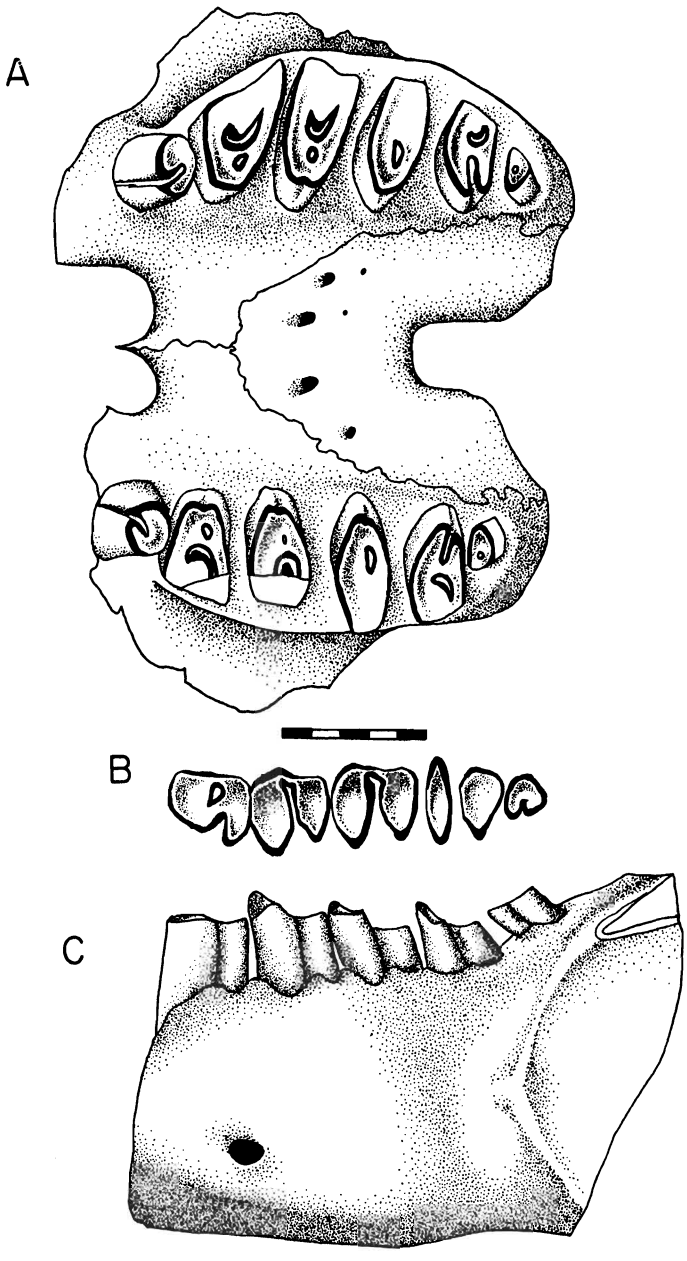

FIGURE 3. Holotype of *Palaeolagus hemirhizis,* UNSM 15483. **A,** palate with complete upper dentition. **B,** occlusal view of LP_3-M_3. **C,** lateral view of mndible. Bar scale = 5mm.

Discussion. The skull, skeleton and dentition of *Megalagus turgidus* have been thoroughly described (Wood, 1940; Dawson, 1958). None of the Sioux County specimens adds to knowledge of the morphology of this species.

The most notable aspect of the sample of *M. turgidus* from Nebraska is its increase in size through the Orellan (Fig. 2; Table I). *Megalagus* is sufficiently rare in Oligocene faunas, where it is known that a statistically significant sample has never been recovered from a sequence of strata. The Nebraska sample is sufficiently large (38 specimens) to demonstrate that specimens of *M. turgidus* are larger from each higher stratigraphic level. The holotype of *M. turgidus* from Colorado falls within the range of the larger specimens from Orella A in the Nebraska sample (Fig. 2).

A single mandible of *Megalagus* with M_2-M_3 (UNSM 17489) from the Lower Whitney Member (Whitney A) is present in the UNSM collections. This specimen is not complete enough to establish whether it belongs to *M. turgidus* or a different Whitneyan species. Both Wood (1940) and Dawson (1958) suggested that *M. turgidus* may occur in the Whitneyan of the Great Plains but cited no specimens or localities. UNSM 17489 demonstrates that *Megalagus* definitely occurs in the Whitneyan, but the species cannot be determined with any certainty. UNSM 17489 is here referred to *Megalagus* cf. *M. turgidus.*

Palaeolagus Leidy, 1856

Palaeolagus hemirhizis new species

(Figs. 3, 4; Table II)

Type specimen. UNSM 15483, palate and both mandibles with all cheek teeth and fragments of skull and postcranial skeleton.

Horizon and locality. Type from UNSM locality Sx-5, referred specimens from UNSM localities Sx-5, Sx-8, Sx-9, Sx-11, Sx-13, Sx-14, Sx-18, Sx-19, Sx-23, Sx-24, Sx-25, Sx-26, Sx-32, Orella A, Orella Member, Brule Formation, Sioux County, Nebraska.

Age. Early Orellan (middle Oligocene).

Referred specimens. Approximately 600 specimens in the UNSM collections.

