Reassessment of Chadrolagus and Litolagus (Mammalia: Lagomorpha) and a New Genus of North American Eocene Lagomorph from Wyoming

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ŁUCJA FOSTOWICZ-FRELIK[1]

ABSTRACT

Lagomorphs from the late Eocene and Eocene-Oligocene transition of North America, apart from the abundant and fairly speciose *Palaeolagus*, are represented by some rare and enigmatic genera, including monospecific *Chadrolagus* and *Litolagus*, of uncertain infraordinal relationship. In this paper new specimens of lagomorphs from the Chadronian and Orellan of Montana and Wyoming are presented. They include *Chadrolagus emryi* from the early Chadronian of the Renova Formation, Beaverhead Basin (Montana), and the late Chadronian of the Dunbar Creek and Cook Ranch Formations (Montana), extending the stratigraphic range of this species to the entire Chadronian interval. Further, previously unreported material, originally collected by M.F. Skinner during his fieldwork in Wyoming (near the Chadronian-Orellan boundary in age), is described and figured. This includes an exquisitely preserved skull of *Litolagus molidens*, and *Limitolagus roosevelti*, gen. et sp. nov., represented by mandibular and dental material from the Chadronian-Orellan boundary. *L. roosevelti* shares many similarities in dental structure with *Chadrolagus,* but its size is close to *Litolagus molidens*. The information provided by newly described material and a revision of the type specimens and topotypic series of *Chadrolagus emryi* and *Litolagus molidens* allow for an extended diagnosis of these taxa and a preliminary phylogenetic analysis of Paleogene North American lagomorphs with *Desmatolagus gobiensis* as an outgroup. The skull of *Litolagus molidens* shows many derived characters: shortening of the palatal bridge and the reduction of its palatine portion, greater skull height, and an increase in the size of the auditory bullae. The greater basicranial angle and relatively

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wider choanae indicate increased cursorial adaptations. A cladistic analysis shows that there is no immediate ancestral relationship between *Chadrolagus* and *Litolagus*, and it supports an advanced phylogenetic position for *Litolagus* closer to Archaeolaginae, suggested by the cranial and dental morphology. *Limitolagus* is related closely to *Chadrolagus* and paraphyly of *Palaeolagus* is strongly suggested, due to a placement of *P. burkei* between *Limitolagus* and the clade composed of *Archaeolagus + Litolagus*.

INTRODUCTION

Stem lagomorphs are an informal group of lagomorphs containing duplicidentates (Lagomorpha and Mimotonidae) outside crown Lagomorpha (Wyss and Meng, 1996; Asher et al., 2005). Among others, they include some members traditionally recognized as belonging to families Leporidae and Ochotonidae. Most often they are placed in a separate family, Palaeolagidae (López Martínez, 2008; Fostowicz-Frelik et al., 2012a,b), erected (as a subfamily) by Dice (1929); recently, Averianov and Lopatin (2005) placed some Eocene Asian taxa (*Aktashmys*, *Gobiolagus*, *Lushilagus*, *Shamolagus,* and *Strenulagus*) in Strenulagidae, but see Fostowicz-Frelik et al. (2012b). Stem lagomorphs are represented from the Early Eocene to the Late Miocene in Asia (Averianov and Lopatin, 2005; Li et al., 2007; Lopatin and Averianov, 2006, 2008; López Martínez, 2008; Rose et al., 2008), from the Early Oligocene to the Late Miocene in Europe (López Martínez, 2008; Fostowicz-Frelik et al., 2012a) and from the Middle Eocene to the Late Miocene in North America (Dawson, 2008).

The Paleogene lagomorphs, unlike closely related mimotonids and eurymylids, have been only occasionally the subject of phylogenetic analysis. A limited number of taxa, mainly North American *Palaeolagus* and, on rare occasions, other genera such as *Desmatolagus*, *Lushilagus*, and *Sinolagomys*, were included in large-scale analyses of Glires relationships (Dashzeveg et al., 1998; Meng and Wyss, 2001; Meng et al., 2003; Asher et al., 2005). McKenna (1982) performed the first comprehensive cladistic analysis of Lagomorpha, which included a number of Paleogene taxa. It utilized 52 characters and 32 fossil and extant taxa of Duplicidentata, including most North American genera known at that time. Recently, Dawson (2008: fig. 17.2) presented a cladistic analysis of extant North American taxa, containing 16 genera.

In the Paleogene of North America, besides more common and widespread *Mytonolagus* (Uintan to Duchesnean; Fostowicz-Frelik and Tabrum, 2009), *Palaeolagus* (Chadronian to Arikareean; Dawson, 2008), and *Megalagus* (Chadronian to Hemingfordian; Dawson, 2008), two rare monotypic genera of restricted spatiotemporal ranges and uncertain phylogenetic relationships stand out. These are small *Chadrolagus emryi* and larger *Litolagus molidens* known only from a few specimens (Prothero and Whittlesey, 1998). They both are fully hypsodont and are characterized by a developmental acceleration of the occlusal dental pattern, which can be perceived as derived and specialized in comparison with other contemporaneous lagomorphs.

Chadrolagus emryi is best known from the middle to late Chadronian of its type locality at the Flagstaff Rim area in Wyoming (Gawne, 1978; Emry and Gawne, 1986) and is the first North American lagomorph whose upper and lower dentition is totally devoid of buccal rootlets (Dawson, 2008). About *Litolagus molidens* from the Chadronian-Orellan transition of Wyo-

ming very little was said; Dawson (1958, 2008) stated that it expresses a mixture of primitive and advanced characters.

The present contribution provides new information on the morphology, phylogeny, and dental evolution of three taxa of the arguably most enigmatic North American Paleogene lagomorphs. First, a revision of the type material of *Chadrolagus emryi* is presented along with a discussion of its known fossil record. Second, a new, exceptionally well-preserved skull of *Litolagus molidens* is described. Such a rare discovery, as regards Paleogene lagomorphs, yields new morphological data for phylogenetic analysis. Furthermore, a reassessment of the lagomorph material collected under supervision of Morris F. Skinner (1906–1989) from the Frick Laboratory of Vertebrate Paleontology in the AMNH results in a description of a new lagomorph genus and species. This Chadronian taxon shares full hypsodonty, among other morphological characters, with *Chadrolagus emryi* and *Litolagus molidens*. Finally, a preliminary phylogenetic analysis based on dental and cranial characters allows for the first reconstruction of Paleogene North American lagomorph relationships below the genus level. Due to newly added morphological characters, it is possible to resolve the position of some extinct taxa, notably of *Chadrolagus* and *Litolagus*, tentatively clustered as sister taxa by Dawson (2008).

MATERIALS AND METHODS

The material discussed herein comes from 14 localities of the late Eocene (early to late Chadronian) and early Oligocene (early Orellan) deposits of Montana and Wyoming (figs. 1, 2), chrons C16n2 to C13n in Prothero and Emry (2004); more detailed geologic information is provided below.

Measurements (figs. 3, 4) were taken using a SYLVAC digital caliper with an accuracy of 0.1 mm for bones and 0.01 mm for teeth. The anatomical terminology follows comprehensive papers by Craigie (1945) and Wible (2007), who in some instances used different terminology, and for general anatomical nomenclature the paper follows Evans (1993). The dental nomenclature is mainly descriptive and follows Meng et al. (2005). The quantitative data were analyzed with JMP 8 package for Windows (SAS Institute Inc., 2008). The list of comparative material is included in appendix 1.

Due to disparities between the sample sizes some of the statistical tests (parametric tests) could not be used in certain instances and so box plots were used to estimate central tendency and variability. Each box plot displays the 10th, 25th, 50th (the median), 75th, and 90th percentiles of variability. The gray box covers the central 50% of the data (the interquartile range). Because all values above the 90th and below the 10th percentile are plotted separately, the box plots are especially useful for displaying outliers. The Kruskall-Wallis nonparametric test (an extension of the Wilcoxon/Mann–Whitney U test of multiple-group comparisons) was used to test the interspecific differences, because it does not require equal sample sizes and normal distribution of data.

The phylogenetic position of the newly described species within stem lagomorphs was evaluated by cladistic analysis. The data matrix (appendix 2) is composed of 44 characters and 11 strictly fossil taxa. The data set was analyzed using equally weighted parsimony with TNT v. 1.1 (Goloboff et al., 2008).
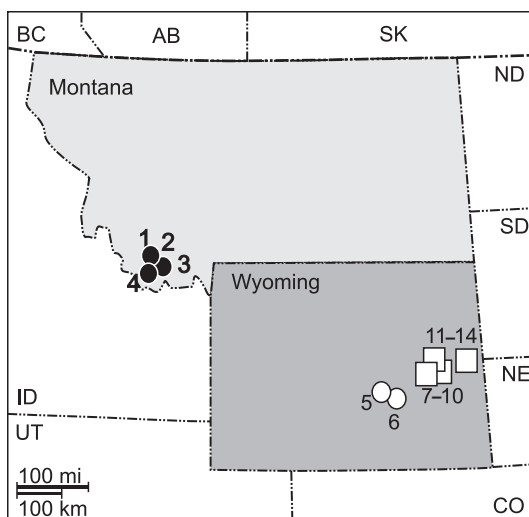
FIG. 1. Map of study area with abbreviated collection repositories in parentheses (based on Asher et al., 2002). **1,** McCarty's Mountain (CM, BMUW); **2,** Pipestone Springs area (CM); **3,** Little Spring Gulch (CM); **4,** 10N highway (CM, UMVC); **5,** Bates Hole (AMNH); **6,** Flagstaff Rim (USNM); **7,** Reno Ranch (AMNH); **8,** Hermann Wulff Ranch (AMNH); **9,** unnamed locality 2 mi NE of Indian Creek (AMNH); **10,** unnamed locality six to eight miles SE of Douglas (AMNH, LACM); **11,** Seaman Hills (AMNH); **12,** Lower Spring Draw (AMNH); **13,** Boner Brothers' Ranch (AMNH); **14,** Jim Christian Hill (AMNH). Localities with *Chadrolagus emryi* indicated by circles, the remainder by squares. Black marks exclusively Chadronian localities, white, localities with a sediment series including the Chadronian-Orellan transition. Standard abbreviations for U.S. states and Canada provinces.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, NY
ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, PA
BMUW	Burke Museum of Natural History and Culture, University of Washington, Seattle, WA
CM	Carnegie Museum of Natural History, Pittsburgh, PA
FH	Fort Hays State University Museum, Hays, KS
FMNH	Field Museum of Natural History, Chicago, IL
LACM (CIT)	Natural History Museum Los Angeles County (previously: Collection of Vertebrate Paleontology of the California Institute of Technology), Los Angeles, CA
UMVC	University of Montana Paleontology Center, Missoula, MT
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.

Localities

The new material studied herein comes from 12 localities in Chadronian and Chadronian/Orellan deposits of southwest Montana and southeast Wyoming (fig. 1). McCarty's Mountain in the Beaverhead Basin is the oldest of all localities in Montana described in this paper, and has the longest history of exploration, being discovered by Earl Douglass in July 1903 (Tabrum et al., 2001). It includes an 850 ft thick sequence, originally divided by Douglass into successive layers designated Q to Z. The sequence crops out over an area of approximately 0.25 mi² in section 28, T4S R8W in Madison County, about 5 mi south-southeast of McCarty's (now McCartney) Mountain and north of the Big Hole River (Tabrum et al., 1996; Tabrum et al., 2001). The locality was included in the Renova Formation and the exact time span represented by the sediment series was eventually established as early Chadronian, based on the faunal assemblage (Tabrum et al.,
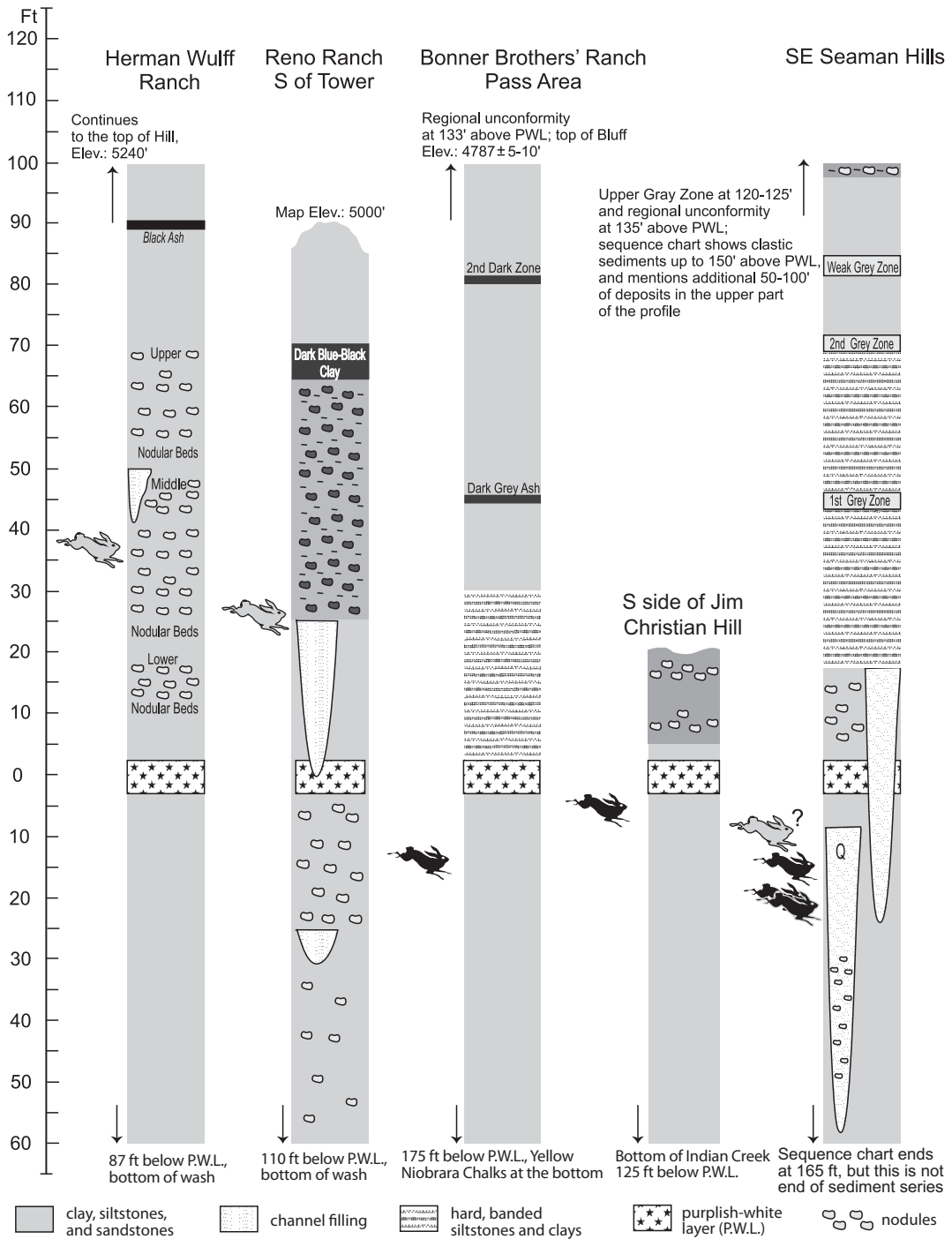
FIG. 2. Generalized stratigraphic sections of the White River Formation in SE Wyoming (Douglas and Lusk areas), showing distribution of *Litolagus molidens* (marked as gray rabbit) and *Limitolagus roosevelti*, new species (marked as black rabbit) in the sediment series near the Eocene-Oligocene boundary. P.W.L. used as correlation level 0; all data after Skinner (ᴍs).
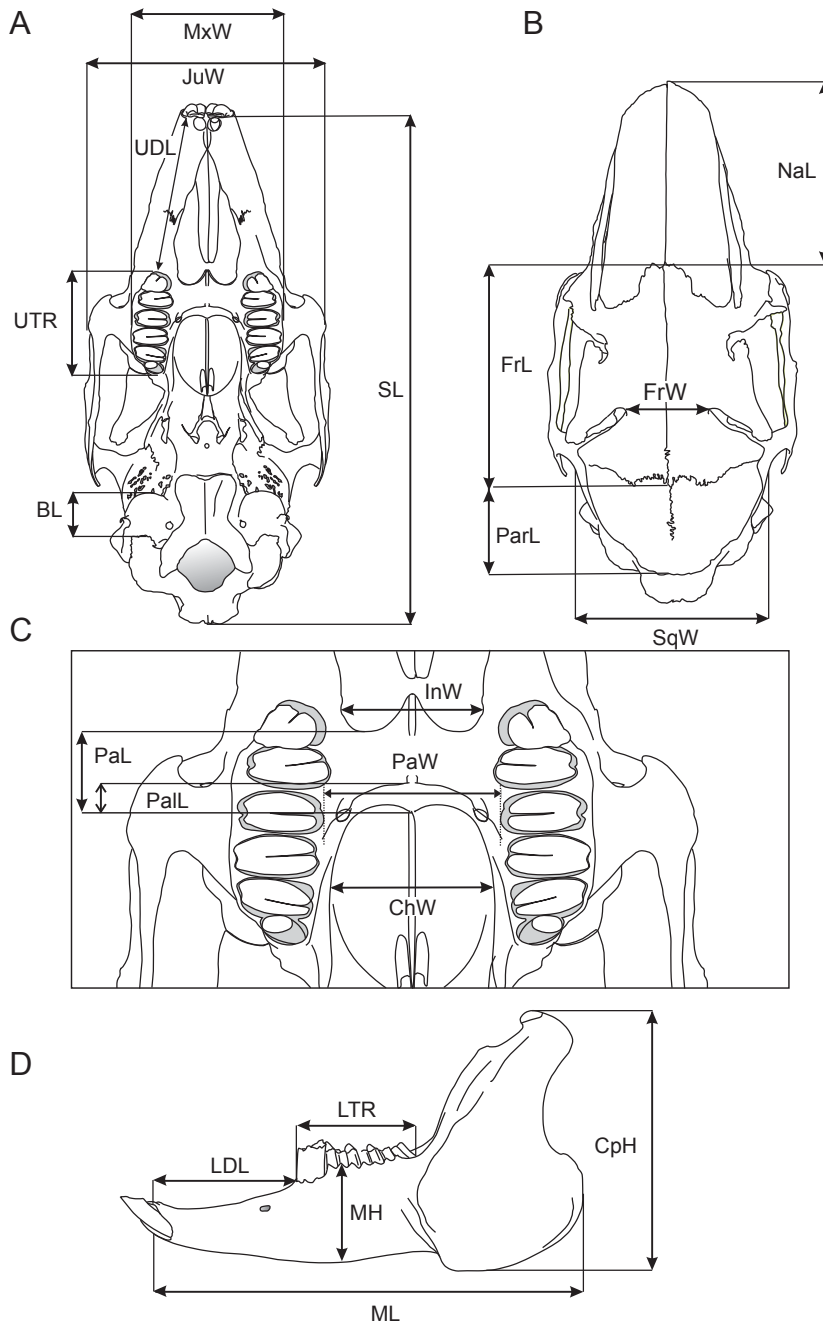
FIG. 3. Skull measurements based on *Lepus*; ventral (**A, C**, closeup of palatine region), and dorsal (**B**) views of cranium, and mandible in lateral view (**D**). Abbreviations: **BL**, bulla length; **ChW**, choanae width; **CpH**, condylar process height; **FrL**, frontal length; **FrW**, minimal frontal width; **InW**, distal incisive width; **JuW**, jugal width of the skull; **LDL**, lower diastema length; **LTR**, lower toothrow length; **MH**, mandible height; **ML**, mandible length; **MxW**, maxillar width of the skull (at alveolar processes of maxilla); **NaL**, nasal length; **PaL**, hard palate length; **PalL**, palatine length; **ParL**, parietal length; **PaW**, palate width (measured between tooth row at the level of P4/M1); **SL**, skull length; **SqW**, squamosal width of the skull; **UDL**, upper diastema length; **UTR**, upper toothrow length.

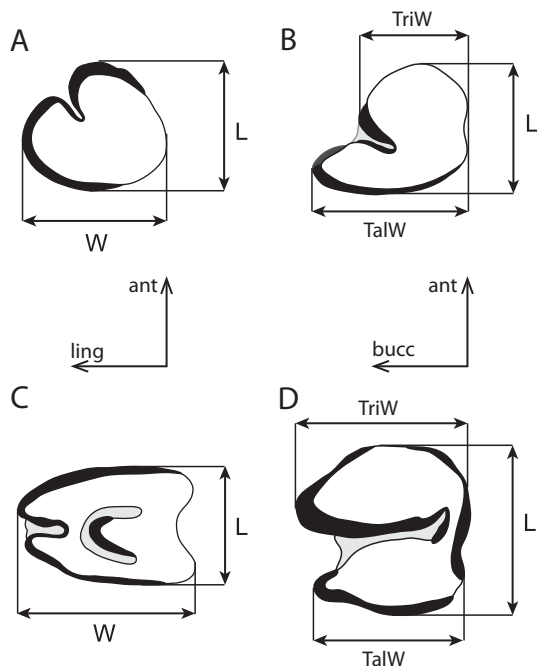FIG. 4. Tooth measurements (occlusal surface). P2 (**A**), p3 (**B**), P3–M2 (**C**), and p4–m3 (**D**). Abbreviations: **ant,** anterior direction; **bucc,** buccal direction; **L,** length; **ling,** lingual direction; **TalW,** talonid width; **TriW,** trigonid width; **W,** width.

1996, 2001; Tabrum and Fostowicz-Frelik, 2009).

The Pipestone Springs area in Jefferson County, Montana, includes three small local faunas: the Pipestone Springs Main Pocket, Pipestone Springs Fence Pocket, and Little Pipestone Creek. The first two local faunas are dated to the middle Chadronian, while Little Pipestone Creek is considered to be slightly younger, middle to early late Chadronian (Tabrum et al., 2001; Dawson, 2008; Janis et al., 2008). The Pipestone Springs area lies in the Jefferson Basin and the sediments are part of the Climbing Arrow Member of the Renova Formation. The Main Pocket of Pipestone Springs is one of the classic localities discovered and studied by Douglass (1901) and is the type locality for *Palaeolagus temnodon*.

Two other localities in southwest Montana, 10N locality of the Dunbar Creek Formation and Little Spring Gulch local fauna, which is regarded as coming from the lowest part of the Cook Ranch Formation, are of late Chadronian origin (Tabrum et al., 2001). The material from the 10N area was collected at several exposures located on the east side of U.S. Route 287 (formerly U.S highway 10N) in the Three Forks Basin, near the connection with Interstate 90 (Tabrum et al., 2001; Asher et al., 2002). The fossiliferous beds of Little Spring Gulch crop out on the north side of the gulch in the Sage Creek Basin, southwestern Montana, and are located a few miles north of the Cook Ranch type area, NE of Lima (Tabrum et al., 1996, 2001; Prothero and Emry, 2004).

The eight localities in Wyoming that yielded the new specimens described here, are located in the vicinity of Douglas, Converse County (Reno Ranch, south of tower, Herman Wulff Ranch, and an unnamed locality 8 mi SE of Douglas) and Lusk, Niobrara County (Bonner brothers' Ranch–Pass area, Seaman Hills, S side of Jim Christian Hill, Lower Spring Draw, and an unnamed locality 2 mi NE of Indian Creek), the classic area of the Frick Laboratory expeditions led by Morris Skinner.

The specimens were recovered during the 1953–1963 field seasons, according to Skinner's field journal (Archives of the Department of Paleontology, AMNH). They all come from the upper Chadronian and the Chadronian-Orellan transition part of the White River Formation sequence in that area (Emry et al., 1987; Evanoff et al., 1992; Prothero and Emry, 2004).

The detailed field journals kept by Skinner give an exact position of each finding with reference to a so-called persistent white layer (see fig. 2), otherwise known as "purple-white layer" of Schultz and Stout (1955, 1961), "tuff 5" of Evanoff (1990), or "Upper Purplish White layer" of Zanazzi et al. (2009), and dated by the $^{40}Ar/^{39}Ar$ method to 33.7 ± 0.7 Ma (Evanoff et al.,

1992), which falls within the interval of the Eocene/Oligocene boundary (Prothero and Emry, 2004). Evanoff et al. (1992) give correlations for some localities studied herein, while others were approximately correlated on the basis of Skinner's unpublished material (Skinner, ms).

The stratigraphy and fauna of the Flagstaff Rim and Bates Hole areas in Wyoming, which yielded the type series of *Chadrolagus emryi*, were described in detail by Emry (1973, 1992), Gawne (1978), and Emry and Gawne (1986), who established the age of these remains as Middle Chadronian (see also Prothero and Emry, 2004). The fauna from the Pipestone Springs area used for comparison is of middle Chadronian age (Tabrum et al., 2001; Prothero and Emry, 2004).

SYSTEMATIC PALEONTOLOGY

Lagomorpha Brandt, 1855
Palaeolagidae Dice, 1929
Chadrolagus Gawne, 1978
Chadrolagus emryi Gawne, 1978

Type Species: *Chadrolagus emryi* Gawne, 1978, by monotypy.

Holotype: AMNH F:AM 99106. Partial skull with palate and both alveolar processes of maxilla with teeth present (right tooth row complete, left P2–M2; figs. 5, 6E, table 1) and right and left mandible with incisors (the right one broken) and p3–m3 (figs. 7, 8E).

Newly Referred Specimens: 10N locality No. 2, Dunbar Creek Formation, Montana: CM 78302, fragment of left maxilla with P2–M2; CM 78348, fragment of right maxilla with P3–M1; CM 78303, fragment of left maxilla with P2–M1; CM 78342, fragment of right premaxilla with dI2; CM 78320, fragment of right maxilla with P2–P4; CM 78332, fragment of left maxilla with M1–M2; CM 78312, right P3; CM 78318, right P4; CM 78311, CM 78321, CM 78330, left M1; CM 78313, CM 78298, right M1; CM 78308, CM 78310, damaged M1; CM 78300, CM 78345, CM 78326, left M2; CM 78344, CM 78349, CM 78309, CM 78329, CM 78316 (juv.), right M2; MPUM 8404/MV8007, fragment of left mandible with p3–p4; UMVC 8405/MV8007, fragment of left mandible with p3–m2; UMVC 8406/MV8007, fragment of right mandible with p3–p4; CM 78305, right mandible with complete cheek dentition; CM 78336, left mandible with complete cheek dentition; CM 78306, fragment of juvenile right mandible with p3 and m1–m2; CM 78347, fragment of left mandible with di2 and p4–m2; CM 78324, fragment of left mandible with p4–m1; CM 78304, fragment of left mandible with p4–m2; CM 78339, fragment of right mandible with m1–m3; CM 78296, fragment of left mandible with m1–m2; CM 78337, fragment of right mandible with m1–m2; CM 78327, fragment of right mandible with m1–m2; CM 78338, fragment of left mandible with m1–m2; CM 78295, juvenile right p3; CM 78343, CM 78334, CM 78301, right p3; CM 78314, CM 78319, CM 78317, CM 78322, CM 78350, right p4 CM 78325, left p4, CM 78335, left p4 or m1; CM 78340, CM 78346, right m1; CM 78315, juvenile right m2; CM 78341, CM78351, left m2. 10N locality No. 6: CM 78353, fragment of left mandible with m2–m3. Little Spring Gulch, Cook Ranch, Montana: CM 78927, right M1–M2 associated; CM 78931, right P2; CM 78932, right P3; CM 78943, left P3; CM 78935, right P4; CM 78928, CM 78944, CM 78929, right M1; CM 78936, right M2; CM 78937, right p3; CM 78945, CM 78938, left p4; CM 78940, right m1; CM 78941, CM 78930, left m1; CM 78946, m1 or m2; CM 78942, left m2; CM 78939, CM 78947, right m2. McCarty's Mountain, Montana: BMWU 38535, right P4; BMWU 40750 left M1; BMWU 38577, upper molar; BMWU 38613, left p3; BMWU 38576, m1.

Revised Diagnosis: Small, fully hypsodont lagomorph, smaller than most Eocene-Oligocene lagomorphs, except *Palaeolagus primus*, *Mytonolagus wyomingensis*, and *Palaeolagus burkei*.
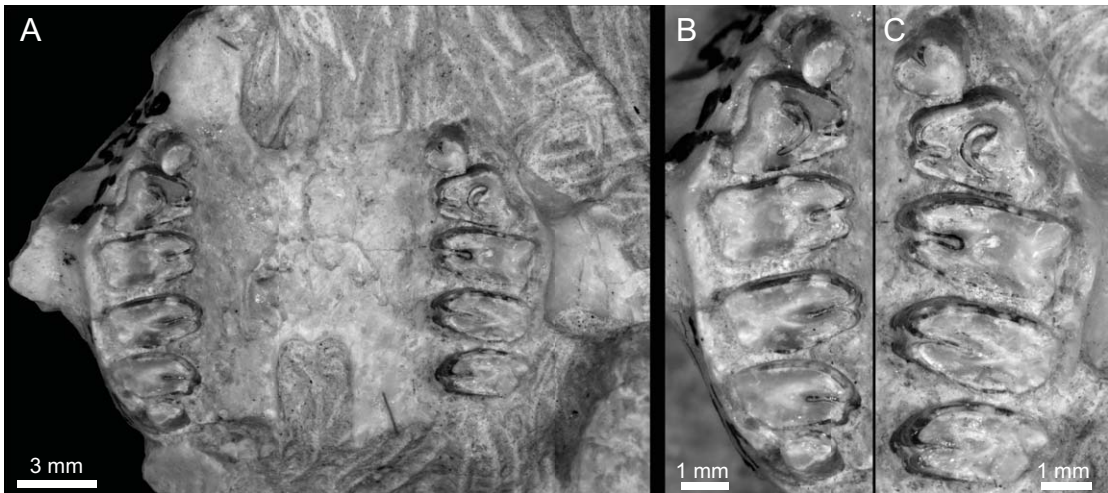
FIG. 5. Skull of *Chadrolagus emryi* (holotype, AMNH F:AM 99106) from Bates Hole, Flagstaff Rim area, Natrona Co., Wyoming. **A,** ventral view; **B,** right tooth row (P2–M3); **C,** left tooth row (P2–M2), both in occlusal views.

FIG. 6. Ontogenetic development of the upper dentition (occlusal surface) in *Chadrolagus emryi* from type locality at Flagstaff Rim, Wyoming. **A,** left P2–M3 (AMNH F:AM 99108); **B,** left P2–M3 (AMNH F:AM 99107); **C,** left P2–M2 (AMNH F:AM 99112); **D,** left P3–M2 (AMNH F:AM 99114); **E,** left P2–M2, and right M3 in reversed view (AMNH F:AM 99106); **F,** right P2–M2 (AMNH F:AM 99111) (reversed view). **A–C,** light wear stages; **D–E,** moderate wear stages; **F,** heavily worn stage (senile).

TABLE 1. Measurements of cranial and mandibular elements of the topotypic sample of *Chadrolagus emryi*. Approximate values italicized.

Skull measurement	AMNH F:AM 99106 (holotype)	AMNH F:AM 99107	AMNH F:AM 99108	AMNH F:AM 99109
UDL	–	11.2	–	10.2
UTR	9.9	9.9	9.9	–
InW	–	3.5	*3.9*	3.2
MxW	15.1	14.2	14.5	13.5
PaW	7.7	7.1	7.5	6.8
ChW	2.7	2.1	2.3	2.2
PaL	6.6	7.4	6.9	6.4
PalL	3.4	4.8	4.0	3.2
NaL	–	–	–	12.8
FrW	–	–	7.5	–
LDL	L: *6.6*/R: *6.7*	L: 7.9/R: 8.0	–	–
LTR	L: 10.5/R: 10.0	–	–	–
MH	L: 7.8/R: 7.6	–	–	–

Chadrolagus emryi has stronger tapered muzzle than *Megalagus* and any *Palaeolagus* species except *P. hypsodus*, and has shorter incisive foramen than those genera, ending at the anterior margin of P2. Differs from *Megalagus*, *Mytonolagus*, and *Palaeolagus* in bilobate, mediolaterally compressed P2, bilobate dP2, shorter lower incisor reaching p3/p4 level, long and persistent hypostriae, and in early formation of lingual bridges in the lower premolars and molars, and quick obliteration of the crescents and buccal cusps at the upper teeth. *Chadrolagus* differs further from *P. burkei* in smooth hypostriae on P3 and P4 without any indentations in the posterior wall, earlier closure of the crescent valley of P3 but shorter lingual lobe of P3, and axes of the trigonid and talonid of p3 perpendicular to the sagittal plane. *Chadrolagus* differs from *Litolagus* in considerably smaller size. Further, it differs in longer palate with dominating palatine portion, zygomatic processes of the maxillae more extended laterally, frontal process of maxilla strongly bent backward, orbits not enlarged, and more level and broad squamosal zygomatic processes. Additionally, it differs from *Litolagus* in persistent anterior reentrant of P2, less molarized P3, shallower hypostria unevenly deep on different loci, formation of the lingual lake on p3, and proportionally narrower talonid of p3.

