A Paleopopulation of *Coryphodon lobatus* (Mammalia: Pantodonta) from Deardorff Hill *Coryphodon* Quarry, Piceance Creek Basin, Colorado

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Abstract

A unique early middle Wasatchian paucispecific bone bed from Deardorff Hill in the Piceance Creek Basin of Colorado contains a minimum of 12 individuals of *Coryphodon lobatus* that range in age from subadult ''yearlings'' to senescent individuals. The preponderance of *Coryphodon* material in this assemblage (92% of the 700+ complete bones represent a single species of *Coryphodon*) argues for a ''catastrophic'' origin for this assemblage. The Deardorff Hill *Coryphodon* Quarry preserves one of the most complete dental eruption sequences reported to date for *Coryphodon* and allows interpretation of demographic and life history attributes not ordinarily observable, such as evidence of seasonality in births. In addition, females are disproportionate in number to males, further confirming that this species had a polygynous social structure. Mass mortality assemblages are useful in eliciting a better understanding of the range of variation in single populations. Metrically, the molars of *C. lobatus* specimens from Deardorff Hill *Coryphodon* Quarry have coefficients of variation ranging from 4 to 11, which are comparable to metric variation observed in other mass death *Coryphodon* assemblages. An understanding of the range of variation in this highly variable taxon is of particular importance in the taxonomy and phylogenetic relationships of this ubiquitous Eocene mammal.

Introduction

Coryphodon was a large-bodied, subdigitigrade browsing mammal common in North America, Europe, and Asia from the latest Paleocene to the early Eocene. In addition to the ubiquitous occurrence of isolated teeth and partial jaws in fossil outcrops, there are several instances of mass death assemblages of *Coryphodon*, such as Roehler's *Coryphodon* Catastrophe Quarry (RCCQ) in Wyoming (McGee, 2001, 2002) and AMNH Quarry 242 in New Mexico (Lucas, 1984). Here we report an additional early middle Wasatchian paucispecific assemblage from Deardorff Hill in the Piceance Creek Basin of Colorado. Originally excavated in the 1940s by Bryan Patterson and colleagues, this assemblage provides tantalizing details on intraspecific and interspecific variation in *Coryphodon*. Below we describe the geologic and taphonomic setting of Deardorff Hill *Coryphodon* Quarry and provide a detailed description of the dental material of *Coryphodon lobatus*, including a reconstruction of the eruption sequence of the dentition. As a ''death assemblage,'' Deardorff Hill *Coryphodon* Quarry provides an unusual opportunity to assess paleobiological and paleodemographic attributes of a population not normally preserved in the fossil record.

Abbreviations and Institutions

AMNH = American Museum of Natural History, New York, NY; RCCQ = Roehler's *Coryphodon* Catastrophe Quarry, WY; UCMP = University of California Museum of Paleontology, Berkeley, CA; FMNH or FM = Field Museum, Chicago, IL; PM or P = Field Museum fossil mammal collection.
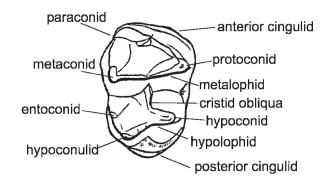
Dental Terminology and Measurements

L = length; AW = anterior width; PW = posterior width; MNI = minimum number of individuals; N = number of specimens; CV = coefficient of variation; SD = standard deviation. All measurements are in millimeters. Cusp and loph designations for the M_3 and M^3 are illustrated in Figure 1. Length and width of individual teeth were measured along maximum dimensions in anteroposterior and transverse planes, respectively. Measurements were taken using Fowler Ultra-Cal II electronic calipers.

Geologic Setting and History of Discovery

Deardorff Hill *Coryphodon* Quarry is situated on the east side the Piceance Creek Basin in northwestern Colorado. The eastern margin of the Piceance Creek Basin, which formed during the Late Cretaceous, is framed by the Axial Basin arch, White River uplift, and Elk Mountains, while the western margin comprises the Uncompahgre uplift, Douglas Creek arch, and the Uinta arch and was formed during the Late Paleocene and Early Eocene (Figure 2; Kihm, 1984). The three early Tertiary rock units include the Debeque (originally identified as Wasatch by Hayden, 1873), Green River, and the Uinta Formations.

In the 1930s and early 1940s, Bryan ''Pat'' Patterson of the Field Museum led collecting expeditions to the Plateau Valley region in the Piceance Creek Basin (western Colorado). In 1941, crew member John M. Schmidt discovered Deardorff Hill *Coryphodon* Quarry (''42-41''), which was subsequently excavated by Schmidt and the chief fossil preparator for the Field Museum, James H. Quinn. While Patterson's work in western Colorado culminated in a number of publications on
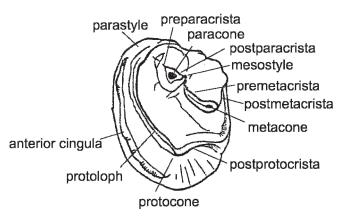
FIG. 1. Terminology of the cusps and lophs of the upper and lower molars of *Coryphodon lobatus* as illustrated by a left M^3 and a right M_3. The terminology used in describing *Coryphodon* lower dentition follows Lucas (1984). Lucas's (1984) terminology is derived from Szalay (1969) and Simpson (1929) with the exception that the cusp identified by Simpson (1929, fig. 8A') as the entoconid is most likely the hypoconulid (Uhen and Gingerich, 1995). This is a significant point since the presence or absence of the entoconid is an important nonmetric trait in distinguishing species of *Coryphodon*. After Lucas (1984, figs. 50F and 51F).

Titanoides and other Tertiary mammals, his work on *Coryphodon* was restricted to a single paper (Patterson, 1939) published prior to the discovery of the Deardorff Hill *Coryphodon* Quarry.

Kihm (1984) described the "Plateau Local Fauna" as a series of Middle Clarkforkian (Earliest Eocene) through late Wasatchian (late Early Eocene) faunas. He identified three Tertiary mammal locality sequences in the Piceance Creek Basin: 1) White River in the northern end of the basin and in the Gray Hills region, 2) farther south, the Roan Cliff region (northwest of Battlement Mesa), and 3) the Mamm Creek region (northeast of Battlement Mesa). Deardorff Hill *Coryphodon* Quarry is located in the southeastern margin of the Mamm Creek region. This region, which extends northward to the Grand Hogback mountains and southward to the northeast corner of Battlement Mesa, contains predominantly Clarkforkian to Wasatchian exposures.

