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Philip D. Gingerich, Director

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EVOLUTION OF *CORYPHODON* (MAMMALIA, PANTODONTA) IN THE LATE PALEOCENE AND EARLY EOCENE OF NORTHWESTERN WYOMING

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Abstract—Six species of *Coryphodon* are recognized from the late Paleocene and early Eocene of the Bighorn and Clarks Fork Basins in northwestern Wyoming. These are, in order of temporal appearance: *Coryphodon proterus*, *Coryphodon eocaenus*, *Coryphodon radians*, *Coryphodon armatus*, and *Coryphodon lobatus*. *C. proterus* is the only species known from the Clarkforkian land-mammal age. The remaining taxa are restricted to some portion of the Wasatchian land-mammal age. The *Coryphodon* lineage including *C. proterus* and *C. eocaenus* decreased in body size from the late Clarkforkian through the early Wasatchian. Subsequently, *C. eocaenus* gave rise to *C. radians*, which differs in lacking an entoconid on the lower third molar and in being larger. *Coryphodon radians* evidently gave rise to two daughter lineages, *C. armatus* of smaller body size, and its larger sister species, *C. lobatus*. All species of *Coryphodon* exhibit variability that is attributed to sexual dimorphism. Upper and lower canines are strongly dimorphic; larger canines are attributed to males, while smaller canines are attributed to females.

INTRODUCTION

Coryphodon is a large herbivorous mammal placed in the archaic, extinct order Pantodonta. The first specimen of *Coryphodon* to be discovered was named and described by Richard Owen in 1845. The specimen consisted of a portion of a right dentary with an incomplete M_2 and complete M_3 . According to Owen, the name *Coryphodon* is derived from Greek *κορυφή*, point, and *όδους*, tooth, in allusion to development of the angles of crests into points (on the talonid on M_3 of the specimen that later became the type of *Coryphodon eocaenus* Owen, 1846).

The first fossils of *Coryphodon* found in North America were collected by F. V. Hayden from the "Wahsatch strata" of Wyoming. These were described by E. D. Cope (1872a) and placed in the genus *Bathmodon*, which was later synonymized with *Coryphodon* by Osborn (1898b). Taxonomy of the genus *Coryphodon* and the family Coryphodontidae (Marsh, 1876) has been in disarray since their fossilized remains were first collected. Five genera were described and later synonymized with *Coryphodon* (*Lophiodon*, *Bathmodon*, *Metalophodon*, *Manteodon*, and *Ectacodon*; Osborn, 1898b).

The most recent revision of *Coryphodon* systematics was published by Lucas (1984a,b), with a cladistic analysis of *Coryphodon* species. Thirty-five species of *Coryphodon* had been described by that time, of which Lucas regarded eight as valid (see Lucas, 1984a, p. 216, table 14). The early proliferation of genera and species now subsumed within *Coryphodon* came about because small differences between individual specimens were considered to represent interspecific rather than intraspecific variation.

Lucas' cladistic analysis of species of *Coryphodon* is problematic for two reasons. First, there are few synapomorphies that delimit groups of *Coryphodon* species in his cladogram. The cladogram presented (Lucas, 1984a, figure 57B) is only one of ten equally parsimonious cladograms that result from an analysis of the data matrix presented (Lucas, 1984a, table 29). Since there are few informative characters in the cladistic analysis, the addition of more characters would be likely to change the resulting cladograms. Lucas (1984a) expressly excluded size as a morphologic character in his cladistic analysis. Size variation and size change among species of *Coryphodon* are significant. In addition, Lucas' cladistic analysis did not take into account the stratigraphic distribution of species of *Coryphodon*. Stratigraphic position is the only direct evidence of relative temporal ordering of species. This information should not be ignored when reconstructing phylogenies of fossil organisms.

The approach to *Coryphodon* systematics and phylogeny reconstruction taken in this paper is somewhat different from the cladistic study of Lucas. We have numerous specimens from a relatively short interval of geologic time, which permits quantification of morphological variation and examination of how the variation changes (or does not change) through time. The study of evolution is fundamentally the study of covariation of morphology and time. A result of this approach when applied to *Coryphodon* is that small differences in size and shape between populations present in closely spaced stratigraphic intervals are less important than the continuity of morphologic variation through time.

The Bighorn and Clarks Fork basins of Wyoming contain a long and continuous depositional sequence that has been well sampled with respect to *Coryphodon*. In this setting, the range of variation expressed in the *Coryphodon* lineage during a series of time intervals can be documented. In this paper, the evolutionary history of North American late Paleocene and early Eocene *Coryphodon* is reviewed, and the species-level taxonomy of *Coryphodon* is revised to conform to our understanding of its phylogeny.

