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A RODENT AND A LAGOMORPH (MAMMALIA) FROM CAMERON SPRINGS, WYOMING (CHADRONIAN: LATEST EOCENE) AND THE USE OF THE OCCLUSAL WEAR PATTERN OF CHEEK TEETH IN DETERMINING ONTOGENETIC AGE OF INDIVIDUALS OF SUBHYPSODONT SPECIES

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ABSTRACT

Large samples (>100 specimens each) of a cylindrodont rodent, *Cylindrodon natronensis* Emry and Korth, 1996, and a lagomorph, *Chadrolagus emryi* Gawne, 1978, are reported from the Chadronian Cameron Springs, Wyoming. This is the first identification of *C. natronensis* outside of their type area (Flagstaff Rim, Wyoming).

Both species have subhysodont cheek teeth, so the occlusal pattern was used to determine the stage of dental attrition (=ontogenetic age), as has been done for larger mammals. The results demonstrate that the use of the dental patterns based on wear is applicable to these smaller species and it allows for a better specific definition of the species because it accounts for the amount of variability often seen in small mammals with this type of dentition. It also allows for the use of ontogenetic age in future taphonomic studies of attritional and catastrophic death assemblages.

INTRODUCTION

The first fossil mammal reported from Cameron Springs, Wyoming was by Hough (1956) with the description of a new species of the apternodontid lipotyphlan *Oligoryctes*. Hough (1956:531) gave the legal location of the locality, and cited it as being "Lower Oligocene" in age, equivalent to the Pipestone Springs fauna of Montana. Van Houten (1964) presented a detailed description of the stratigraphy and included the exposures in the White River Formation. To date, very few mammalian species have been described from this fauna. However, Van Houten (1964: 70) provided a preliminary mammalian faunal list from the locality and referred it to the early Chadronian North American Land Mammal Age (latest Eocene). Later, Emry et al. (1987: fig. 5.3) placed the fauna in the middle Chadronian. This was followed by Janis et al. (2009: appendix I) who assigned it an age of Ch2-3.

Among the best represented species from this fauna are a cylindrodont rodent and a leporid (Lagomorpha), both consisting of samples of more than 100 specimens. A detailed study of these specimens has allowed for specific identifications. Since both of the identified species have subhypsodont cheek teeth, the large size of the sample also has allowed for a study of the ontogenetic changes in dental dimensions of these species.

MATERIALS AND METHODS

Measurements—All measurements were taken at the occlusal surface of the cheek teeth with an optical micrometer to the nearest 0.01 mm. Dental terminology for rodents follows that of Wood and Wilson (1936) and for lagomorphs follows Dawson (1958) and White (1987). Upper teeth are represented by capital letters, lower teeth by lower-case letters (e.g., P3 or p3).

Locality.—All specimens included in this study were surface collected by parties from the Carnegie Museum of Natural History (CM) and the National Museum of Natural History, Smithsonian (USNM) at irregular intervals since the 1940s, and are from Cameron Springs, Fremont County, central Wyoming (Fossil Locality 19 of Van Houten, 1964). The exposed rocks are White River Formation (undifferentiated) with a thickness of approximately 77 m (250 ft), and were deposited as a valley-fill cut into the subjacent Eocene Wagonbed Formation (Van Houten, 1964: 64-65).

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Cylindrodontidae Miller and Gidley, 1918
Cylindrodon Douglass, 1901
Cylidrodon natronensis Emry and Korth, 1996
(Figures 1, 2; Table 1)

Referred Specimens—Dentaries with cheek teeth: CM 17168-17179, 18777-18789, 21236, 21239, 27641, 27644, 60340, 60342, 60343, 62053, 62057, 60858, 62060, 2061, 62063, 62064, 62066, 62096; USNM 20906-20924, 20969, 21109-21121, 21138, 21139, 21143-21145, 21149-21160, 21163, 21164, 21169, 361802, 361804. Palate or partial cranium with cheek teeth on both sides: CM 17181, 27639, 62065; USNM 19906-19908, 19910, 19912, 19913, 19991, 20914, 21107, 21123, 21125-21128, 21130, 21133-21136, 21141, 21142, 21161, 21162, 61165, 361810, 361815, 361828. Maxillae with cheek teeth: CM 17162, 17163, 17165, 17166, 17180, 18784, 18787, 27642, 27643, 62062, 62067, 62070, 62071; USNM 21129, 21131, 21132, 21137, 21146, 21147, 21168.