Composition and Condition of the Deardorff Hill *Coryphodon* Quarry Assemblage

The Deardorff Hill *Coryphodon* Quarry is a paucispecific assemblage consisting of over 700 recognizable skeletal elements (not including ribs) and over 600 fragments of *C.*
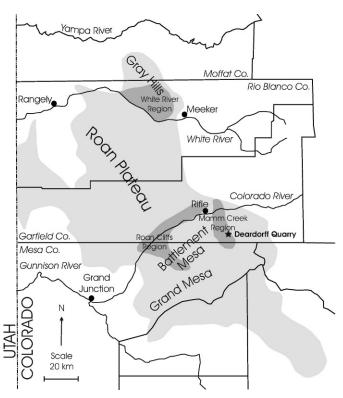

FIG. 2. Piceance Creek Basin in northwestern Colorado. The extent of the basin is demarcated in light gray. Tertiary mammal locality sequences worked by Kihm (1984) in the Piceance Creek Basin are shown in darker gray and include White River in the northern end of the basin and in the Gray Hills region, the Roan Cliff region (north of Battlement Mesa), and the Mamm Creek region (east of Battlement Mesa). Deardorff Hill *Coryphodon* Quarry is located in the southeastern margin of the Mamm Creek region.

lobatus. The MNI based on mandibular and maxillary elements is 10, while MNI based on the right humerus is 12. Information loss is clearly evident in the inventory of bones from this quarry, as depicted in Figure 3 and Table 1, which show the relative abundance of different postcranial elements in the assemblage based on an MNI of 12. The assemblage is biased against smaller elements (e.g., clavicle, sternum, and bones that make up the manus and pes) that, according to the classic taphonomy studies of Voorhies (1969), are the first to be removed by water currents on deposition. Voorhies (1969) suggests that shape of an element influences its potential for transport, so flat bones that float more easily, such as the scapula and innominate, should likewise be absent in an assemblage dominated by larger, heavier bones (i.e., humerus, femur). The profile in Figure 3, however, shows that innominates and scapulae are only slightly less common than larger bones such as the femur. The humerus, the stoutest bone in the *Coryphodon* skeleton, is noticeably more common than any other single element. These biases would suggest that the assemblage was only briefly worked by water currents before deposition and burial.

Fragmentation and compression are characteristic postmortem alterations in the material from Deardorff Hill *Coryphodon* Quarry. Few of the elements were preserved articulated in situ (e.g., PM 39705: atlas through 5th cervical vertebrae; PM 39392: articulated pelvic girdle with left and right innominates, sacrum, and several caudal vertebrae) despite careful preparation of the blocks in the lab at the Field Museum.
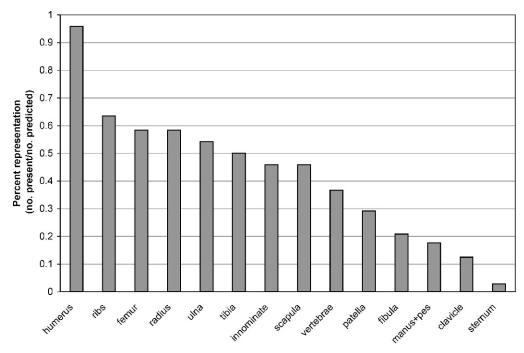
Fig. 3. Relative representation of postcranial elements of *Coryphodon lobatus* from Deardorff Hill *Coryphodon* Quarry. Percentages are based on an MNI of 12.

Hill (1979) suggested that the taphonomic profile of an assemblage may reflect the sequence of disarticulation (Hill, 1979). Water, long known to play an important role in the dispersal of bones (Voorhies, 1969; Behrensmeyer, 1975, 1991), also is a factor in determining the disarticulation sequence of a carcass. In humid conditions, for example, a bovid will disarticulate from the extremities inward, whereas in drier conditions, disarticulation proceeds outward from the body to the extremities. If an assemblage is affected by the sequences of bone disarticulation, a bias against proximal or distal bones would be predicted. Counts of distal (i.e., radius, ulna, tibia, and fibula) and proximal (i.e., humerus, scapula, innominate, and femur) elements in the Deardorff Hill *Coryphodon* Quarry were analyzed using the Mann–Whitney test for independence of means. There is no significant difference between the number of proximal vs. distal elements in this assemblage ($p = 0.686$). The assemblage was also analyzed to determine if there were differences between left and right elements of the limb. Similarly, there was no statistically significant difference between left and right ($p = 0.931$).

Information on relative representation of different elements, the assessment of proximal vs. distal, and left vs. right elements, plus visual inspection of the physical characteristics of the bones, all suggest that burial was rapid and that reworking was minimal.

More than 97% of the assemblage is monospecific. Additional mammals present include primates (*Cantius abditus*: P26477, P26656, P26660), rodents (*Paramys copei*: P26659), creodonts (*Oxyaena forcipata*: P26647), carnivores (*Didymictis protenus*: P26649), condylarths (*Phenacodus primaevus*: P15697; *Hyopsodus* sp. nr. *H. latidens*: P26650, P26697; *Meniscotherium tapiacitis*: P26658), and perissodactyls (*Hyracotherium* sp. C. sensu Kihm 1984: P15705, P26516, P26566, P26567, P26646, P26651, P26655, P26657, P26661, P26664, P26665). The assemblage also contains a few

TABLE 1. Inventory of postcranial elements of *C. lobatus* from Deardorff Hill *Coryphodon* Quarry, and associated relative abundance estimates.