Type Locality: "Divide area between the south fork of Lone Tree Gulch and Blue Gulch, Flagstaff Rim area, . . . Natrona County, Wyoming" (Gawne, 1978); between 10.5 m below Ash D to 12.0 m above Ash G in the generalized section of Emry (1973).

Stratigraphic and Geographic Distribution: Late Eocene, early to late Chadronian of Wyoming and Montana. Confirmed occurrences include: the White River Formation in the Flagstaff Rim area, Wyoming (between ashes C–H, Gawne, 1978; Emry and Gawne, 1986; Dawson, 2008), McCarty's Mountain (Renova Formation), Little Spring Gulch (Cook Ranch Formation), and 10N (Dunbar Creek Formation), all in Montana.

Description and Comparisons: The newly described material consists mainly of jaw fragments and isolated teeth. These previously unreported specimens, especially the isolated teeth,

FIG. 7. Mandibles of *Chadrolagus emryi* (holotype, AMNH F:AM 99106). **A–C,** left mandible body with p3–m3, in buccal (A) and lingual (B) views; **C,** tooth row magnified, in occlusal view. **D–F,** right mandible body with p3–m3, in buccal (E) and lingual (F) views; **D,** tooth row magnified, in occlusal view.
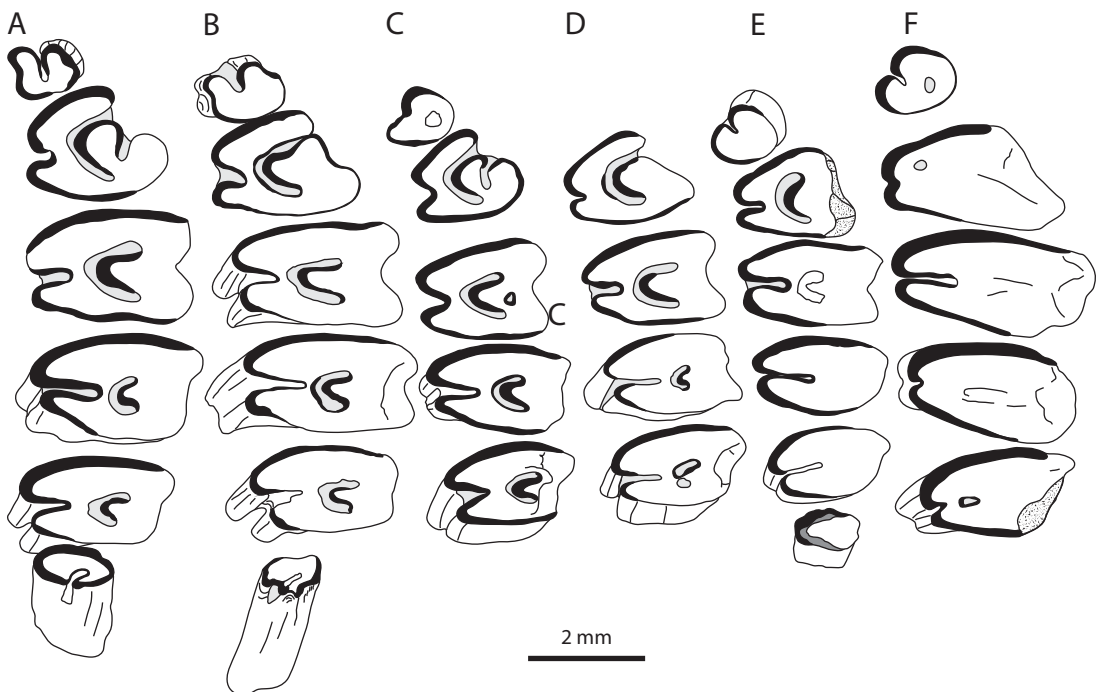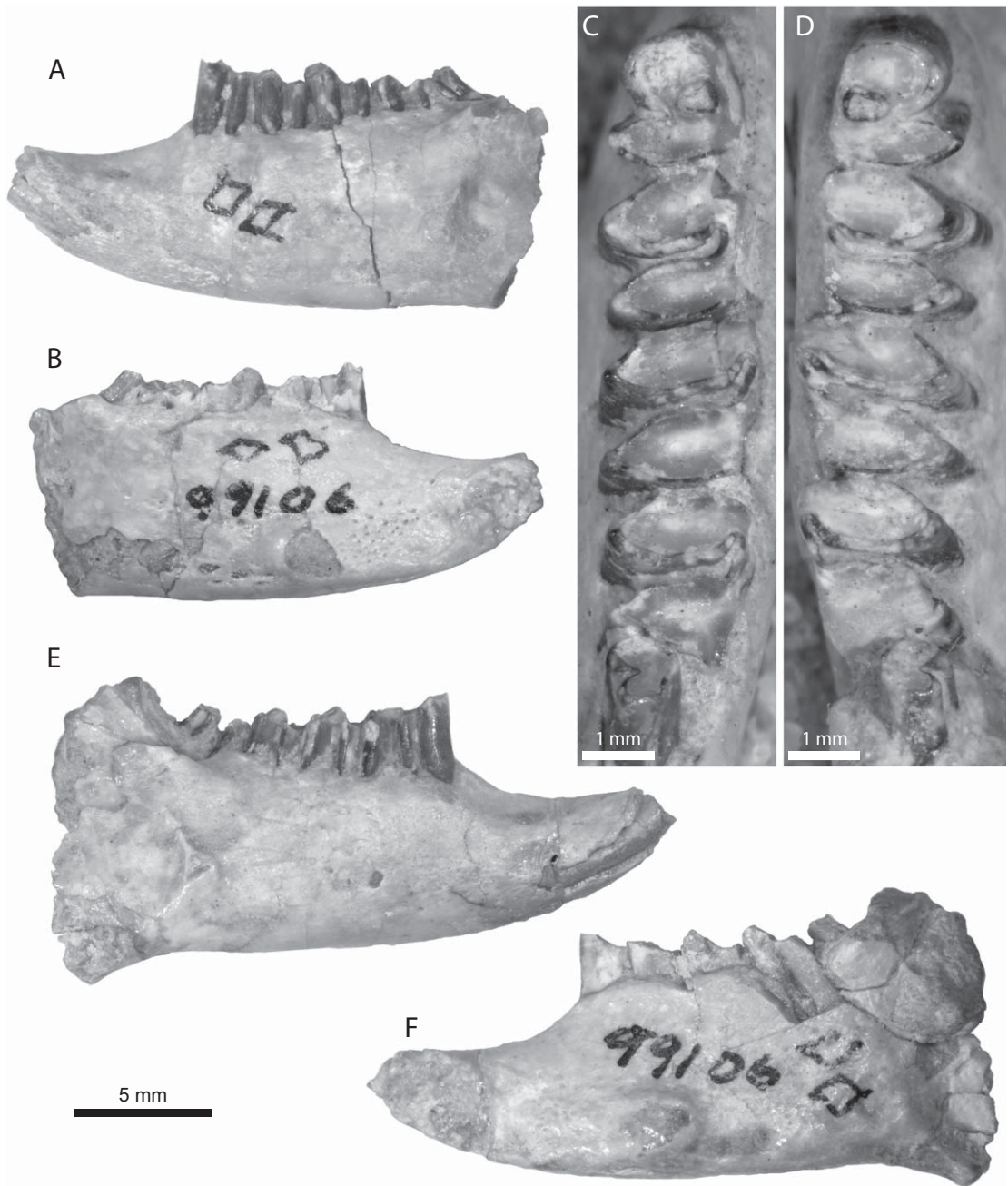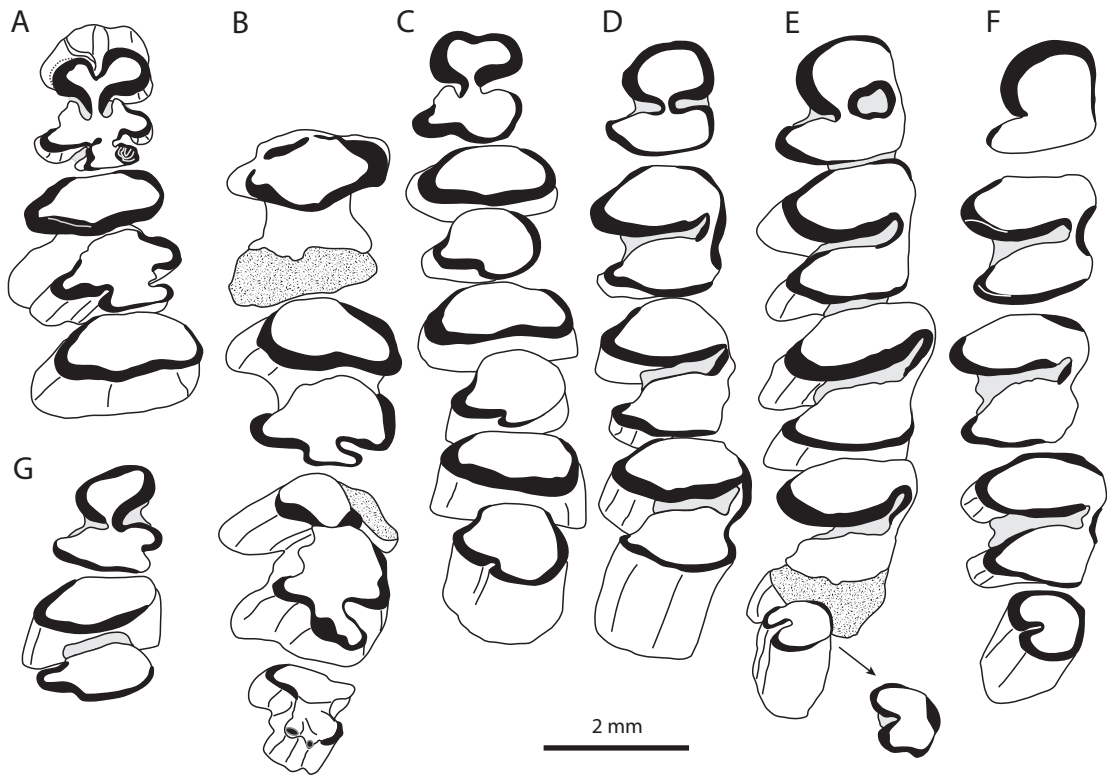
FIG. 8. Ontogenetic development of the lower dentition (occlusal surface) in *Chadrolagus emryi* from type locality at Flagstaf Rim, Wyoming. **A,** left p3–m1 trigonid (AMNH F:AM 99127), juvenile wear stage; **B,** right p4–m3 (AMNH F:AM 99118, reversed view), juvenile wear stage; **C,** left p3–m2 (AMNH F:AM 99120), light wear stage; **D,** left p3–m2 (AMNH F:AM 99119), light wear stage; **E,** right p3–m3 (AMNH F:AM 99106, reversed view), moderate wear stage; **F,** left p3–m3 (AMNH F:AM 99123), heavy wear stage; **G,** left p3–p4 (AMNH F:AM 99115), light wear stage.

were helpful in elucidation of the variability of the wear pattern and allowed study of some aspects of morphology usually hidden in better-preserved jaw material. Moreover, some new observations, measurements (table 1), and photographs of the revised cranial material of the topotypic sample were included to complement the description given by Gawne (1978).

The skull fragments described by Gawne (1978) include two complete rostra (fig. 9), one of them of a juvenile specimen (AMNH F:AM 99109; fig. 9A–C), and a partial skull with the frontals and partly preserved parietals (fig. 10). The skull roof is flat and resembles that of *Palaeolagus haydeni,* but all cranial elements are smaller (Gawne, 1978). The rostrum is relatively narrow (fig. 9) and tapers more strongly than in *P. temnodon* and *P. haydeni,* and it is more elongated in relation to the upper tooth row than in those two species (table 2). The nasals are not distorted in the studied specimens; they narrow anteriorly and raise, forming a relatively high and level roof of the nasal cavity.

The frontal spine is short and wedged between the nasal bones, forming an irregular triangle, as in *Palaeolagus* and other studied genera, but reaches less anteriorly. The frontal processes of the premaxilla end anteriorly to the posteriormost tips of the nasals, as in *Palaeolagus*. The frontals are best preserved in AMNH F:AM 99108 (fig. 10C). They are ornamented by shallow pitting,
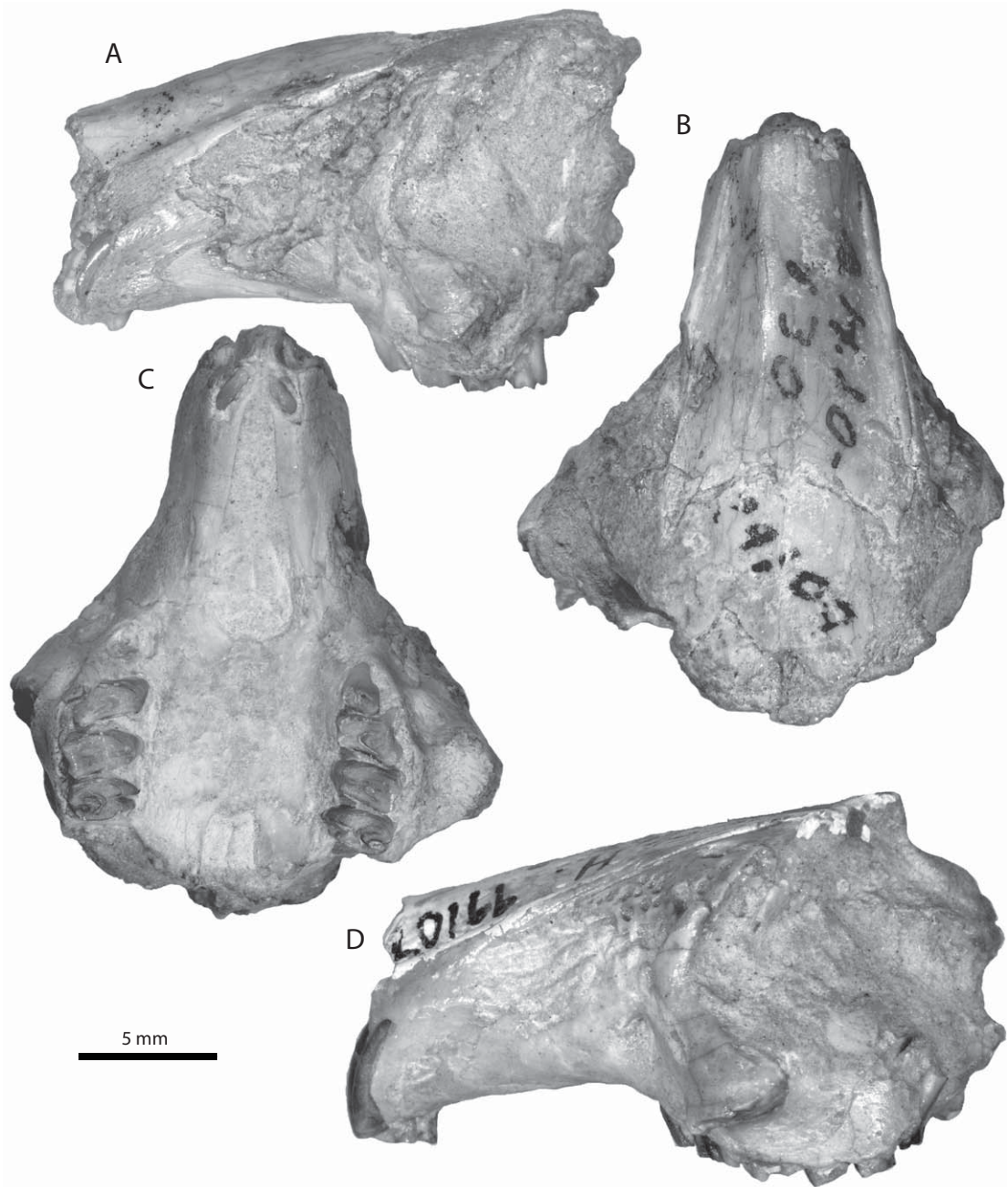
FIG. 9. Anterior skull fragments of *Chadrolagus emryi* from Bates Hole, Natrona Co. Wyoming. **A–C,** juvenile specimen (AMNH F:AM 99109) with dP2–dP4 in lateral (A), dorsal (B), and ventral (C) views; **D,** AMNH F:AM 99107, in lateral view.

which runs along the lateral margins and both sides of the anterior part of the frontal suture, as in *P. haydeni*. The ornamentation is lacking in a juvenile (still with milk dentition) specimen, AMNH F:AM 99109 (see Gawne, 1978: fig. 3). The lateral margins of the frontals in *Chadrolagus* form weakly developed supraorbital processes. The frontoparietal suture is almost straight.
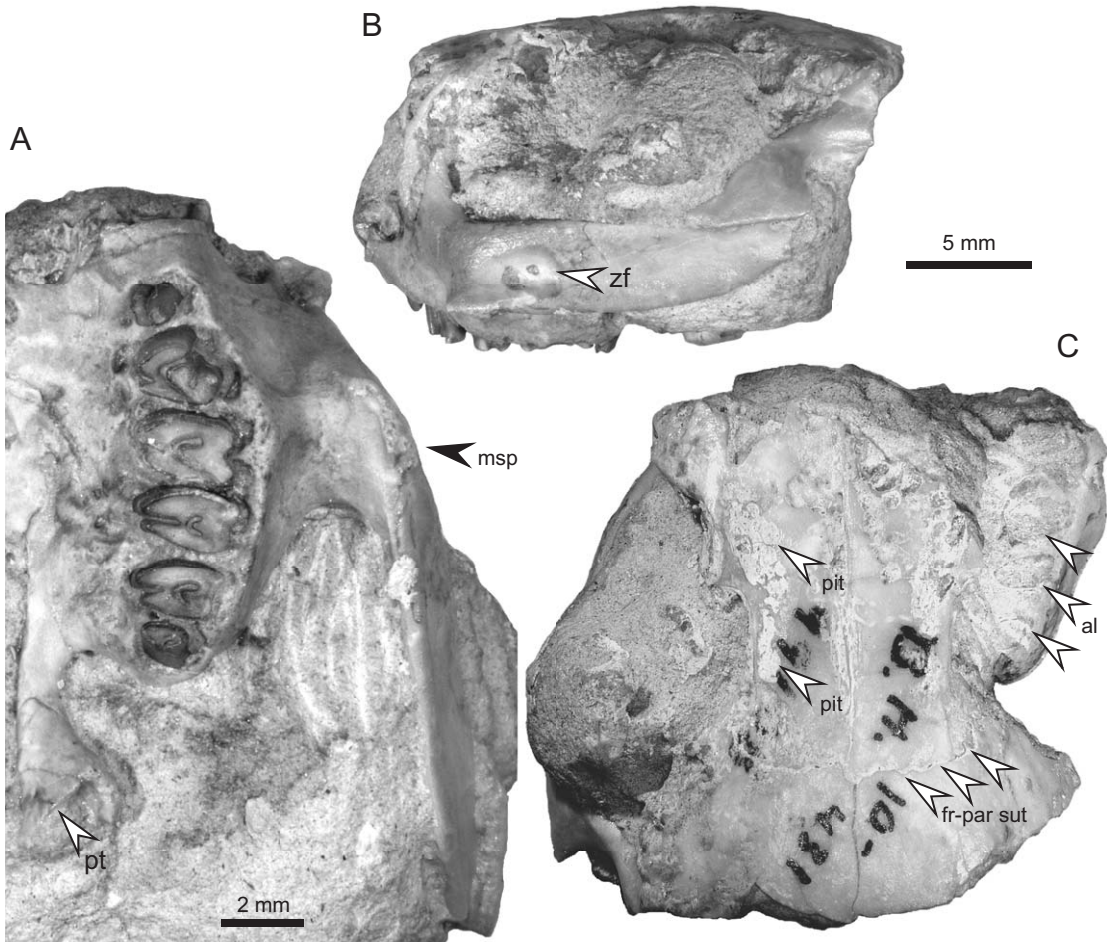
FIG. 10. Partial skull of *Chadrolagus emryi* (AMNH F:AM 99108) from the central fork of Blue Gulch, Bates Hole, Natrona Co., Wyoming. **A,** left side fragment in palatal view, note large and rotated pterygoids; **B,** lateral view; **C,** dorsal view; note pitting of the frontals. Abbreviations: **al,** alveoli; **fr-par sut,** frontoparietal suture; **msp,** masseteric spine; **pit,** pitting; **pt,** pterygoid; **zf,** zygomatic fossa.

The hard palate of *Chadrolagus* is slightly longer than in *Palaeolagus*, spanning the posterior margin of the incisive foramen (anterior to the P2 alveolus) and the anterior brim of the choanae, which falls at the level of M1/M2. The palatine portion of the hard palate is as large as in *Mytonolagus*, *Megalagus*, *Palaeolagus temnodon,* and *P. haydeni* (Dawson, 1958; Gawne, 1978; Fostowicz-Frelik and Tabrum, 2009). It has two pairs of large palatine foramina; its anterior margin is either sharply triangular or rounded, and reaches the level of P3 alveolus (Gawne, 1978).

The ventral view of AMNH F:AM 99108 shows the well-developed, long, and relatively massive pterygoids, with the ectopterygoid crests folded laterally, similar to *Palaeolagus haydeni*. The zygomatic arch is shaped as in *Palaeolagus temnodon* and *P. haydeni*, although the anterior roots formed by the maxilla are slightly less expanded laterally. Gawne (1978: 1106) stated that, in ventral view, the anterior margin of the anterior root of the zygomatic arch lies opposite the

TABLE 2. Comparison of the cranial and mandibular indices for selected species of North American lagomorphs. For abbreviations, see figure 3; number of specimens in parentheses.

Species	UDL/ UTR	PalL/ PaL	PaW/ ChW	PaL/ UTR	BL/ UTR	MH/ LTR	LDL/ LTR
Archaeolagus ennisianus		(1) 0.5	(1) 2.2	(1) 49.6	(1) 1.1	(1) 0.7	(1) 0.8
Chadrolagus emryi	(1) 1.1	(4) 0.6	(3) 3.2	(3) 71.3		(8) 0.7	(3) 0.7
Limitolagus roosevelti, sp. nov.						(4) 0.8	
Litolagus molidens	(1) 1.1	(1) 0.4	(1) 2.8	(1) 48.4	(1) 1.2	(3) 0.9	(1) 0.9
Megalagus brachyodon						(7) 0.7	(1) 0.7
Megalagus turgidus	(1) 1.0	(1) 0.6	(1) 2.3	(1) 64.1		(2) 0.7	
Palaeolagus burkei	(2) 1.1	(3) 0.5	(3) 2.9	(5) 60.7	(2) 1.2	(10) 0.8	(1) 0.8
Palaeolagus haydeni	(3) 0.9	(3) 0.6	(3) 3.3	(3) 60.3	(3) 1.0	(3) 0.7	(2) 0.7
Palaeolagus intermedius	(1) 1.0	(1) 0.6	(1) 2.4	(1) 50.4	(1) 0.7	(8) 0.8	(3) 0.8
Palaeolagus temnodon	(2) 0.7				(2) 0.9	(9) 0.7	(4) 0.6

anterior margin of P4, which resembles *Mytonolagus* rather than *Palaeolagus*. Taking into account the studied specimens of *Chadrolagus* and comparative material of *Palaeolagus* (appendix 1), as well as recently described new material of *Mytonolagus* (Fostowicz-Frelik and Tabrum, 2009), it can be said that the position of the anterior zygomatic root in all three genera is variable. In three *Chadrolagus* specimens of the topotypic sample and the maxilla fragment (CM 78303; fig. 11C) from the 10N locality, the anterior margin of the anterior zygomatic root lies laterally to the P3/P4. In *Palaeolagus temnodon* and *P. haydeni*, and in *Mytonolagus ashcrafti* its position slightly varies, from the midlength of P3 to P3/P4. The posterior margin of the anterior root of the zygomatic arch in *Chadrolagus* is placed laterally to the distal margin of P4 alveolus or P4/M1 as in *Palaeolagus temnodon* and *P. haydeni*. The jugal bone has a relatively flat lateral surface with well-pronounced, oval zygomatic fossa (fig. 10B).

The mandible of *Chadrolagus emryi* does not differ markedly from those of *Palaeolagus temnodon* and *P. haydeni*. The relative depth of the mandible body (calculated as MH/LTR) in *C. emryi* is closer to that of *P. haydeni*, which is also a fully hypsodont species, and slightly higher than that of *P. temnodon*. The morphology and size range of the mandibles (fig. 12A–D, table 3) and maxillae fragments (fig. 11C) conform to the type series with the specimens from Montana on average slightly smaller.

The P2 is bilobate and similar to *Palaeolagus haydeni* and *P. burkei*. It is simplified in morphology in comparison with other contemporaneous lagomorphs, especially *Mytonolagus*, which has a well-developed trilobate P2, as well as *P. temnodon*, in which the third (buccal) lobe persists in some individuals relatively long in ontogeny. In specimens of the type series of *Chadrolagus emryi* representing juvenile individuals, there is a very shallow wrinkle at the anterobuccal margin indicating the position of the vestigial fold (figs. 6A, B, 10A, 13A) that, if fully developed, would separate the buccal lobe, as can be observed in young specimens of *Palaeolagus temnodon* and *P. haydeni*. Gawne (1978) noted that the buccal lobe is "absent or greatly reduced" in *Chadrolagus emryi*; thus, it can be safely assumed for the purpose of the character analysis that this species virtually lacks the buccal lobe at any stage of wear in any of the known specimens. On the other hand, in juvenile specimens the lingual lobe has visibly concave lingual margin

TABLE 3. Mandible measurements (in mm) in *Chadrolagus emryi* from Montana. Approximate values italicized; for abbreviations, see figure 3.

Specimen	LDL	LTR	MH
UMVC 8404	7.3		7.4
UMVC 8405		*9.7*	6.8
UMVC 8406	2.2		6.7
CM 78295	6.7		6.7
CM 78304			7.0
CM 78305	7.3	10.0	7.2
CM 78306		10.0	6.7
CM 78327			7.3
CM 78336		9.7	6.9
CM 78337			*7.7*
CM 78347	*5.6*		7.2

and is relatively long and narrow, which was not mentioned in the original description by Gawne (1978). The P2 changes its shape during ontogeny and the lingual lobe becomes round and similar to the central lobe (figs. 6, 11A, B, 13C). Most of the wear stages of P2 in *Chadrolagus emryi* (apart from the juvenile ones) show a highly symmetrical heart-shaped occlusal surface with the central axis, drawn along the anterior fold, directed more lingually than in *Palaeolagus*. The anterior reentrant is persistent and well marked even in strongly worn specimens (figs. 6F, 11B). It is also generally narrow and free of cement.

The dP2 structure is highly progressive as it lacks the buccal lobe and resembles adult P2 rather than the adult P3 at an early stage of wear, unlike in *Mytonolagus* and *Palaeolagus*, and other stem lagomorphs (Tobien, 1986). Gawne (1978: text-fig. 3; fig. 9C) attributed the lack of the buccal lobe in the specimen AMNH F:AM 99109 to its advanced wear; however, reexamination of the specimen indicates that the stage of wear is not so advanced as to justify such an assumption. In particular, the dP2 has a long shaft visible above the alveolus, but also the occlusal pattern of hypostriae and crescents in dP3 and dP4 is well preserved—by virtue of the "short life" of deciduous teeth, these structures disappear very quickly. In addition, because the lingual lobe does not surround the central lobe in any way, as it does in all other species of *Mytonolagus*, *Megalagus,* and *Palaeolagus*, it seems that the structure of dP2 in *Chadrolagus* is different from that observed in other stem lagomorphs and probably represents an advanced state.

The P3 is not fully molarized, the lingual lobe is relatively short and does not reach the buccal margin (Gawne, 1978). Furthermore, the closure of the P3 crescent is delayed in ontogeny, although not so much as in *Palaeolagus burkei*. Nevertheless, the crescentic valley closes after the crescents on other teeth in the row begin to wear out. It is still open when the crescent of M1 is already visibly decreased and that of M2 begins to disintegrate, but has closed when traces of the crescent are almost gone on P4 (fig. 6). There is no specimen of P3 exhibiting a hypostrial lake, both within the type series (Gawne, 1978) and in the new material; thus, it can be assumed that such a structure, frequent in *Palaeolagus temnodon* but not observed in *P. primus* (Emry and Gawne, 1986), does not appear in *Chadrolagus emryi*. The completely worn isolated P3 can be recognized by more strongly bent shaft and asymmetrical shape of the occlusal surface, with posteroloph much wider than the anteroloph (mentioned by Gawne, 1978) and a sharp buccal projection formed by the remains of the transformed buccal lobe (figs. 11D, E, 13D, E). The structure continues at the shaft forming a marked ridge at the buccal side, in the position of a distal root in *Palaeolagus temnodon*.