Discussion—In Van Houten's (1964: 70) preliminary faunal list of Cameron Springs, he listed two species of *Cylindrodon*, *C. fontis* and *Cylindrodon* sp. However, only one species of cylindrodont appears to be present and it is determined to be *Cylindrodon natronensis* Emry and Korth, 1996, previously only reported from Flagstaff Rim area, Wyoming. A detailed description of *C. natronenis* and comparisons with other species has been provided elsewhere (Emry and Korth, 1996). The identification of the Cameron Springs sample is based on its small size relative to all other species (Table 1; Emry and Korth, 1996: tables 1, 2) and presence of a loph connecting the metaconule to the center of the posterior cingulum on P4-M2 (Figure 1). It differs from *C. solarborus* Emry and Korth, 1996, also from Flagstaff Rim, in its smaller size and the presence of a complete hypolophid on p4. (In the original description of *C. solarborus* the table of measurements provided was a duplication of the measurements for *C. natronensis* [Emry and Korth, 1996: tables 2, 3]. A corrected table of measurements for *C. solarborus* is provided as an Appendix to this paper.)

One of the characters originally used to separate *C. natronensis* from *C. solarborus* was the presence of the anteroposterior loph connecting the metaconule to the posterior cingulum on M3 of *C. solarborus* (similar to P3-M2) and that absence in M3 of *C. natronensis*. However, in the sample from Cameron Springs this was variably present. This accessory loph on M3 could not be determined for specimens with moderate to heavy wear, so evidence of this loph could only be observed on unworn or little-worn specimens. Of the 16 little-worn observable M3s, eight were in palates or partial skulls with both right and left tooth rows. Seven of the observable M3s lacked the posterior loph and had the posterior basin enclosed (as originally defined for the species), six had no accessory loph with the posterior basin open posteriorly, two had the accessory loph in the posterior basin (as diagnosed for *C. solarborus*), and one lacked the posterior basin entirely. Notably, one of the specimens with both right and left M3 (USNM 11910) lacked the accessory loph on the left, but it was present on the right (Figure 2). Clearly, this loph is a variable character (at least in this population) but is lacking in the majority of the specimens. This variability does not warrant the recognition of a new species or reference of this material to another species due to its variable occurrence. The presence of the remainder of the diagnostic features for *C. natronensis* in this sample makes it referable to the latter.

Order Lagomorpha Brandt, 1855
Family Leporidae Fischer de Waldheim, 1817
Chadrolagus Gawne, 1978
Chadrolagus emryi Gawne, 1978
(Figure 3; Table 2)

Referred Specimens—Dentaries with cheek teeth: CM 17185 (three specimens), 17186, 18190, 18804, 21241, 21242, 26750 (both dentaries of one individual), 27651, 27652, 62121, 62122, 62124 (two specimens), 62125-62130, 361762 (four specimens); USNM 20875, 20954-20960, 21187, 21190-21195, 21198, 21203, 21207, 21208, 21210, 21212-21215, 21217, 21218, 361762, 361763 (six specimens), 361764, 361766, 361767, 361768, 361770, 361771, 361772, 361773, 361779, 361782, 361785 (both dentaries of one individual), 361787, 361789, 361791, 361792, 361832 (two specimens). Palate or partial cranium with cheek teeth on both sides: CM 17188; USNM 361770, 361786. Maxillae with cheek teeth: CM 18794-18798, 18805, 21240, 21241, 21243, 27649, 62118-62120, 62131, 91731; USNM 20873, 20874, 20961, 21196, 21197, 21199-21206, 21209, 21211, 21216, 21219-21224, 361765, 361769, 361774, 361178, 361780, 361781, 361783, 36831, 36132.

Discussion—Van Houten (1964: 70) recognized two lagomorphs from Cameron Springs, *Palaeolagus temnodon* Douglass 1901, and *Megalagus brachyodon* (Matthew, 1903). The *Megalagus* material was excluded from this study, and the material previously identified as *P. temnodon* is referred here to *Chadrolagus emryi* Gawne, 1978. The specimens from Cameron Springs differ from contemporaneous species of *Palaeolagus* in having the diagnostic characters of *C. emryi* (Gawne, 1978; Dawson, 2008; Frostowicz-Frelik, 2013): 1) P2 narrow with absent or slight buccal lobe; 2) p3 relatively short and the protoconid is smaller and located further posteriorly than the metaconid; 3)