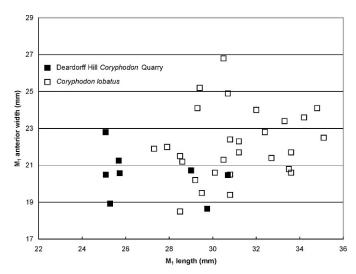|	Number in assemblage	Number per individual	Number expected in assemblage if MNI = 12	Relative abundance
Humerus (L = 11; R = 12)	23	2	24	0.96
Radius (L = 2; R = 3; indet. = 9)	14	2	24	0.58
Scapula (L = 6; R = 4; indet. = 1)	11	2	24	0.46
Ulna (L = 6; R = 7)	13	2	24	0.54
Femur (L = 6; R = 8)	14	2	24	0.58
Innominate (L = 6; R = 4; indet = 1)	11	2	24	0.46
Tibia (L = 7; R = 5)	12	2	24	0.50
Fibula (L = 0; R = 2; indet = 3)	5	2	24	0.21
Ribs	259	34	408	0.63
Vertebrae	207	47	564	0.37
Patella (L = 1; R = 3; indet. = 3)	7	2	24	0.29
Manus+pes	225	106	1272	0.18
Clavicle (indet. = 3)	3	2	24	0.13
Sternum	2	6	72	0.03

FIG. 4. Metric variation in the lower first molar of *Coryphodon* from Deardorff Hill *Coryphodon* Quarry compared with lower first molar of *Coryphodon lobatus* reported by Lucas (1984). The Deardoff Quarry specimens slightly extend the size range of *C. lobatus*.

specimens of turtles (Chelonia: Trionychidae?). The preponderance of *Coryphodon* material in this assemblage (700+ complete bones) and the relative absence of material from other species (21 specimens total, representing eight species of mammals, plus a small assortment of turtle scrap) argues strongly for a "catastrophic" origin for this assemblage.

A catastrophic or mass death accumulation is also characterized by the predominance of a single taxon which shows an age profile that is representative of a living population (Kurtén, 1953; Voorhies, 1969; Turnbull & Martill, 1988). In contrast, assemblages formed over an extended period of time have an age profile that reflects greater mortality in juveniles and old adults (Klein & Cruz-Uribe, 1984; Haynes, 1985, 1987). The Deardorff Hill *Coryphodon* Quarry has an age profile in which each age-group (see below) is represented by about the same number of individuals and is therefore more comparable to a mass death accumulation.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Pantodonta (Cope, 1873)
Family Coryphodontidae (Marsh, 1876)
Coryphodon lobatus (Cope, 1877)
(Figures 1, 5–8)

REFERRED SPECIMENS—P15628: mandible with LI_1–M_3, RI_1–M_3 and skull with LI^{1-3}, LC, LP^2–M^3, RI^{1-3}, RC, RP^2–M^3; PM 35865: mandible with LI_{1-2}, LP_1–M_3, RI_2–I_3, RP_1–M_3 and associated lower L/C and LI_3; PM 35870: dentary with LP_1–M_2, associated lower LC and two incisors, and skull with LC, LP^{2-4}, LM^{1-3}, RP^{2-4}, RM^{1-3}; PM 35871: skull with LI^1–M^3, RI^2–C, RP^2–M^3; PM 35873: mandible with LI_1–M_3, RI_1–C, RP_2–M_3; PM 35878: mandible with LI_1–M_3, RI_1–I_2, RC–M_3; PM 35879: maxillary fragment with LdP^{2-4}, LM^1; PM 35903: skull with LP^2–M^3 and RP^2–M^3; PM 39374: mandible with LI_{1-2}, LP_2–M_3, RI_{1-2}, RP_1–M_3; PM 39375: mandible

with LdP_{1-3}, LM_1 and RM_1; PM 39381: maxillary fragment with RdP^{1-4}–M^1 (possibly the other half of PM 39686); PM 39385: skull with LC–M^3 and RC, RP^2–M^3; PM 39436: mandible with LdP_{2-4}–M_1 (possibly part of PM 35879); PM 39605/39665: skull with LI^3?, LdP^4, LM^{1-2} and RdP^4, RM^{1-2}; PM 39673: skull with LI^3, LC, LP^2–M^3 and RI^3, RC, RP^2–M^3; PM 39686: maxillary fragment with LdP^{1-4}–M^1; PM 39702: mandible with LdP_1, LdP_{3-4}–M_2 and RI_3?, RdP_{1-4}–M_2.

DESCRIPTION—*Coryphodon* species have historically been difficult to distinguish (Earle, 1892; Patterson, 1939) because of individual, sexual, and interspecific variation. Lucas's (1984) treatment remains the most comprehensive to date and provides a basis for identifying the species present at Deardorff Quarry. Lucas (1984) argues that the following characteristics of the M^3 are useful in identifying species of *Coryphodon* (Figure 1): 1) presence and size of M^3 metastyle, 2) relative length and orientation of the postparacrista–premetacrista crest, 3) presence or absence of postprotocrista, and 4) size of the postero-lingual cingulum. For the M_3, the following characteristics are distinctive (Lucas, 1984): 1) length and orientation of the hypolophid, 2) size of the posterior cingulid, 3) presence or absence of the entoconid, entocristid, and other postero-lingual cuspulids and their position and relative size, and 4) size and orientation of the cristid obliqua.

We assign the Deardorff Quarry *Coryphodon* specimens to *C. lobatus*. The M_3 of these specimens possess 1) a semitransverse hypolophid (although not quite as parallel as in *C. subquadratus*), 2) a small but distinct entoconid (absent in *C. molestus*; *C. anthracoideus* has numerous lingual cusps), and 3) a well-developed posterior cingulum with an incipient cusp on the lingual side. The hypoconulid in the Deardorff specimens is more lingual (as in other species) than in *C. proterus* in which the hypoconulid is very centrally placed. The M^3 of the specimens from Deardorff Hill *Coryphodon* Quarry 1) typically lack an M^3 metastyle (or otherwise have a very small one), 2) have a distinctive ectoloph because of the orientation of the postparacrista–premetacrista crest, and 3) have a well-developed postprotocrista. Although several of the *Coryphodon* from Deardorff Hill *Coryphodon* Quarry possess a postero-lingual cingulum, Lucas (1984) argues this is not a feature of *C. lobatus*. A large postero-lingual cingulum is seen in *C. proterus*. The Deardorff Hill *Coryphodon* Quarry specimens cannot be *C. proterus*, however, because of the angle formed by the postparacrista–premetacrista; in *C. proterus*, the postparacrista–premetacrista is straight and nearly transverse (Lucas, 1984).