The other characteristic of the wear pattern in the upper dentition of *Chadrolagus*, not mentioned by Gawne (1978) but frequently observed in the specimens from Montana, is the way the

FIG. 11. Upper dentition and maxilla fragment of *Chadrolagus emryi* from 10N highway locality 2, late Chadronian, Montana. **A,** associated right P2–P4 (CM 78320); **B,** line drawing of P2–M2; and **C,** left maxilla fragment (CM 78303); right P3 in occlusal (**D**) and anterior (**E**) views (CM 78312); **F,** right M1 (CM 78330); right M1 in occlusal (**G**) and distal (**H**) views (CM 78298); **I,** left M1 (CM 78311) in occlusal view; **J,** heavily worn right M2 (CM 78308) in occlusal view; **K,** heavily worn left M2 (CM 78326) in occlusal view; juvenile left M2 (CM 78316) in occlusal (**L**) and distal (**M**) views.
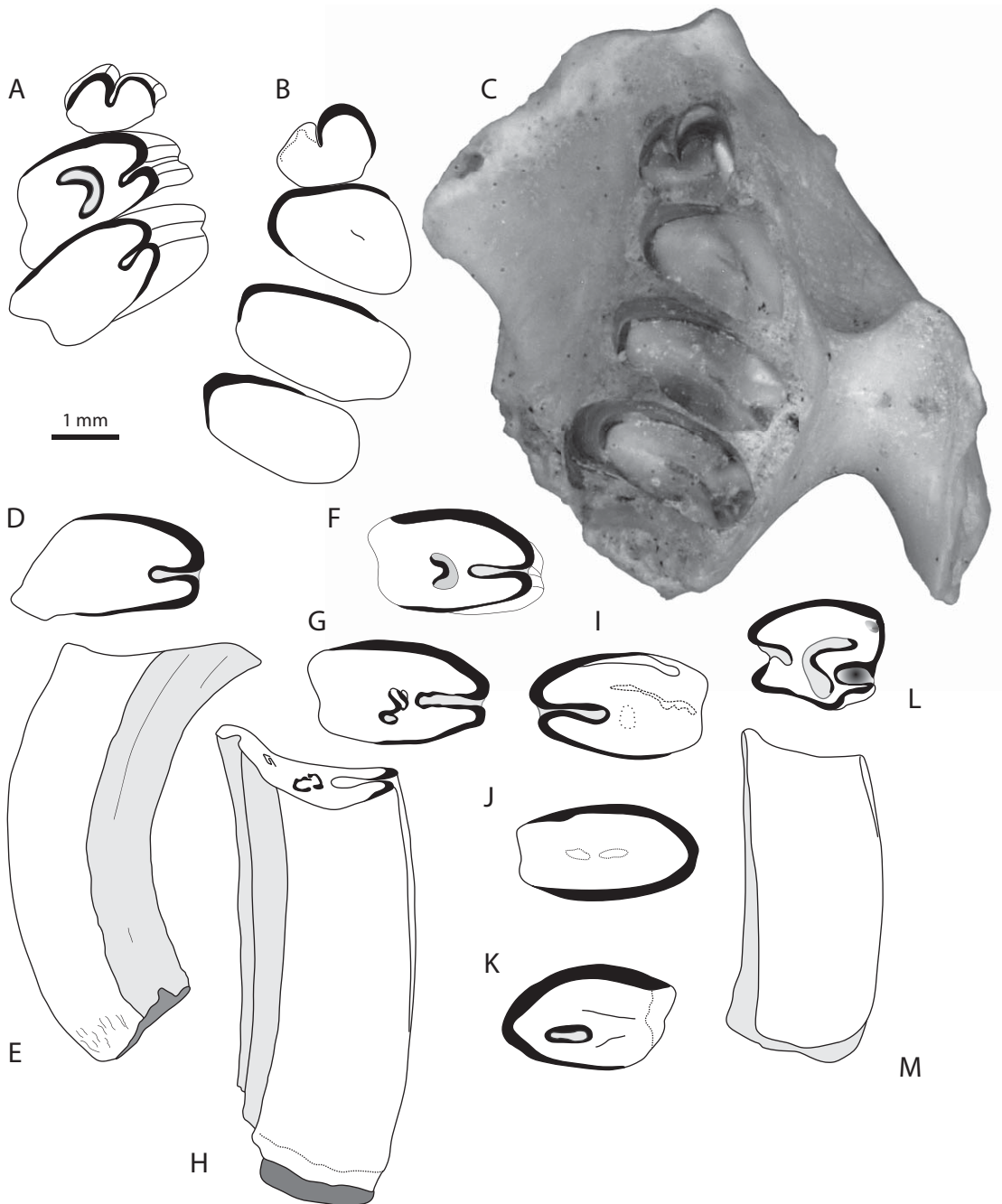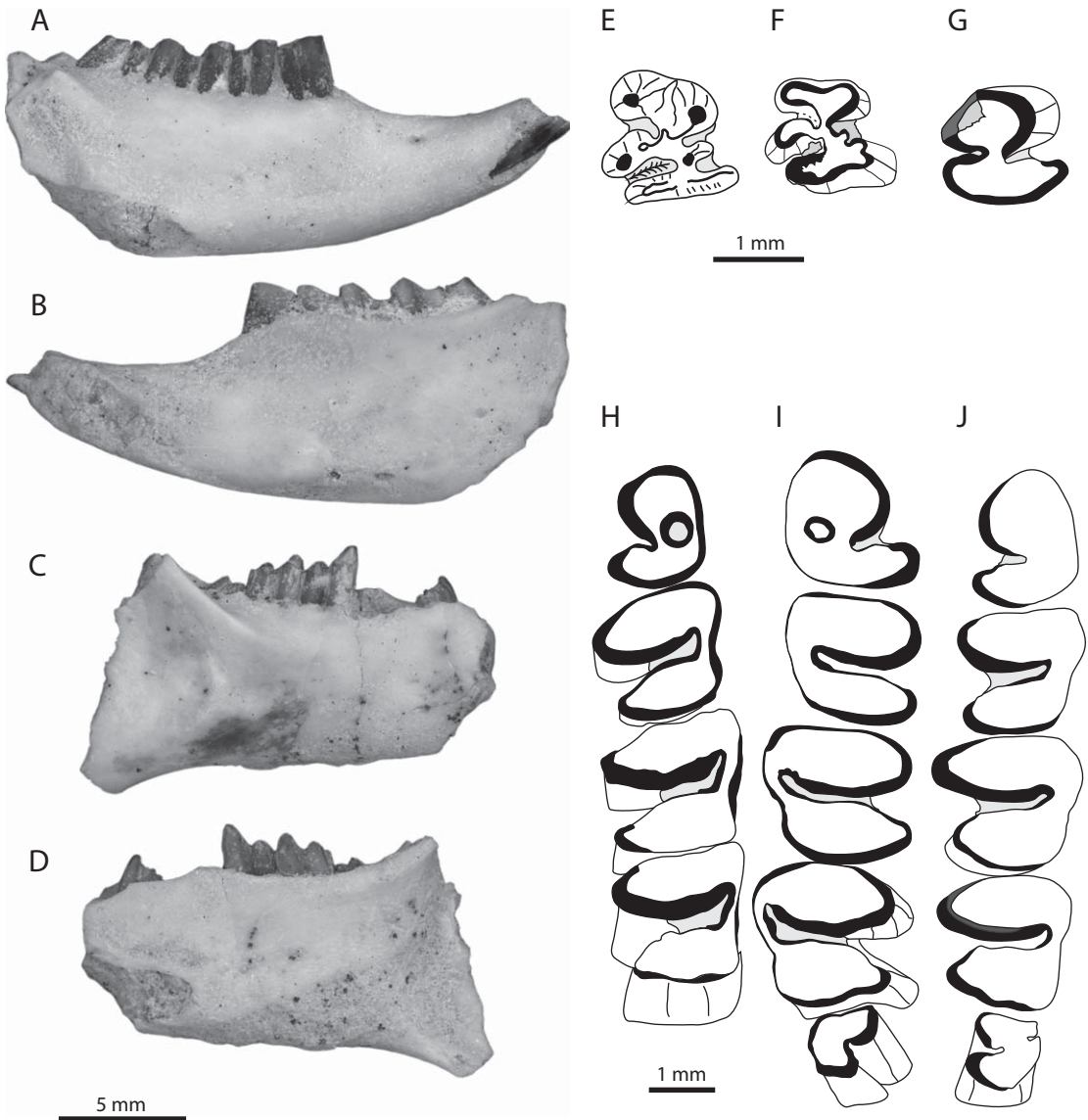
FIG. 12. Lower dentition and mandible fragments of *Chadrolagus emryi* from 10N highway locality 2, late Chadronian, Montana. Right mandible (CM 78305) in buccal (**A**) and lingual (**B**) views; juvenile right mandible (CM 78306) in buccal (**C**) and lingual (**D**) views, with unworn p3 in occlusal view (**E**) and m1–m2. **F,** juvenile right p3 (CM 78295) in occlusal view; **G,** right p3 (CM 78301) in occlusal view, light wear stage; **H,** left tooth row p3–m2 (UMVC 8405/MV 807) in occlusal view, moderate wear stage; **I,** line drawing of p3–m3 (CM 78305) in occlusal view, moderate wear; **J,** left tooth row with p3–m3 (CM 78336) in occlusal view, heavily worn.

crescents of M1 and M2 dissolve. They have a tendency to dissipate into a few smaller lakes creating a chainlike pattern with the lakes connected by a wavy string of enamel, which persist longer, forming buccolingually oriented striae (fig. 11G, I–J). This kind of wear is not observed in *Palaeolagus temnodon* or *P. haydeni*, which instead form round lakes that diminish in size while still

retaining their form. The crescent of M2 breaks up into two elongate lakes in *Mytonolagus* (Fostowicz-Frelik and Tabrum, 2009); however, it does not exactly form the chainlike pattern afterward and the isolated teeth of *Mytonolagus* can be easily distinguished from *Chadrolagus* by the presence of roots, larger curvature, and lower crowns in the former. The heavily worn isolated teeth of *Chadrolagus* with concave, oval occlusal surfaces, unmarked by any structure are quite common among the specimens from Montana, especially from the 10N locality (fig. 11B–D, J).

The lower cheek teeth of *Chadrolagus emryi* are rootless, with the enamel layer on the buccal side stretching to the very base of the tooth. Moreover, the division into two columns, the trigonid and talonid, which is clear on the crown portion, manifests throughout the entire tooth length up to the open root portion, which leaves the pulp chamber divided into two distinct compartments joined only lingually by a thin isthmus (enamel bridge at the occlusal surface). This morphology differs from the structure of the lower teeth of *Palaeolagus temnodon*, which has a more distinct root portion, devoid of the enamel. The single pulp chamber shows bipartite morphology. The only exception to the bipartite morphology of the pulp chamber is p3: in *Chadrolagus* it has one large chamber, whereas in *P. temnodon* it varies from a poorly expressed division into two compartments to a two-root condition, especially in older individuals. Moreover, in ontogenetically old specimens of *Palaeolagus temnodon* the root openings of p3–m2 gently tighten, which indicates a noticeable slowing of the tooth growth, whereas in fully hypsodont *Chadrolagus emryi* the teeth maintain vertical walls and wide root openings regardless of their ontogenetic status.

FIG. 13. Teeth of *Chadrolagus emryi* from Little Spring Gulch, late Chadronian, Montana. Right P2 (CM 78931) in occlusal (**A**), anterolingual (**B**), and ventral (**C**, root) views; left P3 (CM 78943) in occlusal (**D**) and distal (**E**) views; right M1 (CM 78932), in occlusal (**F**) and distal (**G**) views, strong wear; right p3 (CM 78937) in occlusal (**H**) and distal (**I**) views, moderate wear stage.

The morphological development of the p3 occlusal surface is similar in *Chadrolagus emryi* and *Palaeolagus* species, but the timing of the appearance of particular structures is accelerated in *Chadrolagus*. Thus, the specimens showing completely worn p3, without the traces of the lake (figs. 8F, 12J), are more common in this species. Gawne (1978) argued that p3 of *Chadrolagus*
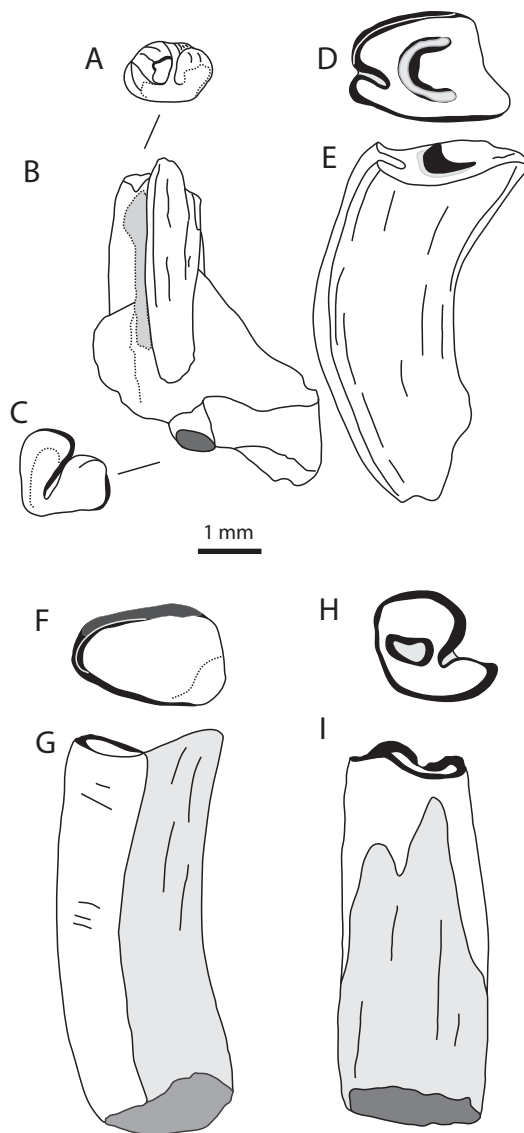
emryi has "larger metaconid than protoconid and [the former] projects farther anteriorly, the reverse condition in *Palaeolagus*." The specimens from the localities in Montana, especially those from the 10N locality, include a representative sample of p3 at different ontogenetic stages (fig. 12E–J). The relative size of the cusps can be best compared in unworn specimens, as even light wear quickly obliterates the original cusp arrangement and produces notable variability of the occlusal surfaces. In two juvenile specimens (one of them unworn) from the 10N locality (fig. 12E, F) the metaconid and protoconid are of similar size, but the metaconid indeed protrudes slightly more anteriorly. Both cusps are divided by a symmetrical deep anterior reentrant characteristic of *Chadrolagus* (Gawne, 1978). A similar, although generally shallower and not so symmetrical groove can be observed in more primitive lagomorphs such as *Tachylagus* (see Storer, 1992) and *Mytonolagus* (Fostowicz-Frelik and Tabrum, 2009), and is occasionally also encountered in *Palaeolagus temnodon* (Wood, 1940: fig. 89; personal obs.).

Reexamination of the topotypic sample revealed that only in specimens AMNH F:AM 99115 and 99121 do the metaconids protrude significantly anteriorly, but they are more or less the same size as protoconids (fig. 8G). Similarly, in specimen AMNH F:AM 99107 the metaconid in both mandibles is positioned slightly farther anteriorly, although that results from the gentle clockwise rotation of the tooth in the tooth row, in comparison with other specimens of *Chadrolagus*. Furthermore, in lightly worn AMNH F:AM 99127 (fig. 8A), the metaconid is indeed larger than the protoconid and its anterior margin is more anteriorly protruded than that of the protoconid, although in AMNH F:AM 99120 both parts seem of equal size (but here the metaconid is less worn and projects higher on the occlusal plane). Concluding, the structure of the p3 trigonid is variable in *Chadrolagus* and dominance of the metaconid over the protoconid in terms of size is not absolute. Although in unworn specimens both cusps tend to be of equal size, the anterior position of the metaconid is observed in most of the specimens, and therefore it can be used in species recognition. At worn stages, the protrusion of the metaconid is equally frequent in *Palaeolagus temnodon* and *Chadrolagus*, which even has a tendency to maintain a flattened anterior margin of p3. The general observation by Gawne (1978: fig. 4) that the length of p3 in *Chadrolagus emryi* changes less during ontogeny than in *Palaeolagus temnodon* is probably related to fully developed hypsodonty; the value of the W/L ratio for p3 does not seem correlated with wear stage in this species, nor is it in *Litolagus molidens* or in the newly described species to any great extent (fig. 14), both having rootless teeth. Moreover, the p3 in *Chadrolagus emryi* is indeed relatively shorter than that of *Palaeolagus temnodon* if larger samples are analyzed (fig. 15), although the difference is not statistically significant, and the ranges of the W/L ratio greatly overlap with *P. temnodon* and the newly described species (fig. 15), especially for some strongly worn specimens from the 10N localities. On the other hand, the teeth of *Chadrolagus emryi* are more frequently flattened at the anterior margin, which is best displayed in moderately worn specimens with large oval lingual lakes or in lightly worn ones that retain open lingual and buccal reentrants (figs. 8D–F, 13H). In *P. temnodon* the anterior margin of p3 tends to be more convex, from lightly through strongly worn stages, and forms rounded anterior tooth edge.

The isolated p3 of both species can be recognized by the higher crown in *Chadrolagus* and the condition of the radical part, showing stronger division in *Palaeolagus temnodon* which may result in the two-root condition. It is worth mentioning that the lake resulting from the closure
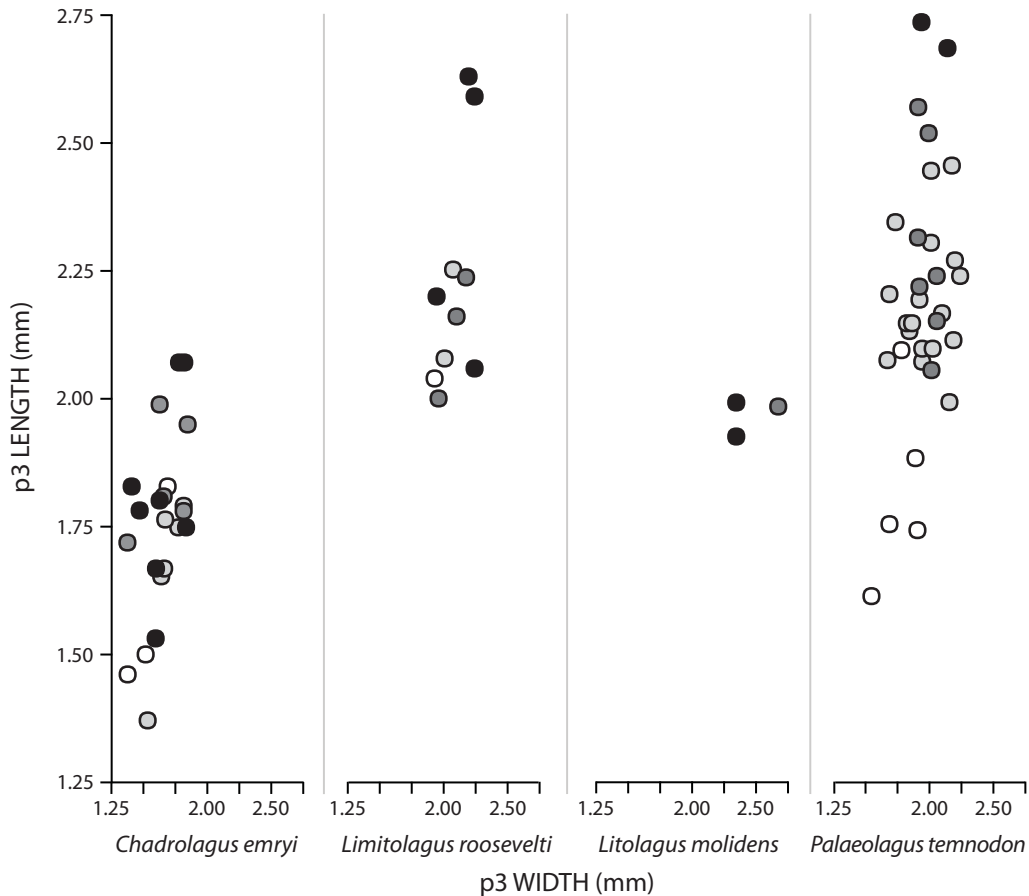
FIG. 14. Changes of p3 length (Lp3) to width (Wp3) related to ontogenetic stage, in lagomorph species across the Chadronian-Orellan boundary. Note virtual lack of interrelation between wear stage and W/L index for *Chadrolagus emryi* (stages well mixed) and strong relationship for *Palaeolagus temnodon*. Circles: white, juvenile specimens; light gray, light wear stage; dark gray, moderate wear stage; black, heavily worn specimens (senile stage).

of the lingual reentrant persists in *Palaeolagus* much longer than in *Chadrolagus*, and is observed even in strongly worn specimens as a small round lake, whereas in *Chadrolagus* the lake vanishes early and quicker.

The lower molariform teeth (p4–m2) form lingual bridges in *Chadrolagus* when the p3 still shows the two-reentrant stage (fig. 8D), whereas in *Palaeolagus temnodon* their formation is postponed until the lingual reentrant closes, at the lake stage. In both species, m1 forms the bridge first (after m3), and is the first permanent tooth to erupt.

COMMENTS: *Chadrolagus emryi* is a rare species and thus far its morphology and variability has been described by Gawne (1978) only on the basis of its type series from Bates Hole, Flagstaff Rim, Wyoming. The stratigraphic range of this species was previously restricted to the middle Chadronian (Gawne, 1978), as *Chadrolagus* appeared in the profile "from 50 ft below Ash B to 50 ft above Ash G at Flagstaff Rim" (Emry, 1973, 1992; Gawne, 1978). The findings from Montana extend the geographic and stratigraphic range of this species. The material from

McCarty's Mountain mentioned by Tabrum and Fostowicz-Frelik (2009) moves the first appearance datum (FAD) of *Chadrolagus emryi* to the early Chadronian, whereas the remains from 10N locality and Little Spring Gulch extend its last appearance datum (LAD) to the late Chadronian. The remains from early Chadronian McCarty's Mountain Local Fauna are very rare and fragmentary: in total only five isolated teeth are known from this locality and only from the highest levels of the profile, Z–Y according to the division by Douglass (Tabrum et al., 2001). However, these specimens show marked vari-

FIG. 15. Box plot of the p3 W/L ratio in lagomorph species occurring near the Chadronian-Orellan boundary.

ability in size, with the upper teeth (P4, M1) among the smallest observed of all samples of *Chadrolagus emryi* described here (table 4); the lower teeth (p3, and m1) include the largest specimens (p3, BMUW 38613: L = 2.18 mm; m1, BMUW 38576: TriW = 2.43 mm, L = 2.28 mm), and are the outliers in the entire analyzed material (table 5). The explanation of these results is problematic. The McCarty's Mountain sequence is of considerable thickness and the upper and lower teeth were not found associated; thus, these isolated specimens may have been separated by a noticeable time interval. The age of the McCarty's Mountain Local Fauna was estimated as early Chadronian (Tabrum et al., 2001). During that time, other fully hypsodont lagomorph lineages (*Palaeolagus haydeni*, *P. burkei*, and *P. intermedius*) had not appeared yet (Prothero and Whittlesey, 1998). Thus, unless the age of the McCarty's Mountain Local Fauna is challenged, these large teeth represent either variability within *Chadrolagus emryi*, which is rather unlikely, or, more probably, a different, larger species (or genus) of fully hypsodont lagomorph, possibly conspecific with a form described herein from Wyoming (see below). The morphology of p3 (BMUW 38613) with a developed lingual lake, rules out *Litolagus molidens*. At present, the two larger specimens from McCarty's Mountain have been left in open nomenclature as *Lagomorpha* indet.

Nevertheless, the scarce remains of the upper cheek teeth from McCarty's Mountain discussed herein confirm the presence of *Chadrolagus emryi* in the early Chadronian. Thus, the early Chadronian may have been close in time either to the origination of this species in situ or its immigration into the Rocky Mountains. The first hypothesis seems more plausible judging from the fact that a few specimens found in the Duchesnean locality of Diamond O Ranch in Montana share some morphological features with *Chadrolagus emryi* (Fostowicz-Frelik and Tabrum, 2009: fig. 12). These specimens, displaying the semihypsodont condition, were preliminarily assigned to ?*Palaeolagus* sp.; however, the development of the occlusal enamel pattern and weakness of the buccal roots indicate rather affinity to the *Chadrolagus* lineage. Thus, an estimated time of origin for *Chadrolagus emryi* in the early Chadronian seems reasonably founded. The species becomes more abundant in the middle Chadronian and maintained this status until the late Chadronian, but probably did not cross the Chadronian/Orellan boundary.
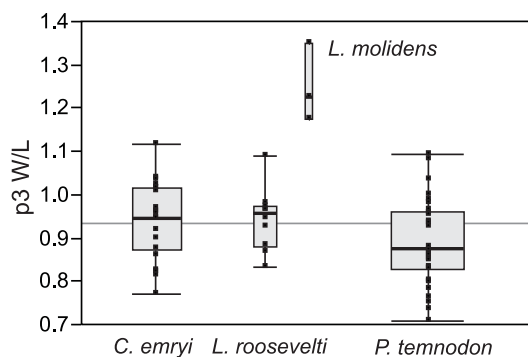
TABLE 4. Upper tooth measurements (in mm) of *Chadrolagus emryi* and ?*Chadrolagus* from the Chadronian of Montana. For abbreviations, see figure 4.

Specimen	P2 L	P2 W	P3 L	P3 W	P4 L	P4 W	M1 L	M1 W	M2 L	M2 W
						Chadrolagus emryi				
CM 78302	1.16	1.44	1.33	2.33	1.33	2.60	1.30	2.75	1.22	2.10
CM 78303	1.25	1.56	1.60	2.44	1.50	2.87	1.38	2.69		
CM 78320	1.06	1.64	1.61	2.98	1.67	3.00				
CM 78931	0.88	1.31								
CM 78348			1.57	2.62	1.57	2.91	1.54	2.89		
CM 78332			1.59	3.16	1.44	2.92				
CM 78312			1.56	2.91						
CM 78932			1.60	2.63						
CM 78943			1.84	2.69						
CM 78330					1.64	2.55				
CM 78318					1.71	2.49				
CM 78323					1.78	2.52	1.52	2.61		
CM 78716					1.56	1.96				
CM 78935					1.59	2.28				
CM 78928					1.47	2.65				
BMUW 38535					1.71	2.73				
CM 78311							1.59	2.61		
CM 78321							1.54	2.73		
CM 78308							1.46	2.69		
CM 78298							1.49	2.65		
CM 78313							1.56	2.69		
CM 78927							1.57	2.49		
CM 78944							1.44	2.67	1.38	2.32
CM 78929							1.57			
BMUW 40750							1.46	2.32		
CM 78344									1.50	2.81
CM 78333									1.49	2.52
CM 78309									1.43	2.35
CM 78345									1.34	2.44
CM 78326									1.59	2.56
CM 78936									1.58	1.80
						?*Chadrolagus* sp.				
CM 9059			1.41	2.79	1.61	2.76	1.51	2.84		

?*Chadrolagus* sp.

Referred Specimens: Pipestone Springs Main Pocket: CM 8620/1, left p4. Little Pipestone Springs: CM 9059, fragment of right maxilla with P3–M1, CM 84350, left p4. Pipestone Springs Fence Pocket: CM 78825, left p4.

Description and Comments: The presence of *Chadrolagus emryi* in the Pipestone Spring area was reported by Garcia (1992) and supported by Tabrum et al. (2001) and Dawson (2008). The four specimens discussed here show a striking similarity to *Chadrolagus emryi* in size (tables
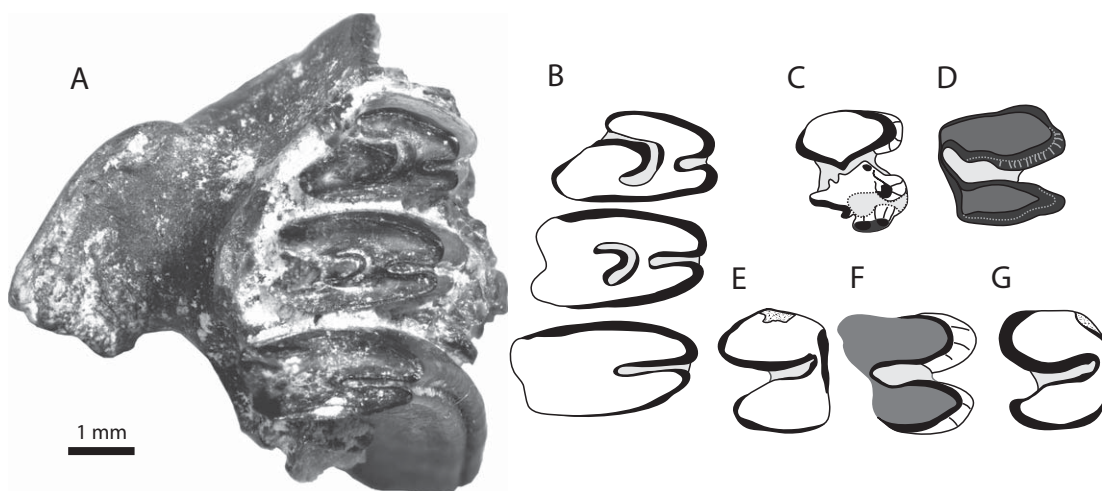
FIG. 16. Tooth morphology of ?*Chadrolagus* sp. from Pipestone Springs area (Montana). **A,** Right maxilla (CM 9059) with P3–M1 in occlusal view; **B,** line drawing of occlusal view of the teeth. Left p4 (CM 84350) in occlusal (**C**) and radical (**D**) views; left p4 (CM 78825) in occlusal (**E**) and radical (**F**) views; **G,** left p4 (CM 8620/1), occlusal view.

4, 5) and in the development of the occlusal enamel pattern, including early appearance of the lingual enamel bridges on the lower teeth (fig. 16). However, the anterior root of the zygomatic process of the maxilla is noticeably different, showing more lateral extension than that in the topotypic material of *Chadrolagus emryi*. Furthermore, the anterior root of the zygoma of CM 9059 is more robust than in *Chadrolagus emryi*, with the masseteric spine more strongly developed. This array of characters is typical for *Palaeolagus temnodon* and *P. haydeni*. Because the structure of the anterior root of the zygoma is recognized as a taxonomically and phylogenetically important character for North American stem lagomorphs (Dawson, 1958; see Character Analysis), such a difference is rather an indication of different species assignation and not intraspecific variability. Additionally, the occlusal outline of the P3 is more oval and more strongly compressed anteroposteriorly in CM 9059 (fig. 16A, B), while in *Chadrolagus emryi* from Flagstaff Rim it is distinctly extended anteroposteriorly (fig. 6), with a relatively short lingual lobe projecting slightly anteriorly. There are no important morphological differences between the lower teeth, which are probably p4 or m1, and the topotypic series of *Chadrolagus emryi*. They are fully hypsodont, with the pulp chamber completely divided into two compartments corresponding to the trigonid and talonid, and the enamel bridges are high on the shafts. CM 84350 is a juvenile tooth showing a not very persistent hypoconulid (fig. 16C). The remainder of the specimens represent adult teeth. All depart slightly from typical *Chadrolagus* in the ratio of tooth length to trigonid width; that is, they are less extended mediolaterally (fig. 17A), and thus, the p4 L/triW shows values more characteristic of *Palaeolagus temnodon* than of *Chadrolagus* (fig. 17B).

Preliminary statistical analysis of this material showed no significant differences in size (Alan R. Tabrum, personal commun.); however, there is variability in the degree of hypsodonty and in the morphology of the root portion, where some of the teeth display a root structure consistent with that typical for *Chadrolagus* (personal obs.). Thus, the taxonomic status of this material remains problematic and they are left in open nomenclature as ?*Chadrolagus*. Whether

TABLE 5. Lower tooth measurements (in mm) of *Chadrolagus emryi* and ?*Chadrolagus* from Montana.

Specimen	p3 L	TriW	TalW	p4 L	TriW	TalW	m1 L	TriW	TalW	m2 L	TriW	TalW	m3 L	TriW	TalW
Chadrolagus emryi															
UMVC 8405/ MV8007	1.71		1.40	1.81	1.99	1.58	1.90	2.06	1.70	1.94	1.98	1.61			
CM 78295	1.46	1.09	1.38												
CM 78343	2.07	1.43	1.81												
CM 78334	2.07	1.35	1.78												
CM 78305	1.75	1.36	1.81	1.64	1.77	1.53	1.74	1.95	1.71	1.92	1.86	1.55	0.85	0.88	0.67
CM 78336	1.83	1.24	1.41	1.61	1.69	1.36	1.74	1.84	1.46	1.77	1.62	1.47	0.99	0.83	0.91
UMVC 8404/ MV8007	1.78	1.34	1.47	1.69	1.94	1.62									
CM 78301	1.79	1.35	1.82	2.10	1.72										
CM 78937	1.95	1.51	1.84												
CM 78324				1.84	1.87	1.44	1.90	1.80	1.63						
CM 78304				1.92	1.72	1.42	2.01	1.87	1.56	2.01	1.84	1.57			
CM 78219				1.81	2.02	1.55									
CM 78317				1.65	2.06	1.61									
CM 78347				1.91	1.88	1.76	1.94	2.11	1.79	2.15	1.83	1.76			
CM 78938				1.88	1.88	1.58									
CM 78945				1.97	1.88	1.82									
CM 78327							2.13	1.99	1.80	1.98		1.55			
CM 78337							2.03	2.25	1.78	2.11	2.03	1.47			
CM 78339							1.99	1.75	1.67	1.92	1.85	1.51	0.84	0.87	0.70
CM 78939							2.13	2.11	1.78						
CM 78940							1.98	2.10	1.68						
CM 78930							2.09	1.99	1.83						
CM 78946							1.79	1.89	1.24						
CM 78341										2.16	1.95	1.71			
CM 78942										2.08	1.95	1.70			
CM 78947										2.15	2.07	1.70			
?*Chadrolagus* sp.															
CM 78825				1.80	1.58	1.66									
CM 84350				1.82	1.68	1.56									

the specimens discussed here represent a smaller species of *Palaeolagus* from the Pipestone area or should be included into *Chadrolagus* remains open until the revision of the Pipestone Springs material is completed.

Limitolagus roosevelti, new genus and species

Holotype: Left mandible body (AMNH F:AM 105995) with p3–m3 but lacking diastemal part (figs. 18, 19F).

Referred Specimens: AMNH F:AM 105992, fragment of left mandible with p3–m2; AMNH F:AM 105993, fragment of left mandible with p3–m2; AMNH F:AM 105996, fragment of left mandible with p4–m2; AMNH F:AM 105997, fragment of right mandible with p3–m2; AMNH F:AM 105998, fragment of right mandible with m1–m3; AMNH F:AM 105999, fragment of left mandible withp3–m2; AMNH

F:AM 106000, fragment of right mandible with p3–m3; AMNH F:AM 106001, fragment of right mandible with p3–m3; AMNH F:AM 106002, fragment of left alveolar process of maxilla with P2–M2, fragment of left mandible with p3–m2, head of right humerus; AMNH F:AM 143385, fragment of right mandible with p3–m2; AMNH F:AM 143386, fragment of right mandible with p4–m2 AMNH F:AM 143387, juvenile left mandible with p3–m1; AMNH F:AM 143391, fragment of left mandible with p3–p4.

DIAGNOSIS: Fully hypsodont lagomorph of medium size, comparable to *Litolagus molidens*, significantly larger than *Chadrolagus emryi* and most *Palaeolagus* species (except *P. intermedius*), but smaller than *Megalagus*. Full hypsodonty distinguishes it from *Megalagus* and *Palaeolagus temnodon*.