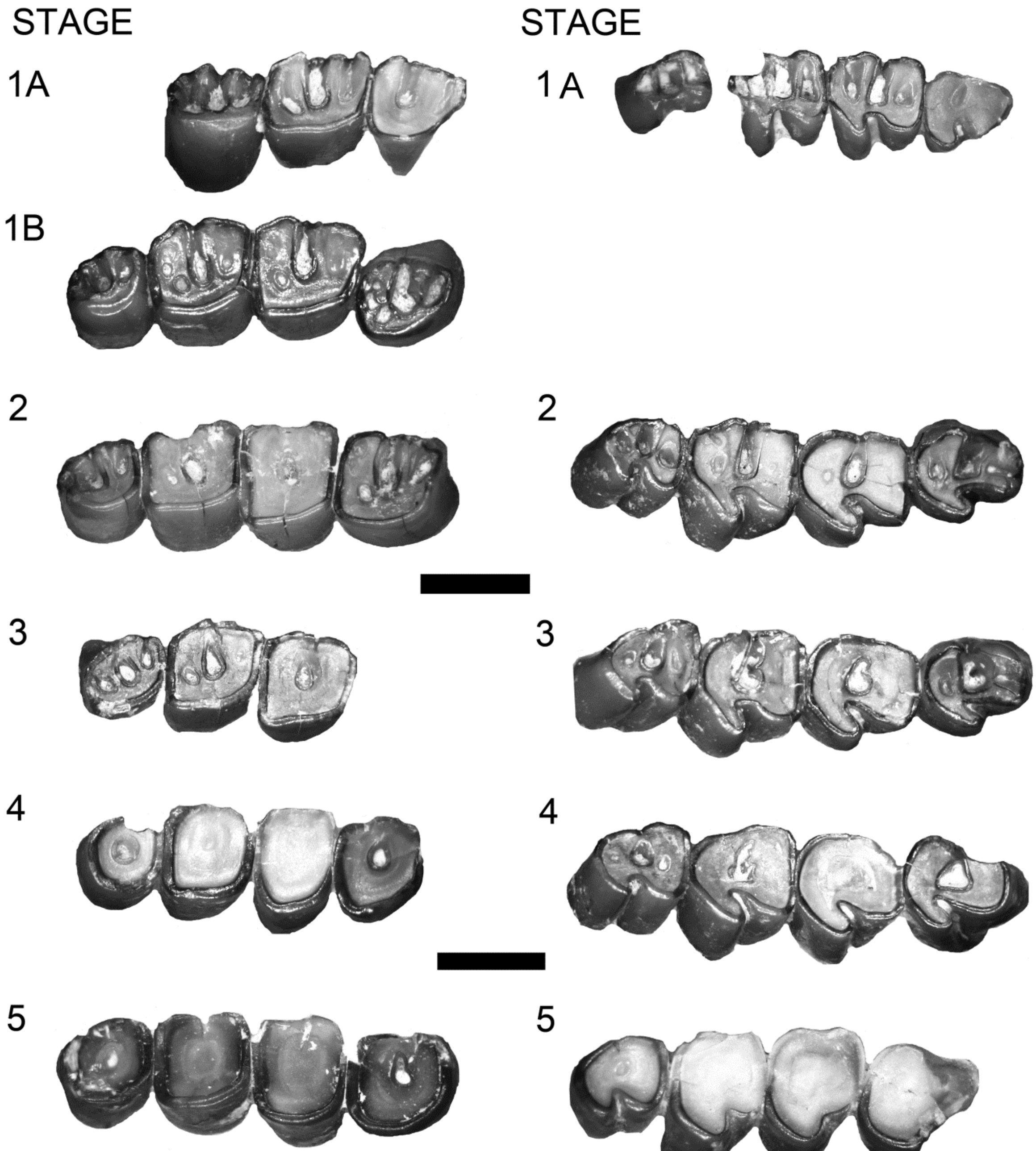

FIGURE 1. Wear stages of cheek teeth of *Cylindrodon natronensis*. Uppers in left column, lowers in right column. Anterior to the right in all specimens. **Stage 1A**, CM 62071, right dP3-M2; USNM 603825, left dp4-m3 (reversed). **Stage 1B**, CM 17180, left P4-M3. **Stage 2**, USNM 19908, right P4-M3; CM 21236, p4-m3. **Stage 3**, CM 17162, right M1-M3; CM 18715, right p4-m3. **Stage 4**, CM 18787, left P4-M3 (reversed); CM 18779, right p4-m3. **Stage 5**, USNM 21135, left P4-M3 (reversed); CM 62061, left p4(partial)-m3 (reversed). Bar scale = 2 mm.

early loss of crescents from P4-M2 and persistent a hypostria that is retained later in wear; and 4) no buccal roots present on the upper cheek teeth. These specimens are also similar in size to the topotypic and referred material of *C. emryi* (Table 2; Gawne, 1978: tables 2, 3; Frostowicz-Frelik, 2013: tables 4, 5) and smaller than those of *P. temnodon* (Wood 1940: 322; Galbreath 1953: 51; Emry and Gawne 1986: table 1). Previously, *C. emryi*, has been reported from the type area, Flagstaff Rim area of Wyoming (Gawne, 1978), McCarty's Mountain, Little Spring Gulch, and 10N (Dunbar Creek Formation), all in Montana (Frostowicz-Frelik, 2013) and possibly Pipestone Springs, Montana (Dawson, 2008; Frostowicz-Frelik 2013).