Lucas (1984) assigns Deardorff Hill *Coryphodon* Quarry specimens to two *Coryphodon* species, *C. lobatus* (P15628, PM 35865, PM 35873) and *C. molestus* (PM 35870, PM 35871, PM 35903, and PM 35878). We observe most, if not all, of the characteristics noted above for *C. lobatus* on the specimens Lucas (1984) designates to *C. molestus*. For PM 35870, the upper third molars lack a metastyle, the postprotocrista is present, and there is a distinctive ectoloph. Both PM 35871 and PM 35903 have a very small metastyle on M^3; a postprotocrista is present, and the ectoloph is distinctive. PM 35878 has a very small entoconid on the M_3; the hypolophid is nearly transverse, and the posterior cingulid is present and well developed. Metrically, PM 35870, PM 35871, PM 35903, and PM 35878 (see below) are smaller than the other Deardorff Hill *Coryphodon* Quarry specimens noted by

TABLE 2. Summary statistics of molar measurements for *C. lobatus* from Deardorff Hill *Coryphodon* Quarry. All measurements in mm.

	N	Mean (mm)	SD	Range (mm)	CV
Lower dentition					
P_4L	6	23.11	1.58	20.71–24.80	6.84
P_4W	6	19.40	1.14	17.97–20.58	5.87
M_1L	9	27.73	2.70	25.08–32.57	9.75
M_1AW	9	20.45	1.18	18.31–22.66	5.77
M_1PW	9	20.68	0.88	19.54–22.32	4.27
M_2L	6	34.84	3.46	30.17–39.47	9.94
M_2AW	7	25.83	1.59	24.20–28.64	6.16
M_2PW	6	24.87	1.60	22.97–27.18	6.45
M_3L	4	38.91	4.46	35.29–44.83	11.45
M_3AW	5	28.01	1.80	26.24–30.15	6.42
M_3PW	4	25.25	1.39	23.63–26.94	5.50
Upper dentition					
P^4L	6	20.15	1.70	18.16–22.58	8.41
P^4W	6	32.00	1.36	30.64–34.34	4.26
M^1L	10	27.92	3.03	22.81–31.71	10.84
M^1AW	10	31.03	1.61	28.77–34.83	5.18
M^1PW	9	30.14	2.69	26.37–36.15	8.93
M^2L	7	33.52	2.68	30.28–36.92	7.99
M^2AW	7	38.40	1.28	37.28–40.54	3.34
M^2PW	7	37.43	1.70	35.78–40.23	4.53
M^3L	6	32.74	3.44	28.40–38.40	10.51
M^3W	6	44.16	3.76	40.14–49.55	8.51

Lucas (1984), but we argue that these specimens should be classified with *C. lobatus*.

Coryphodon species have also traditionally been differentiated metrically. An important caveat, however, is that interspecific variation of taxonomic consequence is best assessed using metric measurements on elements that are not sexually dimorphic. Gingerich (1981) suggests that the central cheek teeth (P_4^4, M_1^1, and M_2^2) are unimodally distributed within a species; of the three, the first molar shows the least variation within mammalian species (Gingerich, 1974). A bivariate plot depicting the relationship between length vs. width of the lower first molar for the Deardorff Hill *Coryphodon* Quarry specimens and other *C. lobatus* is presented in Figure 4. The Deardorff Hill *Coryphodon* Quarry assemblage moderately extends the size range for *C. lobatus* with the individuals from Deardorff Hill *Coryphodon* Quarry being smaller on average with respect to other *C. lobatus*.

Coefficients of variation, a standard measure of the relative amount variation in a sample, for P4 through M3 of the *Coryphodon* from Deardorff Hill *Coryphodon* Quarry are given in Table 2. Simpson et al. (1960) noted that coefficients of variation for mammalian species characteristically range between 4 and 10. Gingerich and Schoeninger (1979) observed a more narrow range of approximately 6 to 9 for P4, M1, M2, and M3 for primates, while Gingerich and Winkler (1979) observed a slightly broader range of approximately 3 to 12 for the same teeth in the red fox (*Vulpes vulpes*). The *Coryphodon* from Deardorff Hill *Coryphodon* Quarry have CV values ranging from approximately 4 to 11. Variation in specimens from Deardorff Hill *Coryphodon* Quarry is within an acceptable range for a species of *Coryphodon*, especially given that this taxon is sexually dimorphic.

Age Determination

Lucas and Schoch (1990) and Lucas (1984) proposed a dental eruption sequence in *Coryphodon* that is confirmed by the *C. lobatus* specimens from Deardorff Hill *Coryphodon* Quarry. In addition, the specimens from this quarry permit us to fine-tune some of the details of the eruption sequence. We observe the following at Deardorff Hill *Coryphodon* Quarry (Figure 5):

- None of the anterior deciduous dentition is intact in the Deardorff Hill *Coryphodon* Quarry specimens. Lucas and Schoch (1990) believe that the anterior deciduous dentition precedes the posterior deciduous dentition. Given the teeth present in the Deardorff Hill *Coryphodon* Quarry specimens, we believe that the deciduous premolars dP4, dP3, and dP2 erupt sequentially, starting with the dP4.
- The first molar (M1) erupts next at about the same time as I3 and followed by the last of the deciduous teeth, the dP1. Unlike other deciduous teeth, the dP1 is retained in the adult dentition.
- The M2 erupts next, followed by the permanent premolars P4, P3, and P2, which replace the deciduous premolars.
- The I1 probably erupts next, followed by the adult canine, I2, and M3, which erupt at approximately the same time. From the Deardorff Hill *Coryphodon* Quarry specimens, we can determine that these teeth erupt simultaneously, whereas previously it was suggested that the I2 and M3 erupted after the canine.

As in other mammals, deciduous teeth are identified by their weak or flaring roots, a light brown color, and thin, less rugose or striated enamel. Corresponding teeth of the upper and lower dentition erupt at the same time. These patterns and
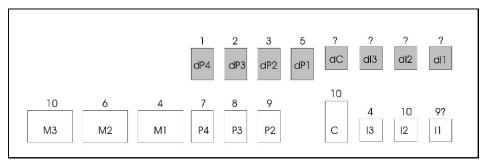

FIG. 5. Dental eruption sequence for *Coryphodon*. Data from Deardorff Hill *Coryphodon* Quarry confirm postulated sequence of Lucas and Schoch (1990). After Lucas and Schoch (1990).
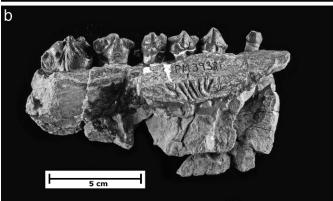
FIG. 6. (**A**) *Coryphodon lobatus*, PM 39436, mandible with LdP$_{2-4}$–M$_1$. (**B**) *C. lobatus*, PM 39381, maxillary fragment with RdP$^{1-4}$, M^1. Deciduous premolars still present and first permanent molar present. I3 is in the process of erupting (indicated by arrow in Fig. 6A). Deardorff Hill *Coryphodon* Quarry contains four individuals from age class 1 that are nearly identical in eruption and wear patterns. This suggests these individuals were the same age at death and therefore were born at the same time of year (i.e., births could have been seasonal).