Differs from *Chadrolagus emryi* in significantly larger size, more distally extended incisive foramen (reaching to the posterior margin of P2), wider but shorter P2 (more oval in outline), wider anteroloph of P3 (more advanced molarization), more elongated p3, and deeper mandible body. Differs from *Palaeolagus haydeni* in larger size, deep and persistently open hypostria, and development of the occlusal dental pattern (vanishing of crescents, early formation of lingual bridges on lower cheek teeth). Differs from *P. intermedius* in having a more elongate p3 with a well-developed lingual lake at the moderate stage of wear, and accelerated maturation of the occlusal tooth pattern. Differs from *Litolagus molidens* in lower mandible body, the lower incisor ending close to ventral margin of mandible body, a more persistent anterior reentrant on P2, the longer and narrower p3, with a well-developed lake stage after closure of the lingual reentrant, in its longer and more square P3, generally shallower, less persistent hypostriae on P3–M2 at comparable stages of ontogeny, and broader and straighter enamel bridges in the lower p4–m2.

ETYMOLOGY: The generic name refers to *limitis*, genitive singular of *limes* (Latin for "border") and *lagos* (Greek for "hare"). It alludes to the stratigraphic occurrence of this lagomorph near the Eocene-Oligocene boundary. The specific name is after Theodore Roosevelt, the 26th president of the United States of America and a keen naturalist.

TYPE LOCALITY AND AGE: SE Seaman Hills, 16–20 mi N of Lusk, Niobrara County, southeastern Wyoming, 15 ft below P.W.L., late Chadronian, late C13r chron (according to Prothero and Whittlesey, 1998).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: Late Chadronian, about 30 to 5 ft below the P.W.L. in the following localities in Wyoming: Seaman Hills (S side, SE side, SE end, SW, and "Channel Quarry") Niobrara County, 2 mi NE of Indian Creek (SE of Seaman Hills), Lower Spring Draw, Niobrara County, S side of Jim Christian Hill (SE of Indian Creek), Niobrara County, Boner Brothers' Ranch, Pass area, Niobrara County, 8 mi SE of Douglas, Converse County.

INCLUDED SPECIES: Only the type species.

DESCRIPTION OF THE TYPE SPECIMEN: The holotype mandible includes complete lower tooth row (LTR = 13.7 mm), showing advanced wear stage. The p3 is relatively elongated, has no lake, and its lingual side is gently concave (figs. 18, 19F). The p4 shows a very wide, straight, and short lingual bridge; similarly the bridges of m1 and m2 are relatively straight and wide. The m3 is rounded and compact. The mandible is 10.3 mm high at the p4 level. The lateral side of the mandible body, below the p3/p4 transition, is finely perforated. The lower incisor reaches the trigonid of p4 (fig. 18) and its distal end lies close to the ventral margin of the mandible. The masseteric line is angular with pointed apex directed anteriorly and reaching the level of m2/m3 transition.

DESCRIPTION AND COMPARISONS: The new species is represented only by fragmentary material. Mandibular bodies with teeth are the most common elements (table 6); additionally, a single alveolar portion of maxilla with P2–M2 (fig. 20, table 7) and the proximal part of a humerus are known.

The mandible body of *Limitolagus roosevelti* has a slightly longer tooth row than *Litolagus molidens* but is proportionally lower. The ratio of the mandible height to the length of the tooth row (MH/LTR) in *Limitolagus roosevelti* is in fact comparable to that of *Palaeolagus intermedius* and *Archaeolagus ennisianus*, two relatively large fully hypsodont species; it also partly overlaps with ratio values for *Chadrolagus emryi*, but is higher than that in *P. temnodon* (fig. 21, table 2). The Kruskal-Wallis test for MH/LTR at α = 0.05 confirmed that the differences between *Limitolagus roosevelti* ($N = 4$, median 0.761), *Chadrolagus emryi* ($N = 8$, median 0.706), *Litolagus molidens* ($N = 3$, median 0.833), and *Palaeolagus temnodon* ($N = 9$, median 0.658) are significant ($\chi^2 = 35.636$, df = 9, $p < 0.0001$), but because of the small sample sizes these results should be treated as approximate only.

The length of the lower tooth row is on average slightly larger than that of *Litolagus molidens* and *Palaeolagus temnodon*, although values are comparable and differences statistically insignificant. The lower incisor ends below p4 similarly as in *Chadrolagus emryi* and *Litolagus molidens*. However, the root of the incisor in *L. roosevelti* is not recurved dorsally as in *L. molidens*, resulting in its being closer to the ventral margin of the mandible body than in the latter species. The diastemal part is destroyed in all specimens of *L. roosevelti*. A relatively large foramen (probably, the anterior mental foramen) is located about 2.0–3.5 mm in front of the p3 alveolus on the lateral side. The surface of the mandible between this foramen and the ventral margin of the bone is finely perforated, similarly to that of *Litolagus molidens*.
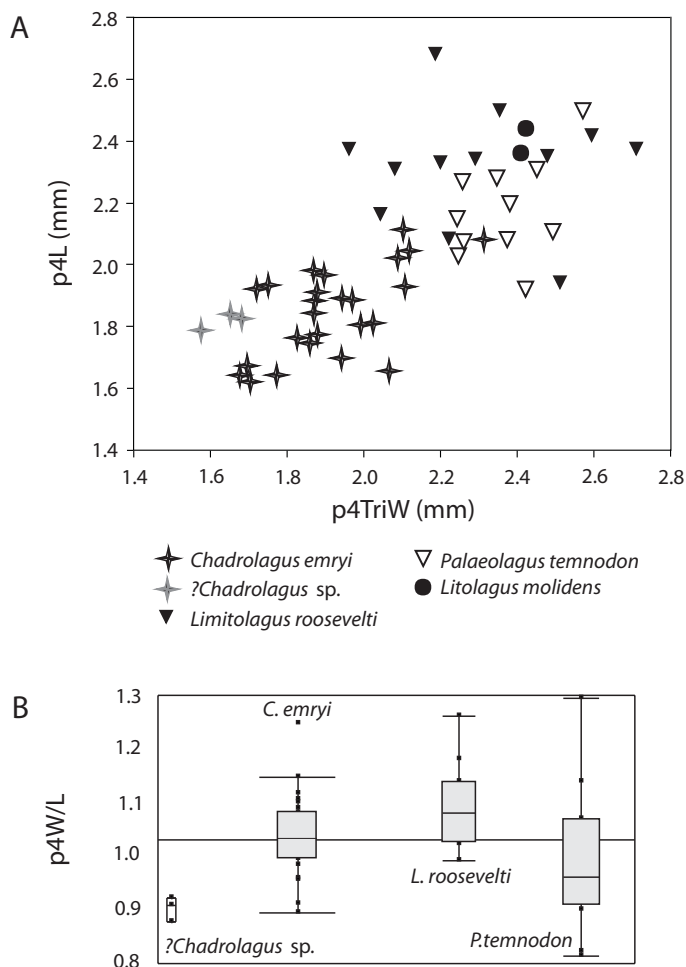

FIG. 17. Proportions of p4 in ?*Chadrolagus* sp. from the Pipestone Springs area, compared with morphologically closest lagomorph species from the middle Chadronian–early Orellan interval. **A,** scatter-plot of the tooth length (p4L) to the trigonid width (p4TriW) ratio; **B,** box plot of this ratio.

The near complete upper dentition of *Limitolagus roosevelti* is known only from one specimen (AMNH F:AM 106002), which lacks M3 (fig. 20). The teeth display a relatively worn stage, although the crescent is still present on P3 and the remnants of the occlusal structures on P4–M2 are manifested by a thin ridge sculpting the surface, as in *Chadrolagus emryi* (figs. 6, 11). P2 has a deep and persistent reentrant as in *Chadrolagus emryi*, which is one of the characters differentiating it from *Litolagus molidens*, in which P2 loses its reentrant relatively earlier in ontogeny.

The P3 in *L. roosevelti* is not as strongly compressed anteroposteriorly as in *Litolagus*, being more square, similar to *Chadrolagus emryi* and *Palaeolagus temnodon*. The lingual lobe seems to reach more buccally than in *C. emryi* at the comparable stage of wear (figs. 6, 20), indicating more advanced, although not complete, molarization of P3, in a manner similar to that observed in *Litolagus molidens* (Dawson, 1958). In general, the upper cheek teeth are proportionally less compressed anterodistally (thus longer) and more rounded in outline in *Limitolagus roosevelti* than in *Litolagus molidens* and this character is also manifested in AMNH F:AM 106002. Moreover, in comparison with *Litolagus molidens* the hypostriae are relatively shallower in *Limitolagus roosevelti* and in *C. emryi*, and they vary in depth at different loci, which changes throughout ontogeny. By contrast, in *Litolagus* they have very similar depth in all teeth in the row, from P3 to M2, and persist through ontogeny. The average depth of the

FIG. 18. Left mandible body with p3–m3 of the holotype of *Limitolagus roosevelti*, new genus and species (AMNH F:AM 105995). **A,** occlusal; **B,** buccal; and **C,** lingual views.

hypostriae in *Limitolagus roosevelti* calculated for the teeth of AMNH F:AM 106002 is ca. 30% of the total tooth width (ranging from 23%–36%). The comparative values for *Chadrolagus emryi* at the similar stage of wear are 33% (ranging 23%–40.5%), whereas for *Litolagus molidens* the comparative values are 40% (37%–42%).

The ontogenetic development of the enamel pattern of the lower teeth occlusal surface is similar in *Limitolagus roosevelti* (fig. 19) to *Chadrolagus emryi* (fig. 8). In a juvenile, almost unworn specimen (AMNH F:AM 105993, fig. 19A), the metaconid is markedly larger and oriented more anteriorly, similar to *Chadrolagus emryi* (Gawne, 1978). Moreover, metaconid and
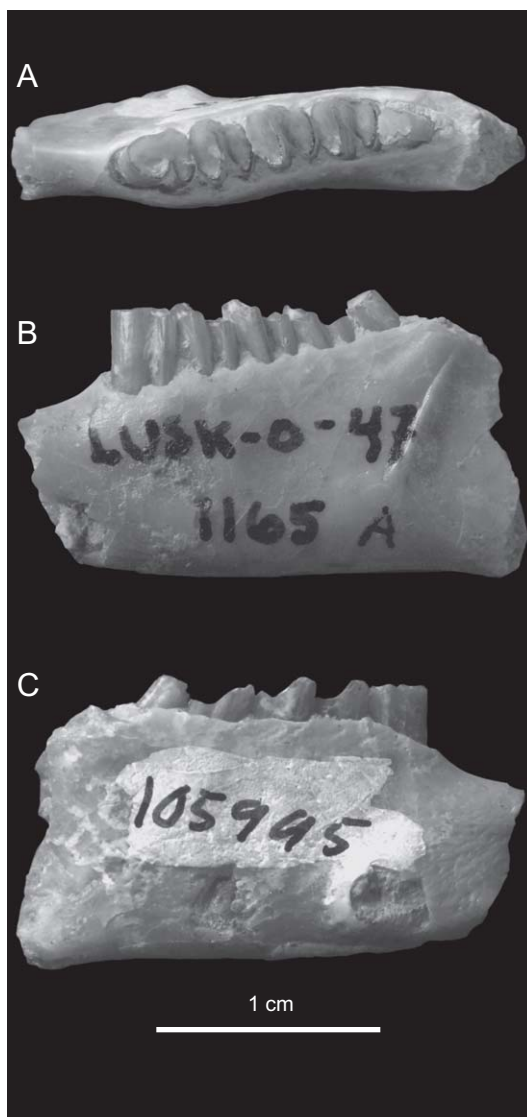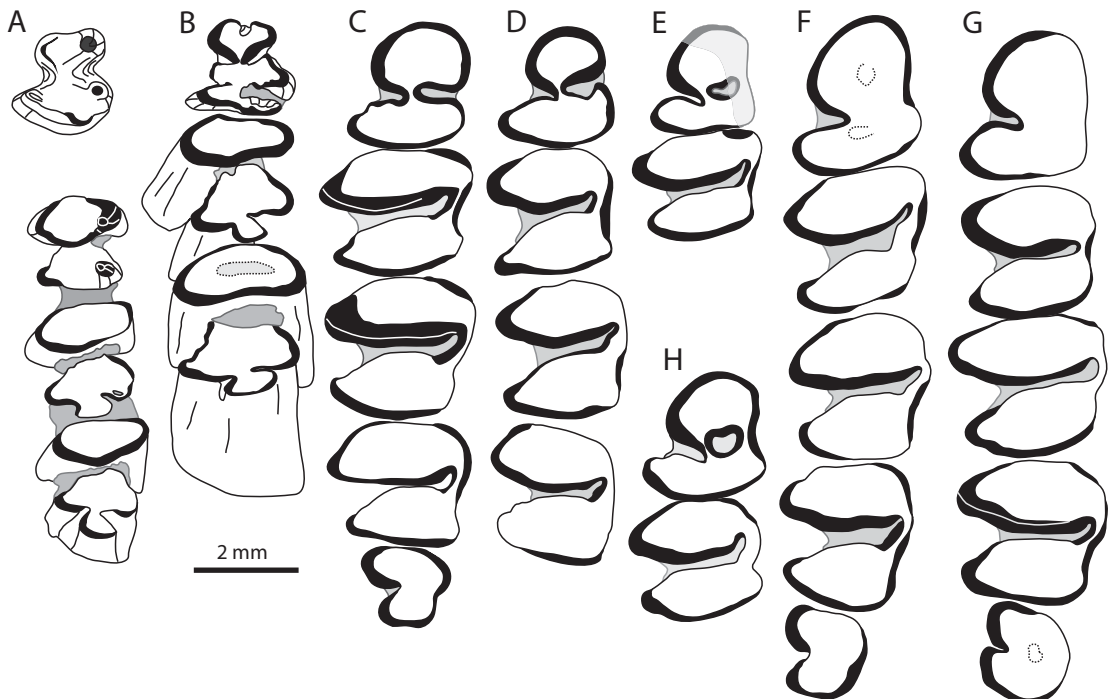
FIG. 19. Ontogenetic development of the lower tooth row (occlusal surface) in *Limitolagus roosevelti*, new genus and species. **A,** left p3–m2 (AMNH F:AM 105993), note position of metaconid in unworn p3; **B,** left p3–m1 (AMNH F:AM 143387); **C,** right p3–m3 (AMNH F:AM 106000, reversed view); **D,** left p3–m2 (AMNH F:AM 105999); **E,** right p3–m1 (AMNH F:AM 143385, reversed view); **F,** left p3–m3 of the holotype (AMNH F:AM 105995); **G,** right p3–m3 (AMNH F:AM 106001, reversed view); **H,** left p3–p4 (AMNH F:AM 143391). A–B, juvenile wear stage; C–D, light wear stage; E, H, moderate wear stage; F–G, heavily worn stage.

paraconid are separated by a deep anterior reentrant, as in *C. emryi* (Gawne, 1978). The predominance and anterior position of the metaconid is poorly expressed during light and moderate wear stages, when the anterior margin of the trigonid is more flattened. It becomes more visible after closure of the lingual reentrant and more pronounced in a strongly worn stage (fig. 19), when the anterior margin of the trigonid becomes oblique to the frontal plane. The lingual lake is relatively persistent as can be observed in AMNH F:AM 143386, where the damaged lingual wall of the tooth exposes the vertical extent of this structure, at least 2.0 mm in height (a moderately worn tooth, 9.0 mm high in total), already expressing a lake, at the occlusal surface. The presence of the lingual lake on p3 is one of the most significant characters distinguishing *Limitolagus roosevelti* from *Litolagus molidens* because such a structure is unknown in the latter, even in the type specimen, which is a young individual whose limb bones show incompletely fused epiphyses (Dawson, 1958).

The p3 is relatively short (table 8) but longer than in *Litolagus molidens* and the differences are statistically significant between these two species. The W/L ratio of p3 for *L. roosevelti* overlaps with both *C. emryi* and *P. temnodon* (fig. 15). In ontogeny *Limitolagus roosevelti* shows slightly larger elongation than *C. emryi* and the length of the tooth seems to correlate more with the stage of wear than with its width, although the analyzed sample is too small to be conclusive (fig. 14).

TABLE 6. Mandible measurements (in mm) of *Limitolagus roosevelti* from the Chadronian of Wyoming.

Specimen	LTR	MH
AMNH F:AM 105992	12.6	9.5
AMNH F:AM 105993		8.2
AMNH F:AM 105995	13.7	10.3
AMNH F:AM 105996		8.9
AMNH F:AM 105998		9.9
AMNH F:AM 105999		9.6
AMNH F:AM 106000	11.5	9.3
AMNH F:AM 106001	13.4	10.4
AMNH F:AM 106002		8.0
AMNH F:AM 143385		8.7
AMNH F:AM 143386		9.7

TABLE 7. Upper tooth measurements (in mm) of *Limitolagus roosevelti* from the late Chadronian, Wyoming.

Measurement	AMNH F:AM 106002
P2 W	2.18
P2 L	1.65
P3 W	3.60
P3 L	2.40
P4 W	4.17
P4 L	2.51
M1 W	3.76
M1 L	2.28
M2 W	3.49
M2 L	2.18

Similarly, as in *Chadrolagus emryi* and *Litolagus molidens,* the enamel bridges in lower cheek teeth (p4–m2) are formed early in ontogeny and are well developed before the lingual reentrant closes. They are relatively broad and have a relatively straight line, similar in structure to those of *Chadrolagus emryi,* rather than of *Litolagus molidens.* The m3 does not differ markedly in *L. roosevelti* from that of *C. emryi* and *L. molidens*, although it resembles the former species more. It has similar bilobate, slightly irregular shape, with slightly wider trigonid, through most of its ontogenetic stages (fig. 19). However, the differences in trigonid and talonid width are less than in *Litolagus molidens*, and some of the m3 in *Limitolagus roosevelti* are well rounded as in *Chadrolagus*.

COMMENTS: The preliminary assignment of the material of *Limitolagus roosevelti* according to Skinner's fieldnotes was to *Litolagus molidens.* However, close reexamination of that material revealed the differences in the development of the occlusal enamel pattern of upper and lower dentition, different proportions of the teeth (especially p3) and the mandible body (figs. 15, 21, table 2) from the holotype of *Litolagus molidens* (LACM CIT 1568) and two new skulls described in this paper. Initially, Fostowicz-Frelik and Meng (2011: 111) assigned the newly examined material to a new, unnamed species of *Chadrolagus.* However, the present author, on the basis of morphological differences assigned the referred specimens to a new genus and species, *Limitolagus roosevelti.*

Limitolagus roosevelti is significantly larger than *Chadrolagus emryi*, but shares with this species an array of characters related to the ontogenetic development of the occlusal tooth surface, such as predominance and anterior position of the metaconid on p3, formation of the p3 lingual lake structure, persistent anterior reentrant of P2, the dissolution pattern of upper tooth occlusal enamel structures, and developmental pattern of the hypostriae. Moreover, the mesowear of the upper dentition is similar in *Chadrolagus emryi* and *Limitolagus roosevelti*, showing more primitive characters shared also with *Palaeolagus* and *Mytonolagus*. Mesowear in these genera produces smooth and gently concave tooth surfaces except at the buccalmost parts, but not contributing to a hypostrial fold and tending to obliterate it, which as a result causes this structure to become shallow and finally disappear, whereas in *Litolagus molidens* mesowear observed on the upper teeth favors the formation of the centrally positioned eminence directed buccolin-
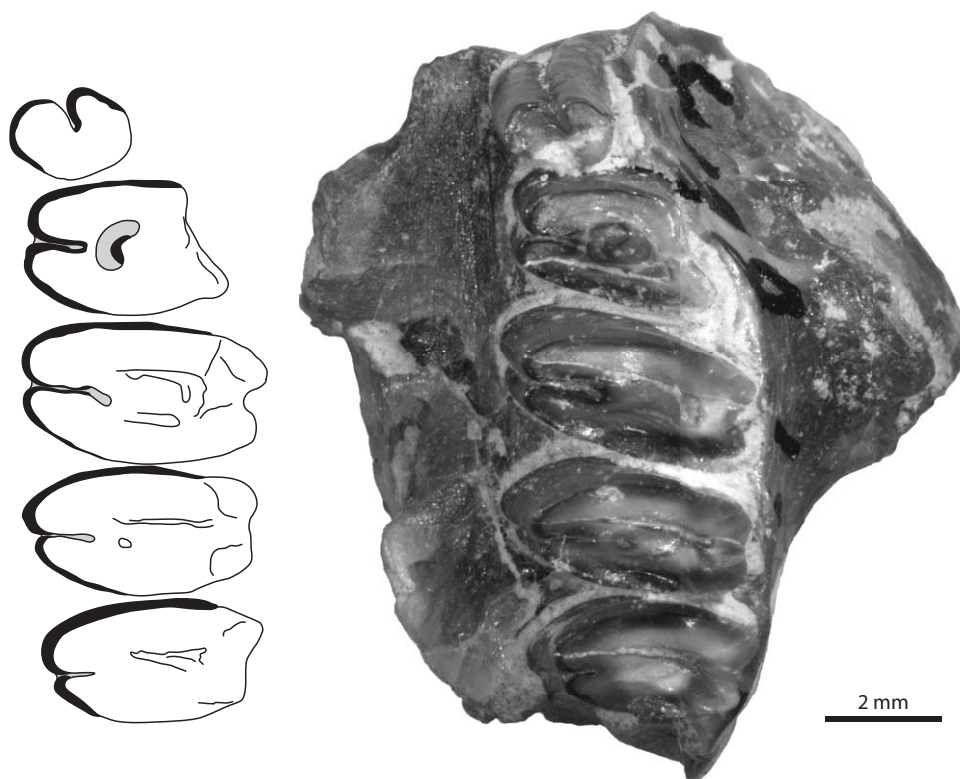
FIG. 20. Left upper P2–M2 of *Limitolagus roosevelti*, new genus and species (AMNH F:AM 106002) in occlusal view.

gually, which is virtually an extension of the hypostriae and preserves this fold during wear. The major differences in the mesowear imply differences in mastication and tooth occlusion, which stems from different functional capacities of the cranial muscles (e.g., range of action, forces and their points of application) and ultimately points to differences in skull construction of the respective genera. Additionally, the material assigned here to *Limitolagus roosevelti*, although it comes in part from the same area in Wyoming (Douglas, Converse County) as that of *Litolagus molidens* (Dawson, 1958; Skinner, ms), does not occur in the same localities and the two species show different stratigraphic occurrence (fig. 2). All specimens of *Limitolagus roosevelti* appear below the borderline white tuff ("Persistent White Layer" or P.W.L. of Skinner, ms.) marking the Eocene-Oligocene boundary (Evanoff et al., 1992; Prothero and Emry, 2004), whereas those assigned to *Litolagus molidens* were found almost exclusively above that layer, and are thus according to their position most likely of Oligocene age.

<div align="center">

Leporidae Fischer von Waldheim, 1817

Litolagus Dawson, 1958

Litolagus molidens Dawson, 1958

</div>

Type Species: *Litolagus molidens* Dawson, 1958, by monotypy.

Holotype: LACM-CIT 1568. Partial skull, mandibles, and associated postcranial skeleton (figs. 22–24).
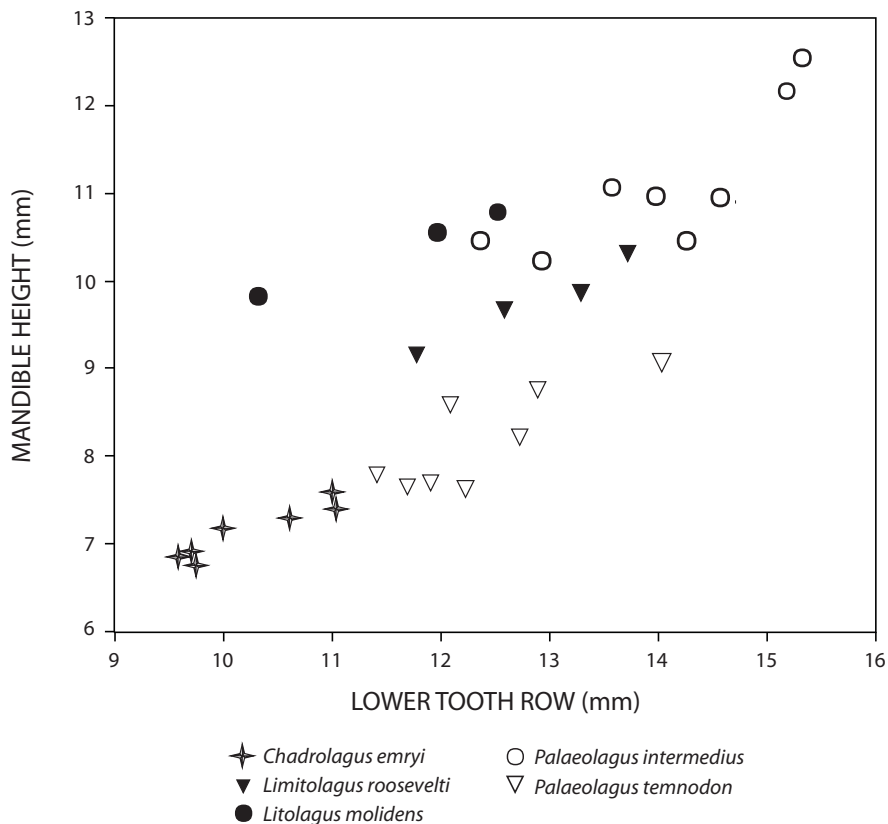
FIG. 21. The mandible proportions (MH/LTR ratio) in lagomorph species occurring near the Chadronian-Orellan boundary.

Newly Referred Specimens: AMNH FM 143955, complete, partly crushed skull with both mandibles; AMNH F:AM 105991, skull with partly damaged rostrum and associated two mandibles and epistropheus; AMNH F:AM 105994, isolated P3.

Revised Diagnosis: Medium-size, fully hypsodont lagomorph, larger than *Palaeolagus haydeni*, but slightly smaller and more gracile than *P. intermedius*, *Megalagus*, and *Archaeolagus*. Significantly larger than *Chadrolagus emryi*, but similar in size to *Limitolagus roosevelti*. It differs from *Chadrolagus*, *Megalagus*, and *Palaeolagus* by the skull structure: larger orbit and lower position of the jugal arch, greater basicranial angle, shorter palate bridge with reduced palatine portion, slenderer and less expanded laterally zygomatic processes of the maxilla and squamosal, more erect frontal process of the maxilla, and deeper mandible body. Moreover, it differs from the above genera in the upper incisor (dI2) having both lobes similarly wide, not persistent anterior reentrant of P2, longer anteroloph of P3, more compressed anterodistally upper cheek teeth, P2–M2, with deeper and more persistent hypostriae, comparably deep on all loci, P3–M2 (last two characters shared with *P. burkei*), shorter p3 with a wider talonid, lacking lake stage, but with a wide concavity at the lingual side, framed by eminent entoconid and metaconid, in young specimens. It differs from *Palaeolagus haydeni*, *P. intermedius*, *P. burkei*, and *Megalagus* in lack of hypostrial lakes and overall acceleration of the development of the enamel pattern at the occlusal surfaces (as in *Chadrolagus*), resulting in

early loss of crescents and early formation of lingual bridges, which are thinner and more strongly bent than in any of *Palaeolagus* or *Chadrolagus*. Further, *Litolagus* differs from *Archaeolagus* in less-angled skull and smaller orbit, slightly shorter and more distally positioned palatal bridge (stretched between P3 and M1/M2), narrower frontals and parietals, the latter also more flattened and elongated, more slender zygomatic process of squamosal, significantly larger auditory bulla, higher mandible body, upper incisors less compressed anterodistally, with wide mesial lobe, simpler P2 structure, P3–M2 with deeper hypostria and crescents obliterated earlier in the ontogeny, shorter p3 with shorter, round trigonid and wider talonid, and m3 expressing early wide lingual connection between the trigonid and talonid.

TYPE LOCALITY AND AGE: Douglas area, Converse County, Wyoming, lower nodular layer of "Oreodon beds," ca. 6.5 mi SE of Douglas (Dawson, 1958).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: Early Orellan and Chadronian/Orellan deposits of Wyoming. The exact localities according to Skinner's field journal: Reno Ranch S of Tower (25 ft above 100 ft white marker layer), 5 mi SE of Douglas and Hermann Wulff Ranch (middle part of the "nodular layer"), 3.5 mi SE of Douglas, ?SE Seaman Hills (Channel Quarry, 10 ft below P.W.L.), 16–20 mi north of Lusk, Niobrara County.

DESCRIPTION AND COMPARISONS: *Litolagus molidens* is an extremely rare species. The remains of this lagomorph are known only from the early Oligocene deposits of the White River Formation cropping out SE of Douglas, Wyoming (Dawson, 1958, 2008; Prothero and Whittlesley, 1998). Up to now only two specimens were known, both including parts of the skull and one associated with the postcranial elements (Dawson, 1958). In the present work two new skulls are described, of which the best preserved (AMNH FM 143955) is a fairly complete specimen of *Litolagus molidens* (figs. 25–28). In the comparisons, all North American lagomorph taxa known from the Chadronian and Orellan deposits of the Wyoming are included. Furthermore, because of the advanced structure of the skull of *Litolagus*, comparisons with the Miocene archaeolagine *Archaeolagus ennisianus* are provided to assess its relationships to Archaeolaginae.

MORPHOLOGY OF THE SKULL

SKULL IN GENERAL: The skull of *Litolagus molidens* is longer than that of *Chadrolagus emryi*, *Palaeolagus temnodon*, *P. burkei*, and *P. haydeni*. The measurements for the specimens described here are given in table 9. The skull AMNH FM 143955 (figs. 25–27) is slightly smaller and more delicate and gracile than the skulls of *Megalagus*, and *P. intermedius*, being comparable to *Archaeolagus ennisianus*, but slightly more slender. The skull of *Litolagus molidens* is relatively higher and more angled than the skulls of *Palaeolagus* and *Megalagus*, but the basicranial bending is less profound than in *Archaeolagus*. Moreover, the braincase structure with elongated, flat parietals, well-pronounced sagittal crest, and prominent dorsally exposed mastoids seems to be more similar to that of *Palaeolagus*.