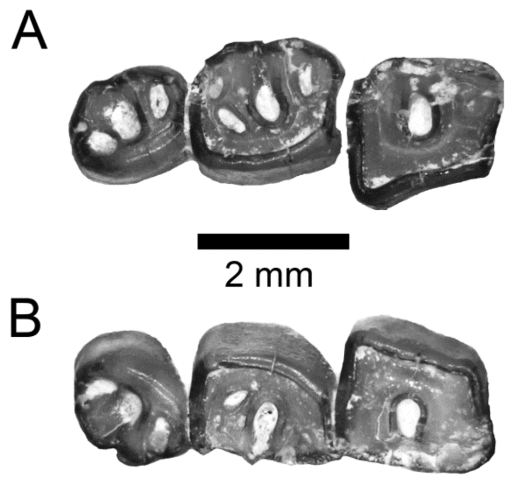

FIGURE 2. Upper molars of *Cylindrodon natronensis*, USNM 19910, from Cameron Springs, demonstrating the variability in morphology of M3. A, right M1-M3. B, left M1-M3. Anterior to the right.

ONTOGENETIC AGE DETERMINATION

Several authors have used the occlusal pattern of the cheek teeth of hysodont larger mammals to determine the relative ontogenetic age of individuals in a fossil population (Kurten, 1953; Van Valen, 1964; Voorhies, 1969; Shipman, 1981). Ontogenetic age determination of small fossil mammals previously has been done based on species with cheek teeth that were brachydont, where the amount of wear could be measured directly from the height of the individual teeth (Korth and Evander, 1986; Korth, et al., 2015). Czaplewski (2011: fig. 7, table 2) used both occlusal pattern and crown-height measurements on a Pliocene owl-pellet accumulation of the subhypsodont heteromyid rodent *Prodipodomys*. He found that the crown-height measurements (based on height of dentine tracts) and the occlusal wear-pattern produced different results (Czaplewski, 2011: fig. 12.1), questioning its applicability to smaller mammals. Recently, Fostowicz-Frelik (2013: figs. 6, 8) figured and discussed the ontogenetic changes in the occlusal morphology of the dentition of *Chadrolagus*. In this study, the samples of *Cylidrodon natronenis* and *Chadrolagus emryi* from Cameron Springs were examined and ontogenetic ages were determined based on occlusal pattern of the cheek teeth similar to the methods used in hypsodont larger mammals.

RESULTS

Cylindrodon—Emry and Korth (1996) demonstrated that the occlusal pattern of the cheek teeth of species of *Cylindrodon* changed through the life of the animal. They defined five stages (Table 3; Emry and Korth, 1996: 412) from virtually no wear (Wear Stage I) to the complete removal of all enamel from the occlusal surface of all the cheek teeth except the outline of the crown (Wear Stage V). This was done to demonstrate the change in proportions of the cheek teeth at these different wear stages (Emry and Korth, 1996: tables 4-13). However, these stages were based on the individual teeth within the tooth row, and not the entire tooth row itself. Since all of the cheek teeth in the jaw do not erupt at the same time, the same individual would have cheek teeth at different stages of wear (Emry and Korth, 1996: figs. 2, 4).

In this study, the age of the individual is based on the combined wear stages of all of the cheek teeth remaining in the jaw. To achieve this, the wear stage was determined for all of the cheek teeth individually as Stages 1-5 (= Wear Stage I-V of Emry and Korth, 1996), then the average of the stages was taken of all of the teeth present to determine an overall stage (or age) of the individual. Any deciduous premolars were given the value of zero. This process was applied to all specimens regardless of the number of cheek teeth retained (minimum number of cheek teeth retained in any individual in the sample was two). The calculated stages were divided into five age groups. Each group was based on a scale from one to five with a range of 0.7 used to define each stage: Stage 1 =1.0-1.7; Stage 2 = 1.8-2.5; Stage 3= 2.6-3.3; Stage 4 = 3.4-4.2; Stage 5= 4.3-5.0.

Chadrolagus—As with the sample of *Cylindrodon*, the occlusal pattern of cheek teeth was used to separate the sample of *Chadrolagus* into different age ranges. However, this was only possible on P3 and p3. The last premolar (P4/p4) and molars of *Chadrolagus* vary little and can only be distinguished when very young (first eruption) or very old (latest stages wear) and no definite intermediate wear stages can be defined with confidence (Fostowicz-Frelik, 2013:15-21). Wear

TABLE 1. Combined dental measurements of *Cylindrodon natronensis* from Cameron Springs. Abbreviations: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; MIN, minimum measurement; MAX, maximum measurement; SD, standard deviation; CV, coefficient of variation. Measurements in mm.

	dP4L	dP4W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	14	13	49	44	67	60	64	58	38	35	25
M	1.71	1.52	1.82	1.73	1.74	1.76	1.74	1.63	1.50	1.36	7.11
MIN	1.40	1.14	1.54	1.31	1.33	1.19	1.53	1.06	1.28	0.95	6.24
MAX	2.04	1.77	2.04	2.38	2.22	2.31	2.01	2.12	1.67	1.86	8.00
SD	0.19	0.21	0.13	0.25	0.22	0.25	0.13	0.23	0.11	0.21	0.48
CV	11.02	13.50	7.08	14.70	12.46	13.93	7.24	14.01	7.09	15.45	6.71