INSTITUTIONAL ABBREVIATIONS

AMNH	—American Museum of Natural History, New York
NHML	—Natural History Museum, London
UM	—University of Michigan Museum of Paleontology, Ann Arbor
UNM	—Department of Geology, University of New Mexico, Albuquerque
USNM	—National Museum of Natural History, Smithsonian Institution, Washington, D. C.
YPM	—Yale Peabody Museum of Natural History, New Haven
YPM-PU	—Princeton collection at Yale Peabody Museum

DENTAL TERMINOLOGY

Dental terminology follows Van Valen (1966) in general, and Simpson (1929) in particular for cusp homologies of *Coryphodon* teeth. The single exception to Simpson's identification of *Coryphodon* cusps concerns identification of the entoconid on M_3 . The cusp Simpson identified as the entoconid is almost certainly the hypoconulid (see Simpson, 1929, figure 8). Some spe-

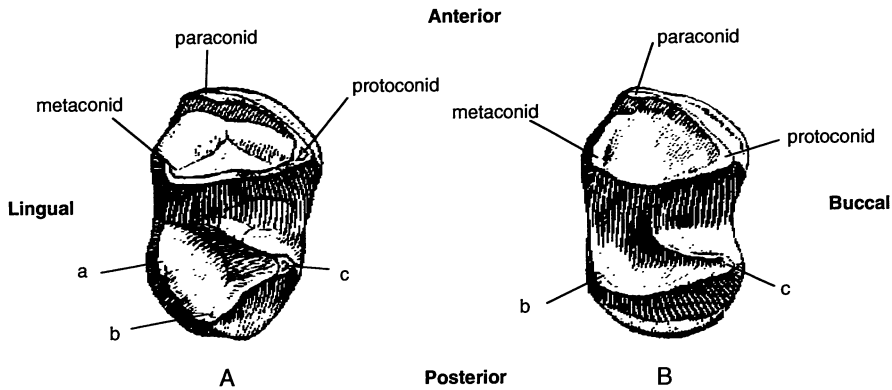


FIG. 1—Cusp homologies of *Coryphodon* lower third molars. A, M_3 of early Wasatchian *C. eoacaenus*. B, M_3 of middle to late Wasatchian *C. armatus*. Cusp *a* is identifiable as the entoconid, cusp *b* as the hypoconulid, and cusp *c* as the hypoconid in *C. eoacaenus* (A), as in most Eocene mammals, because all three cusps are present in their usual positions on the talonid. Cusp *b* in *C. armatus* (B) is here identified as the hypoconulid because specimens intermediate between *C. eoacaenus* and *C. armatus* show *a* to be the cusp that is reduced and lost through time (see Fig. 10). Figures are from Osborn (1898b); not to scale.

cies of *Coryphodon* have two cusps on the M_3 talonid, while others have three (Fig. 1). In species with three cusps, the most lingual cusp is identified here as the entoconid. It is connected by a crest to the posterior-most cusp (the hypoconulid of this study). The hypoconulid is connected in turn by another crest to the hypoconid. The M_3 figured by Simpson shows two cusps connected by a crest. If the most buccal cusp on M_3 is the hypoconid, then the second cusp must be the hypoconulid rather than the entoconid, since the hypoconid and entoconid are not directly connected by a crest in the species with three cusps. Individuals exist with intermediate conditions in which the entoconid is reduced, and the crest connecting the hypoconid and hypoconulid is subparallel to the protolophid, as in forms with only two cusps. Figure 1 shows two types of *Coryphodon* lower third molars and the identification of cusps on each tooth as used in this paper. The M_3 in Figure 1A, *C. eoacaenus*, has an entoconid, while the M_3 in Figure 1B, *C. armatus*, lacks the entoconid.

STRATIGRAPHIC SETTING

The evolution of *Coryphodon* can be traced through the late Paleocene and early Eocene in strata of the Bighorn and Clarks Fork Basins of northwestern Wyoming. These basins contain stratigraphic sections characterized by relatively continuous and rapid deposition of sediment from the Clarkforkian (late Paleocene) through the Wasatchian (early Eocene) land-mammal ages. The Clarkforkian and Wasatchian are subdivided into multiple biostratigraphic chrons or biozones. The Clarkforkian is partitioned into three biochrons, numbered from Cf-1 (earliest) to Cf-3 (latest). Eight biochrons, numbered Wa-0 to Wa-7, delimit the earliest to latest Wasatchian. Gingerich (1991) provided a full discussion of the indicative taxa for each biochron, alternative biochron names, and the stratigraphic limits of each biochron.