The muzzle of *Litolagus molidens* is long and slender with a relatively elongate diastema (compared to the length of the upper tooth row; table 2), which is similarly long in *Litolagus molidens*, *Palaeolagus temnodon* and *P. haydeni*. Moreover, the palate area is wider in *Litolagus* than in *Palaeolagus temnodon* and *P. haydeni*, which have similar length of the upper tooth row, but is visibly narrower than in *Archaeolagus* (table 2).
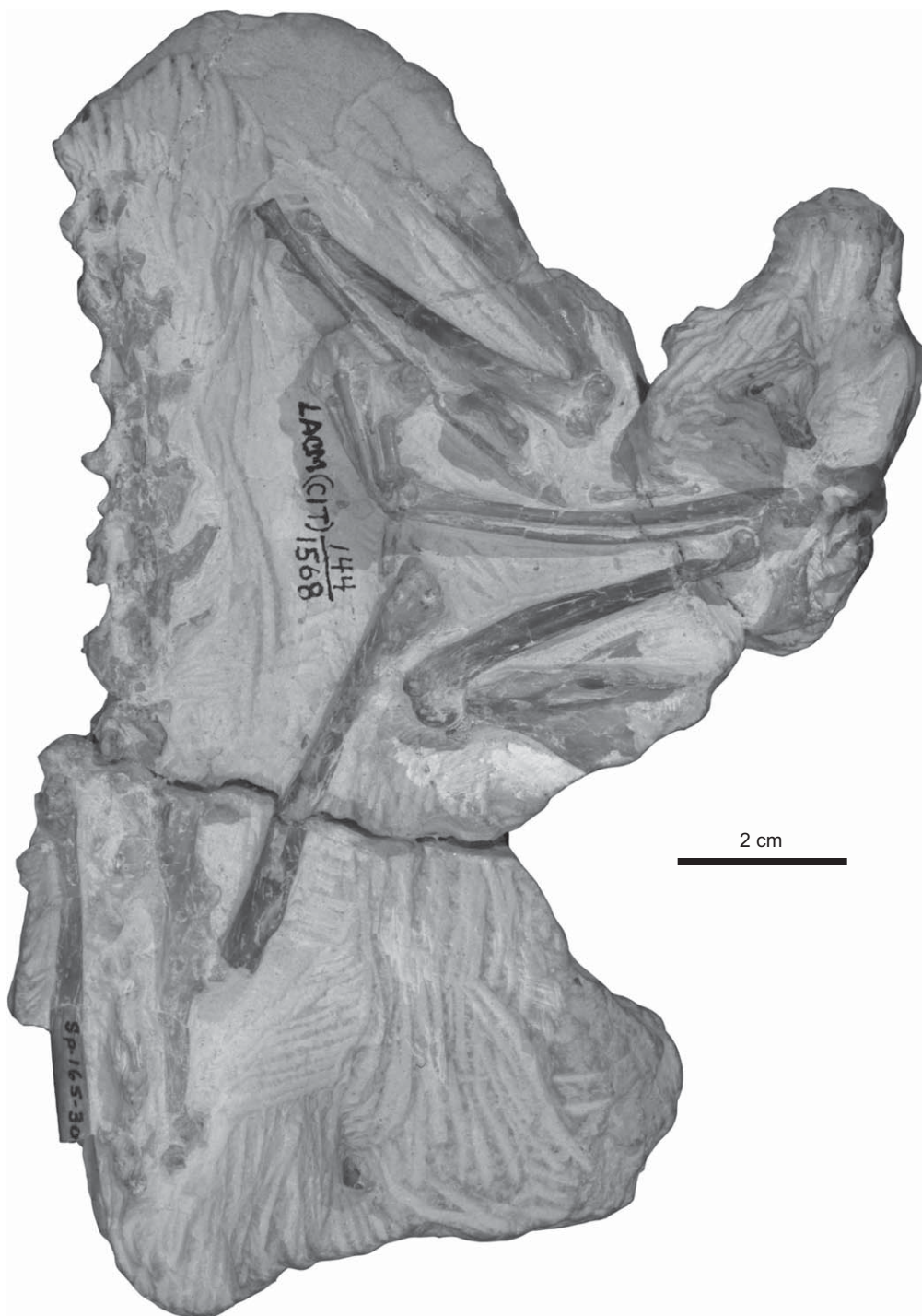
FIG. 22. The holotype of *Litolagus molidens* (LACM-CIT 1568) in a slab.
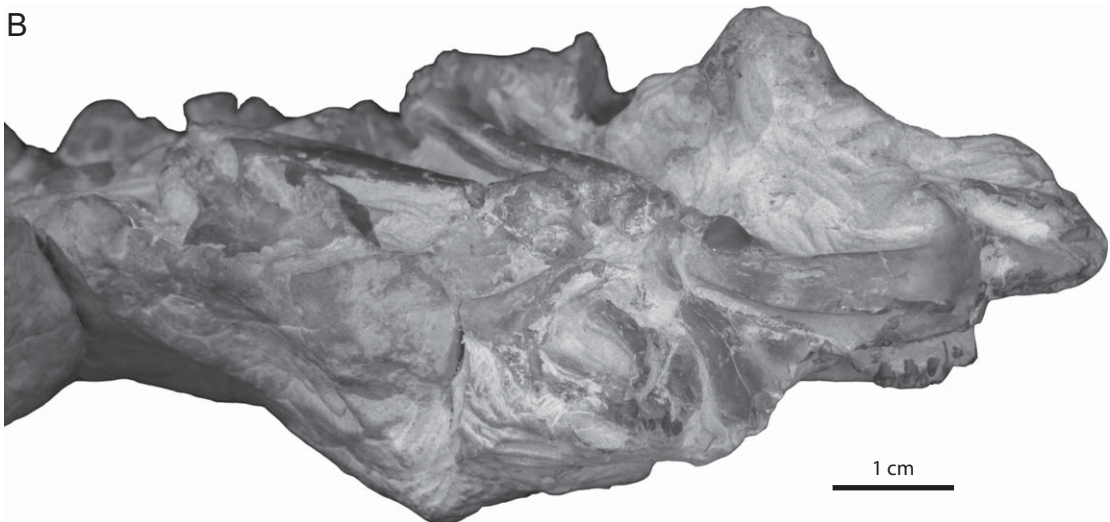
FIG. 23. Skull of the holotype of *Litolagus molidens* (LACM-CIT 1568) in ventral (**A**), and lateral (**B**) views.

Both skulls of *Litolagus* described here (AMNH F:AM 105991 and AMNH FM 143955) have strongly marked ornamentation expressed as a series of minute concavities covering nasal and frontal bones, especially the region above the olfactory lobes, running in two plies along the sagittal suture on parietals, and concentrating at the parietal-mastoid suture (figs. 25–26, 29). That kind of ornamentation is weaker in all other palaeolagine lagomorphs, although perforation of the frontals can be observed in *Chadrolagus* (fig. 10C) and *Palaeolagus*. It is also common in modern leporids, but it concentrates mostly on the parietals and in most cases is not extensive. The only extant species with such well-developed ornamentation covering most of the skull
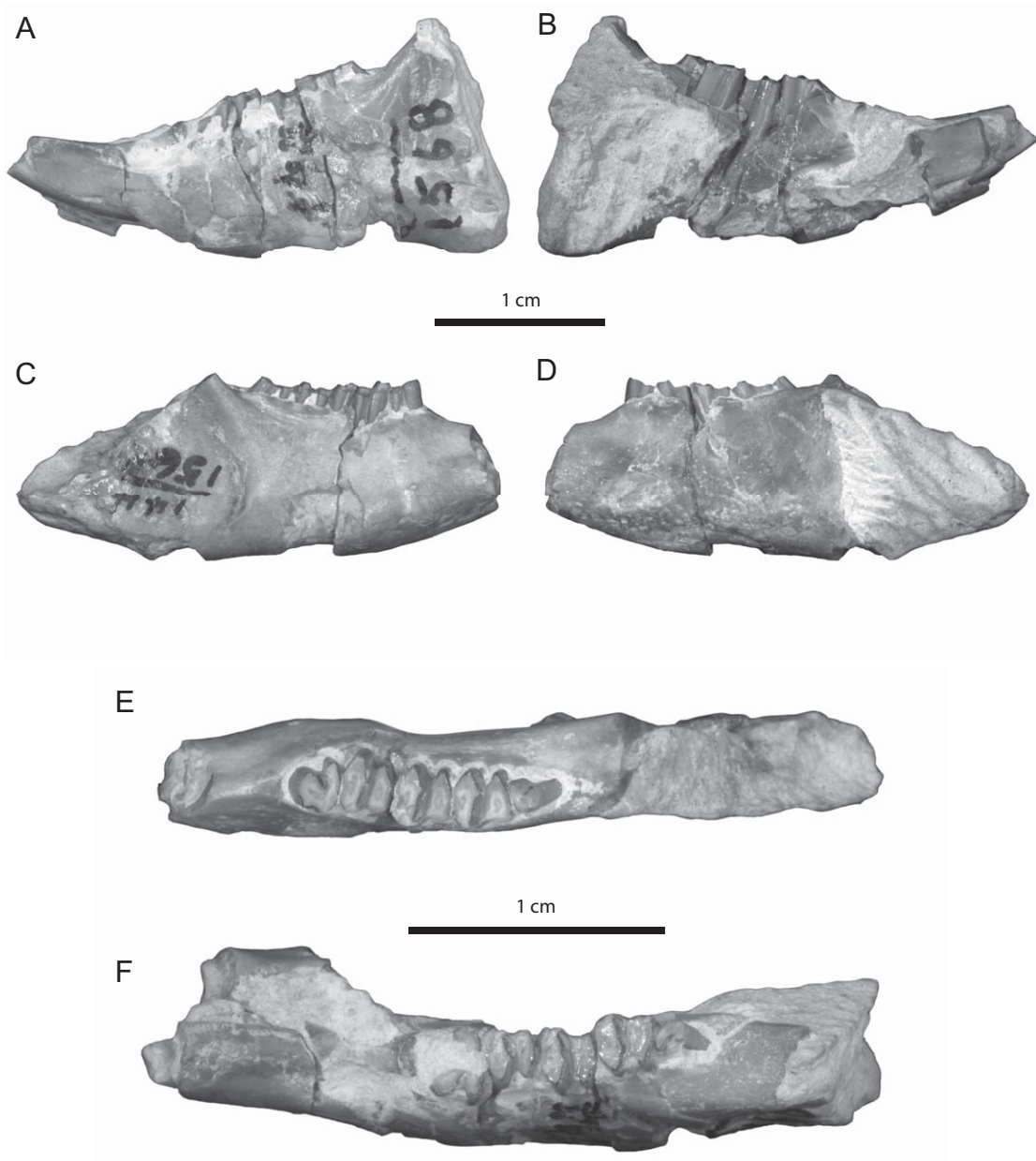
FIG. 24. Mandibles of the holotype of *Litolagus molidens* (LACM-CIT 1568). Left mandible in buccal (**A**), lingual (**B**), and occlusal (**F**) views. Right mandible in buccal (**C**), lingual (**D**), and occlusal (**F**) views.

roof is the volcano rabbit *Romerolagus diazi* (personal obs.; see also Wible, 2007: fig. 1B). The original description of *Litolagus* lacks any comment on this character, but the material presented by Dawson (1958) was almost completely devoid of the skull roof and the holotype specimen is in major part still embedded in the matrix (figs. 22–23).

Nasals: The nasals are long and generally equally wide over the entire length, not tapering visibly as in *Chadrolagus emryi*. They are located relatively high, not gently arched as in *Palaeo-*

lagus, forming a more spacious nasal cavity. The anterior part of the nasals, where the bones detach from the premaxillae and form the roof of the piriform foramen (the external nasal opening), is higher than in *Palaeolagus haydeni* and *P. temnodon*. Two-thirds of the posterior part of the nasals have a visible ornamentation in the form of minute irregular concavities, located especially along the external margins of the nasal bones. This kind of ornamentation is displayed more distinctly in AMNH F:AM 105991, where the posterior part of the right nasal bone is heavily perforated. Similar perforation of the nasal bones is also observed in a specimen of *P. temnodon* (CM 8620), but is much weaker in *P. haydeni*.

PREMAXILLA: The premaxilla accommodates the upper incisors, which are embedded in the dorsal part of the body of premaxilla, although slightly more ventrally than in *Palaeolagus*. The length of the incisor alveolus is shorter in *Litolagus* (as well as in *Palaeolagus* and *Chadrolagus*) than in modern leporids, although the distal opening of the root ends similarly at the premaxillary-maxillary suture, but it is located higher laterodorsally (in the upper 40% of the dorsoventral extent of the body of the premaxilla), whereas in modern lagomorphs the end of dI2 is located at the ventral side of premaxilla, in the vicinity of the premaxillary-maxillary suture.

The alveolar part of the body of the premaxilla in *Litolagus* is not as elongated as in modern leporids (e.g., *Lepus* or *Sylvilagus*), and the thin crests at the base of the frontal processes of premaxilla (the posterodorsal process sensu Wible, 2007) that frame the lateral margins of the piriform aperture anteriorly descend to the very anterior margin of the incisor alveoli, as in *Palaeolagus* and *Chadrolagus*. Nevertheless, the body of the premaxilla is slightly elongated in *Litolagus* in comparison to those of *Palaeolagus* and *Chadrolagus*. The frontal process of the premaxilla in *Litolagus* is long and thin, reaching as far as the nasal-frontal contact at the lateral side of the skull, only ≤1.0 mm shorter than the greatest posterior extent of the nasals, as in *Chadrolagus*, *Palaeolagus*, and *Archaeolagus*.

MAXILLA: The anterior part of the maxilla is heavily perforated, forming, as is characteristic of Lagomorpha, lacework bone on both sides of the muzzle (Meng and Wyss, 2001; Meng et al., 2003; Asher et al., 2005; Wible, 2007). The fenestration is similar in *Litolagus* to that in *Chadrolagus* and *Palaeolagus*. The bone ventral to the lacework is solid and forms an acute-angled process that cuts anteriorly into the premaxilla. This prominent process is sharper, narrower, and longer in *Litolagus* than in *Chadrolagus*, but shorter than in *Palaeolagus haydeni*. It is oriented more laterally in *Litolagus*, higher at the muzzle than in *Chadrolagus emryi*, as in *Palaeolagus haydeni*. The remainder of the premaxillary-maxillary suture is located at the ventral side of the muzzle and forms a deeply overlapping serrated bone contact. The infraorbital foramen is slightly smaller than in *P. haydeni* and *P. temnodon* and positioned over the anterior part of the alveolus for P2, like in *Chadrolagus emryi*, and slightly more anteriorly than in *Palaeolagus*.

The frontal process of the maxilla is straighter and more erect than in *Palaeolagus haydeni,* in which it reclines distally ca. 45°, and in *Chadrolagus emryi*, which expresses a slightly less inclination of this process. In *Litolagus* it forms a gentle arch framing the anterior part of the orbit.

In ventral view, the incisive foramen bordered by the premaxilla and maxilla is long in *Litolagus*. It extends to the distal part of the P3 alveolus, whereas in *Chadrolagus emryi* it reaches the anterior margin of P2 alveolus; in *Palaeolagus temnodon*, the midlength of P2 alveolus; and in *P. haydeni*, the P2/P3 contact. This shortens the palatal bridge in *Litolagus* more than in North American stem lagomorphs (fig. 30, table 2). Moreover, the choanae reach the M1/M2 in *Lito-*
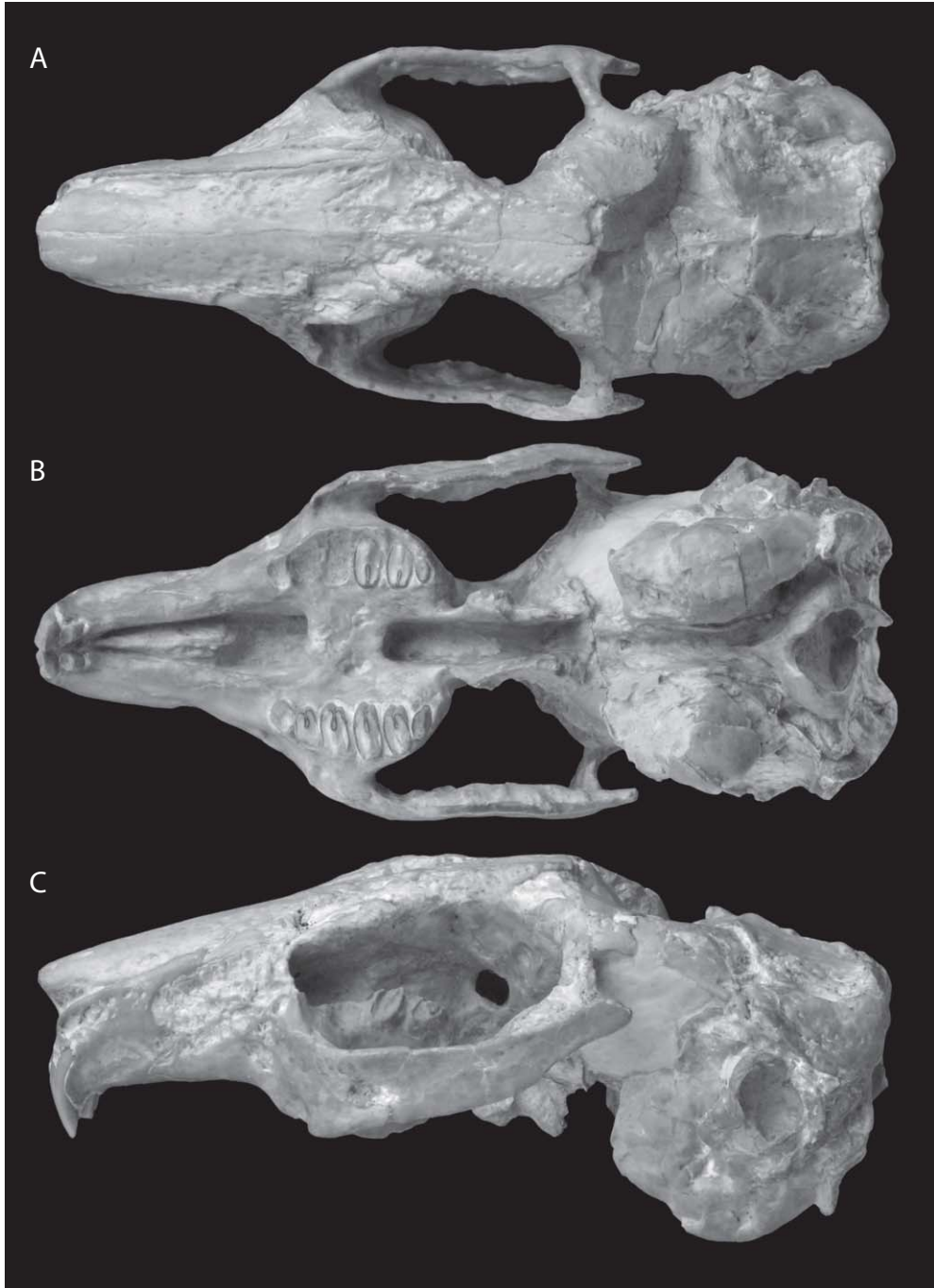
FIG. 25. Skull of *Litolagus molidens* (AMNH FM 143955) from Herman Wulff Ranch, Converse County, Wyoming in dorsal (**A**), ventral (**B**), and lateral (**C**) views. See figure 26 for explanations.
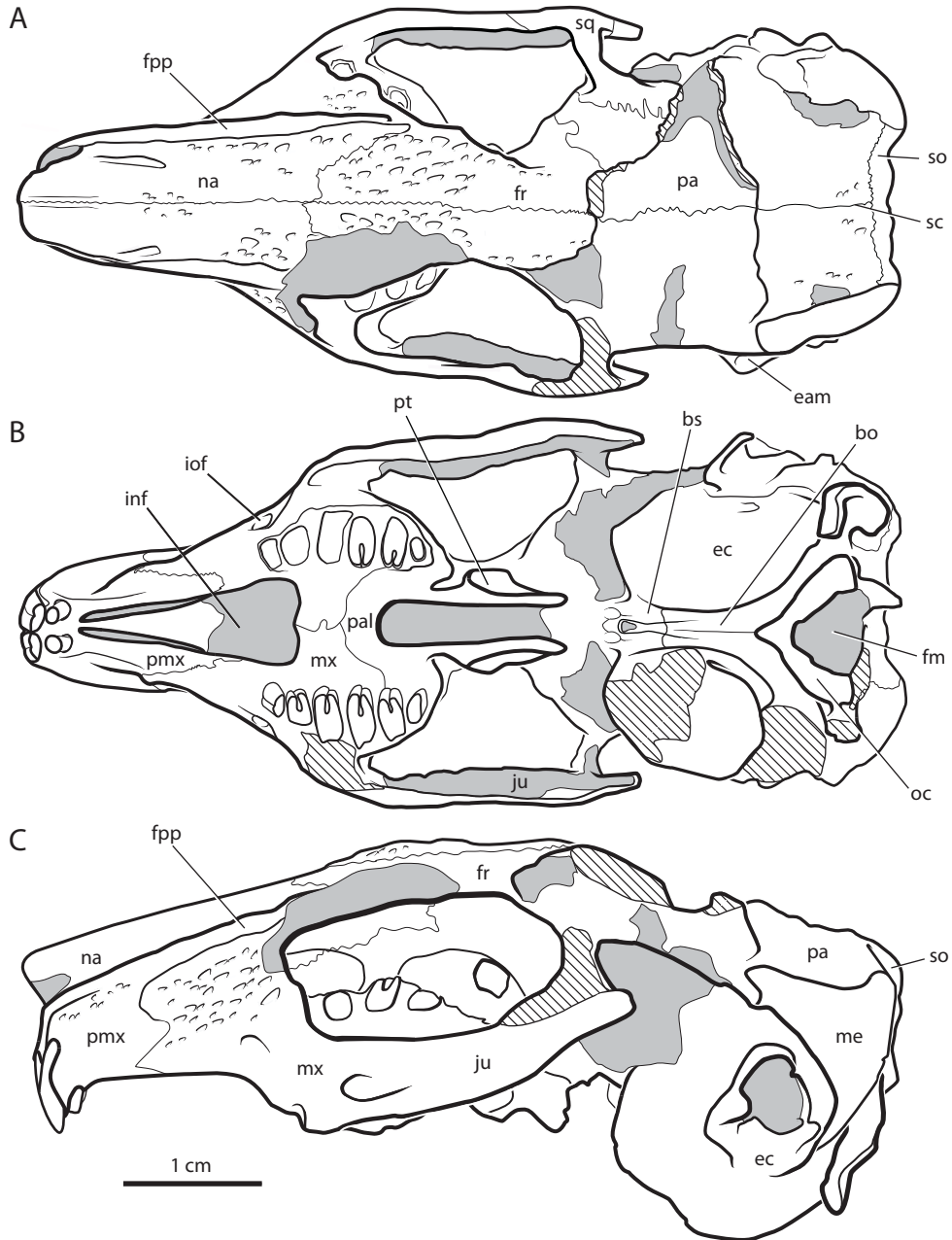
FIG. 26. Line drawing of skull of *Litolagus molidens* (AMNH FM 143955) in dorsal (**A**), ventral (**B**), and lateral (**C**) views. Abbreviations: **bo,** basioccipital; **bs,** basisphenoid; **eam,** external acoustic meatus; **ec,** ectotympanic; **fm,** foramen magnum; **fpp,** frontal process of premaxilla; **fr,** frontal; **inf,** incisive foramen; **iof,** infraorbital foramen; **ju,** jugal; **me,** mastoid exposure of petrosal; **mx,** maxilla; **na,** nasal; **oc,** occipital condyle; **pa,** parietal; **pal,** palatine; **pmx,** premaxilla; **pt,** pterygoids (ento- and ectopterygoid crests); **sc,** sagittal crest; **so,** supraoccipital; **sq,** squamosal. Hatched areas correspond to missing or damaged bone.
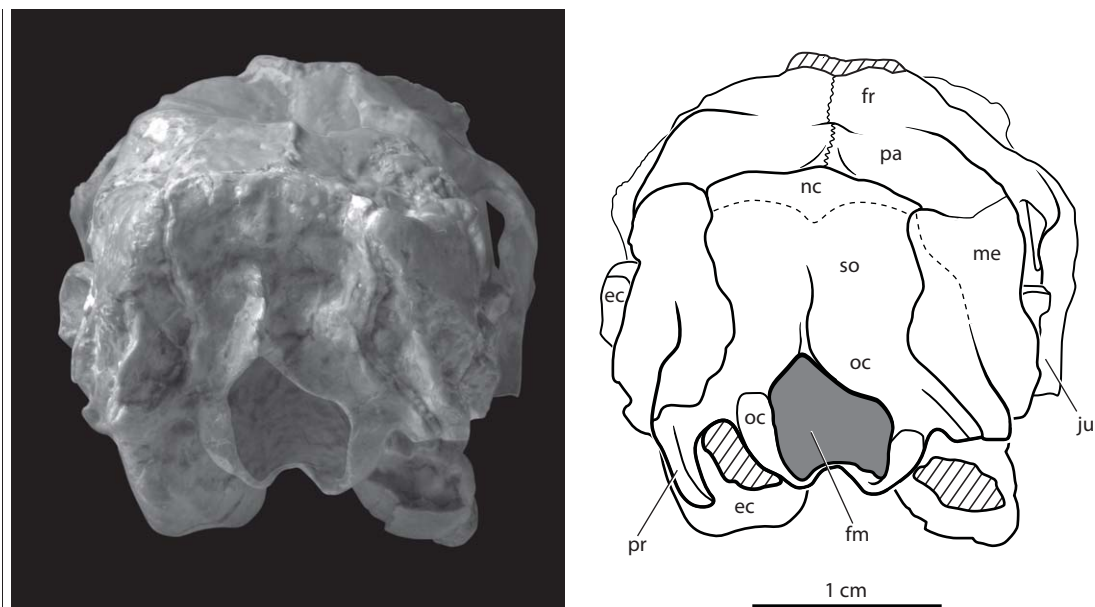
FIG. 27. **A,** Occipital region of *Litolagus molidens* skull (AMNH FM 143955) in caudal view, and **B,** line drawing. See figure 26 for abbreviations; **nc,** nuchal crest. Hatched areas correspond to missing or damaged bone.

lagus as in *Chadrolagus emryi*, whereas in *P. haydeni* they open closer to the middle of M2. In *Litolagus* the maxillary part of the palate formed by the palatine process of the maxilla occupies 57% of the length of the palatal bridge, comparable to *Archaeolagus ennisianus* (53%), whereas in *Chadrolagus emryi*, *Palaeolagus temnodon*, and *P. haydeni* it constitutes only 36%–49%, 42%, and 38%–46% of the palate, respectively.

The alveolar process of the maxilla is deep and occupies the lower part of the orbit as in other palaeolagines and modern lagomorphs (Craigie, 1945; Wible, 2007). The lateral border of the alveolar process on the left side of the skull in AMNH FM 143955 is complete and frames a partly destroyed dentition. It allows view of the spatial relation of the zygomatic process and the ventral margin of the alveolar process of the maxilla, which are closer to each other in *Litolagus molidens* than in *Palaeolagus haydeni*, creating simultaneously a more spacious and round orbit.

The morphology of the zygomatic process of the maxilla was one of the characters differentiating *Litolagus* from *Palaeolagus* emphasized by Dawson (1958). In ventral view the zygomatic process of *Litolagus*, especially the masseteric spine is less expanded laterally than that of *Palaeolagus* (*P. temnodon*, *P. haydeni*, and *P. burkei*), *Chadrolagus emryi*, and *Archaeolagus ennisianus* (fig. 30). It is also longer and resembles the shape of this structure in the European rabbit (*Oryctolagus cuniculus*), although it is located closer to the alveolar process of the maxilla. On the other hand, in *Palaeolagus* the masseteric spine is shorter and more compact in ventral view, but flares more laterally, similar to the condition found in the mountain hare (*Lepus timidus*). In lateral view, the anterior tip of the masseteric spine in *Litolagus* forms a sharp apex (as in *Chadrolagus emryi*) pointing anteroventrally, whereas in *Palaeolagus* the tip is blunt, directed more ventrally, and the zygomatic process is swept somewhat backward.
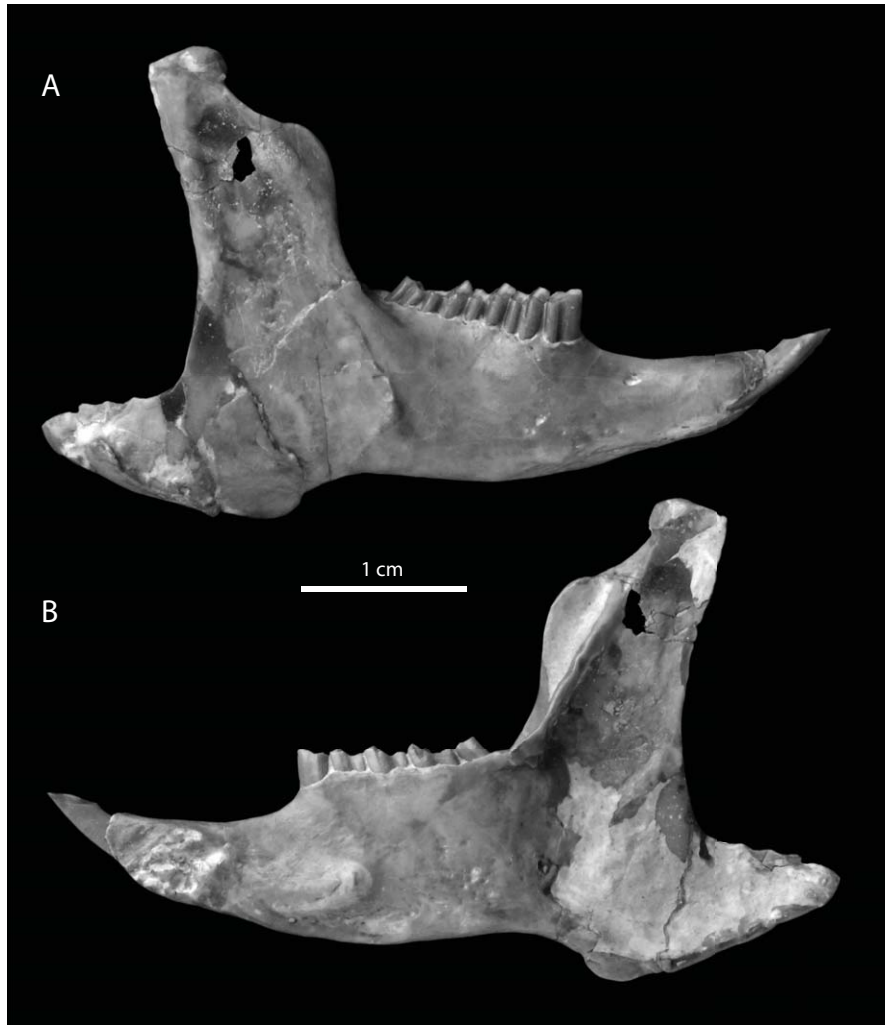
FIG. 28. Mandible of *Litolagus molidens* (AMNH FM 143955) in lateral (**A**), and lingual (**B**) views.

In *Litolagus molidens* a shallow fossa occurs anterior to the zygomatic process of the maxilla, forming a nascent depression almost completely lacking in *Palaeolagus* and *Chadrolagus emryi,* but well marked, although shallow, in *Megalagus*, deeper in *Archaeolagus*, and well developed and deep in extant leporids (in some species perforated). The fossa was mistakenly marked as the infraorbital foramen in *Romerolagus*, by Wible (2007: fig. 2B), but in fact the infraorbital foramen in leporids lies within the ventral part of the fenestrated area of the maxilla (Craigie, 1945: 179, fig. 79) and is obscured by the extensive fenestration of the whole region.

JUGAL: The zygomatic arch in *Litolagus molidens* is positioned relatively lower on the skull than in *Palaeolagus*, which creates more space in the orbit. This is a result of simultaneous lowering of the position of the zygomatic process of the maxilla (moving it closer to the occlusal tooth surface), and stronger bending ventrally of the zygomatic process of the squamosal, unlike

FIG. 29. Skull of *Litolagus molidens* (AMNH F:AM 105991) in dorsal view. Note the strongly perforated frontal.

the condition observed in *Palaeolagus, Megalagus,* and *Archaeolagus ennisianus*. In *Chadrolagus emryi* the zygomatic process of the maxilla lies equally low (fig. 10B) as in *Litolagus*, but the squamosal zygomatic process is not bent ventrally more than in *Palaeolagus*.

The exact position of the bone contact between the zygomatic process of the maxilla and the jugal bone is not clear in any of the specimens of *Litolagus molidens* because this suture is obliterated very early in ontogeny (Craigie, 1945). The lamina of the jugal bone is relatively broad in *Litolagus* and positioned exactly parallel to the sagittal plane. It has neither the masseter margin gently inclined outward nor both the jugal plates swung aside backward, flaring slightly, increasing the distance from the orbit, as it is in *Palaeolagus*. The jugal bone of *Litolagus* is broadest at its anterior end near the zygomatic process of the maxilla; it then narrows slightly toward the posterior terminus. The lateral surface of the jugal is flatter in *Litolagus* (and *Chadrolagus*) than in *Palaeolagus*. Although a shallow zygomatic fossa occurs in both species, it is not emphasized by the additional lateral bending of the orbital and masseter margins observed in *Palaeolagus haydeni* and *Archaeolagus ennisianus* (expressed more weakly in *P. burkei*). In *Litolagus molidens* the zygomatic fossa is a single, well-defined oval depression about 3.5 mm long and 2.2 mm high, unlike *Palaeolagus haydeni*, which has a spade-shaped zygomatic fossa shallowing distad.

The posterior part of the jugal arises slightly upward to join the zygomatic process of the squamosal. In lagomorphs the part of the jugal plate along the jugal-squamosal suture is generally narrower than the rest of the bone plate. In *Litolagus molidens* this part is relatively longer and less narrow than in *Palaeolagus haydeni*, and the distal end of the jugal seems blunter than in *Palaeolagus*.

PALATINE AND PTERYGOID: The palatine bone forms the posterior part of the hard palate and surrounds the opening of the internal nares. The palatine portion of the palatal bridge is relatively short in *Litolagus molidens*, in comparison to *Chadrolagus emryi* and *Palaeolagus*. The anteromedial part of the maxillo-palatine suture in *Litolagus molidens* is profoundly flattened, apart from

the minute anterior spinelike apex, and is perpendicular to the sagittal plane differentiating this species from *Chadrolagus emryi, Palaeolagus*, and *Archaeolagus ennisianus,* which have the maxillo-palatine contact rounded with the convex margin directed anteriorly (figs. 26, 30; Gawne, 1978: fig. 2a). One pair of major and one pair of minor palatine foramina are located closer to the maxillo-palatine suture, and more laterally in *Litolagus* than in *Chadrolagus* and *Palaeolagus*. The foramina are also relatively smaller in *Litolagus* than in *Palaeolagus* or *Chadrolagus*.