FIG. 7. (**A**) *Coryphodon lobatus*, PM 39605/39665, skull with LI$^{3?}$, LdP^4, LM$^{1-2}$ and RP^3–M^2. (**B**) *C. lobatus*, PM 39702, mandible with LdP$_1$, LdP$_{3-4}$–M$_2$ and RI$_{3?}$, RdP$_{1-4}$–M$_2$. These specimens represent age class 2. The second permanent molar is partially erupted; third and fourth permanent premolars in process of erupting (indicated by arrow in Fig. 7A).

characteristics are verified here and also reported by Lucas and Schoch (1990).

We group the *C. lobatus* specimens from Deardorff Hill *Coryphodon* Quarry into five age classes. The first three classes are distinguished by eruption sequences, while the last two classes are differentiated on the basis of wear.
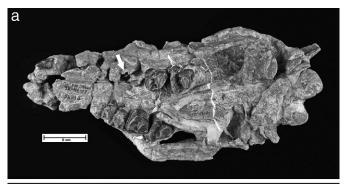
Age Class 1 (young subadult)

(Figure 6)

Deciduous premolars are still present, and the first permanent molar is fully erupted; I3 is in the process of erupting (arrow, Figure 6). Specimens in age class 1 include the following:

PM 39436 (LdP$_{2-4}$–M$_1$): M$_1$ is fully erupted and I3 is partially erupted. An alveolus is present for dP$_1$ but the tooth is missing. The dP$_{2-4}$ are well worn; the M$_1$ shows minimum wear, appearing as a shear surface along the metalophid.

PM 39381 (RdCP$^{1-4}$–M^1): Permanent right I$_3$ in the crypt exposed through breakage, suggesting that this would be the next tooth to erupt (possibly in advance of M$_2$).
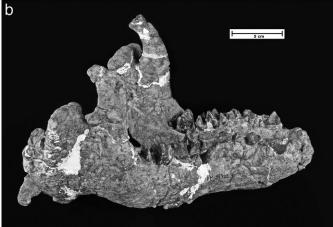
PM 35879 (LdP$^{2-4}$–M^1): Possibly from the same individual as PM 39381. These two specimens are very similar in eruption and wear stage to PM 39436.

PM 39686 (LdP$^{1-4}$–M^1): Similar in eruption and wear to PM 39436, PM 39381, and PM 35879. This specimen preserves the area posterior to the M^1, and there is no evidence of the M^2 or even a crypt for M^2.

PM 39375 (LdP$_{1-3}$, LM$_1$, and RM$_1$): M$_1$ and dP$_1$ are fully erupted. The crypt of the M$_2$ is visible, but no tooth is apparent. It is also uncertain if the P$_4$ was shed or fell out postmortem. LdP$_{1-3}$ are present with wear (dP$_4$ is missing, but the alveolus is present and well defined), and there is no wear on M$_1$. The presence of the M$_2$ crypt suggests that this individual was older than PM 39686, PM 39436, PM 39381, and PM 35879.

Deardorff Hill *Coryphodon* Quarry contains four individuals from this class (PM 39686, PM 39436, PM 39381, and PM 35879) that are nearly identical in eruption and wear patterns. This suggests the same age at death and thus would have been born at the same time of year. Although these four are the youngest in the assemblage, the presence of the permanent M$_1$ suggests that even the youngest individuals in this *Coryphodon* herd were probably weaned and that births could have been seasonal. In two extant analogues of *Coryphodon*—*Sus scrofa* and *Hippopotamus amphibius*—subadults are weaned (3.38 months and 10.13 months, respectively; Ernest, 2003) before the first molar has completely erupted (5.6 months and 24 months, respectively; Smith, 2000).
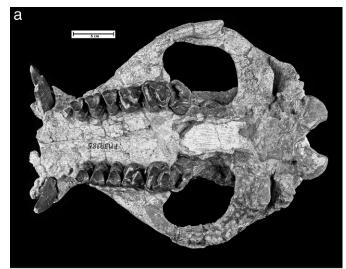
FIG. 8. (A) *Coryphodon lobatus*, PM 39385, skull with LC–M^3; RC, P^2–M^3. (B) *C. lobatus*, PM 35873, mandible with LI$_1$–M$_3$, RI$_1$–C, P$_2$–M$_3$. These specimens represent age class 3. Permanent canine and third molar partially erupted, and the adult second incisor (one of the last teeth to erupt in adult dentition) is also erupting.

Age Class 2 (subadult)

(Figure 7)

PM 39702 and PM 39605/39665, which may represent the same individual, are considered a subadult:

PM 39702 (mandible with LdP$_1$, LdP$_{3-4}$–M$_2$ and RI$_{3?}$, RdP$_{1-4}$–M$_2$): M$_1$ and dP$_{1-4}$ are fully erupted and show some wear. The M$_2$ is partially erupted. On the left, a permanent premolar is partially exposed under the dP$_4$. There is a very small alveolus anterior to the right dP$_1$, presumably for a deciduous canine; the left side of the mandible is too badly damaged to determine the status of this area. There is a large, spatulate tooth anterior to this alveolus, which is interpreted to be the RI$_3$.
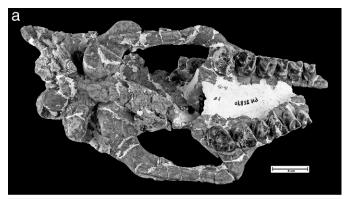
PM 39605/39665 (skull with LI$^{3?}$, LdP^4, LM$^{1-2}$, and RP^3–M^2): As with PM 37902, the M^1 shows some wear and the M^2 is partially erupted. Permanent premolars are partially exposed under the LdP^3, LdP^4, RdP^3, and RdP^4.