Evidence from Koch et al. (1992) indicates that the Paleocene-Eocene boundary as recognized in the northern Atlantic by a large extinction of benthic foraminifera is also marked by a large $\delta^{13}\text{C}$ shift in planktonic and benthic marine foraminiferal tests and is correlative with a similar $\delta^{13}\text{C}$ shift seen in mammalian tooth enamel and soil carbonate nodules from the Wa-0 stratigraphic level (earliest Wasatchian). If these two shifts in carbon isotopes are produced

TABLE 1—Variability of molar tooth size in species of early Eocene *Coryphodon* compared to that in extant *Hippopotamus amphibius*. The *C. armatus* quarry sample is from American Museum of Natural History Quarry 242 in the San Juan Basin, New Mexico (data from Lucas, 1984a). The *H. amphibius* sample is from various sites in Africa (data from Hooijer, 1950). Note the similarity of molar size variation in individual species of *Coryphodon* to that in *H. amphibius*. *N*, number of specimens; *Range*, range magnitude of natural log ($L \times W$) for upper or lower molar (expected range magnitude within a species is ca. 0.40); *V*, coefficient of variation of tooth crown area (standard deviation divided by mean, expressed as a percentage).

Species	N	M1 Area Range	V	N	M2 Area Range	V	N	M3 Area Range	V
Upper dentition									
<i>Coryphodon proterus</i>	9	0.36	10.8	4	0.28	11.7	7	0.40	15.2
<i>Coryphodon eocaenus</i>	14	0.61	17.9	14	0.60	18.1	17	0.66	18.5
<i>Coryphodon radians</i>	8	0.59	17.1	7	0.62	22.8	7	0.49	17.0
<i>Coryphodon armatus</i>	2	0.09	6.2	3	0.20	10.1	5	0.22	8.9
<i>Coryphodon lobatus</i>	1	--	--	6	0.33	14.6	7	0.42	17.2
<i>Coryphodon armatus</i> quarry sample	9	0.35	11.0	9	0.28	10.6	8	0.35	12.9
<i>Coryphodon</i> all species	40	0.88	19.7	41	0.94	23.6	46	0.99	28.8
<i>Hippopotamus amphibius</i>	30	0.57	15.2	25	0.58	13.5	13	0.44	12.5
Lower dentition									
<i>Coryphodon proterus</i>	6	0.21	7.4	5	0.29	11.8	4	0.52	24.9
<i>Coryphodon eocaenus</i>	14	0.43	13.3	14	0.47	13.7	19	0.44	9.8
<i>Coryphodon radians</i>	4	0.21	9.1	6	0.45	17.5	4	0.31	14.6
<i>Coryphodon armatus</i>	9	0.41	13.1	11	0.22	7.8	11	0.26	7.9
<i>Coryphodon lobatus</i>	3	0.12	6.6	6	0.16	6.6	4	0.27	11.2
<i>Coryphodon armatus</i> quarry sample	9	0.38	13.2	9	0.45	14.6	8	0.45	15.3
<i>Coryphodon</i> all species	41	0.76	20.1	45	0.71	17.8	52	0.83	22.5
<i>Hippopotamus amphibius</i>	24	0.58	13.9	23	0.49	12.2	16	0.46	16.5

by the same phenomenon, then the Paleocene-Eocene boundary roughly coincides with the Clarkforkian-Wasatchian boundary. Correlations of North American stratigraphic horizons with those of Europe have greatly improved in recent years. A similar carbon isotopic excursion has been identified in Europe associated with biozone PE-I of Hooker (in press). If these geochemical markers are indicative of the same event, then biochron Wa-0 and biozone PE-I represent approximately the same time, which is also supported by similarity in the faunas (Hooker, in press). If the carbon isotopic excursion is also taken to be at the Paleocene-Eocene boundary, then no Paleocene *Coryphodon* are known from Europe.

DENTAL VARIATION AND SEXUAL DIMORPHISM IN CANINE SIZE

It has been shown in previous studies that for species of mammals, crown area of M_1 has a range of variation of approximately 0.4 units on a natural logarithm scale (e.g., Gingerich and Winkler, 1979). This standard has been used to recognize and distinguish contemporaneous species of many mammalian genera, including *Coryphodon* in this study. Sample sizes, coefficients of variation, and ranges of the natural log of crown area of upper and lower cheek teeth of *Coryphodon* species are listed in Table 1. The same statistics for *Hippopotamus amphibius* are also reported for comparison with a species that has been cited as a modern analog of *Coryphodon* (Lucas, 1984a: data from Hooijer, 1950). The coefficients of variation of early Eocene *Coryphodon* from northwestern Wyoming are comparable to those of *Hippopotamus* (Table 1) and other modern mammalian species (see Gingerich, 1974). In addition, a quarry sample from American Museum of Natural History quarry 242 in the San José Formation, New Mexico, is included in Table 1 (data from Lucas, 1984a, table 15). All individuals in the quarry sample almost certainly represent a single species, *C. armatus*. This sample has comparable variability to the samples of species from northwestern Wyoming. More complete statistics of variation of linear measurements of cheek teeth are listed in Tables 3 to 7 as part of the summary description of each species of *Coryphodon* found in northwestern Wyoming.