	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	2	2	34	33	59	57	63	62	50	48	22
M	1.72	1.41	1.82	1.61	1.78	1.81	1.80	1.80	1.61	1.35	7.26
MIN	1.56	1.38	1.44	1.19	1.31	1.29	1.47	1.36	1.30	0.96	6.73
MAX	1.87	1.44	2.21	1.83	2.17	2.39	2.18	2.77	2.22	1.94	7.78
SD	0.22	0.04	0.16	0.12	0.16	0.17	0.12	0.22	0.17	0.19	0.32
CV	12.78	3.01	8.82	7.75	9.07	9.45	6.77	12.22	10.51	13.74	4.42

TABLE 2. Combined dental measurements of *Chadrolagus emryi* (all wear stages) from Cameron Springs. Abbreviations as in Table 1. Measurements in mm. High coefficients of variation reflect the ontogenetic change in dimensions and shape of the individual teeth (see Gawne, 1978: table 3; Korth and Hageman, 1988: table II).

	dP3L	dP3W	dP4L	dP4W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	P2-M3
N	1	1	1	1	18	18	47	44	53	49	46	44	36	34	18	9
M	1.63	2.42	1.77	2.70	1.42	1.65	1.88	2.74	1.86	3.01	1.72	2.89	1.62	2.57	0.85	10.97
Min					0.97	1.22	1.41	1.74	1.12	1.21	1.40	1.63	1.19	1.62	0.63	10.37
Max					1.99	2.19	2.43	3.53	2.53	4.47	2.14	3.76	1.96	3.45	1.22	11.70
SD					0.25	0.22	0.21	0.41	0.22	0.55	0.19	0.42	0.17	0.40	0.12	0.43
CV					17.42	13.13	11.16	14.87	11.87	18.15	11.30	14.65	10.36	15.53	14.24	3.94

	dp3L	dp3W	dp4L	dp4W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p3-m2
N	4	4	5	5	31	32	48	48	47	46	40	40	21	20	7
M	2.39	1.71	2.30	1.69	2.09	1.84	2.23	2.18	2.24	2.16	2.18	2.13	1.16	1.13	11.18
Min	2.00	1.37	2.24	1.53	1.34	1.25	0.98	1.47	0.99	1.19	1.04	1.30	0.93	0.90	10.52
Max	2.93	2.14	2.38	2.00	2.98	2.90	2.70	2.65	2.69	2.73	2.93	2.67	1.48	1.38	11.56
SD	0.39	0.37	0.06	0.19	0.30	0.27	0.28	0.27	0.35	0.29	0.42	0.32	0.14	0.13	0.38
CV	16.53	21.57	2.43	11.30	14.55	14.76	12.49	12.19	15.48	13.22	19.18	14.79	11.72	11.41	3.37