Diagnosis. Larger than *P. haydeni* and smaller than *P. temnodon:* roots on P^3-M^2 small and present on only 50% of the specimens; those without roots possess shallow grooves along buccal side of tooth running entire height of tooth; crown height of cheek teeth slightly less than that of *P. haydeni;* internal reentrant valley on P_3 closes in early wear, leaving isolated lake as in *P. haydeni;* I_1 ends posteriorly below M_1.

Etymology. Greek, *hemi,* half; *rhizis,* rooted.

Description. No complete skull of *P. hemirhizis* is known, but several specimens consist of partial skulls. There is no detectable difference between the skulls of *P. hemirhizis* and *P. haydeni.*

Posterior end of I_1 below center of M_1 to below talonid of P_4. Roots present on 50% of specimens of P^3-M^2; roots reduced, smaller than those of *P. temnodon;* crown height of cheek teeth

TEXT—*(Continued on page 146)*

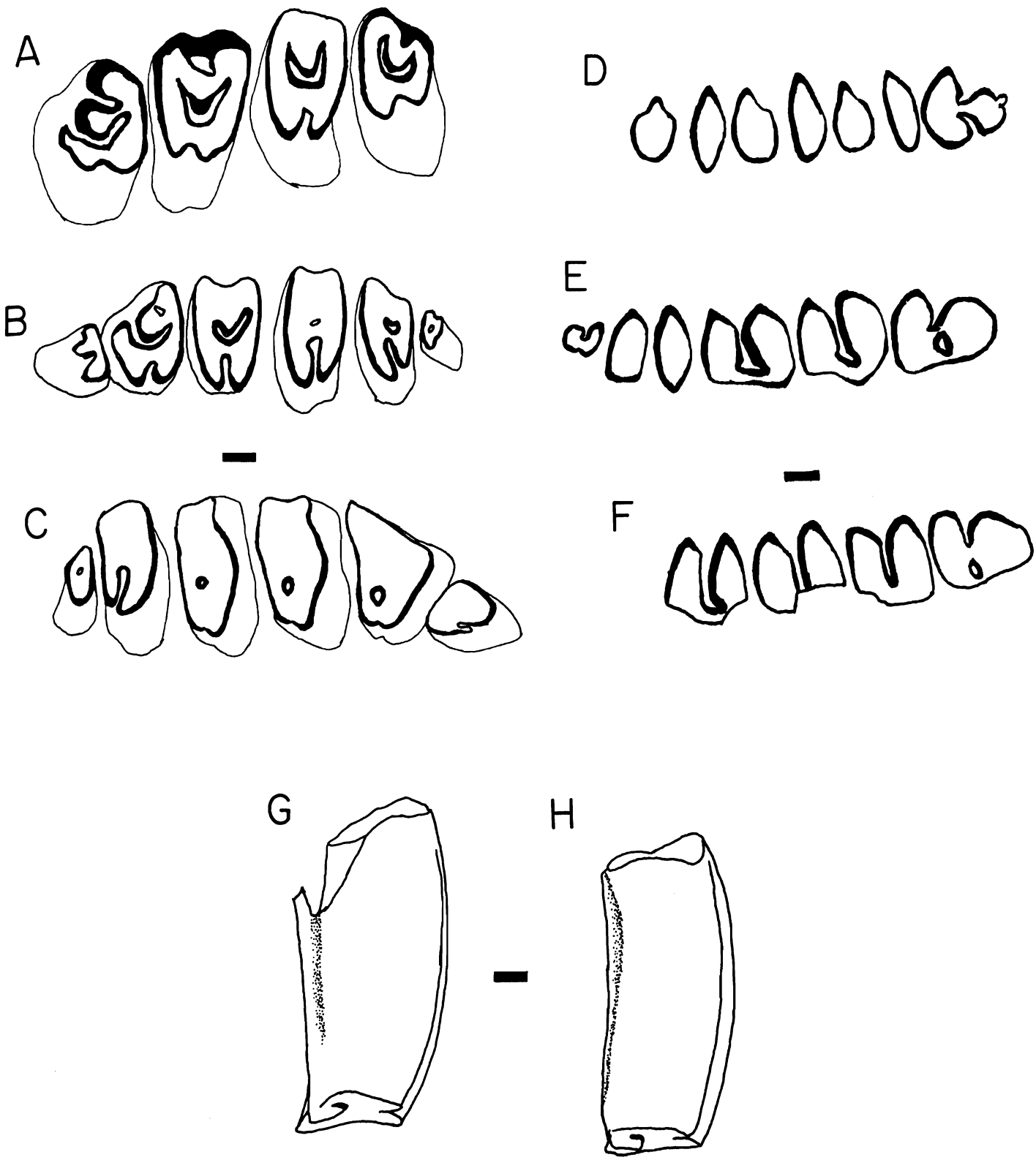

FIGURE 4. Dentitions of *Palaeolagus hemirhizis*. **A, D,** early stage of wear; **B, E,** intermediate stage of wear; **C, F,** late stage of wear. **A,** UNSM 15522, LP^3-M^2. **B,** UNSM 81088, LP^2-M^3. **C,** UNSM 15133, RP^2-M^3. **D,** UNSM 15485, LP_3-M_2. **E,** UNSM 15453, LP_3-M_3. **F,** UNSM 15221, LP_3-M_2. **G, H,** posterior view of M^2; **G,** UNSM 15522; **H,** UNSM 15075. Bar scale = 1 mm.