Age Class 3 (young adult)

(Figure 8)

PM 35873 and PM 39385 are considered young adults:

PM 35873: The C and M$_3$ are partially erupted on both sides. The anterior dentition of this specimen is unusual in that there are three fully erupted and worn incisors that appear to be part of the adult dentition, but there is also another incisor erupting into the position occupied by RI$_2$; it is unknown
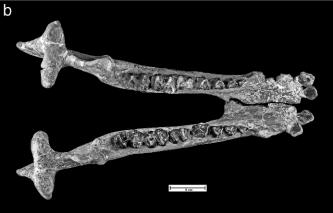

FIG. 9. (A) *Coryphodon lobatus*, PM 35870 skull with L/C, LP$^{2-4}$, LM$^{1-3}$, RP$^{2-4}$, RM$^{1-3}$. (B) *C. lobatus*, PM 35865 (mandible with LI$_{1-2}$, P$_1$–M$_3$, RI$_2$–I$_3$, P$_1$–M$_3$ and associated lower LC and LI$_3$ not pictured). All teeth present are part of the permanent dentition (dP1 is retained). First and second molars are worn (especially the M1); incisors also show wear.

whether this tooth is supernumerary or if it is an adult incisor displacing the dI2. (This confirms Lucas's observation that the I2 is the last incisor to erupt.) All other teeth present in the mandible are permanent. The canines are about 28.71 mm (right side) at the gum line, but the dentary is broken away to expose the rest of the canine (on both sides), which appears large. PM 39385 is a skull that similarly has partially erupted M^3 and almost fully erupted canines; the incisors are not preserved in this specimen.

Age Class 4 (adult)

(Figure 9)

In age class 4, all of the adult teeth are erupted:

PM 35870 (dentary with LP$_1$–M$_2$, associated lower LC and two incisors, and skull with LC, LP$^{2-4}$, LM$^{1-3}$, RP$^{2-4}$, RM$^{1-3}$): All teeth are part of the permanent dentition. The protoconids and hypoconids on the lower M1 and M2 are worn (especially in M1). In the skull, the protocones and postprotocristae of the M1 and M2 are similarly worn; the third molar, which is present in the skull but absent in the dentary fragment, shows only the beginning stages of wear. The permanent premolars are not significantly worn in either the skull or the dentary fragment.

PM 35865 (mandible with LI$_{1-2}$, LP$_1$–M$_3$, RI$_2$–I$_3$, RP$_1$–M$_3$ and associated lower LC and LI$_3$): All teeth are part of the permanent dentition. There is a small amount of wear on the RM$_3$; wear increases anteriorly from M$_3$ to M$_1$. P$_4$ is not worn,

but P_3 is. The left dentary of this mandible is similar in wear features except that the P_4 is more worn than the P_3, and overall there is considerably more wear on the teeth on the left than on the right. There is a fair amount of wear on RI_3 and to a lesser extent, RI_2; on the left side, I_1 shows more wear than I_2.

PM 35903 (skull with LP^2–M^3 and RP^2–M^3): The lower and upper M1 are very worn, and the protoloph and ectoloph on M^3 are fairly worn.

PM 35871 (skull with LI^1–M^3, RI^2–C, RP^2–M^3) and PM 35878 (mandible with LI_1–M_3, RI_1–I_2, RC–M_3): The protocone of the M^3 is moderately worn, along with the protoloph and ectoloph; as with PM 35903, the upper and lower first molar are very worn. The left and right I^3 in PM 35871 are the most worn of the upper incisors; on the lower dentition (PM 35878), the I_2 are the most worn of the incisors.

Age Class 5 (advanced/old adult)

As with age class 4, in age class 5, all of the adult teeth are erupted. Age class 5 exhibits extreme wear on many of the teeth:

PM 39673 (skull with LI^3, LC, LP^2–M^3 and RI^3, RC, RP^2–M^3), PM 39374 ($LI_{1–2}$, LP_2–M_3, and $RI_{1–2}$, RP_1–M_3), and P15628 (mandible with LI_1–M_3, and RI_1–M_3 and skull with $LI^{1–3}$, LC, LP^2–M^3, $RI^{1–3}$, RC, RP^2–M^3) are the most worn of the specimens. Both upper and lower M1 and M2 are extremely worn, and M3 is beginning to show excessive wear along the metalophid and protoconid/hypolophid on the lowers; in the uppers, the protoloph and ectoloph are completely worn. There is still enamel present elsewhere on the occlusal surface of both the upper and lower M3; there is almost no enamel left on the occlusal surfaces of the upper and lower M1 and M2. The P3 and P4 are also well worn (especially in the lower dentition).

Aspects of *Coryphodon* Life History

The preservation of the eruption sequence of the Deardorff Hill *Coryphodon* provides an opportunity to consider life history characteristics of *Coryphodon*. Smith (2000) suggests that relative eruption sequences of select extant taxa can be used to predict the tempo of life histories for species of extinct mammals. She examined eruption sequences in Insectivora, Archonta, and Ungulata to test "Schultz's Rule" that permanent incisors, canines, and premolars (= replacement teeth) erupt earlier in slow-growing, long-lived species. She noted that in rapidly growing mammals (e.g., *Antidorcas*), the three sets of teeth (deciduous, molars, and replacement) erupt sequentially (deciduous → molars → replacement), whereas in slow-growing mammals (e.g., *Homo*), the eruption of molars and replacement teeth is mixed (e.g., the permanent canine erupts after M1 and before M3, as in the case of the collared peccary, *Tayassu tajacu*). Age classes 1 and 2 of *C. lobatus* from Deardorff Hill *Coryphodon* Quarry clearly indicate a sequence in which the molars and replacement teeth are mixed, a pattern that is suggestive of a prolonged development.