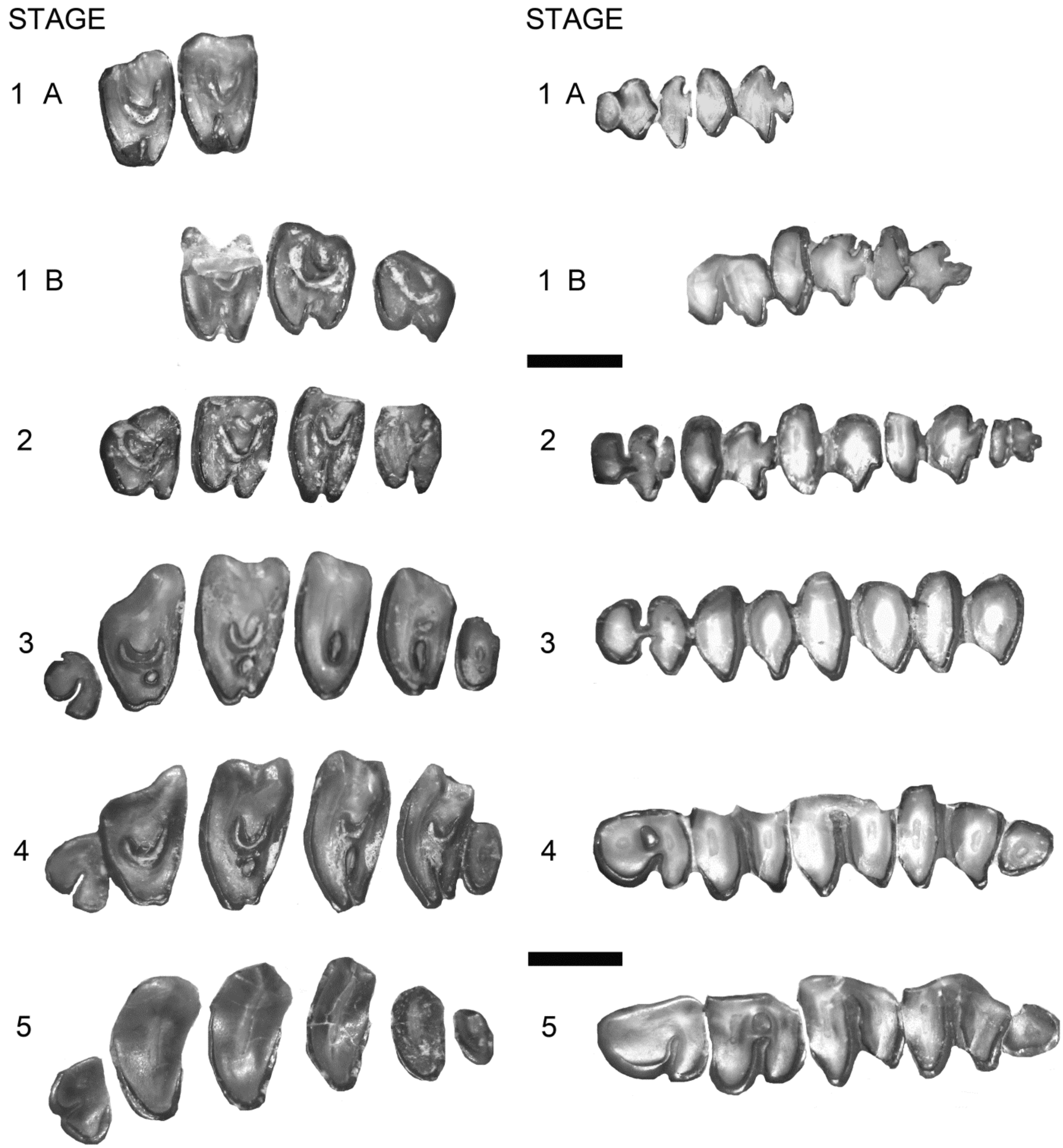

FIGURE 3. Wear stages of cheek teeth of *Chadrolagus emryi* (also see Fostowicz-Frelik, 2013: figs. 6, 8). Uppers in left column, lowers in right column. Anterior to the left on all specimens. **Stage 1A**, CM 91731, left dP3-dP4; USNM 20959, right dp3-dp4 (reversed). **Stage 1B**, USNM 21200, right dP3 (partial)-M2 (reversed); USNM 21194, left dp4-m2. **Stage 2**, USNM 361769, left P3-M2; CM 17190, right p3-m3 (reversed). **Stage 3**, USNM 21194, left P2-M3; USNM 21192, right p3-m2 (reversed). **Stage 4**, USNM 361778, right P2-M3 (reversed); USNM 361782, left p3-m3. **Stage 5**, USNM 21205, right P2-M3 (reversed); USNM 361791, left p3-m3. Bar scale = 2 mm.

TABLE 3. Wear stages of individual cheek teeth of species of *Cylindrodon* as defined by Emry and Korth (1996: 412).

Stage I	Unworn, or worn so slightly that dentine is exposed only at the poins of the main cusps.
Stage II	Dentine exposed on occlusal surface of lophs, but three enamel lakes or basins still present.
Stage III	Anterior basin eliminated, only two basins remain.
Stage IV	Posterior basin eliminated, only central basin remains.
Stage V	Central basin eliminated, occlusal surface is dentine surrounded by a band of enamel, but no internal enamel pattern.

TABLE 4. Definition of wear stages for *Chadrolagus emryi* (also see Fostowicz-Frelik, 2013).

Stage 1	dP3/dp3 present
Stage 2	P3/p3 erupted; slight amount of wear on the chewing surface; all reentrants are still open.
Stage 3	P3/p3 slightly worn; anterior re-entranced closed and central crescent formed on P3; posterior internal and external re-entrant remain open on p3.
Stage 4	P3/p3 heavily worn; hypostria completely eliminated on P3, but a crescent or circular fossette remains; on p3 the posterior external re-entrant remains open, internal re-entrant reduced to circular fossettid.
Stage 5	The chewing surface of the P3/p3 completely worn, little to no pattern to the tooth, only enamel outline of crown remains.

stages could not be defined for P2 of *Chadrolagus* because of its simplified occlusal pattern (Gawne, 1978; Fostowicz-Frelik, 2013). Five wear stages for *Chadrolagus* were defined based on the change in the occlusal patterns of P3 and p3 only (Table 4). Because the wear stages were based on P3/p3, only specimens retaining these teeth could be included in the study.