TEXT—*(Continued from page 144)*

nearly equal to that of *P. haydeni,* greater than in *P. temnodon;* intermediate in size, larger than *P. haydeni* and smaller than *P. temnodon* with approximately 50% size overlap with each; cementum present on all cheek teeth as in *P. haydeni.*

P^2 three-lobed; buccal lobe smallest, disappearing in early wear; lingual lobe angular anteriorly; central lobe round; valley between central and lingual lobes disappears in late wear, leaving circular outline.

P^3 as in *P. haydeni* in occlusal pattern; buccal lobe circular and restricted to posterior half of tooth; central lobe also circular with no anterior projecting spurs; valley between buccal and central lobe first to disappear with wear; crescent between central and lingual lobes remains open until hypostria closes lingual end; central crescent disappears before enamel lake of hypostria; hypostria shallow; half of specimens containing roots have only the posterobuccal root; origin of anterobuccal root a minimum of 2.9 mm higher on crown than origin of posterobuccal root.

P^4 similar to molars; P^3 and P^4 retain central enamel crescent longer than molars; hypostria shallower than in molars; lingual end of hypostria closes long before central crescent disappears; enamel lake of hypostria retained longer than central crescent.

M^1-M^2 similar, M^2 narrower; hypostria straight-walled, deeper than in premolars; central crescent disappears rapidly before lingual end of hypostria closes; enamel lake of hypostria retained until very late wear.

M^3 very small; enamel lake between lingual and buccal lobes circular rather than crescentic; hypostria very shallow, lost in early wear; central enamel lake retained until late wear.

TABLE II. Dental measurements (mm) of a sample of *Palaeolagus hemirhizis.* Abbreviations: **S,** standard deviation; **CV,** coefficient of variation; other abbreviations as in Table I.

							UNSM 15483 type	
		N	**M**	**OR**	**S**	**CV**	left	right
P^2	a-p	8	1.41	0.99-1.84	.30	19.4	1.52	1.46
	tr	8	1.88	1.48-2.21	.02	13.3	1.94	1.95
P^3	a-p	10	2.18	1.92-2.51	.25	8.9	2.51	2.01
	tr	6	3.22	2.86-3.58	.30	9.6	3.52	—
P^4	a-p	10	2.06	1.76-2.35	.16	7.8	1.97	2.12
	tr	9	3.52	3.15-4.02	.28	8.1	3.69	—
M^1	a-p	10	1.86	1.64-2.16	.15	8.2	1.75	1.64
	tr	10	3.32	3.04-3.67	.20	6.1	3.40	3.67
M^2	a-p	10	1.75	1.61-1.90	.09	5.3	1.65	1.81
	tr	10	2.85	2.55-3.27	.19	6.8	2.78	2.92
M^3	a-p	9	0.99	0.92-1.44	.09	9.3	1.06	0.93
	tr	9	1.51	1.37-1.61	.16	10.7	1.38	1.37
P_3	a-p	11	2.17	1.68-2.39	.24	11.0	2.37	2.39
	tra	11	1.58	1.31-2.01	.17	11.3	1.56	1.55
	trp	11	1.99	1.85-2.36	.19	9.4	1.87	2.28
P_4	a-p	11	2.19	1.96-2.41	.18	8.0	2.16	2.31
	tra	11	2.24	2.10-2.45	.12	5.2	2.23	2.24
	trp	11	2.02	1.77-2.26	.15	7.6	2.07	2.21
M_1	a-p	11	2.25	2.01-2.37	.12	5.3	2.27	2.37
	tra	11	2.34	2.24-2.50	.12	5.1	2.34	2.41
	trp	11	2.08	1.80-2.39	.16	7.8	2.05	2.17
M_2	a-p	11	2.11	1.90-2.35	.18	8.3	2.28	2.35
	tra	11	2.25	2.11-2.41	.09	4.1	2.33	2.41
	trp	11	1.95	1.76-2.14	.13	6.8	2.01	2.00
M_3	a-p	5	1.31	1.21-1.39	.07	5.6	1.39	1.30
	tra	5	1.32	1.24-1.41	.06	4.6	1.30	1.33
	trp	5	1.03	0.97-1.09	.04	4.2	1.09	1.03

P_3 similar to *P. primus, P. temnodon* and *P. haydeni;* lingual reentrant valley closes lingually after little wear leaving isolated enamel lake; enamel lake retained until very late wear; anterior margin rounded.

P_4-M_2 as in all other *Palaeolagus;* trigonid wider than talonid; lingual bridge between trigonid and talonid forms after moderate wear.

M_3 small; trigonid not elevated above talonid; talonid rounded posteriorly; valley between trigonid and talonid disappears in late wear.

Discussion. *Palaeolagus hemirhizis* is intermediate between the Chadronian *P. temnodon* and the later Orellan *P. haydeni* in size and development of dental characteristics (see Wood, 1940; Dawson, 1958; Storer, 1981; Emry and Gawne, 1986). In size, *P. hemirhizis* is almost exactly intermediate between the Chadronian and Orellan species. The size range of the cheek teeth of *P. hemirhizis* overlaps that of the older and younger species by approximately 50% each; the larger specimens are within the range of *P. temnodon* and the smaller specimens are in the size range of *P. haydeni*.