The distal margin of the palatal bridge forming the rim of the choanae has a weakly developed tubercle, which can be homologized with the posterior spine of the palatine, not detected in *Chadrolagus* and *Palaeolagus*, but well developed in more advanced lagomorphs, including archaeolagine leporids (see Dawson, 1958: fig. 27a; Fostowicz-Frelik, 2007: fig. 8a) and some leporine genera (Craigie, 1945, for *Oryctolagus*; personal obs. for *Sylvilagus*).

The choanae are wider in *Litolagus molidens* in relation to the width of the palate than in *Palaeolagus haydeni* and *P. burkei* or *Chadrolagus emryi*, but slightly narrower than in *Archaeolagus ennisianus*, *P. intermedius*, and *Megalagus turgidus* (table 2). The medial walls of the basipharyngeal canal (sensu Evans, 1993), formed anteriorly by the palatine and posteriorly by the entopterygoid crests (Wible, 2007), are parallel and show no tendency toward narrowing in the midlength, as can be observed in some *Palaeolagus haydeni* specimens (e.g., AMNH FM 143956), where the choanae are somewhat heart shaped. The entopterygoid crests are positioned almost vertically in *Litolagus molidens*, with the ectopterygoid crests (lateral laminae of pterygoid processes sensu Craigie, 1945: fig. 81) spread out laterally, at an oblique angle of about 45°. The entopterygoid crests in *Litolagus molidens* are much more vertical than those of *Chadrolagus emryi* and *Palaeolagus*. The hamuli of the pterygoids are partly preserved in AMNH FM 143955. They lie in the plane of the entopterygoid crests (sagittally), project ventrodistally, and do not deviate laterally as in some species of extant lagomorphs, e.g., *Oryctolagus* (Craigie, 1945) or *Sylvilagus* (personal obs.).

BASISPHENOID: The basisphenoid is well preserved in specimen AMNH FM 143955, although its anterior part is broken and contact with the pterygoid is obscured. The basisphenoid in *Litolagus molidens* appears relatively narrow in comparison with *Palaeolagus* and extant *Lepus* and *Sylvilagus*, and this narrowing seems rather more natural than artificial because the entire distal part of the skull of AMNH FM 143955 is not crushed or distorted significantly (fig. 25–27). The bone is also gently grooved longitudinally. The craniopharyngeal canal (Evans, 1993; Wible, 2007: fig. 4B), or foramen cavernosum (Craigie, 1945), is visible in *Litolagus molidens* but hard to locate even in the best-preserved specimens of *P. haydeni*. The intersphenoidal synchondrosis is well marked in *Litolagus* and flanked by the auditory bullae, unlike in modern leporids, where it occurs anterior to the bullae. The bone, immediately anterior to the contact with the basiooccipital, forms two gently swollen tuberosities, indicating the position of the synchondrosis.

OCCIPITAL: The ventral part of the occipital region, the basioccipital, in *Litolagus molidens* is relatively long compared with *Palaeolagus haydeni*. The posterior part bears a thin spine that continues as a conelike structure located at the ventral side of the intercondyloid notch, a structure found in *Palaeolagus* but very poorly developed in modern leporids. Although the supraoccipital in *Litolagus molidens* (fig. 27) is partly crushed, it seems higher and more vertically positioned than in *Palaeolagus haydeni* and *P. burkei*, and even more than in extant leporids, in which the distal surface of the skull is strongly inclined backward and faces ventrodistally. The
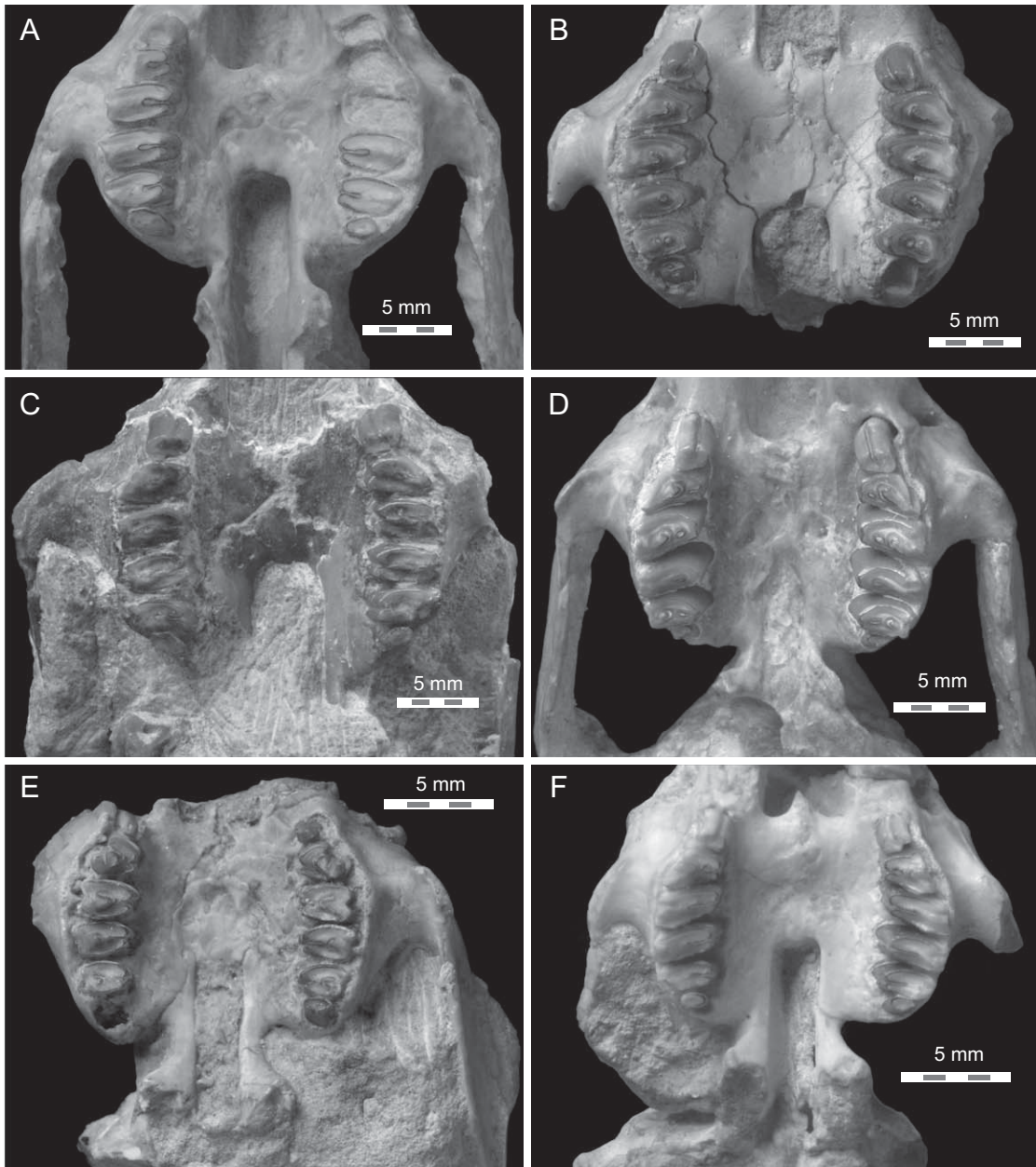
FIG. 30. Structure of hard palate. **A,** *Litolagus molidens* (AMNH FM 143955); **B,** *Megalagus turgidus* (AMNH FM 141012); **C,** *Archaeolagus ennisianus* (AMNH FM 7190); **D,** *Palaeolagus haydeni* (AMNH FM 143957); **E,** *Chadrolagus emryi* (AMNH F:AM 99108); **F,** *Palaeolagus burkei* (AMNH FM 8704).

exoccipital in *Litolagus molidens* is similar to that of *Palaeolagus* and the jugular process or paracondylar process of the exoccipital (sensu Wible, 2007: fig. 5B) has a length similar to that in *P. haydeni*, but is longer than in *P. burkei*. However, they all differ markedly from the structure in *Archaeolagus ennisianus* and extant leporids. The paired exoccipital bones in *Litolagus*

and *Palaeolagus* are much smaller and narrower than in extant species and *Archaeolagus*. They constitute relatively narrow lateral margins of the foramen magnum with the L-shaped jugal processes detaching lateroventrad, with their tips pointing slightly mesiad. In leporids the exoccipital bones are much wider, not L-shaped but semicircular, with a flared, round dorsolateral margin, covering a significant part of the mastoid exposure of the petrosal in distal aspect.

The articular surface of the occipital condyle is slightly broader in *Litolagus molidens* than in *Palaeolagus haydeni* and the intercondyloid notch is deeper and narrower. The whole structure of the condyles seems stronger in *Litolagus*, which is not surprising, given the larger skull compared with *Palaeolagus*.

Frontal: The skull roof in AMNH FM 143955 is partially crushed, although most of the frontals are intact (fig. 25A). The frontal region is less complete in skull AMNH F:AM 105991, but the parietal region is better preserved (fig. 29).

The anterior part of the frontal bones in *Litolagus* is heavily ornamented, especially in the region covering the olfactory lobes (figs. 25A, 26A, 29). The ornamentation is stronger in *Litolagus* than in any species of *Palaeolagus* or *Chadrolagus emryi*. The nasal spine of the frontal is blunted and irregular at its anterior margin, wedged between the nasal bones. It does not form such a triangular wedge as in *Palaeolagus* and *Chadrolagus*. The supraobital processes are lacking in both specimens, as well as in the holotype (Dawson, 1958), although the presumption is that only the posterior supraorbital processes were present and they were similarly developed as in *Palaeolagus* or *Chadrolagus* (Wood, 1940; Dawson, 1958; Gawne, 1978). The orbital part of the frontal is significantly higher in *Litolagus* than in *Palaeolagus* or *Chadrolagus* resulting in elevating the skull roof.

Two distinct gently ornamented frontal ridges follow along the orbital margins (fig. 25A), cross the frontoparietal suture, and meet medially midway along of the parietal (figs. 25A, 29). The ridges are much better developed in *Litolagus* than in any species of *Palaeolagus,* where only delicate lines can be discerned, or in *Chadrolagus emryi*, where they are lacking entirely. The frontals join with the parietals by means of an irregular suture generally perpendicular to the sagittal plane. This suture in both specimens of *Litolagus molidens* described here is similar in its appearance to that of *Chadrolagus emryi*, more irregular and flatter than the suture of *Palaeolagus haydeni*, which shows two symmetrically located processes wedged into the parietals.

Parietal: The parietal region of *Litolagus molidens* is similarly structured as in Palaeolaginae (Dawson, 1958: pls. 1, 2). The anterior part is slightly convex dorsally, whereas the distal part flattens and extends caudally. The morphology markedly distinguishes *Litolagus* from modern leporids and *Archaeolagus ennisianus*, whose braincases have a shorter and rounded parietal portion. The skull of *Litolagus* has visible narrow V-shaped ornamented crests terminating distally at the sagittal suture on the parietals (figs. 25A, 29). From the place of their fusion, the sagittal crest arises and continues distally to the suture with the supraoccipital. The sagittal crest is more pronounced in both specimens of *Litolagus* than in any *Palaeolagus haydeni* and *P. burkei*. The condition of this character is unknown in *Chadrolagus*, whereas in *Archaeolagus ennisianus*, although the crest is not present, the parietals narrow slightly and form a longitudinal ridgelike eminence, not as sharp as a crest, but visible.

SQUAMOSAL: The parietal joins the squamosal via a strongly serrated suture. The ventralmost parts of both squamosals are missing in both skulls of *Litolagus*, but the zygomatic processes of the squamosal are well preserved. They join the jugal dorsally forming a relatively long, straight suture in the horizontal plane. The zygomatic process of the squamosal is formed as a right-angled triangle with its right angle directed distally and the base joined with the jugal. In *Litolagus molidens* the structure is more slender and elongate (with its sides either gently convex or concave) resembling the processes of *Lepus* or *Sylvilagus* more than those of *Palaeolagus haydeni*, *P. temnodon*, *P. burkei*, *Chadrolagus emryi*, and *Archaeolagus ennisianus*, in which it is sturdier and fully triangular. Moreover, the base of the zygomatic process, which connects the zygomatic arch with the skull, is more strongly bent ventrally in *Litolagus molidens* (as in modern leporids) than in *Chadrolagus emryi* and *Palaeolagus*, resulting in a lower position of the jugal arch in relation to the skull roof, and creating more space in the orbit. Also, the bending of the zygomatic processes in *Litolagus* brings the plate of the jugal closer to the skull.

ORBIT REGION: The orbit in *Litolagus* is markedly larger and more round than in all species of *Palaeolagus* analyzed here, *Megalagus*, and *Chadrolagus emryi*. This is caused by the lowering of the zygomatic arch, the more vertical position of the frontal process of the maxilla, the higher orbital portion of the frontal, and the raised orbital margin of the frontal at the supraorbital process. Size of the orbit in *Litolagus molidens* is comparable to that of *Archaeolagus ennisianus* or slightly smaller, but AMNH FM 7190, a specimen of *Archaeolagus,* has one of the supraorbital processes of its frontal preserved, and it defines the orbit more accurately than can be determined for any of the *Litolagus* specimens (all of which lack the supraorbital processes).

The orbitosphenoid is mostly preserved, and sutures with the frontal, squamosal, and parietal are clearly visible. The optical foramen is large, and the position of the alisphenoid canal is well marked, especially on the right side of the skull in AMNH FM 143955. However, the alisphenoid is mostly damaged on both sides of the skull (figs. 25–26).

The lacrimal bone, which is usually reduced in Lagomorpha and forms a small tubercle connected to the anterolateral extremity of the frontal (Craigie, 1945), is mostly lacking in the fossil material. The skull of *Litolagus molidens* (AMNH FM 143955) has a small protuberance at the orbital margin of the frontal process of the maxilla, possibly the remains of the lacrimal bone, not different in size from that in modern taxa.

PETROMASTOID AND ECTOTYMPANIC: The ear region in lagomorphs consists of two distinct elements: the ectotympanic, which forms the auditory bullae, and the petromastoid, which encapsulates the inner ear structures (Craigie, 1945). The auditory bullae are crushed or embedded in the matrix in all specimens of *Litolagus*, although the partially preserved auditory bullae of AMNH FM 143955 give some insight into the external morphology of the ear region (fig. 25). The auditory bullae are relatively large in *Litolagus* compared to *Palaeolagus haydeni*, *Archaeolagus ennisianus* (table 2), and extant leporids. They are similarly enlarged in *P. burkei* in relation to the skull size, although in *Litolagus molidens* the bullae were probably more dorsoventrally extended than in *P. burkei*, which has a generally flattened skull and bullae. However, they are relatively smaller than in *P. hypsodus* (see Dawson, 1958: pl. 2:1a–d). The auditory bullae have, as far as can be ascertained after taking

into account alteration caused by the sedimentation processes, their long axes directed more parallel to the sagittal plane than in *Palaeolagus*, in which the long axis of the auditory bulla forms an angle of about 45° with the sagittal plane of the skull. The external meatus of *Litolagus molidens* is equally long in *Palaeolagus haydeni*, and the position of the stylomastoid foramen is clear in *Litolagus molidens* AMNH FM 143955, on the left side of the skull.

The dorsal exposure of petromastoid (Craigie, 1945), or the mastoid exposure of the petrosal (Meng et al., 2003), is massive in *Litolagus molidens*, somewhat swollen, and covered with delicate ornamentation that is finer than that of the frontal (fig. 25); this ornamentation, while typical for this element in lagomorphs (Craigie, 1945), is better expressed in *Litolagus* than in *Palaeolagus*. It protrudes over the surface of the parietal as a noticeable, right-angled triangle with ventrally directed mastoid process (Craigie, 1945), otherwise called the paroccipital process of petrosal (sensu Wible, 2007). The general outline of the mastoid exposure of petrosal is similar in all lagomorphs, but the exact position of this element in the skull differs between modern leporids and Paleogene genera discussed herein. In modern leporids it is bent ventrally together with the entire occipital region and part of the parietals, whereas in palaeolagines and *Litolagus* it is oriented much more horizontally. Thus, the right angle of the triangular form of the mastoid exposure is directed distad, with the mastoid process pointing ventrally with slight anterior inclination (figs. 25–26).

MANDIBLE: The mandibles of *Litolagus molidens* (AMNH FM 143955) are almost complete (fig. 28), the left one having a partly damaged condylar process. In AMNH F:AM 105991 only mandible bodies with dentition are preserved, and the left mandible produced its impression in the underlying matrix. The whole mandible is larger than that of *Chadrolagus emryi* and *Palaeolagus haydeni* and more slender. Moreover, the mandible of *Litolagus molidens* has a higher and more delicate condylar process and slightly longer diastema (almost equal in length to the LTR) than in *Palaeolagus* and *Megalagus* (fig. 21, table 2). The ratio of the LTR to the LDL in *Litolagus* is closest to that of *Archaeolagus ennisianus* (table 2).

The articular head in *Litolagus molidens* is wider and proportionally shorter than that of *Palaeolagus*. The coronoid process is of similar size in both species, although in *Litolagus* it seems to be less projecting than in *Palaeolagus*. The coronoid crest is strongly developed and similar in both species, although the mandibular notch is slightly deeper and more flared out in *Litolagus* than in *Palaeolagus*.

The angular process in *Litolagus* is visibly longer than in *Palaeolagus*, protruding more distally. The distal margin of the mandibular ramus is incised more deeply, producing an angular process that is more pointed. The masseteric line has a similar course and the masseteric fossa in *Litolagus* is similarly formed as in *Palaeolagus*, occupying almost the whole lateral area of the mandible ramus. The anterior margin of the masseteric fossa has a distinct triangular tubercle also seen in *Megalagus* and *Mytonolagus*. The tubercle is located more posteriorly in *Litolagus* (under m3) than in *Palaeolagus* (under the m2/m3 contact).

The ventral margin of the mandible body below m3 is not as concave as in *Palaeolagus*; thus, it seems to gently increase in depth distally, whereas in *Palaeolagus haydeni* the greatest depth is at the level of p4. The lower incisor in *Litolagus molidens* reaches only the anterior part of p4, similar to that in *Chadrolagus emryi* and *Limitolagus roosevelti*, and unlike in *Palaeolagus*

TABLE 8. Lower tooth measurements (mm) of *Limitolagus roosevelti*.

Specimen	p3			p4			m1			m2			m3		
	L	TriW	TalW	L	TriW	TalW	L	TriW	TalW	L	TriW	TalW	L	TriW	TalW
AMNH F:AM 06000	2.08	1.62	2.01	2.11	2.49	2.11	2.40	2.55	2.02	2.06	2.43	1.90	1.32	1.51	0.97
AMNH F:AM 05995	2.63	1.78	2.19	2.32	2.45	2.02	2.48	2.44	1.92	2.64	2.39	1.91	1.58	1.38	1.00
AMNH F:AM 05993	2.04	1.45	1.93												
AMNH F:AM 43391	2.16	1.58	2.10	2.04	2.24	2.10									
AMNH F:AM 05992	2.20	1.60	1.94	2.07	2.26	1.90	2.31	2.57	2.11	2.38	2.45	2.05			
AMNH F:AM 06001	2.59	1.82	2.25	2.29	2.34	2.14	2.47	2.71	2.31	2.54	2.52	2.19	1.74	1.48	1.52
AMNH F:AM 05999	2.25	1.50	2.08	2.28	2.26	2.16	2.46	2.41	2.10	2.50	2.32	2.11			
AMNH F:AM 43385	2.00	1.62	1.96	1.92	2.42	1.97	2.61	2.47	2.14	2.32	2.44	1.99			
AMNH F:AM 43386	2.06	1.62	2.24	2.08	2.37	2.13	2.27	2.55	2.20	2.08	2.37	2.01			
AMNH F:AM 05997	2.24		2.16	2.20	2.38	2.23	2.44	2.59	2.18	2.35	2.62	2.20			
AMNH F:AM 06002			2.35	2.50	2.57	2.41	2.66	2.76	2.41	2.76	2.74	2.41			
AMNH F:AM 05996				2.15	2.24	2.05	2.49	2.53	2.05	2.33	2.37	2.05			
AMNH F:AM 05998							2.26	2.60	2.28	2.10	2.63	2.18	1.45	1.41	1.00

haydeni, *P. temnodon*, and *P. burkei*, where the di2 reaches to the level of m1. Additionally, the lower incisor is less procumbent in *Palaeolagus*, erupting from the alveolus at a greater angle than in *Litolagus*, which has relatively less recurved incisor, although its distal end is slightly bent upward, so it is embedded farther from the ventral margin of the mandible than in *Limitolagus roosevelti*. The p3 in *Litolagus* is erect in its alveolus and its distal end produces a gentle impression at the lateral side of the mandibular body. In *Palaeolagus* the p3 is gently bent anteriorly and no such impression can be recognized.

The arrangement and number of the mental foramina is variable in lagomorphs, especially in palaeolagines. Whereas the first (anterior) mental foramen is located at the diastemal part of the mandible body, the second can be either clearly developed in the area near the p3–p4 alveolus or it can be indistinguishable from other perforations on the lateral surface of the mandibular body. In *Litolagus molidens* (AMNH FM 143955), the first mental foramen is located at two-thirds of diastema length, more anteriorly and medially than in some specimens of *Palaeolagus haydeni* (e.g., AMNH FM 143956), whereas in AMNH F:AM 105991 it is oriented more laterally on the mandibular body. The second mental foramen appears below the talonid of p3 in AMNH FM 143955, accompanied by a few smaller fenestrae and is completely obscured by a series of crude ornamentations spreading between the distal part of the diastema and the alveolus of p4 at the ventrolateral part of the mandible body.

DENTITION: The upper incisors (dI2) are relatively wider and flatter than in *Chadrolagus emryi*, *Palaeolagus haydeni,* and *P. temnodon*, but relatively less flattened than in *Archaeolagus ennisianus*. Also, the mesial lobe in *Litolagus* is wider (almost equal in width to the lateral lobe) than in the other species. The lower incisor (di2) resembles that of *Palaeolagus haydeni*, in that it is relatively narrow and high, but with a markedly wider anterior margin.

The upper and lower teeth of *Litolagus molidens* (figs. 31–32; tables 9–10) show fully hypsodont morphology and relatively early in ontogeny form the lingual enamel bridges, thus expressing some ontogenetic acceleration, in which respect they resemble *Chadrolagus* (figs. 6, 8). Nevertheless, the development of the occlusal enamel pattern, especially of P2, P3, and p3 differentiates this species from *Chadrolagus* and the fully hypsodont *Palaeolagus* species.

The early stages of wear of P2 are not known, but at a moderate stage of wear it is bilobate, showing no trace of the buccal lobe. The P2 of *Litolagus* is more oval than those of *Chadrolagus* or *Palaeolagus*, with the longer axis positioned transversely, as in *Limitolagus* (fig. 20) and *P. burkei*. The lingual lobe is full and round, larger than the buccal one. Heavily worn specimens lose the anterior reentrant and their occlusal surface becomes completely smooth and gently concave (fig. 31).

The P3 is relatively slender and compressed anterodistally in comparison with *Chadrolagus* or *Palaeolagus haydeni*. Its buccal side is oblique and the distalmost part forms a long projection. In *Litolagus*, as in *Chadrolagus*, there is an asymmetrical structure of the P3 shaft with pronounced distal ridge, homologous to the distal root in the semihypsodont species. The P3 closes and loses a crescent very quickly but preserves open and deep hypostriae for a long time in ontogeny. The crescent is already lost in the holotype specimen (LACM-CIT 1568) described by Dawson (1958), which is a subadult specimen with long bones showing incomplete fusion of the epiphyses. All other specimens of *Litolagus* have open and deep hypostriae, which are similarly deep on P3–M2, resembling in this respect *Palaeolagus burkei* and *P. hypsodus* rather than *Chadrolagus*, which maintains the deepest hypostria on P4 at comparable stage of wear (fig. 6). The M3 is slightly smaller than in *Chadrolagus* and *Palaeolagus* and its occlusal surface is rounder than in these two genera. The enamel pattern of M3 is completely obliterated in all known specimens of *Litolagus* (fig. 31; see also Dawson, 1958: fig. 15).

The lower dentition in two newly described skulls (AMNH FM 143955 and F:AM 105991) does not depart in morphology from the holotype described by Dawson (1958: fig. 16). The p3 shows simple morphology, even in the holotype, which is a young individual (Dawson, 1958: 33). The tooth is relatively short in comparison to *Palaeolagus* or even *Chadrolagus* (figs. 15, 32, table 10). It has a single buccal reentrant filled with cement and no traces of the lingual reentrant or a lake. Dawson (1958) stated that the lingual reentrant is lost early in ontogeny, but in fact it is not certain that it was ever present, because in all known specimens no trace of it can be found. The trigonid of p3 in *Litolagus molidens* is round with a smooth outline and is markedly narrower than the talonid, which is distinctively short in comparison with other contemporary lagomorphs. The lingual margin of the tooth in the holotype bears a visible concavity flanked by an eminent metaconid anteriorly and well-developed entoconid distally (fig. 24E; see also Dawson, 1958: fig. 16). The new specimens described herein display slightly more advanced wear and this concavity was either completely or greatly eradicated, but the proportions of the trigonid and talonid remain the same (fig. 32).
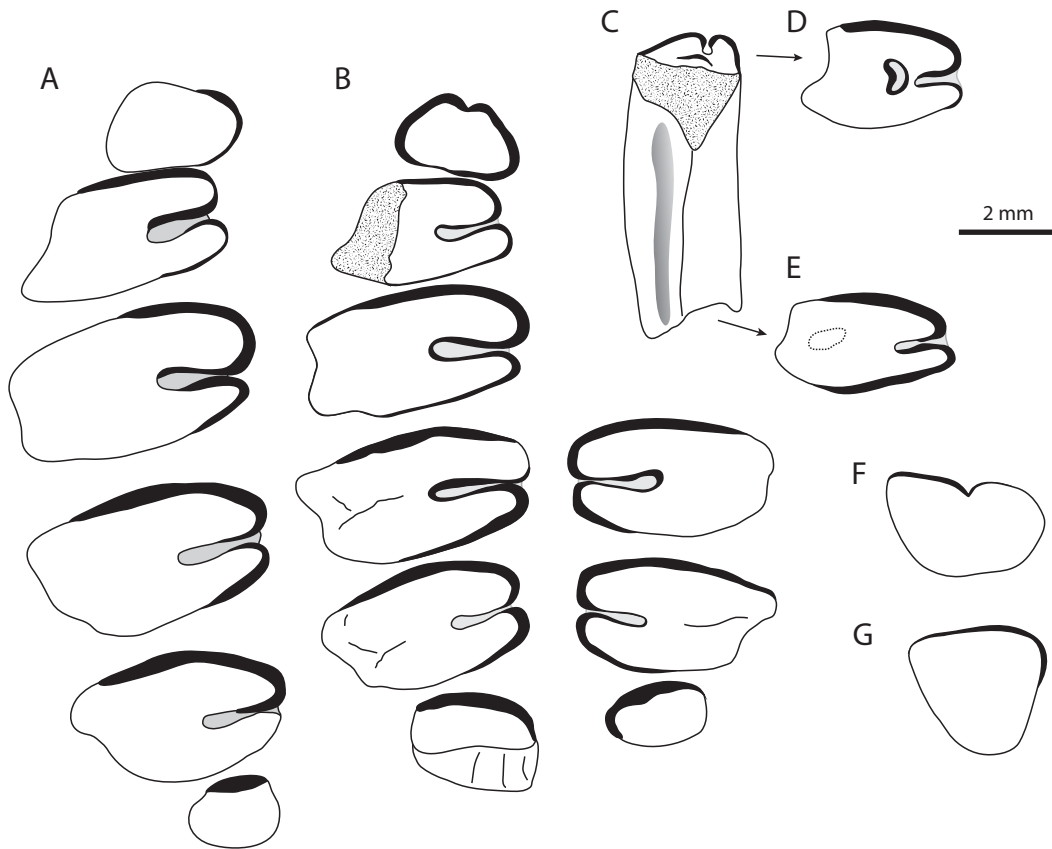
FIG. 31. Incisors and upper cheek teeth of *Litolagus molidens*, the Chadronian-Orellan transition, Wyoming. **A,** right tooth row (AMNH F:AM 105991) in occlusal view, Reno Ranch; **B,** right and partial left tooth rows (AMNH FM 143955) in occlusal view, Herman Wulff Ranch; right P3 (AMNH F:AM 105994) in buccal (**C**), occlusal (**D**), and ventral (**E**) views, Seaman Hills; **F,** left upper and **G,** left lower incisors of AMNH FM 143955.

The lower molariform teeth, p4–m2, are very similar and form thin enamel bridges very early in ontogeny, similarly to *Chadrolagus* and *Limitolagus*. The cement is well developed on both upper and lower teeth and fills the hypostriae and space between the trigonids and talonids.

The m3 of *Litolagus molidens* does not differ markedly from that of *Chadrolagus*, although it is more buccolingually extended and has a visibly wider trigonid (fig. 32). The m3 forms a wide enamel bridge and persists in this form for a long time, whereas its wear is marked only by the shallowing of the buccal reentrant, which does not form a lake as seen in *Palaeolagus temnodon*.

COMMENTS: *Litolagus molidens* is an extremely rare species, known only from a few specimens found in a limited area a few miles SE of Douglas, Wyoming (Dawson, 1958). The original description of the species included only two specimens, the holotype (LACM CIT 1568) and an adult skull FH 10283 (Dawson, 1958). Prothero and Whittlesey (1998) refer to five known specimens from the Lusk and Douglas area, but did not give a precise description of the material or collection numbers, although it is possible that they refer to the specimens collected by the Frick Laboratory of AMNH, which are revisited in this paper.

Both skulls assigned to *Litolagus molidens*, described herein (AMNH FM 143955 and F:AM 105991) come from sediments above the P.W.L., roughly marking the Eocene-Oligocene transition (Evanoff, 1990; Evanoff et al., 1992), and the same applies to both specimens mentioned by Dawson (1958). The only specimen known from a different horizon is an isolated P3 (AMNH F:AM 105994) found in Channel Quarry (SE Seaman Hills), which according to Skinner (ms) lies below the Chadronian-Orellan boundary. Prothero and Whittlesey (1998) stated that one of the specimens from the Douglas area attributed to *Litolagus* was found ca. 10 m below "the 5 tuff" correlated to P.W.L., but revision of the material excavated by the Frick Laboratory revealed that all specimens below P.W.L. from the Douglas vicinity were either *Limitolagus*, which otherwise is similar in size to *Litolagus* (tables 6–10), or *Palaeolagus temnodon*.

CHARACTER ANALYSIS

In the fossil record of lagomorphs teeth are the most common and often the only accessible material available for study; thus, dental characters are the predominant source of information for reconstructing the phylogenetic relationships of the taxa. Two important morphological dental character sets can be analyzed in Lagomorpha from the evolutionary perspective: the hypsodonty-related features (see Tobien, 1978) and the occlusal enamel pattern. The first character set includes the presence (or absence), formation, and structure of the buccal rootlets of the tooth, and the height of the main root and of the crown. The second character set comprises the formation of crescent, buccal valley, and hypostriae, the persistence of these structures at open or closed (lakelike) stages, and the interplay between these characters in ontogeny, which among fossils is observed as a sequence of the wear pattern.