CONCLUSIONS

There is a clear change in the occlusal pattern of the cheek teeth of these two subhypsodont mammals so that individual ontogenetic ages can be assigned. This allows for future work on individual sites, and can be used to determine taphonomic factors such as attritional or catastrophic death assemblages or population dynamics of small hypsodont mammals, as has been done for larger mammals. It also allows for the recognition of the range in size of the dental elements for a single population. Since the measurements vary for different levels of attrition for these species, the overall measurements have very large ranges of variation (Tables 1, 2). However, if the ontogenetic age (=wear stage) is taken into consideration, the ranges of variation are much more limited (Tables 5, 6). This allows for better comparison of size in samples of such subhypsodont species from different localities and a better definition of individual species based on size.

Age-frequency histograms or survivorship curves have been used to determine whether a fossil assemblage was catastrophic or attritional for larger mammals (Kurten, 1953, Van Valen, 1964; Voorhies 1969; Shipman, 1981). An attritional assemblage would consist of mainly very young and very old individuals, whereas a catastrophic assemblage would have the same profile as a living population with many more individuals of “middle age” and very few of the oldest age (Voorhies 1969: plate 13, figs. 1, 2). Histograms for small mammals also have been done, but were based on species with cheek teeth that were brachydont, where the amount of wear could be measured directly from the height of the teeth (Korth and Evander, 1986: fig. 1; Czaplewski, 2011: fig. 12; Korth, et al., 2015: fig. 5).

Based on the histograms for the age-frequency of both species examined from Cameron Springs (Fig. 4), the fossil assemblage appears to be the result of attritional death. In both cases, the greatest number was that of the oldest individuals (Stage 5), the number for Stage 3, the middle-aged or young adult stage (Figure 5), was among the lowest. This is typical of an attritional assemblage (see Voorhies, 1969: fig. 1; Korth and Evander, 1986: fig. 1). Theoretically, the number of Stage 1 individuals (youngest with deciduous premolars) should be the highest, but it is much lower than predicted for both species from Cameron Springs. This is not unexpected because the samples were surface collected over a relatively thick sequence of sediment so that the larger, more complete adult jaws were more likely collected and the bones of the very youngest individuals, being smaller and much more fragile, were more likely destroyed or washed away due to weathering and surface exposure and therefore less likely to survive (Voorhies, 1969; Korth, 1979). Korth and Evander (1986: fig. 6) demonstrated that a combination of attritional and catastrophic assemblages of small mammals would produce a histogram of this type in a similar depositional environment. This is consistent with the sedimentology of the White River Formation. The source of the sediment of this formation is weathered volcanic ash accumulated over a long period of time that has been reworked by surface processes (Evanoff et al., 2010). Therefore, the Cameron Springs samples cannot be directly used to determine whether the initial accumulation was catastrophic or attritional. A determination of this kind can only be

TABLE 5. Mean measurements of cheek teeth of *Cylindrodon natronensis* separated into wear stages. Abbreviations as in Table 1. Measurements in mm.

Stage	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3
1	1.88	1.19	1.87	1.55	1.87	1.65	1.52	1.23	6.96
2			1.86	1.73	1.83	1.66	1.49	1.17	7.50
3	1.65	1.56	1.85	1.71	1.81	1.73	1.55	1.30	7.10
4	1.80	1.61	1.78	1.82	1.81	1.80	1.66	1.38	7.30
5	1.92	1.67	1.70	1.92	1.75	1.94	1.69	1.50	7.23

Stage	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3
1	1.77	1.44	1.95	1.52	1.78	1.38	1.50	1.05	7.08
2	1.87	1.62	1.87	1.75	1.83	1.65	1.55	1.29	7.53
3	1.93	1.65	1.79	1.96	1.74	1.75	1.49	1.30	
4	1.81	1.74	1.60	1.84	1.67	1.67	1.45	1.43	6.99
5	1.84	2.01	1.60	2.02	1.74	1.90	1.54	1.57	6.92

TABLE 6. Mean measurements of cheek teeth of *Chadrolagus emryi* from Cameron Springs separated into wear stages. Abbreviations as in Table 1. Measurements in mm.

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p3-m3L
Stage 1					2.27	2.09	2.32	1.58			
Stage 2	1.68	1.61	2.06	2.00	2.29	2.26	2.10	2.09	1.13	0.93	
Stage 3	2.22	1.89	2.25	2.28	2.04	2.04	2.04	2.29	1.22	1.38	11.17
Stage 4	2.20	1.75	2.22	2.17	2.42	2.33	2.43	2.23	1.25	1.20	11.56
Stage 5	2.30	1.89	2.21	2.21	2.17	2.32	2.40	2.33	1.20	1.02	11.34

	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P2-M3L
Stage 1							1.89	2.49	1.41	1.88			
Stage 2			1.76	2.47	1.89	2.55	1.84	2.31	1.66	2.18			
Stage 3	1.41	1.66	1.89	2.68	1.87	2.95	1.79	3.12	1.71	2.70	0.96	1.46	11.70
Stage 4	1.38	1.65	1.94	2.78	1.96	3.19	1.73	3.00	1.57	2.55	0.82	1.33	10.90
Stage 5	1.46	1.68	1.72	2.86	1.73	3.25	1.61	3.03	1.55	2.63	0.83	1.32	10.57

done with confidence if it can be shown that the accumulation was over a very short period of time (e.g., Czaplewski, 2011; Korth, et al., 2015),and that the fossils were carefully collected form a single horizon.