P^3-M^2 on all specimens of *P. temnodon* are rooted, and only 50% of those of *P. hemirhizis* are rooted. Burt and Wood (1960) cited several isolated specimens of *P. haydeni* from the Orellan of South Dakota that had very fragile roots. Of the specimens in the UNSM collections of *P. haydeni* from Nebraska, 15% of the specimens from Orella B possess very fragile roots, and none of the specimens from Orella C or D have roots. Again, the morphology of *P. hemirhizis* is intermediate. The rootless specimens of *P. hemirhizis* have shallow grooves that isolate thin ridges along the buccal height of the tooth, clearly homologous to buccal roots (Fig. 4H). Emry and Gawne (1986, Table I) noted that the buccal roots on P^3 of *Mytonolagus* originated at the same level on the tooth, and in *Paleolagus* the posterobuccal root originated nearer the occlusal surface than the anterobuccal root. In *P. primus* the distance between the origin of the two roots ranged from 0.3 to 2.0 mm. In *P. temnodon* it ranged from 2.2 to 2.8 mm. In the specimens of *P. hemirhizis* that possess both roots (anterobuccal root not present in 50% of specimens with roots) the closest measurement is 2.93 mm.

The only difference in the occlusal pattern of the cheek teeth of *P. hemirhizis* and *P. haydeni* is that the hypostriae close lingually on the upper cheek teeth, and the enamel lake on P_3 forms at an earlier stage of wear in *P. hemirhizis.* The lingual bridge between the trigonid and talonid on the lower cheek teeth appears perhaps slightly earlier in *P. hemirhizis* than in *P. haydeni*.

The crown height of the cheek teeth of *P. hemirhizis* is almost equal to that of *P. haydeni,* higher than in *P. temnodon*.

Gawne (1978) demonstrated in a sample of *P. temnodon* that P_3 increased in size relative to the remainder of the tooth row at increased wear stages. This is evident in the measurements of P_3 in the sample of *P. hemirhizis* (Table II), which have coefficients of variation greater than 10. This change in size due to wear is also reflected in the size of P^2 and complements the increase in size of P_3.

All specimens of *P. hemirhizis* are from the lowest level of the Orella Member (Orella A of Schultz and Stout, 1955) and *P. haydeni* is known from the Orella B horizon through the lower Whitney Member.

It is possible that specimens of *P. haydeni* may be contained in the sample referred here to *P. hemirhizis.* However, because the species of *Palaeolagus* can be identified only with a large sample due to the large amount of overlap in size and morphology between species, there would be no way to separate only a few specimens of these two species. The upper dentitions that lack roots cannot be separated from those with roots by size or any occlusal morphology.

Galbreath (1953) identified specimens of *P. intermedius* from the Chadronian Horsetail Creek Member of northeastern Colorado. Later, Dawson (1958) noted that these specimens were not referable to *P. intermedius,* but were intermediate in size and hypsodonty of the cheek teeth between *P. temnodon* and *P. haydeni*. She referred these specimens to *P. haydeni,* but suggested that they may represent a distinct subspecies. The Colorado specimens were not examined as a part of this study, but they may prove to represent *P. hemirhizis.*

Palaeolagus haydeni Leidy, 1856

(Fig. 5A)

Type specimen. ANSP 11031, mandible with RP_3-M_3.

Horizon and locality. Type from "Turtle bed, head of Bear Creek, Nebraska" (Dawson, 1958:20). Referred specimens from UNSM localities Sx-1 (Orella C), Sx-2 (Orella C), Sx-4 (Orella B, C), Sx-5 (Orella C, D), Sx-6 (Orella B, C), Sx-10 (Orella D), Sx-11 (Orella D), Sx-13 (Orella C), Sx-14 (Orella D), Sx-17 (Orella C, D), Sx-19 (Orella C, D), Sx-23 (Orella C), Sx-24 (Orella B, C), Sx-26 (Orella B), Sx-102 (Orella B), Orella Member, Brule Formation, Sioux and Scotts Bluff counties, Nebraska; and Sx-17 (Whitney A), and Sx-48 (Whitney A), Whitney Member, Brule Formation, Sioux County, Nebraska.

Age. Orellan (B through D) and early Whitneyan (middle to early late Oligocene).

Referred specimens. Approximately 1,000 specimens in the collections of the UNSM.

Discussion. *Palaeolagus haydeni* is the most common lagomorph represented from the Brule Formation. It is definitely known from the B through D horizons of the Orella Member, and the Whitney A horizon of the Whitney Member. Little morphologic change can be observed through time in the sample of *P. haydeni* from the Orellan of Nebraska. Fifteen percent of the specimens of upper dentitions of *P. haydeni* from Orella B possess very reduced roots on the cheek teeth. No other specimens of *P. haydeni* from any higher levels retain roots. The sample of *P. haydeni* reported by Burt and Wood (1960) from South Dakota that variably retained roots were probably collected from a lower Orellan horizon.

The size of the cheek teeth of *P. haydeni* shows some change through the Orellan. As demonstrated by the dimensions of M_1 (Fig. 6), specimens from later horizons are longer anteroposteriorly but narrower buccolingually.