The present analysis is aimed at resolving the relationships of Eocene and Oligocene lineages of North American lagomorphs, but is limited to the taxa appearing near the Eocene-Oligocene transition. It includes 11 species and is based on 44 dental and cranial characters. The characters were chosen to depict as accurately as possible the often subtle changes in generally uniform lagomorph morphology. Although some of them were already used in the phylogenetic analyses of Duplicidentata (McKenna, 1982; Meng and Wyss, 2001; Meng et al., 2003; Asher et al., 2005), in this analysis these characters were reassessed and made more precise. The increase in the character resolution by a more detailed approach proved successful in the phylogenetic analysis of closely related taxa, namely of *Ochotona* (Fostowicz-Frelik et al., 2010). This analysis has three main purposes: first, to test *Chadrolagus-Litolagus* relationships implied by Dawson (2008); second, to check the suitability of the chosen dental characters for phylogenetic reconstruction of the Paleogene lagomorphs, and, finally, to examine the possible affiliation of *Litolagus* with more advanced lineages, by inclusion of a derived species, *Archaeolagus ennisianus*, a representative of Archaeolaginae (Leporidae). Early Oligocene *Desmatolagus gobiensis* from the Hasanda Gol Formation (Mongolia) was chosen as the outgroup: it is one of the best known and well-represented members of the *Desmatolagus* lineage dating back to the late Eocene of Asia (Meng et al., 2005).
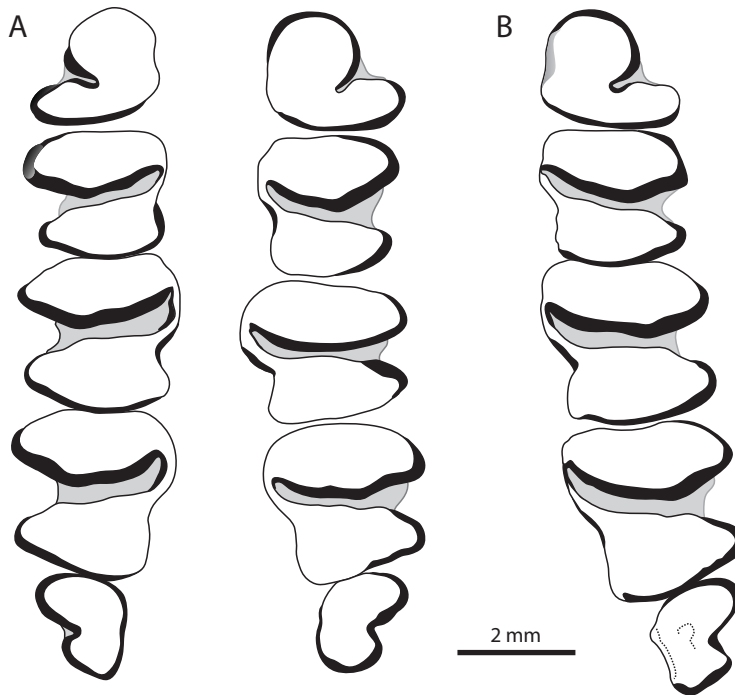
FIG. 32. Lower dentition of *Litolagus molidens* from the Chadronian-Orellan transition of Converse County, Wyoming. **A,** right tooth row p3–m3 (AMNH F:AM 105991); **B,** right tooth row p3–m3 (AMNH FM 143955). Both in occlusal view.

Dentition

1. Upper incisors (dI2) in cross section: (0) heart shaped, distal margin very narrow; (1) trapezoid, ventral margin wider, tooth wider than long; (2) nearly square, anteroposterior compression weak (3) rectangular, strongly compressed anteroposteriorly.

In lagomorphs, the shape of the upper incisor in cross section is characteristic at the generic and specific level, especially among Leporidae (Koby, 1959). It proved variable among stem taxa studied here. The character was not employed previously in cladistic analyses in such detail. Meng et al. (2003: char. 22) distinguished different shapes of the incisor cross section in gliroid mammals, but they stated that all lagomorphs have anteroposteriorly compressed upper incisors and coded *Ochotona*, *Lepus*, and *Palaeolagus* as (1). As this is true for most of the species, some of them (e.g., *Lepus timidus*) express less compression and their W/L ratio for dI2 is close to 1.0. Although most stem taxa have heart-shaped or trapezoid dI2, in *Palaeolagus temnodon* and *P. haydeni* the tooth is more square and less compressed, whereas in *Archaeolagus ennisianus* it is strongly compressed.

2. Medial lobe of dI2: (0) both lobes of similar width, medial one slightly narrower than the lateral one; (1) medial lobe markedly narrower than the lateral lobe; (2) medial lobe wider than the lateral lobe.

3. Position of dI2 medial lobe: (0) projecting anteriorly; (1) level with the lateral lobe.

The size, shape and position of the medial (mesial) lobe of the dI2 is variable among lagomorph taxa. Most species, including modern leporids, have the medial lobe narrower and projecting more anteriorly, although among extinct Paleogene taxa some variation is observed. The

TABLE 9. Skull and upper tooth measurements (in mm) of *Litolagus molidens.* For abbreviations, see figure 3.

Skull measurement	AMNH FM 143955	AMNH F:AM 105991	Upper tooth measurement	AMNH FM 143955	AMNH F:AM 105991
SL	63.1		DI2 W	2.30	
UDL	13.2		DI2 L	1.62	
UTR	12.4	12.8	P2 W	1.90	2.10
InW	5.9		P2 L	1.45	1.43
MxW	18.0		P3 W	3.00	3.30
JuW	24.9	23.9	P3 L	1.85	1.74
PaW	8.4		P4 W	3.58	3.90
ChW	3.0		P4 L	2.00	2.14
PaL	6.0		M1 W	3.24	3.84
PalL	2.6		M1 L	1.80	2.08
NaL	21.9		M2 W	3.13	3.35
FrL	19.3	19.9	M2 L	1.82	1.99
FrW	7.8	8.3	M3 W	1.81	1.43
ParL	21.0	20.4	M3 L	1.14	1.13
SqW	19.6	19.3			
BL	15.3				

medial lobe is level with the lateral one in *Litolagus molidens.*

4. P2 crown morphology: (0) persistently trilobate; (1) bilobate in adults, trilobate in juveniles and could be prolonged in ontogeny until subadult stages; (2) bilobate, third, buccal lobe is present only as a vestigial structure in the freshly erupted teeth.

The P2 in lagomorphs has a very conservative structure with basically two variants observed throughout their evolutionary history. There are either three lobes remaining until late in ontogeny, or two lobes only. However, in some species the buccal lobe (always more weakly developed) persists in ontogeny a little longer, to the more advanced stages of wear marked by closure of the crescents and formation of the hypostrial lakes (in *P. temnodon*) or appears only in juveniles and wears away quickly; thus, the character is somewhat a mixed condition. The trilobate P2 can be considered as more primitive, but it can also be found in more derived genera, such as *Prolagus* (e.g., López Martínez, 1989; Fostowicz-Frelik et al., 2010). Whether this structure of P2 appeared independently twice and thus is homoplastic, or was inherited by *Prolagus* from its stem ancestor (*Piezodus* or "*Amphilagus ulmensis*"; see Tobien, 1974) is uncertain.

5. P2 main anterior fold: (0) deep and persistent; (1) initially deep, but obliterated in older specimens, which leaves a shallow groove at the anterior tooth wall.

The main anterior reentrant of P2 is generally a persistent structure in most lagomorph species, although in some taxa, such as *Litolagus molidens*, it tends to shallow quickly, with progressing wear, until complete obliteration in the mature specimens (fig. 31A).

6. P2 occlusal surface: (0) not compressed, heart shaped or round, central lobe dominating and projected anteriorly; (1) anteroposteriorly compressed, central and lingual lobes of equal size, anterior margin flattened, no lobe projecting.

Within the conservative tri- or bilobate structure of P2, the occlusal surface shows variability in size of particular lobes and its general outline, which can be almost round or heart shaped as in *Chadrolagus emryi* (fig. 6E, F), or an anteroposteriorly flattened oval as in *Litolagus molidens*

TABLE 10. Mandible and lower tooth measurements (in mm) of *Litolagus molidens* from Wyoming. For abbreviations, see figures 3 and 4.

Measurement	AMNH FM 143955	AMNH F:AM 105991
Mandible		
CpH	30.0	28.8
LDL	10.8	
LTR	12.5	12.0
MH	10.7	10.6
Lower dentition		
di2 W	1.87	
di2 L	1.82	
p3 TriW	1.57	1.54
p3 TalW	2.35	2.34
p3 L	1.92	1.99
p4 TriW	2.42	2.41
p4 TalW	2.19	2.07
p4 L	2.44	2.36
m1 TriW	2.79	2.80
m1 TalW	2.36	2.30
m1 L	2.79	2.40
m2 TriW	2.69	2.69
m2 TalW	2.20	2.17
m2 L	2.77	2.70
m3 TriW	1.56	1.44
m3 TalW	1.12	1.07
m3 L	1.75	1.71

(fig. 31A, B) or *Palaeolagus burkei*.

7. dP2 morphology: (0) mimicking the morphology of P3, with extended lingual lobe and small round buccal lobe; (1) similar in morphology to adult P2.

As frequently observed in lagomorphs and other mammals (Tobien, 1986), morphology of the deciduous teeth is in some aspects more progressive than of their permanent counterpart. In most stem lagomorphs the upper deciduous dentition prefigures the morphology of the permanent tooth locus next in row (in this instance, dP2 closely resembles permanent P3). However, this was not observed for *Chadrolagus emryi*, in which dP2 looks more similar to P2 than to P3. The state of this character cannot be ascertained for taxa whose deciduous teeth are missing.

8. P3 molarization: (0) not molarized; (1) semimolarized, molarization not complete and delayed in ontogeny until subadult stages; (2) molarization considerably postponed, until adult stage; (3) molarized.

The P3 expresses notable variability in shape in lagomorphs, which in different lineages display unmolarized to molarized condition. It tends to be unmolarized in ochotonids (Erbajeva, 1988) and molarized in leporids (McKenna, 1982). The molarization manifests, among other things, in the complete closure of the crescentic valley and the full confluence of the three lobes at the labial side. Additionally, the anterior part of the tooth formed by the lingual lobe tends to be elongate and level with the posterior lobe, mimicking the structure of P4. Among stem lagomorphs, the crescentic valley shows different stages of closure, from completely open at all stages of wear (e.g., in *Mytonolagus*), or open long in ontogeny (different in each species of *Palaeolagus* and *Chadrolagus emryi*), through the crescentic valley closing quickly already in the juvenile specimens. The character was scored (1) for *Litolagus molidens* and *Limitolagus roosevelti* on the basis of the strong asymmetry of P3, which in all specimens does not show any trace of crescent; thus, its exact morphology at the juvenile stage is unknown.

9. P3 crown morphology (hypostria): (0) lack of hypostria; (1) shallow but defined hypostria (narrow, not exceeding one-quarter of the width of the occlusal surface), not forming lakes; (2) shallow but defined hypostria, quickly closing and forming lakes; (3) deep (equal to or exceeding one-third of the width of the occlusal surface) persistent, and not forming lakes.

Among the analyzed taxa the P3 hypostria is either poorly defined initially as a very shallow concavity devoid of cement, indented in the lingual margin of the tooth (*Mytonolagus*) and scored here as (0), or narrower, well defined, of variable depth, displayed initially as reentrant. Persistence of this structure in the open state differs greatly among species. It can either close very quickly, producing the hypostrial lake, or remain open for a longer period and consecutively shallowing as the wear progresses. Again, the appearance of the lake stage is a variable character and it does not manifest in all specimens (Emry and Gawne, 1986); nevertheless, the character was coded as (2) if the lake stage was observed in most specimens in a sample.

10. P3 root morphology: (0) two buccal rootlets located symmetrically on the shaft; (1) two buccal rootlets located asymmetrically on the shaft; (2) one buccal rootlet, or extended common base giving rise to two rootlets; (3) buccal rootlets lost.

11. P4 root morphology: (0) two buccal rootlets; (1) one buccal rootlet or extended common base giving rise to two rootlets; (2) buccal rootlets lost.

The number of the buccal rootlets in the premolars and the primitive state of this character in Lagomorpha has been frequently discussed (Wood, 1940; Dawson, 1958, 1970; Sych, 1977). Some Eocene genera (e.g., *Gobiolagus*, *Lushilagus*, and *Procaprolagus*) characterized by primitive low-crowned dentition have two buccal roots on P3 and P4 (Li, 1965, Meng et al., 2005). The same is also true for stem duplicidentate *Gomphos* (Meng et al., 2004; Kraatz et al., 2009; Meng et al., 2009). On the other hand, one of the earliest lagomorphs described so far, *Dawsonolagus antiquus*, from the late Early Eocene of Nei Mongol, has a single root at P3 and P4 (Li et al., 2007), as do North American *Mytonolagus petersoni* and *M. wyomingensis*, which are much more advanced in the development of hypsodonty (Burke, 1934; Dawson, 1970). Dawson (1970), on the basis of observations made on the specimens from the Badwater Creek (Wyoming), proposed the double-rooted condition as derived in the *Mytonolagus* lineage. Interestingly, P3 and P4 are polymorphic in the number of roots in *Mytonolagus ashcrafti* from the Duchesnean of Montana (Fostowicz-Frelik and Tabrum, 2009). However, even double-rooted forms mostly show an extended common base, noted also for the specimens from Badwater Creek (Dawson, 1970). It is possible that the double-rooted condition appeared twice in lagomorph evolution, especially given that some more advanced genera, such as *Palaeolagus* (and *Megalagus*), are different than *Mytonolagus* in the arrangement of the buccal roots on the main root (shaft). In those species, the anterior root is oriented much more ventrally on the shaft, and frequently has even coalesced with it through most of its length, whereas the posterior one is shorter, free, and has a strong base resulting in the buccal extension of the occlusal area of the posteroloph. This extension, as well as the distinct ridge along the shaft, is present also in P3 of fully hypsodont genera such as *Chadrolagus* and *Litolagus*.

12. Hypostriae on P4–M2: (0) shallow; (1) deeper but quickly closing in ontogeny, forming lakes more or less persistent than the crescentic valley; (2) deep and open throughout the ontogeny.

Among stem lagomorphs, two general patterns of the hypostrial change due to wear can be observed, provided that the hypostriae are deep enough (cutting about one-third or more across of the occlusal surface). These are: quick closure of the fold resulting in creation of usually persistent lake, and maintenance of the fold at the original open stage. It seems that the "lake type"

hypostriae are more common in the more primitive genera (e.g., *Megalagus*, *Mytonolagus*, and the Eocene species of *Palaeolagus*, such as *P. primus* and *P. temnodon*), expressing also unilateral hypsodonty (Dawson, 1958, 1970; Emry and Gawne, 1986; Fostowicz-Frelik and Tabrum, 2009). The lake-forming hypostriae are also typical for fully hypsodont *Palaeolagus haydeni*, but *Chadrolagus emryi* mostly lacks hypostrial lakes, and although Gawne (1978) mentioned the presence of some "ephemeral lakes" on P4–M2, these structures are rare. Similarly, hypostrial lakes are lacking in fully hypsodont *Limitolagus roosevelti*, *Litolagus molidens*, *Palaeolagus burkei,* and *P. hypsodus*, as well as *Archaeolagus ennisianus* (Dawson, 1958, 2008).

13. Stages of hypostriae development: (0) hypostriae display unequal depth at different loci during wear; (1) depth of the hypostriae similar at all loci throughout ontogeny.

In the tooth row the depth of the hypostriae is frequently uneven, from very shallow on P3 to deepest on M1 and P4. It changes during ontogeny; for example, in *Chadrolagus emryi* it can be deepest initially on M1, but on P4 during late stages of wear (fig. 6). In the species that form hypostrial lakes, the depth of the external remnants of the hypostriae is always uneven in the tooth row. However, some species, e.g., *Litolagus molidens* (fig. 31) and *Palaeolagus burkei*, which display long-lasting, open hypostriae show uniformly even depth in these structures relative to the width of the occlusal surface (within ca. 10% deviation).

14. p3 occlusal surface morphology: (0) irregularly triangular, trigonid and talonid poorly separated; (1) simple bilobate, trigonid and talonid well defined (reentrant or reentrants moderately deep); (2) bilobate, with trigonid and talonid distinctly separated by deep reentrants, especially at the earlier stages of wear; (3) originally bilobate, but complex, reentrants deep, numerous, and persistent.

The simplest form is the plain bilobate p3 with only one shallow buccal reentrant entering the occlusal surface (e.g., Tobien, 1974; Meng et al., 2005), whereas the most complex p3 may be a bi- or tribilobate structure (sometimes with an isolated anteroconid) and have up to five reentrants of different depths (Hibbard, 1963; López Martínez, 1989; Averianov and Tesakov, 1997; Fostowicz-Frelik et al., 2010).

15. p3 trigonid size: (0) distinctly smaller than talonid; (1) slightly smaller or equal to talonid; (2) larger than talonid.

The p3 trigonid is variably developed, ranging from an indistinct round lobelet (e.g., in *Desmatolagus*) to a large, complex, and dominating structure of the tooth, as in Leporidae and some ochotonids (e.g., *Ochotonoides* or *Pliolagomys*; Erbajeva, 1988; Qiu, 1987; Fostowicz-Frelik et al., 2010).

16. p3 reentrants morphology: (0) lingual reentrant extremely shallow and not persistent, or entirely lacking; (1) in juvenile and moderately worn specimens both reentrants (buccal and lingual) equally deep, later the lingual one forms variably persistent lake; (2) lingual reentrant shallower than buccal one, no lakes.

The reentrants can appear at the occlusal surface of p3 cutting in from buccal, lingual, or anterior sides. Generally, the main buccal reentrant (hypoflexid) is always present, even in the most worn specimens. In most genera with a more or less persistent lingual reentrant, the second main fold (mesoflexid) cuts into the occlusal surface just opposite the hypoflexid. It persists in the open state for some time and either shallows and vanishes, as in *Megalagus* and some

species of *Mytonolagus* (*M. ashcrafti*), or closes, forming a lake if its depth is large enough, such as in *Chadrolagus*, *Palaeolagus temnodon*, *P. haydeni*, and *P. burkei*. The persistence of the lake structure is variable among the species, ranging from relatively short-lived in *Chadrolagus* to prolonged in a heavily worn stage in *Palaeolagus temnodon*.

In some genera, such as *Ochotona* or *Gobiolagus* (Erbajeva, 1988, and Meng et al., 2005, respectively), additional reentrants, located more anteriorly (lingual paraflexid and buccal protoflexid; see Fostowicz-Frelik, 2008: fig. 1) can occur. Furthermore, in some leporids (e.g., *Trischizolagus*, *Serengetilagus*, and most extant genera) as well as in some derived Ochotonidae (*Ochotona*, *Ochotonoides*, and *Pliolagomys*) anterior reentrants can appear (Qiu, 1987; Erbajeva, 1988; Fostowicz-Frelik et al., 2010). All species included in the present analysis display only hypoflexid and occasionally mesoflexid.

17. Position of p3 metaconid in relation to protoconid: (0) posterior; (1) anterior; (2) level.

Gawne (1978) stressed the anterior position of the metaconid as one of the characters distinguishing *Chadrolagus emryi* from *Palaeolagus temnodon* and *P. haydeni*, which have the protoconid positioned anteriorly. The anterior position of the protoconid also is present in *Megalagus brachyodon* and *Mytonolagus ashcrafti* with an even more distinctive and more posteriorly oriented metaconid. In these species the relative position of the cusps is visible most clearly in juvenile specimens when the occlusal surface is forming, whereas in older specimens the exact position of the cusps is obscured and the outline of the anterior margin of the p3 trigonid can be variable and misleading. On the other hand, in *P. burkei* a pronounced anterior position of the metaconid is well expressed, even in the older specimens, due to the deviation of the transverse axes of the trigonid and talonid. In *Litolagus*, *Archaeolagus*, and modern *Lepus*, the position of the metaconid is level with the protoconid and both cusps are positioned relatively posteriorly and are inconspicuous. In younger specimens of *Litolagus molidens* the metaconid forms a distinct projection in the lingual margin of the tooth, as observed in the type specimen (Dawson, 1958: fig. 16), and it is expressed more weakly but still present in the right p3 of AMNH FM 143955 (fig. 32).

18. p3 root morphology: (0) two roots; (1) one root (joint pulp chamber).

19. p4 root morphology: (0) two roots; (1) one root, one pulp chamber; (2) one root, two separate pulp chambers.

20. m1 root morphology: (0) two roots; (1) one root, one pulp chamber; (2) one root, two separate pulp chambers.

21. m2 root morphology: (0) two roots; (1) one root, one pulp chamber; (2) one root, two separate pulp chambers.

The morphology of the root portion in lagomorphs is closely related to the development of hypsodonty. In the fully hypsodont species the lower cheek teeth, p4–m2, maintain separation of the trigonid and talonid also in the radical part, and thus have two independent pulp chambers joined by a thin lamella of the lingual bridge. On the other hand, the structure of roots in the lower teeth of the unilaterally hypsodont species may vary. The root portion either forms a common pulp chamber, which tightens its ventral entrance into an irregular figure-eight shape, as in *Palaeolagus temnodon*, or two independent roots are clearly formed, as in *Mytonolagus* and *Megalagus* (Dawson, 1970, 2008; Fostowicz-Frelik and Tabrum, 2009), and European *Amphilagus*, *Eurolagus,* and *Titanomys* lineages (Tobien, 1974; Fostowicz-Frelik et al., 2012a). A slightly different pattern of root forma-

tion applies to p3, which forms two roots or one root with double tooth chamber in the semihypsodont forms and one root with one tooth chamber in the fully hypsodont forms.

22. Formation of lingual dental bridges: (0) relatively late in ontogeny; (1) early in ontogeny; (2) markedly delayed in ontogeny or absent.

In stem lagomorphs and Leporidae the trigonid joins the talonid lingually by a thin dental lamella or "lingual bridge," formed by the dentine and two enamel layers (of which the external one tends to disappear in Archaeolaginae and Leporinae). The moment in ontogeny when the bridge reaches the occlusal surface varies among the taxa regardless of their degree of hypsodonty, although in modern species the bridges form relatively early. Among stem taxa, in a considerable group, including *Desmatolagus*, *Palaeolagus temnodon*, *Megalagus*, and *Mytonolagus*, bridge formation is delayed to a stage of moderate wear. Nevertheless, in four North American Paleogene fully hypsodont species two extremes can be observed: early formation of bridges marking the overall acceleration of the maturation of the occlusal surface in *Chadrolagus emryi*, *Limitolagus roosevelti*, and *Litolagus molidens*, and extreme retardation in *Palaeolagus burkei*.

23. Relative length of trigonids and talonids: (0) trigonids compressed anteroposteriorly; (1) trigonids of similar length as talonids.

The lower cheek teeth of lagomorphs retain the primitive structure of tribosphenic teeth, which undergoes only slight modification during evolution. The most primitive, Eocene and early Oligocene lagomorphs, such as *Lushilagus* or *Shamolagus* (not included in this analysis) and *Desmatolagus*, *Mytonolagus*, and *Megalagus* still display (as is typical for tribosphenic molars) shortening of the trigonids and elongation of the talonids. These differences tend to lessen in more derived genera, and can be related to strongly marked unilateral hypsodonty, because no fully hypsodont Oligocene species or modern leporids express trigonid compression.

Cranium

24. Basicranial angle: (0) skull flat; (1) skull arched.

Cranial base angulation is related to the ability to balace the head and thus, to locomotor adaptations. An increased basicranial angle most probably appeared more than once independently in Lagomorpha, as it is encountered in some distantly related lineages, such as leporids and prolagids (McKenna, 1982). Even among representatives of *Ochotona*, generally considered as having a flat skull (McKenna, 1982; Dawson, 2008), a degree of variability is observed (Meng et al., 2003; Fostowicz-Frelik et al., 2010).

25. Braincase outline: (0) flat and horizontal; (1) parietal visibly rounded and the occipital region inclined ventrally.

The extended and flattened parietal region of the skull is a character shared by some stem lagomorphs with basal duplicidentates included in Mimotonidae (Li and Ting, 1993; Asher et al., 2005). *Litolagus* and *Palaeolagus* display such a structure of the parietal region; it is slightly convex in the anterior part, flattens posteriorly and forms a well-defined edge at the occipital suture. On the other hand, in Archaeolaginae and extant Leporidae, the parietals are convex over the entire length and bend ventrally, thus strongly inclining the occipital surface ventroposteriorly. The parietal region structured in that way contributes to an increase in the basicra-

nial angle, but these two characters are here coded independently, because the structure of the parietal region is not solely responsible for that character.

26. Exoccipital structure: (0) thin, L-shaped; (1) broad, semicircular.

The structure of the exoccipital is visibly different in *Palaeolagus* and *Litolagus* (not known for *Chadrolagus*) from that of *Archaeolagus* and *Lepus*. In the first two genera exocciptals are delicate and thin. They depart from the foramen magnum at a right angle as thin bone appendices that are connected with ventrally directed jugular processes, forming an L-shaped structure (fig. 27). In *Archaeolagus* and *Lepus*, exoccipitals are significantly wider and more robust, forming (together with the jugular processes directed ventrolaterally) gently semicircular plates; the jugular processes are much less distinguished from the exoccipital base than in *Litolagus* and *Palaeolagus*.

27. Position of posterior margin of incisive foramen: (0) anterior to the P2 alveolus; (1) at the P2 alveolus; (2) posterior to the P2 alveolus; (3) at P3 or farther back.

A large and long incisive foramen is characteristic of Lagomorpha and common in Glires (Novacek, 1985; Li et al., 1987; Li and Ting, 1993). The shape and position of the incisive foramen have been included into analyses of Glires relationships (Meng and Wyss, 2001; Meng et al., 2003; Asher et al., 2005; Wible, 2007). Because in lagomorphs its shape and position do not change much, a more precise character, the posterior reach, was employed in the present study. The position of the posterior margin of the foramen shows a noticeable variability among analysed taxa, with *Chadrolagus*, *Megalagus*, and *Mytonolagus* having relatively short foramina that do not extend beyond the P2 alveolus, and *Litolagus molidens* expressing the largest posterior extension with the incisive foramen ending at the P3 level.

28. Choanae position: (0) at the level of M2; (1) between M1 and M2; (2) farther anteriorly (at M1 or P4/M1).

The position of the posterior margin of the bony palate, marking the choanae, shows some variability among lagomorphs, although less so than in the case of the incisive foramen. The posterior margin of the choanae tends to shift slightly anteriorly in more advanced forms, as the bony palate shortens. In the present analysis, most species display the posterior margin of choanae located at the level of M1/M2 transition and this seems not to be related to the position of the posterior margin of the incisive foramen. Of the two species expressing the most anteriorly shifted choanae, *Litolagus molidens* also displays the most posteriorly extended incisive foramen, but *Archaeolagus ennisianus* has the incisive foramen level with the posterior margin of P2, as in all *Palaeolagus* species and *Limitolagus roosevelti*.

29. Posterior margin of zygomatic process of maxilla: (0) at P4 or between P4 and M1; (1) farther back, at M1 or M2.

The position of the posterior margin of the maxillary root of the zygoma was used for taxonomic purposes in palaeolagines (Dawson, 1958; Gawne, 1978). This character was also included in a cladistic analysis by Meng et al. (2003: char. 123). In the present work, the more anteriorly shifted anterior root of the zygoma is considered more primitive for Lagomorpha and coded (0), contrary to Meng et al. (2003) who coded the posteriorly shifted location of this structure as (0).

30. Lateral reach of zygomatic process of maxilla: (0) wide, extended; (1) not extended.

The maxillary zygomatic process forms a massive base of the zygomatic arch. The anterior-most and ventral part of the process forms the masseteric spine projecting directly anteriorly or inclined posteroventrally. In ventral view, the masseteric spine forms a flat ridged surface for muscle atachment. It can be flared more or less laterally, creating adequate space for the partial attachment of the masseter. Although, Dawson (1958) stated that the laterally extended base of the zygomatic process is an advanced character for palaeolagines, the observations on fossil and extant species of Lagomorpha do not fully support that statement, because substantial variation is observed in the degree of the lateral reach of the maxillary zygomatic process and the masseteric spine even among the extant Leporidae.

31. Inclination of frontal process of maxilla: (0) strongly inclined backward, at an angle ca. 45°; (1) more erect (inclination <15°).

The frontal process of maxilla forms a long spine projecting posterodorsally and framing the anterior margin of the orbit. The inclination of this bone spine varies among the species, with a tendency to be more inclined posteriorly in the less advanced species.

The feature was indirectly incorporated into the analyses of Meng et al. (2003: char. 129), Asher et al. (2005: char. 120), and Wible (2007: char. 12) as "anteroventral orbital rim," which was coded as (1) squared for *Palaeolagus* and leporids, and (0) round for other stem and crown lagomorphs. In the present analysis, all species express "squared" anteroventral orbital rim, but the anteroventral angle is different.

32. Relative length of bony palate: (0) long, palatal bridge equals 70% or more of the length of the upper tooth row; (1) moderate, palatal bridge equals 50%–69% of the upper toothrow length; (2) short, less than 50% of the upper toothrow length.

There is an evolutionary tendency to shorten the palate bridge in lagomorphs, which is achieved either by posterior extension of the incisive foramen or anterior extension of the internal nares opening, although the latter manner is more prevalent. Meng et al. (2003) distinguished long and short palates among analyzed taxa, whereas Averianov (1999) coded the length of the palatal bridge as a percentage of the condylobasal skull length. Because of the lack of well-preserved skull material for most of the taxa studied herein, the index was modified to the ratio of the length of the palatal bridge to the length of the upper tooth row.

33. Palatine portion of palate: (0) long, longer than the maxillary portion; (1) short, forming 40%–50% of the palatal bridge.

The long palatine portion forming an anteriorly rounded wedge is typical for palaeolagines and remains a significant portion of the hard palate in archaeolagines. However, even among palaeolagines the proportion between the maxillary and palatine portions of the hard palate differs.

34. Position of palatine suture: (0) at P3; (1) between P3 and P4; (2) at P4; (3) between P4 and M1.

The position of the palatine suture is partly related to the reduction of the palatine portion of the bony palate, although the most posterior position of this suture was observed in *Litolagus molidens*, which otherwise has a similarly reduced palatine portion as *Archaeolagus*, but a more posteriorly extended incisive foramen.

35. Pterygoid crests: (0) expanded and reclined laterally; (1) more vertical.

The pterygoid crests form the lateral walls of the posterior part of the nasal pharynx. In *Chadrolagus emryi* and most of the studied *Palaeolagus* species (except *P. temnodon*, from which that part is not known) the ectopterygoid crests are more flared laterally.

36. Zygomatic process of squamosal: (0) robust and level; (1) slender and more strongly bent ventrally.

The zygomatic process of the squamosal in *Litolagus molidens* differs visibly from other studied species, resembling the condition in some modern genera, such as *Lepus*. It is more slender and more strongly curved ventrally, which results in bringing the jugal arch closer to the skull and lowering it relative to the skull roof. *Archaeolagus ennisianus* shares the structure of the zygomatic process of the squamosal with *Chadrolagus* and *Palaeolagus*.

37. Frontal pitting: (0) absent; (1) slight; (2) significant.

Pitting (sensu Wible, 2007) is rarely observed in lagomorphs, which, although having delicate skulls fenestrated by large maxillary openings and partly constructed of lacework bone, in general have the bones of the skull roof solid, except for the occipital region. The only living exception appears to be the volcano rabbit, which has most of the dorsal skull surface covered with fine pitting (Wible, 2007) or a shallow texture of fine lacunae. The function of these is unknown, although it is probably related to vascularization of the scalp. Among palaeolagines the best expressed pitting, comparable to that of *Romerolagus diazi*, is in *Litolagus molidens*, especially on the frontals. *Palaeolagus haydeni* and *P. temnodon* also show some skull pitting, mainly at the lateral sides of nasals and in the region of the frontals just above the olfactory bulbs.

38. Orbit: (0) not enlarged, elongated and constricted dorsoventrally; (1) slightly enlarged, oval; (2) enlarged, rounded.

The shape of the orbit in lagomorphs is variable, depending on the position of the zygomatic arch and morphology of the frontal. It is more oval and anteroposteriorly extended in species with a flat skull and having zygomatic arch positioned higher on the maxilla, as in *Chadrolagus emryi*, *Palaeolagus haydeni*, and *P. burkei*. On the other hand, the orbit in some species increases, which then tends to be rounder, by lowering of the jugal arch on the alveolar process of maxilla or uplifting and extending the frontals. In *Litolagus molidens* the orbit increases both ways, although in *Palaeolagus intermedius* and *Archaeolagus ennisianus* the uplifting of the frontals is more prevalent (see Matthew, 1902).

39. Relative size of auditory bulla: (0) small, less than 99% of the upper toothrow length; (1) moderate, 100%–119% of the upper toothrow length; (2) large, 120% or more of the upper toothrow length.