Framing *Coryphodon* evolution within the context of life histories, as suggested by Smith (2000) also leads us to consider which, if any, large-bodied extant herbivore is a good analogue for this taxon. Within the "slow growers," Smith (2000)
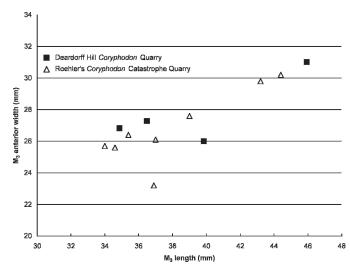

Fig. 10. Metric variation in the lower third molar of *Coryphodon lobatus* from Deardorff Hill *Coryphodon* Quarry compared with lower third molar of *C. anthracoideus* from Roehler's *Coryphodon* Catastrophe Quarry. Both death assemblages indicate the presence of large- and small-size morphs in each assemblage, presumed to indicate males and females, respectively.

suggested that *Coryphodon* is less like the hippo and more like a large deer or pig. She noted that the eruption patterns of I_1 and P_3 seen in *Coryphodon* are found in extant mammals in which the M_1 erupts between 0.34 and 0.88 years and that have a life span of 21 to 35 years. She questions whether the hippo, with a slower life history marked by the emergence of the M1 at two years and a life span of 40 to 50 years, is a suitable analogue for *Coryphodon*. *Coryphodon* shares a sequence pattern $M_1M_2P_3M_3$ with *Equus burchelli*, *T. tajacu*, *S. scrofa*, *H. amphibius*, *Ceratotherium simum*, and *Procavia capensis*. We add to this the observation that all these taxa, with the exception of *E. burchelli*, wean their young before the complete eruption of the first molar (Smith, 2000; Ernest, 2003). These observations serve to underscore the complexity of identifying an analogue. In putting *Coryphodon* in the context of an extant species, Lucas (1984) discussed functional analogues such as the pygmy hippo (*Hexaprotodon liberiensis*), tapirs (*Tapirus* sp.), and the Sumatran rhino (*Dicerorhinus sumatrensis*) as well as ecologic analogues such as the hippo (*H. amphibius*). Dental eruption data suggest that life history can also serve as a basis for analogy between extant and extinct taxa.

Sociality in *Coryphodon* and Future Directions

Death or catastrophic assemblages such as Deardorff Hill *Coryphodon* Quarry potentially provide a unique window into the behavior of extinct populations. A paleopopulation, defined as a well-delimited faunal level spanning a short period of geological time (MacFadden, 2008), may still represent as much as 100,000 years in duration. Mass death assemblages, representing near instantaneous accumulation (e.g., such as that seen over a period of days, weeks, or months during wildebeest migrations when rivers are in flood; Talbot & Talbot 1963), are more comparable to extant populations.

Mihlbachler (2003) argued that because adult sex ratios (ASRs) are linked to sociality in extant species (Berger, 1986;

Byers, 1997), ASRs in fossil assemblages can be used to infer paleodemography in extinct species if males can be distinguished from females through sexually dimorphic features. Sexual dimorphism in *Coryphodon* quarry assemblages is evident in the size of the third molars and the canines (Figure 10). We would expect this to be the case on the basis of Gingerich's (1974) suggestion that the third molar is under greater influence of sex hormones than the first and second molars, which erupt earlier. Sexual dimorphism can also be inferred from canines. However, canines are often missing or broken in *Coryphodon* assemblages that have undergone significant postmortem modifications. Figure 10 indicates that there are two distinct size morphs in the Deardorff Hill *Coryphodon* Quarry assemblage, a pattern that is also seen in the death assemblages of *C. anthracoideus* from Roehler's *Coryphodon* Catastrophe Quarry and *C. molestus* from AMNH Quarry 242. General consensus is that in extant large herbivorous mammals, males are usually larger than females (Ralls, 1977; Jarman, 1983), and this has been inferred for fossil mammals (Kurtén, 1969; Gingerich, 1981).

Ralls (1977) and Jarman (1983) argued that there is a close correlation between sexual dimorphism and polygyny. Using information on sexual dimorphism and body size differences in *C. lobatus* from Deardorff Hill *Coryphodon* Quarry, we can reconstruct a picture of sociality patterns. The ASR at Deardorff Hill *Coryphodon* Quarry is minimally 1:3 (which is also the case for *C. anthracoideus* at Roehler's *Coryphodon* Catastrophe Quarry). We would predict based on the model of Berger et al. (2001) that *C. lobatus* lived in unisex groups except during periods of the year when mating took place. The ASR of the Deardorff Hill *Coryphodon* Quarry indicates that males were present at the time the death event occurred, and therefore this assemblage probably preserves a picture of this population of *Coryphodon* during mating season.

The cranial and postcranial *C. lobatus* material from Deardorff Hill *Coryphodon* Quarry is still largely unstudied beyond basic inventorying, and thus many questions remain regarding the degree and nature of sexual dimorphism in this species. It has been suggested that extreme polygyny and dimorphism are associated with bimaturism; that is, males and females reach sexual maturity at different ages (Ralls, 1977; Jarman, 1983). Jarman (1983) argued that a delay in male maturation is in fact a requirement for the evolution of extreme polygyny and sexual dimorphism. *Coryphodon* mass death assemblages will no doubt be useful in eliciting the degree of sexual dimorphism in this taxon and hence the possibility that males matured later than females. Additional work might also focus on a closer inspection of size differences between the two morphs (i.e., males and females) in the Deardorff Hill *Coryphodon* Quarry assemblage. With respect to interpreting the behavioral and/or demographic significance of sexual dimorphism, the distinction must be made between dimorphism in secondary sexual characteristics and dimorphism in body size. A number of authors have noted that selection pressures including sexual selection may contribute to sexual dimorphism in size (Ralls, 1977; Alexander et al., 1979; Gingerich, 1981; Jarman, 1983; Weckerly, 1998). Ralls (1977) suggests that sexual dimorphism in structures and coloration is more closely related to sexual selection than is body size. That is, different factors can cause dimorphism in size (e.g., neonate size in females), but only sexual selection can affect structure/coloration. Future analysis might test whether *Coryphodon* males and females are different only in size or if differences in morphology beyond allometry exist. If males are relatively and absolutely larger than females, then it may be the case that sexual selection is the driving force.