The relative representation of *P. haydeni*, based on minimum number of individuals, changes throughout the Orellan. In the Orella B and C levels, *P. haydeni* makes up 94 and 87% of the lagomorphs respectively. Only 44% of the lagomorphs from Orella D are *P. haydeni*. This sharp decrease in the abundance of this species coincides with the appearance of *P. intermedius* and the marked increase of *P. burkei* in the Orella D level (see Fig. 7).

As mentioned above for *Megalagus turgidus*, *P. haydeni* was reported as possibly being from the Whitneyan of the Great Plains, without any specific data (Wood, 1940; Dawson, 1958). Two specimens definitely referable to *P. haydeni* (UNSM 17496, UNSM 17494) are present in collections from the Whitney A horizon.

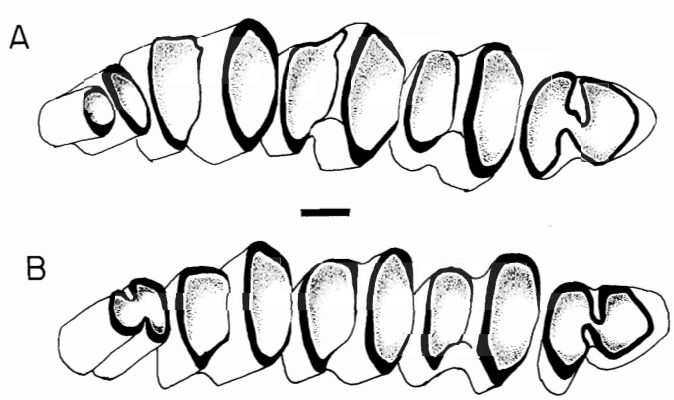

FIGURE 5. Lower dentitions of *Palaeolagus haydeni* and *P. burkei* from the Brule Formation, Nebraska. **A,** *P. haydeni*, UNSM 17333. RP_3-M_3. **B,** *P. burkei*, UNSM 17466, RP_3-M_3.

Palaeolagus burkei Wood, 1940

(Fig. 5B)

Type specimen. AMNH 8704, skull with complete upper dentition.

Horizon and locality. Type from White River Formation (*Leptauchenia* beds), Logan County, Colorado. Referred specimens from UNSM localities Sx-1 (Orella C), Sx-5 (Orella C), Sx-6 (Orella C), Sx-10 (Orella D), Sx-14 (Orella D), Sx-17 (Orella D), Sx-19 (Orella C), Orella Member, Brule Formation, Sioux County Nebraska; and Sx-4 (Whitney A), Whitney Member, Brule Formation, Sioux County, Nebraska.

Age. Middle Orellan (Orella C through D) through Whitneyan (middle to early late Oligocene).

Referred specimens. Approximately 300 specimens in the collections of the UNSM.

Discussion. *Palaeolagus burkei* was originally diagnosed as being smaller than *P. haydeni*. The specimens of these two species from northeastern Colorado showed no overlap in size (Galbreath, 1953). However, Galbreath (1953: 51) noted that several specimens equal in size to *P. haydeni* had the dental morphology of *P. burkei*. He referred these specimens to *P. haydeni*, interpreting size as the more important feature. Dawson (1958) provided a more complete description and comparison of the dental features of *P. burkei*, including lower dentitions with better criteria for easier separation of these species. All the specimens referred here to *P. burkei* were done so according to the morphologic criteria presented by Dawson (1958) before the measurements were made.

The dimensions of the dentitions referred to *P. burkei* show a nearly complete overlap with dentitions of *P. haydeni* (see Fig. 7). The mean of the measurements of the teeth of *P. burkei* is smaller than that of *P. haydeni* from the same horizon. The difference in the means of these species is greater from Orella D than Orella C, and the amount of overlap of size range is accordingly less in the Orella D horizon (Fig. 6).

There is a minor change in the size of *P. burkei* in the Orellan, similar to that of *P. haydeni*. As demonstrated by the dimensions of M_1 (Fig. 6), specimens of *P. burkei* are smaller from the higher level.

The occurrence and relative abundance of *P. burkei* from the Orellan of Nebraska are also significant. Galbreath (1953) reported *P. burkei* from the middle and upper levels of the Cedar Creek Member and the Whitneyan Vista Member of Colorado. In the Nebraska sample, *P. burkei* is known only from the Orella C and D levels (middle and upper), and the lower Whitney. This species first occurs later in the section than the earliest specimens of *P. haydeni*. The relative representation of *P. burkei*, based on minimum number of individuals, also shows a marked change in the Orellan (see Fig. 8). At its lowest level of occurrence, Orella C, *P. burkei* represents only 9% of the total lagomorphs represented. In the sample from Orella D, *P. burkei* constitutes 48% of the lagomorph fauna, a greater percentage than *P. haydeni*.

Based on the level of first occurrence and change in the relative abundance of *P. burkei*, it appears that this species was replacing *P. haydeni* in the late Orellan. The overlap in size and similarity in dental morphology of *P. burkei* and *P. haydeni* at the Orella C level, and further separation in size of these species at the Orella D level, may demonstrate the gradual separation of *P. burkei* from an ancestral species, *P. haydeni*. An alternate explanation is that *P. burkei* migrated into the Great Plains in the middle Orellan and gradually replaced *P. haydeni*.

Palaeolagus intermedius Matthew, 1899

Type. AMNH 8722, skull with upper dentition.