It is extremely difficult to estimate the actual ages of the individuals of these species, so the five age groups that were used in the analysis are essentially arbitrary. In looking at modern analogs of these fossil species, the length of each of the stages can be estimated, as has been done for large mammals (e.g., Kurten 1953; Voorhies, 1969). Since the family to which *Cylidrodon* belongs (Cylindrodontidae) has been extinct since the Oligocene (Walsh and Storer, 2008), it is difficult to find a Recent analog. In size, *C. natronensis* is similar to that of the modern chipmunk *Tamias*, and had a generalized skeleton similar to that of *Tamias* which is mainly terrestrial (Walsh and Storer, 2008). The maximum life-span of *Tamias* is two to three years (Nowak, 2005), thus suggesting the same for *Cylindrodon*. If this is the case, each of the Wear Stages of *C. natronensis* would represent approximately five to seven months. For *Chadrolagus*, a likely Recent analog that is similar in size is the cottontail rabbit *Sylvilagus*. The maximum life span of the latter is approximately five years (Nowak, 2005), suggesting that the Wear Stages for *Chadronlagus* average one year.

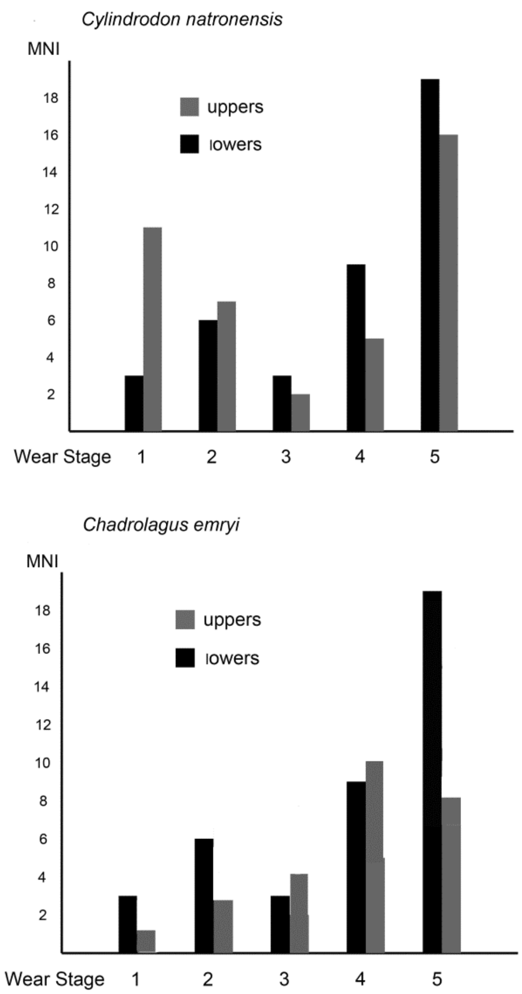

FIGURE 4. Survivorship curves of *Cylindrodon natronensis* (above) and *Chadrolagus emryi* (below). Horizontal axis = wear stages (see above text); vertical axis = minimum number of individuals in each stage. Lower dentition in black; upper dentition in gray.

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APPENDIX

Corrected dental measurements of *Cylindrodon solarborus* from the type area, Flagstaff Rim Wyoming. Abbreviations as in Table 1. Measurements in mm. Intended to replace the incorrect table in Emry and Korth (1996: table 3).

	dP4L	dP4W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	3	3			28	26	30	26	20	18	23
M	1.91	1.67			1.71	1.97	1.73	1.79	1.51	1.43	6.95
MIN	1.83	1.55			1.40	1.55	1.50	1.40	1.35	1.20	6.30
MAX	2.00	1.70			2.15	2.40	2.00	2.25	1.85	1.80	7.95
SD					0.22	0.24	0.15	0.25	0.11	0.18	0.43
CV					13.01	12.27	8.58	14.01	7.12	12.55	6.11

	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	2	2	17	16	24	22	22	21	15	15	13
M	2.05	1.34	1.88	1.69	1.93	1.96	1.92	1.93	1.64	1.41	8.05
MIN	2.00	1.23	1.65	1.45	1.50	1.45	1.70	1.40	1.50	1.25	7.35
MAX	2.10	1.45	2.20	1.90	2.25	2.20	2.15	2.15	1.80	1.60	9.15
SD			0.16	0.13	0.18	0.17	0.12	0.18	0.08	0.10	0.52
CV			8.28	7.91	9.25	8.63	6.37	9.13	5.13	7.26	6.41