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Appendix I. Metric measurements of lower adult dentition of *Coryphodon lobatus* from Deardorff Hill *Coryphodon* Quarry (all measurements in mm)

| | PM 35878 | | P15628 | | PM 35865 | | PM 35873 | | PM 35870 | PM 39374 | |
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Left	Right
I_1	18.51		21.79	20.73	20.02		22.51	21.04		20.59	17.51
I_2	21.45	21.53	21.85	23.68	22.92	23.45	23.02	22.94		22.68	23.09
I_3	20.51		19.54	18.23	23.26	19.48	24.90	23.95			
C-bl	21.52	22.21	27.66	28.03	26.32						
C-md	24.62	25.80	34.53	33.12	23.97						
p_1L	15.93	15.99	16.21	16.39	16.95	16.04	17.13		15.86		15.57
p_1W	9.51	11.06	10.47	11.66	9.73	9.61	9.37		9.45		9.45
p_2L	17.05	18.59	24.92	20.83	19.34	20.35	22.16	21.27	17.47	18.80	21.41
p_2W	13.50	13.25	15.62	16.42	13.97	14.17	15.08	14.78	13.41	13.79	13.59
p_3L	21.43	20.50	23.80	23.50	20.78	20.35	22.60	22.15	22.97	22.34	22.07
p_3W	15.72	17.39	17.89	17.49	16.31	16.24	17.73	17.63	15.52	16.22	16.10
p_4L	21.14	18.24	24.51	25.24	23.68	24.13	23.20	23.82	21.73	23.71	23.51
p_4W	18.49	17.82	20.03	20.55	18.33	19.18	20.44	19.54	17.97	20.27	19.33
m_1L	25.72	24.34	30.69	29.56	25.29	28.69	29.01	29.99	25.08	25.08	24.71
m_1AW	20.58	19.06	20.47	20.89	18.92	19.40	20.72	19.64	20.49	22.80	21.70
m_1PW	21.49	19.68	21.44	25.53	20.42	20.16	21.12	20.44	19.96	21.16	20.61
m_2L	35.24	31.76	36.09	37.12	35.70	37.18	39.18	38.60	30.17	32.42	29.60
m_2AW	23.78	24.92	26.26	31.65	24.73	24.43	25.99	25.61	24.20	27.08	24.58
m_2PW	24.58	24.91	26.67	28.57	23.48	24.61	26.47	26.17	22.97	25.05	22.95
m_3L	34.87	37.68	45.93	42.32	39.84	39.48				36.49	35.62
m_3AW	26.82	27.44	31.01	27.42	26.00	26.21	29.84	26.48		27.28	27.09
m_3PW	25.54	25.04	26.45	28.02	23.55	23.49				24.87	24.14

Appendix II. Metric measurements of upper adult dentition of *Coryphodon lobatus* from Deardorff Hill *Coryphodon* Quarry (all measurements in mm)

	PM 35871		PM 39385		PM 35903		PM 39673		PM 35870		P15628	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
I1	21.81										24.54	24.97
I2	21.31	20.06									25.90	23.27
I3	19.63	17.88					19.01	15.22			23.35	22.35
C-bl	23.42	23.57	27.40	27.27			23.46	21.86	29.75		31.13	32.95
C-md	21.93	21.56	19.48	18.69			21.27	21.68	23.81		29.02	30.54
p^1L	14.31											
p^1W	10.80		11.20									
p^2L	18.14	18.37	19.34	19.22	21.82	21.85	20.18	19.85	18.05	18.61	20.53	20.39
p^2W	28.56	26.64	28.74	29.21	24.80	26.49	27.64	28.50	27.11	26.40	28.59	26.79
p^3L	19.78	18.87	21.75	21.56	21.81	20.88	19.34	19.63	19.33	19.63	23.49	23.64
p^3W	30.21	30.61	30.99	31.43	28.70	29.15	31.41	29.33	29.71	29.09	33.24	32.52
p^4L	18.47	17.83	20.98	20.43	19.77	18.90	17.99	18.46	20.46	20.55	22.51	22.42
p^4W	31.39	31.45	32.50	31.66	30.96	30.65	30.59	31.70	31.41	32.15	34.58	33.32
m^1L	22.65	22.90	30.39	28.43	29.09	27.19	23.23			27.03	32.03	30.78
m^1AW	30.92	30.11	30.54	30.07	31.03	29.08	32.19		27.79	31.43	34.83	
m^1PW	29.58	29.48	30.79	30.09	29.64	27.93	30.56		30.23	31.49	37.32	33.17
m^2L	30.49	30.81	37.75	35.38	34.09	35.14	34.66		31.56	31.60	36.58	34.72
m^2AW	37.22	38.11	37.33	37.99	38.41	37.64	40.54		37.70	37.65	39.75	38.89
m^2PW	35.43	35.05	34.97	35.54	36.38	35.69	38.26		35.76	35.69	39.87	39.68
m^3L	27.72	28.43	32.89	31.45	29.46	31.38	33.41	32.25	32.63	33.40	39.47	35.47
m^3W	40.58	40.22	43.74	44.65	40.54	42.46	45.27	44.43	39.73	43.70	49.55	46.26

Appendix III. Metric measurements of juvenile dentition of *Coryphodon lobatus* from Deardorff Hill *Coryphodon* Quarry (all measurements in mm)

	PM 39375 left	PM 39375 right	PM 39702 left	PM 39702 right	PM 39436 left
I_1					
I_2					
I_3				20.30	
C-bl					
C-md					
dp_1L	16.03		14.15	15.46	
dp_1W	9.80		9.83	10.75	
dp_2L	12.16				15.78
dp_2W	8.56				10.09
dp_3L	17.60		18.15		19.11
dp_3W	10.77		11.94		11.52
dp_4L			20.81		26.71
dp_4AW			14.79		14.17
dp_4PW			17.30		15.69
m_1L	29.75	29.99	25.68	25.33	32.57
m_1AW	18.64	17.77	21.26	19.13	20.61
m_1PW	19.48	19.54	19.59	19.35	19.91
m_2L					
m_2AW			26.07	23.76	
m_2PW					
m_3L					
m_3AW					
m_3PW					

	PM 39605/39665 left	PM 39605/39665 right	PM 39686 left	PM 39381 right	PM 35879 left
I^1					
I^2					
I^3	20.42				
C-bl					
C-md					
dp^1L			16.00	16.34	
dp^1W			13.91	10.54	
dp^2L			14.98	17.71	14.67
dp^2W				15.32	14.55
dp^3L					16.95
dp^3W			18.87	18.26	17.01
dp^4L		22.92	20.69	23.31	20.82
dp^4W		25.64	24.79	23.73	23.29
m^1L	27.42	27.56	27.69	29.29	31.21
m^1AW	30.74	31.05	30.44	30.16	30.33
m^1PW	28.71	31.15		26.37	30.54
m^2L	30.33	31.31			
m^2AW	36.47	37.00			
m^2PW	38.27	35.32			
m^3L					
m^3W					