Horizon and locality. Type from "Oreodon beds, White River formation, Castle Rock, Logan County, Colorado" (Dawson, 1958: 28). Referred specimens from UNSM localities Sx-10 (Orella D), Sx-19 (Orella D), Orella Member, Brule Formation, Sioux County, Nebraska; and Sx-17 (Whitney A), Whitney Member, Brule Formation, Sioux County, Nebraska.

Age. Late Orellan to Whitneyan (middle to early late Oligocene).

Referred specimens. UNSM 17359, mandible with RP_3-M_2; UNSM 17693, mandible with RP_4-M_2; and UNSM 81082, maxilla with LP^2-M^2.

Discussion. The only significant information that can be gained from the Nebraska sample of *P. intermedius* is the level of occurrence. Galbreath (1953) cited this species from throughout the Orellan Cedar Creek Member and the Whitneyan Vista Member of the White River Formation of Colorado. In the Nebraska sample *P. intermedius* is rare and is known only from the Orella D and Whitney A horizons. This may indicate a late Orellan age for the Cedar Creek Member in Colorado because the pattern of occurrence is similar to that of some rodents that occur only at the Orella D level in Nebraska, and throughout the Cedar Creek Member in Colorado (Barbour and Stout, 1939; Korth, 1986).

TEXT—*(Continued on page 151)*

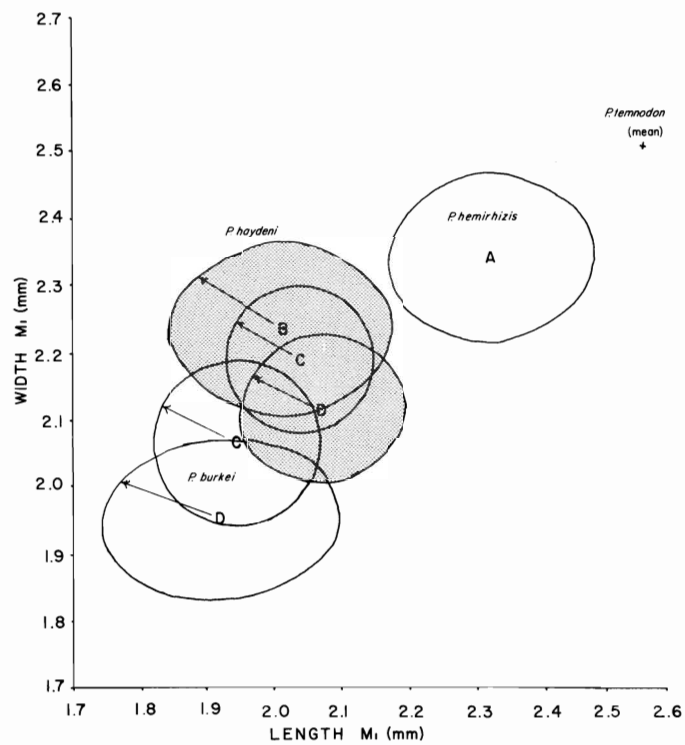

FIGURE 6. Graph showing size change of M_1 of species of *Palaeolagus*. Letter in center of each field indicates horizon within Orella Member and mean measurements for length (a-p) and width (tra) of M_1 for each species. Radius of each field (arrows) represents one standard deviation. Mean of M_1 for *P. temnodon* based on data from Wood (1940), Storer (1981), and Emry and Gawne (1986).