The increase in size of the auditory bulla is observed in several lagomorph lineages, including both extinct and living species; among them *P. hypsodus* has relatively the largest bullae (Dawson, 1958). Also *Palaeolagus burkei* has considerably large auditory bullae, comparable to those of some species of *Ochotona* (Erbajeva, 1988; Fostowicz-Frelik et al., 2010), which in general have larger bullae than any leporid (McKenna, 1982; Wible, 2007). Averianov (1999) compared the size of the auditory bullae with the length of the occipital condyle, while in the present work the anteroposterior length of the auditory bulla was compared to the more accessible length of the upper tooth row.

Mandible

40. Position of the end of di2: (0) under m1 or farther back; (1) under p4 or at the p3/p4 level.

The primitive state for length of the deciduous second lower incisor (di2) in Glires was thoroughly discussed by Meng and Wyss (2001) and Meng et al. (2003). The present work includes only lagomorphs; thus, the states for individual characters are discussed only for that group. Only in the most primitive lagomorphs does the lower incisor extend posteriorly to m2 (Dashzeveg et al., 1998; Meng et al., 2003; Li et al., 2007), whereas in the more derived taxa the length of the incisor tends to shorten and in modern leporids it does not extend farther than p3. Thus, taking into consideration only Lagomorpha, but not all Glires, the lower incisor reaching the end of the cheek tooth row seems to be a primitive character, as stated by Dashzeveg et al. (1998).

The gradual withdrawal of the incisor from the alveolar part of the mandibular body is probably related to the development of full hypsodonty, because in most of the fully hypsodont species the di2 does not reach farther than p4, whereas in the unilaterally hypsodont forms it extends farther (to m1). However, there are exceptions to this rule; in the fully hypsodont *Palaeolagus haydeni* di2 ends most often at the m1 level (in some specimens, however, the incisor open root ends under p4).

41. End of di2: (0) gently curved, but located close to the ventral margin of the mandible body; (1) more strongly bent upward, farther from the ventral margin.

The di2 alveolus varies in course and curvature among the species, resulting in a position of the incisor open root closer to the ventral margin or deeper within the mandible body. The position of the end of the incisor seems, however, to be unrelated to the steepness of the anterior (oral) part of the incisor.

42. Depth of mandible body (MH/LTR): (0) low, less than 70%; (1) deepened, equal to 70%–79%; (2) high, 80% and more.

The ratio MH/LTR measures the relative depth of the mandible body, the character frequently employed in the taxonomic descriptions of the lagomorphs (Erbajeva, 1988; Fostowicz-Frelik, 2008; Fostowicz-Frelik et al., 2010). The deepening of the mandible body in lagomorphs carries a functional and presumably phylogenetic signal, as it is related to the increase of the dental column height and therefore hypsodonty.

43. Anterior edge of masseteric fossa: (0) under m2; (1) at the m2/m3 level; (2) at the m3 level (under talonid portion).

The anterior edge of the masseteric fossa is marked in palaeolagines and *Archaeolagus* by a triangular tubercle with its tip directed anteriorly, whereas in extant leporids this margin is rounded. Meng et al. (2003) noticed that the anterior margin of the masseteric fossa tends to move anteriorly in more advanced rodents. Contrary to that, among lagomorphs analysed here, the more advanced species have more posterior "masseteric tubercles."

44. Size (reflected in LTR): (0) small, LTR 11.0 mm or less; (1) moderate, LTR 11.0–14.0 mm long; (2) large 14.0 mm and larger.

Size as a character is frequently employed in phylogenetic analyses and expressed either by skull length or length of the tooth row (Asher et al., 2002; Fostowicz-Frelik et al., 2010). In the present analysis, the observed length of the lower tooth row in all included taxa was divided arbitrarily into three character states.

DISCUSSION

Phylogenetic Considerations

The present work focuses on the North American lagomorphs near the Eocene-Oligocene transition and their interrelationships at the species level. A cladistic analysis (fig. 33) rejects the immediate relationship between *Chadrolagus emryi* and *Litolagus molidens,* doubted by Gawne (1978) but recently implied by Dawson (2008). *Chadrolagus*, *Limitolagus*, and *Litolagus* do not form a monophyletic group, despite similar dental adaptations that are due to the accelerated development of the occlusal pattern. These similarities include early closure of crescents, early obliteration of all occlusal structures on the upper teeth, except persistently open hypostria, and early formation of the lingual dental bridges on lower cheek teeth. *Chadrolagus emryi* and *Limitolagus roosevelti* seem to be closely related considering the dental characters (fig. 33), which might be misleading because of generally high homoplasy of these characters in lagomorphs and the lack of skull material for *Limitolagus*, which prevents incorporation of cranial characters into the data matrix. On the other hand, the detailed analysis of ontogeny of the dental pattern has proved a reliable tool for deciphering phylogenetic relationships in the case of some middle Eocene (Fostowicz-Frelik and Tabrum, 2009) and Miocene stem lagomorphs (López Martínez, 1986, 1989; Fostowicz-Frelik et al., 2012a), and the development of dental pattern in *Chadrolagus* and *Limitolagus* is strikingly similar (figs. 6, 8, 12, 19, 20). Furthermore, the present cladistic analysis places *Chadrolagus emryi* closest to the *Palaeolagus temnodon–P. haydeni* cluster recognized by Dawson (1958, 2008). This proximity of *Chadrolagus* to *Palaeolagus* was suggested by Gawne (1978), who stated that *Chadrolagus* seems "to be an offshoot of the evolutionary line leading to *Palaeolagus*…." Later, Emry and Gawne (1986) did not rule out that *P. primus* (recovered from the same sediments as *Chadrolagus* but preceding this species stratigraphically) could be tentatively considered ancestral to *Chadrolagus*, although they preferred a common ancestor near *Mytonolagus wyomingensis*. At present, the origins and possible descendant lineage of *Chadrolagus* are unknown, especially because this genus is rare and appears in the early Chadronian already showing a combination of primitive and derived cranial and dental characters, including fully developed hypsodonty. Interestingly, scarce dental remains of Duchesnean age from the Black Rabbit Locality at Diamond O Ranch in Montana show development of the occlusal surface of upper teeth similar to *Chadrolagus* (Fostowicz-Frelik and Tabrum, 2009: fig. 12). Moreover, the buccal roots are slightly weaker in these scarce specimens (attributed to ?*Palaeolagus* sp.) than in *P. temnodon* (Fostowicz-Frelik and Tabrum, 2009). Emry and Gawne (1986) mentioned that *P. primus* does not have a hypostrial lake on P3, the condition found also in *Chadrolagus emryi*. Thus, noting the similarities and earlier occurrence of *Palaeolagus primus* in the White River Formation at Flagstaff Rim, it seems plausible that *Chadrolagus emryi* and *Palaeolagus primus* share a common ancestor dating back at least to the Duchesnean.

The origins and relationships of *Litolagus molidens* are even more enigmatic than those of *Chadrolagus*. *Litolagus* is known only from a few specimens; however, thanks to the exceptionally well-preserved skull described herein, which yielded abundant data, its phylogenetic position can be established with certainty as an evolutionarily advanced species, more closely related to Miocene *Archaeolagus* than to the remaining Eocene and Oligocene stem taxa. Such a placement

within the phylogenetic tree removes *Litolagus* from the Palaeolagidae, a group that at present contains most of the Eocene to Miocene stem lagomorphs (see Gureev, 1964; Erbajeva, 1988; Fostowicz-Frelik et al., 2012a, 2012b), and suggests its closest affinity to a more advanced family, Leporidae. Dawson (1958) noted that the skull structure of *Litolagus molidens* shows a mixture of primitive and advanced characters. The material described here allows for a more detailed analysis. The most evident feature is a highly progressive structure of the hard palate, which shows a relatively reduced palatine portion, mentioned already by Dawson (1958). Further, the skull has visibly stronger basicranial angulation than the other coeval species, and in general is higher, due to the enlargement of the orbital portion of frontal and uplifting of the skull roof. Dawson (1958) argued that the structure of the zygomatic arch, namely the masseteric spine at the maxillary zygomatic process, is primitive in *Litolagus*, in which it is not markedly extended laterally. However, the structure and extent of the masseteric spine is a highly variable character in lagomorphs and can differ within a genus (e.g., in *Lepus*, personal obs.). A relatively long and narrow (in ventral view) masseteric spine can be observed also in archaeolagines (e.g., *Hypolagus beremendensis*, see Fostowicz-Frelik, 2007) and some extant rabbits, e.g., the European rabbit (*Oryctolagus cuniculus*). It is difficult to establish whether this character in the extant species is plesiomorphic or not, as most Eocene taxa are known mainly from dental remains. Nevertheless, according to the present author's observations, the structure of the anterior part of the jugal arch in *Litolagus molidens* does not show a plesiomorphic character, especially when compared with *Dawsonolagus* (Li et al., 2007) or *Desmatolagus* (Lopatin, 1998; Meng et al., 2005). On the other hand, the parietal and occipital regions (especially the exoccipital structure) in *Litolagus* show plesiomorphic conditions. The parietals are positioned relatively horizontally and not bent ventrally as in extant leporids, and the occipital face is almost vertical, not inclined ventrally. This particular structure of the braincase is probably one of the most conservative morphological regions of the skull and is shared not only by the Paleogene stem lagomorphs and *Litolagus*, but also mimotonids, including their basalmost genus, *Gomphos* (Li and Ting, 1993; Asher et al., 2005: fig. 2A–B).

However, looking at derived cranial characters of *Litolagus*, such as the larger basicranial angle, shorter palate, wider choanae, and enlarged auditory bullae, it becomes obvious that they are adaptations to more open and arid habitats. The increased angulation, shorter palatal bridge, and relatively wider choanae have functional meaning, as they facilitate balancing of the head and ventilation (respectively) during locomotion, thus increasing the capability of an animal to withstand greater mechanical effort, resulting in quicker and/or prolonged running. Adaptations of that kind can be observed in most extant nonsylvan species of Leporidae (Fostowicz-Frelik, 2007). Additionally, the enlargement of the auditory bullae is a common adaptation among relatively small mammals that entered open environments (e.g., Cainotheriids; Theodor, 2010), and in the light of other *Litolagus molidens* adaptations it is the most plausible explanation.

The preliminary cladistic analysis of North American Paleogene lagomorphs shows extended paraphyly of some genera and a split within *Palaeolagus*, which disintegrates into at least two groups: the "old core" *P. temnodon*–*P. haydeni* (incidentally, the latter is the type species; Leidy, 1856) clade and *P. burkei,* which is separated from the former clade by *Chadrolagus* and *Limitolagus* (fig. 33). The detailed phylogeny of *Palaeolagus* is beyond the scope of this paper and will be investigated further. Nevertheless, distinctive structure of the skull and dentition of *Palaeolagus*
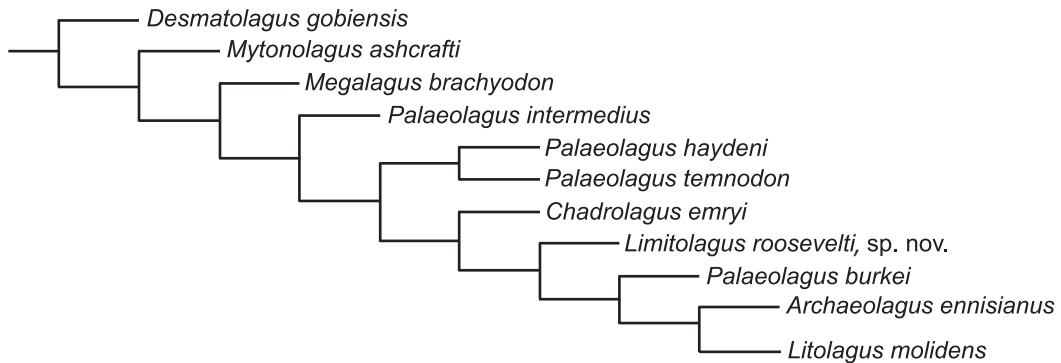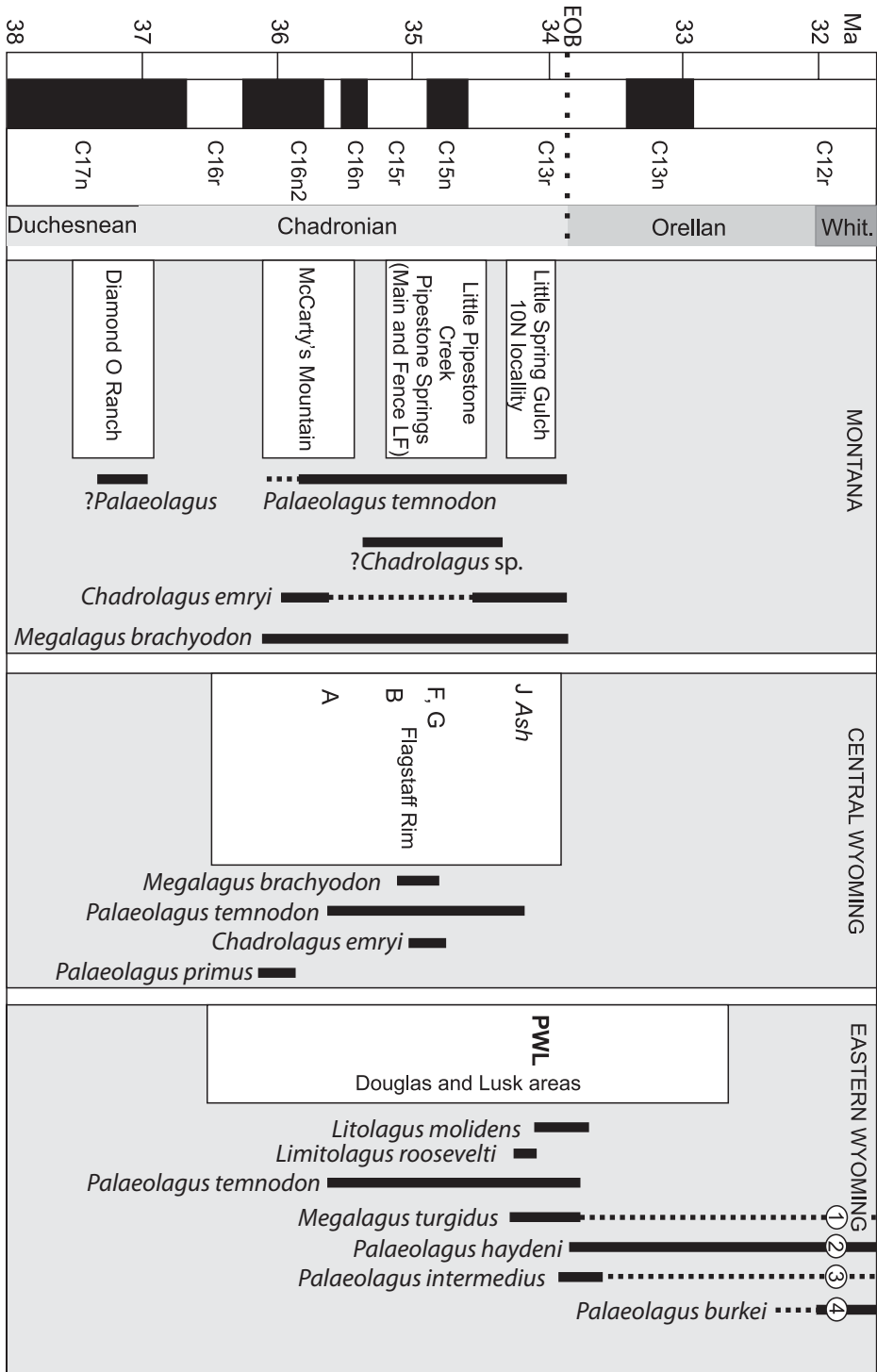
FIG. 33. Phylogenetic position of *Limitolagus roosevelti*, new genus and species within Paleogene North American lagomorph taxa.

burkei needs a brief comment. This species appears as the last of the analyzed taxa after the Eocene-Oligocene transition (Prothero and Whittlesey, 1998; Dawson, 2008). Although its dentition shows a simplified occlusal pattern similar to *Litolagus molidens*, the skull structure expresses quite different specialization displayed, again, in the inflation of the auditory bullae, but also in flattening of the whole skull. In general form and adaptations, the skull of *Palaeolagus burkei* resembles that of extant *Ochotona*, inhabitant of steppes and mountains and a frequent burrower (Nowak, 1999). This analogy is even more surprising when the dental characters are taken into account, as some structural and developmental features are also strikingly similar between these two very distant relatives. The dental features of *Palaeolagus burkei* can be characterized as pedomorphic, the trend opposite to that observed in *Chadrolagus*, *Limitolagus*, and *Litolagus*. The ontogenetic delay in molarization of P3 and no formation of the lingual enamel bridges on p4–m2 even in an advanced age parallel dental structures (nonmolarized P3 and lack of lingual bridges) in the crown ochotonids (Erbajeva, 1988). In any case, even the preliminary phylogenetic analysis presented herein shows the paraphyletic arrangement of stem taxa. *P. temnodon–P. haydeni* form the core of "typical" *Palaeolagus*, while *Litolagus molidens*, the most derived of the Paleogene lagomorph species, links to *Archeaolagus ennisianus* as a sister taxon. Whether this position reflects real relationships or choice of taxa, or is yet another result of the convergent evolution (and thus cranial and dental homoplasies) frequently observed in lagomorphs, remains to be seen.

Diversification of North American Lagomorph Fauna at the Eocene-Oligocene boundary

The Eocene-Oligocene transition about 34.0 Ma was the time of one of the most profound global climate changes (Zanazzi et al., 2007; Lear et al., 2008; Liu et al., 2009) during the entire Cenozoic, and major faunal turnover coincided with the Eocene-Oligocene boundary worldwide (e.g., Evanoff et al., 1992; Prothero and Emry, 2004; Kraatz and Geisler, 2010). In North America, the drying and cooling of the climate gradually turned moist forest habitats of subtropical character into broad-leaved deciduous woodlands, dry and open woodlands, bushlike environments of warm temperate zone, and finally the first Paleogene grasslands (Evanoff et al., 1992; Retallack, 1992; Prothero and Emry, 1996; Sheldon and Retallack, 2004; Woodburne, 2004; Meyer, 2005;

Ma
38   37   36   35   34 EOB   33   32

C17n   C16r   C16n2   C16n   C15r   C15n   C13r   C13n   C12r

Duchesnean   Chadronian   Orellan   Whit.

MONTANA

Diamond O Ranch

McCarty's Mountain

Little Pipestone Creek Pipestone Springs (Main and Fence LF)

Little Spring Gulch 10N locality

?*Palaeolagus*

Palaeolagus temnodon

?*Chadrolagus* sp.

Chadrolagus emryi

Megalagus brachyodon

CENTRAL WYOMING

A

B Flagstaff Rim

F, G

J Ash

Megalagus brachyodon

Palaeolagus temnodon

Chadrolagus emryi

Palaeolagus primus

EASTERN WYOMING

PWL

Douglas and Lusk areas

Litolagus molidens

Limitolagus roosevelti

Palaeolagus temnodon

Megalagus turgidus ①

Palaeolagus haydeni ②

Palaeolagus intermedius ③

Palaeolagus burkei ④

Hembree and Hasiotis, 2007; Boyle et al., 2008; Leopold et al., 2008; Mathis and McFadden, 2010).

The early Chadronian to early Orellan interval, as documented by one of the most complete late Eocene to early Oligocene vertebrate records yielded by the sediment series of the White River Group, is the time of noticeable high biodiversity among Lagomorpha in North America (fig. 34; Evanoff et al., 1992; Prothero and Whittlesey, 1998). The extinction followed by the radiation events can be noted for lagomorphs near the Eocene-Oligocene boundary (Korth, 1989; Prothero and Whittlesey, 1998), similar to those observed for other herbivorous mammals (Janis et al., 2008; Mathis and McFadden, 2010).

The first species disappearing from the fossil record is *Chadrolagus emryi*, one of the smallest and first fully hypsodont, of North American Paleogene lagomorphs (Gawne, 1978). Taking into account the material described herein, the stratigraphic range of this species covers the early to late Chadronian with the latest occurrences in 10N highway (Dunbar Creek Formation) and Little Spring Gulch (Cook Ranch Formation) localities in Montana. It appears that despite fully developed hypsodonty, a specialization typical for grazers, the dentition of *Chadrolagus* was probably not well adapted to feeding on harder, more xerophilous vegetation, as its occlusal enamel pattern was obliterated early. Future microwear study can shed light on this hypothesis. Thus, it can only be said that apparently *Chadrolagus* was not well suited to increasingly drying habitats, either because of dental adaptations or other possibly paleoecological factors such as predation or competition with other species, such as *Palaeolagus temnodon*, as suggested by Gawne (1978). *Chadrolagus emryi* disappears from the fossil record in Flagstaff Rim a little above Ash G bed and well before the change of the sedimentation type from fluvial to eolian, noticeable near Ash I bed (Evanoff et al., 1992), which implies greater susceptibility of this species to subsequent change. Although Evanoff et al. (1992) mentioned that dry land deposition had a west to east progression, the more localized nature of sedimentation in the Montana basins and the higher elevation could be mitigating factors, producing more favorable conditions for *Chadrolagus*, which found a temporary refuge there. Similar buffering processes are known to have operated at the Eocene-Oligocene transition in the northeastern Colorado White River Formation, as detected in paleosols (Hembree and Hasiotis, 2007).

Two other Chadronian lagomorphs, *Palaeolagus temnodon* and *Megalagus brachyodon,* outlasted *Chadrolagus*, reaching or even crossing (*P. temnodon*) the Eocene-Oligocene boundary. However, precise LAD of *P. temnodon* is obscured by the presence of *Palaeolagus hemirhizis*. Prothero and Whittlesey (1998) presumed that the latter species is a nomen dubium and results from mixing of *P. temnodon* and *P. haydeni*, which are closely related and morphologically similar species (Dawson, 1958: fig. 26) in early Orellan localities. They argued that, notwith-

FIG. 34. Lagomorph biostratigraphy in the Chadronian-Orellan sediment series of the studied areas, Montana (Renova Formation) and Wyoming (White River Formation). Data after Dawson, 2008 and Janis et al., 2008; correlation after Prothero and Emry (2004: fig. 5.2). Solid lines: actual presence in studied localities; dashed lines: ranges inferred from data from other parts of the White River Group. LADs of *Megalagus turgidus* (1), *Palaeolagus intermedius* (3), and *P. burkei* (4) established on late Whitneyan–earliest Arikareean (Wh2-Ar1) in Harris Ranch LF (= Harris Ranch Badlands Unit E); LAD of *Palaeolagus haydeni* (2) noted in Lower and Upper Fauna III (= lower Sharps Formation), early Arikareean (Ar1). Presence of *P. burkei* in E Wyoming (Whitneyan deposits of Sherrill Hills) after Dawson (2008), FAD of this species in the White River Group falls to the mid-Chron C12r (after Prothero and Whittlesey, 1998). Abbreviations: **EOB,** Eocene-Oligocene boundary; **Whit.,** Whitneyan.

standing similar size of *P. temnodon* and *P. haydeni*, they can be easily recognized by the presence or absence of roots in their upper premolars and molars (Prothero and Whittlesey, 1998). In any case, despite the putative validity of *Palaeolagus hemirhizis*, the "*hemirhizis*" zone in Orella A demonstrates that there is a species close to *P. temnodon*, with not fully hypsodont teeth, in the early Orellan. Probably, those remains belong to *P. temnodon*, as no actual difference between *P. temnodon* and the rooted specimens of *P. hemirhizis* was provided (Korth and Hageman, 1988). I presume that *P. temnodon* survived major environmental change at the Eocene-Oligocene boundary. The same cannot be said of *Megalagus brachyodon*, which apparently became extinct prior to the Eocene-Oligocene transition (Prothero and Whittlesey, 1998). However, it is sometimes problematic to distinguish this species from *Megalagus turgidus* or *Palaeolagus intermedius* (especially if the roots are hidden in alveoli), both thought to be of Orellan origin (Dawson, 1958; Prothero and Whittlesey, 1998). The stratigraphic range of *Megalagus brachyodon* is well recognized in the Flagstaff Rim area, where it mostly overlaps with *Chadrolagus emryi*, but disappears ca. 25 feet lower in the section than *Chadrolagus* (Gawne, 1978: fig. 7; Emry, 1992). Dawson (1958, 2008) suggested that although *Megalagus* and *Palaeolagus* are not immediately related, the former mimics dental adaptations of the latter. The development of the occlusal surface shows a similar sequence of structures, including early formation of the hypostrial lakes and long persistence of the crescents (Wood, 1940; Dawson, 1958). Such dental adaptations suggest a browser type of foraging, as the occlusal surface, similar to the condition in *Palaeolagus temnodon*, gains a "bunodont" character due to the presence of persistent lakes (at last two of them: hypostrial and crescential). This pattern stands in opposition to the "lophodont-like" type of typical grazers, imitated by *Chadrolagus*, *Limitolagus*, and *Litolagus*, which all have their upper tooth enamel organized in loops; in this case a single loop of relatively deep hypostria. Nevertheless, where *Megalagus brachyodon* failed, *Palaeolagus temnodon* succeeded, although it did not last beyond the "*hemirhizis* zone," roughly correlated with the Orella A Member (Korth, 1989), and was replaced by *Palaeolagus haydeni*, which shows a similar occlusal pattern but is fully hypsodont (Wood, 1940; Dawson, 1958, 2008).

Following the evolutionary patterns in North American lagomorphs at the Eocene-Oligocene boundary two general observations can be made: first, disappearance of the Chadronian semihypsodont species and second, advent of many fully hypsodont species. In the case of the semihypsodont species, basically they were replaced by closely related ecological counterparts: *Palaeolagus temnodon* by *P. haydeni*, and *Megalagus brachyodon* by *M. turgidus* (see Dawson, 2008). A different situation is presented in the fully hypsodont genera, especially those showing acceleration in the development of the occlusal dental pattern in comparison with both species of *Megalagus* and all coeval *Palaeolagus*. Three species have a very similar pattern of dental wear: *Chadrolagus emryi*, *Limitolagus roosevelti*, and *Litolagus molidens*. From the standpoint of functional morphology, their dental characters imply grazer-type dietary adaptations, as they parallel similar lophodont dental structures of some grazers and most extant leporids, which feed mainly on grasslike vegetation and herbs (Nowak, 1999). However, taking a closer look at the extant hares and rabbits, it is highly probable that the relatively simple enamel pattern in *Chadrolagus*, *Limitolagus*, and *Litolagus* was insufficiently abrasive for new post-Eocene vegetation. Today, the most extreme dental adaptations to a hard-leaved diet are seen in the Amami

rabbit (*Pentalagus furnessi*), which feeds on bamboo shoots (Nowak, 1999). This species has a very complicated enamel pattern with all folds strongly crenulated; the crenulation is also quite considerable in some other extant genera, e.g., *Lepus* or *Pronolagus*. However, in the three Paleogene taxa discussed above it is comparatively very simple. Additional argument confirming this hypothesis is the strong wear of the occlusal surfaces, which can be observed in relatively young specimens, even subadults in the case of *Litolagus molidens*, which owes its specific name to that particular character (Dawson, 1958).

The lack of evolutionary success in *Chadrolagus*, *Limitolagus,* and *Litolagus* is further evidenced by their restricted stratigraphic and geographic ranges, especially in the case of *Limitolagus* and *Litolagus* (known only from the Douglas and Lusk areas, Wyoming). *Chadrolagus*, the most widespread of them, went extinct in the late Chadronian. *Limitolagus* is not known later than the Eocene-Oligocene boundary and *Litolagus* was reported from the sediments above P.W.L., with the exception of an isolated P3 found 10 feet below P.W.L. in Channel Quarry, Seaman Hills, Niobrara Co. Furthermore, none of them left identifiable descendants.

The picture of lagomorph faunal turnover at the Eocene-Oligocene boundary in North America is completed by the appearance of *Palaeolagus burkei* in the Orella C horizon of the Orella Member, Brule Formation (Prothero and Whittlesey, 1998). This relatively small species mimics some ochotonid adaptations in skull structure, which suggest similar lifestyle and possible burrowing adaptations not surprising in increasingly open environments. Interestingly, there is no decrease in lagomorph species richness across the Eocene-Oligocene boundary in North America. Five species are known from the latest Chadronian, and the same number from the earliest Orellan.

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APPENDIX 1

Comparative Material

Archaeolagus ennisianus: holotype AMNH FM 7190, John Day Formation, N fork of John Day River, Oregon.

Chadrolagus emryi: type series AMNH F:AM 99107–99127, 99139; USNM 214671, 214681–214683, 214687, 214689, Bates Hole, Flagstaff Rim area, Natrona Co., Wyoming.

Desmatolagus gobiensis: holotype AMNH FM 19102, Hsanda Gol Formation, Red Beds, 10 mi W of Loh, Mongolia.

Litolagus molidens: holotype specimen LACM-CIT 1568.

Megalagus brachyodon: holotype AMNH FM 9652 (mandible 9730), Pipestone Springs, Montana; AMNH FM 99183, FM 99185, FM 99174, FM 99271, FM 99182, Bates Hole, Natrona Co., Flagstaff Rim area, Wyoming; AMNH FM 143966, FM 143967, Morton Ranch, Converse Co., Wyoming.

Megalagus turgidus: AMNH FM 141012, FM 143959, Reno Ranch S of Tower, Converse Co., Wyoming; FMNH UC 1642 Hat Creek Basin, Grines Ranch, Cedar Creek, Sioux Co., Nebraska.

Megalagus sp.: AMNH FM 143960–143963 Wulff Ranch, Converse Co., Wyoming; AMNH FM 143964, Reno Ranch, Reservoir area, Converse Co., Wyoming.

Palaeolagus burkei: holotype AMNH FM 8704 Castle Rock, Logan Co., Colorado; AMNH FM 104307, FM 106287, FM 106312, FM 10695, FM 106289, FM 106245, Rocky Ford, Shannon Co., South Dakota; FM 105710, FM 105719, FM 107258, Sioux Co., Nebraska; FM 106306, FM 106311, Shannon Co., South Dakota; FM 106367, Harvey Springs Range, Shannon Co., South Dakota; 27763, 6 mi SW Bridgeport, Morrill Co., Nebraska; LUSK 0-38-897-9; LUSK 0-39-928 (2, 3), 10 mi E of Harrison, Nebraska; AMNH FM 106367, Harvey Springs Range, Shannon Co., South Dakota.

Palaeolagus haydeni: lectotype ANSP 11031 and syntype ANSP 11028, 11030, 11032–11041; AMNH FM 143957 Herman Wulff Ranch, Converse Co., Wyoming; AMNH FM 143958 8 mi SE of Douglas, Converse Co., Wyoming; AMNH FM 143956 Converse Co., Wyoming.

Palaeolagus intermedius: cast of the holotype AMNH FM 8722 Oreodon beds, White River Formation, Castle Rock, Logan County, Co.; AMNH S 592-25207 (8) Plunnett, Sioux Co., Nebraska; AMNH DICK 30-1075A, DICK 21-463 15 ft above base Leo Fitterer Ranch, Channel, North Dakota; AMNH DICK 21-517 Leo Fitterer Ranch, 42–50 ft above Banded Zone, North Dakota; AMNH 141013 Little Badlands, North Dakota; AMNH 8752 Logan Co., Colorado; AMNH LUSK 0-38-897 (33) 10 mi N of Harrison, Nebraska; AMNH LUSK 0-20-521A above channel, N of Node Road, Wyoming.

Palaeolagus temnodon: lectotype CM 725a and CM 6570, 6575–6577, 6584, 6586, 6590, 6592, 6601, 6602, 6604, 6625, 6628, 6642, 8198, 8962, 8968, 9198, 9205, 10162, 10203, Pipestone Springs Main Pocket, Montana. AMNH FM 99130, 99137, 99140, 99145, 99157, 106004, 106016 Bates Hole, Flagstaff Rim area, Wyoming.

APPENDIX 2

Character-Taxon Matrix

Archaeolagus ennisianus
310211?133221121112221111122001211?0021201122

Chadrolagus emryi
0002001113220211122211100?0100000000100101210

Desmatolagus gobiensis
???00100100000000????0???3100?00??????0?0000

Limitolagus roosevelti
????01?113220211122211????2?0????2?????101112

Litolagus molidens
121211?133221110122211003111121311222112222

Mytonolagus ashcrafti
000000000211021210000???0100?00??????000000

Megalagus brachyodon
2100000011010110000000000011000100??00?110002

Palaeolagus burkei
1201111233221211122221000220001112??2021001?0

Palaeolagus haydeni
2101000123210211111010002100010200100000101

Palaeolagus intermedius
211211?113200111012220111?12001100?001?10102

Palaeolagus temnodon
210100012101021111110100021000101?0100000100