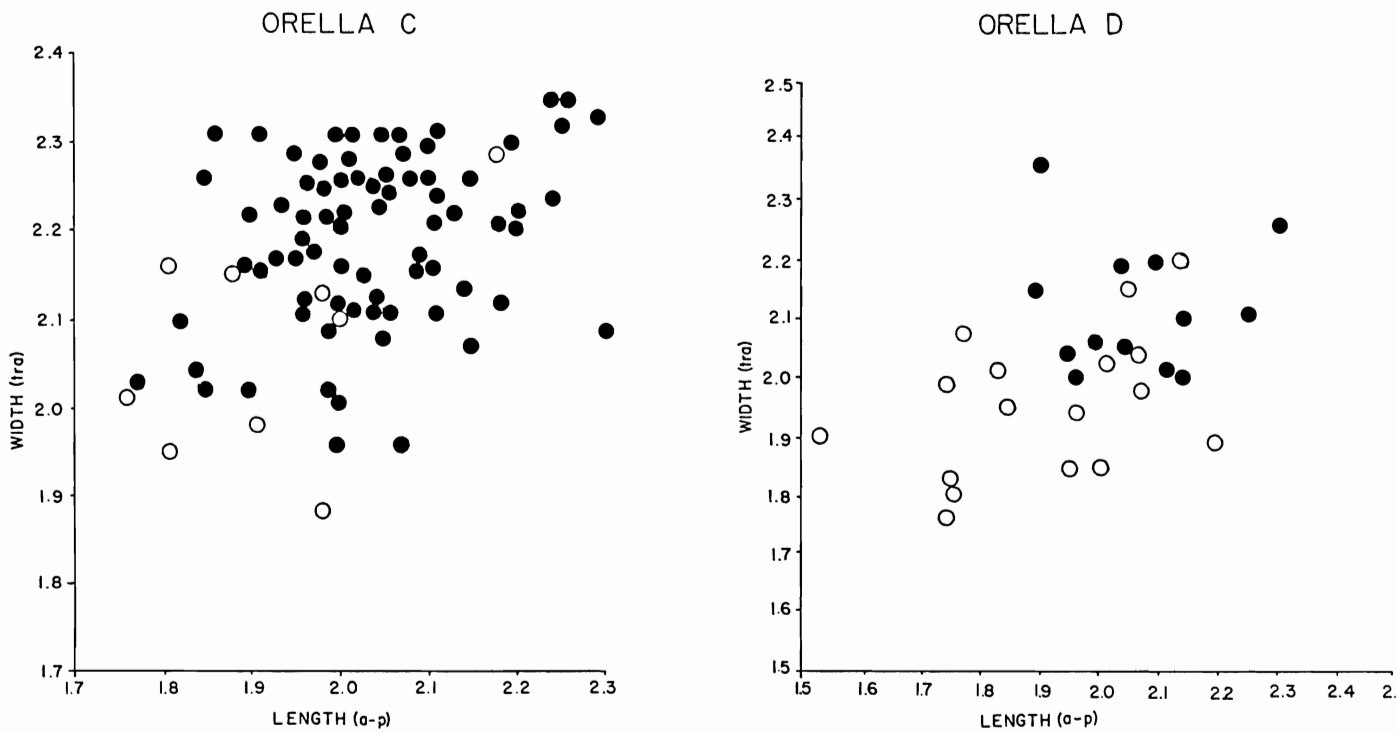

FIGURE 7. Scatter diagrams of the length versus width of M_1 of *Palaeolagus haydeni* (dark circles) and *P. burkei* (open circles) from Orella C and D levels of the Orella Member, Brule Formation, Nebraska. Axes in millimeters.

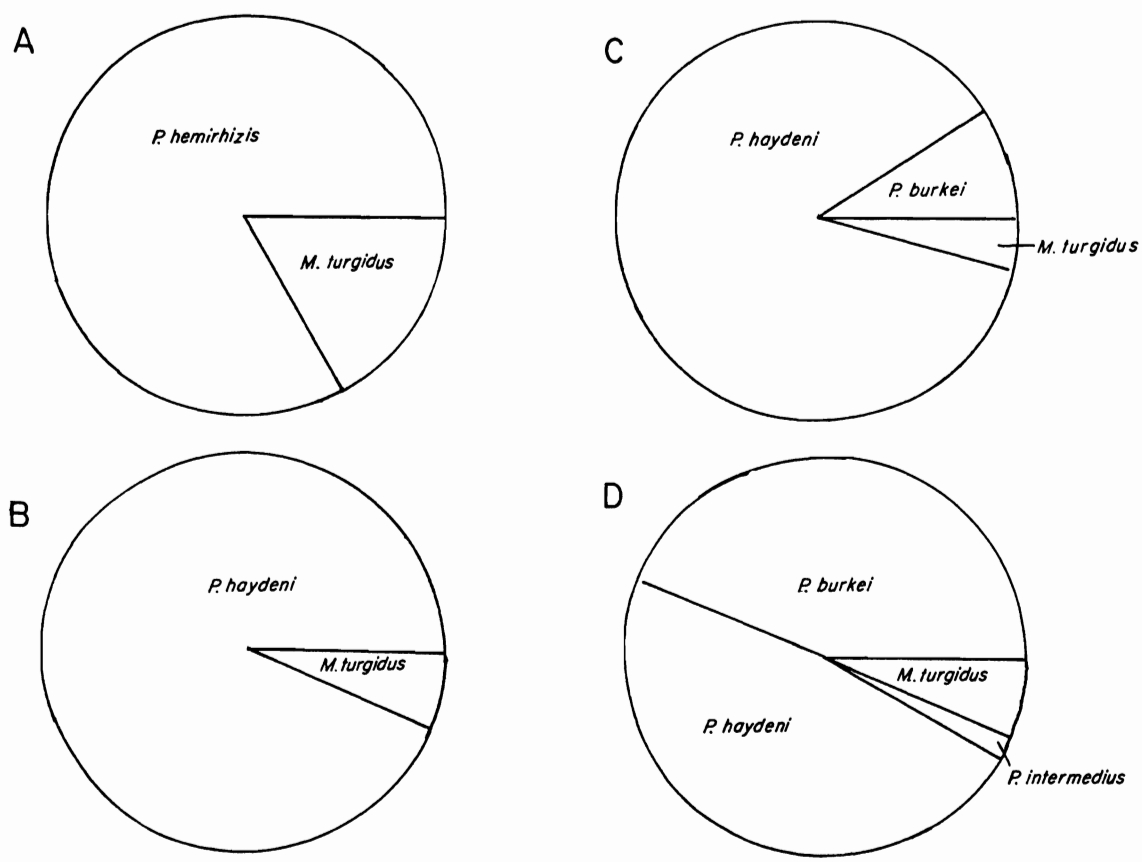

FIGURE 8. Percentage representation of species of the lagomorph fauna from the Orella Member, based on minimum number of individuals. Capital letters next to each chart designate the horizon within the Orella Member.

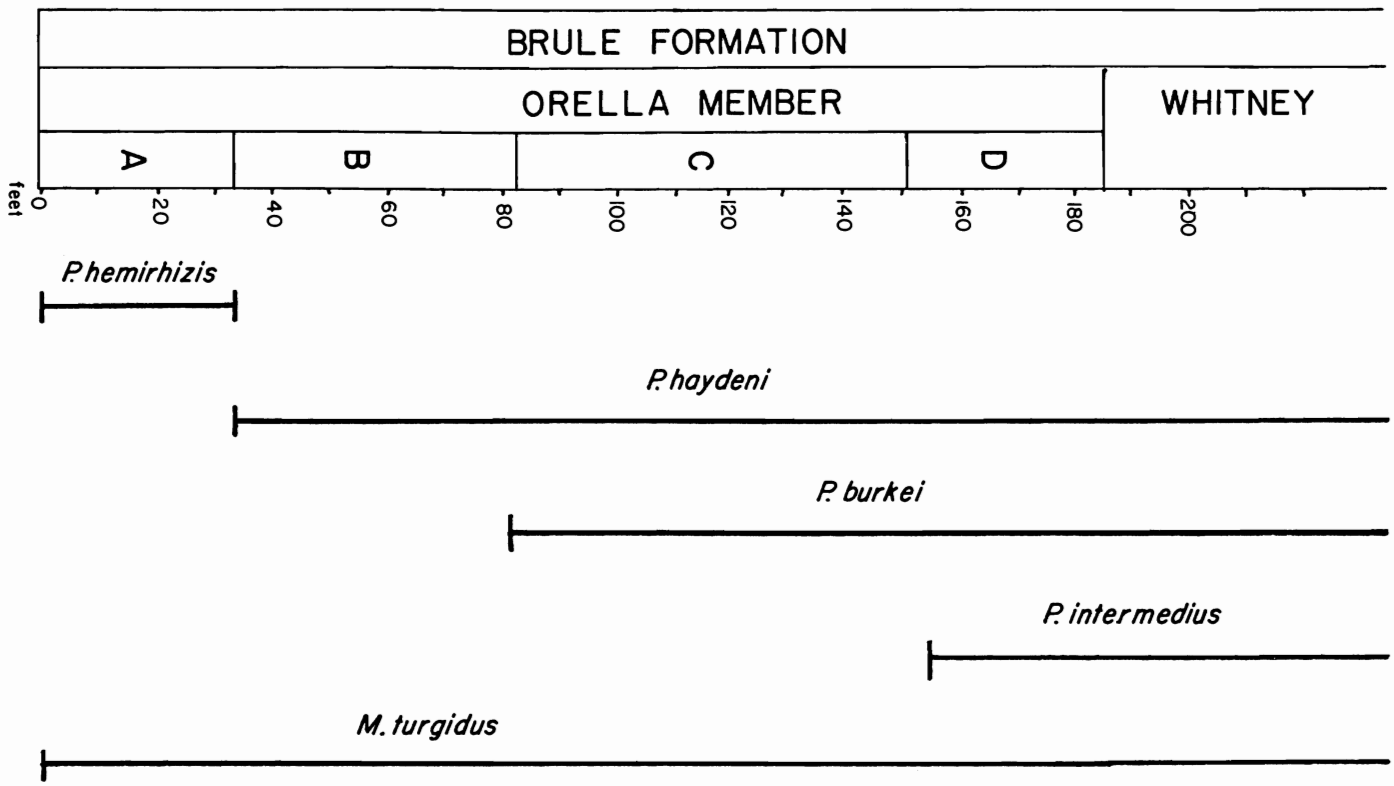

FIGURE 9. Horizons of occurrence of lagomorph species in the Brule Formation, Sioux County, Nebraska. Vertical scale based on minimum thickness of each horizon as defined by Schultz and Stout (1955).

TEXT—*(Continued from page 149)*

CONCLUSIONS

The lagomorph fauna from the Orellan of Nebraska shows little stasis. Only *Megalagus turgidus* is known from all levels of the Orella Member. All other species are restricted to a maximum of three levels (Fig. 9). It is also significant that four of the Orellan species of lagomorhs survive into the early Whitneyan, and there was no notable change in the lagomorph fauna at the Orellan-Whitneyan boundary. Arikareean lagomorphs, while they contain some species similar to those of the Orellan (such as *Palaeolagus hypsodus* and *P. philoi*), also contain the beginnings of the Archaeolaginae. No transitional species are known between the palaeolagines and archaeolagines from the Whitneyan. Because the samples of Whitneyan lagomorphs in the Nebraska collections are restricted to the lowest level of the Whitney Member, nothing can be said about the later Whitneyan. Transitional forms between the palaeolagines and archaeolagines may occur at higher levels in the Whitney not presently known.

Three species, *M. turgidus, P. haydeni,* and *P. burkei* all show a change in size through the Orellan. *Megalagus turgidus* increases, *P. burkei* decreases and *P. haydeni* changes the relative proportions of its cheek teeth through the Orellan. A morphologic change can be demonstrated by the presence of the more primitive *P. hemirhizis* from Orella A, specimens of *P. haydeni* from Orella B with roots on upper cheek teeth, and *P. haydeni* from the remainder of the Orellan with none of the primitive features of *P. hemirhizis* or the Chadronian *P. temnodon*.

The replacement of *P. haydeni* by *P. burkei* can also be demonstrated by the relative representation of these species from the Orella C and D levels.

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