Another component of variation important for interpreting *Coryphodon* is sexual dimorphism. *Coryphodon* has been described as slightly dimorphic sexually in canine size and body size (Lucas, 1984a), and we know that individuals collected from stratigraphic intervals where a single species is present have similar-sized cheek teeth but canines that are either large or small compared to cheek tooth size. Figures 2A and 2B quantify patterns of variation of tooth size in the upper and lower dentitions of individual specimens normalized for M^1 and M_1 size, respectively (samples plotted include several species from a range of different stratigraphic intervals). The greatest deviations from expectation are in canine size, where two distinct clusters of specimens are evident: those with canine size smaller than expected for their M^1 or M_1 size, and those with canine size larger than expected. Other teeth vary less, when normalized for M^1 and M_1 size, and fall into one group with little deviation from expectation. Both upper and lower canines are dimorphic, but the upper canines appear to be slightly more so than the lowers. By comparison with modern species of mammals, we infer that individuals with relatively large canines are males and individuals with relatively small canines are females. Hooijer (1950) found that female *Hippopotamus amphibius* has lower canine diameters ranging from 38 to 49 mm ($n = 10$), while males range from 62 to 78 mm ($n = 22$). There is no overlap in *Coryphodon* either.

BODY MASS

Several attempts have been made to document the body size and estimate the body mass of *Coryphodon*. Marsh (1893), Osborn (1898a), and Patterson (1939) published skeletal restora-

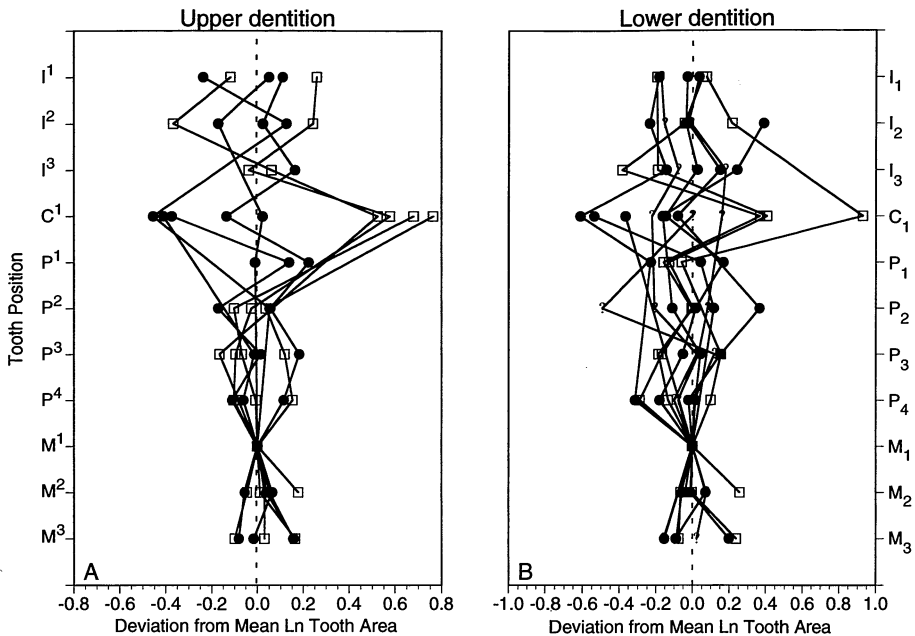


FIG. 2—Tooth size profiles for upper teeth (A) and lower teeth (B) in individual specimens representing several species of *Coryphodon* from the Clarks Fork and Bighorn basins. Profiles were drawn by (1) plotting the difference between each measurement and the sample mean for measurements at that tooth position, (2) subtracting the difference at M¹ or M₁ from all values for each specimen; and (3) connecting values at different tooth positions to link those representing the same specimen. Note that canine size in this sample is much more variable than the sizes of teeth at other positions, as is commonly true in sexually dimorphic species, and canines tend to be either relatively smaller or larger than expected for a given cheek tooth size. Specimens with relatively small canines are interpreted as females (closed circles), those with large canines are interpreted as males (open squares).

tions of *Coryphodon*, but did not attempt to quantify the live weight or live body mass of *Coryphodon*. Lucas (1984a, 1986) followed Jerison (1973) in using shoulder-to-tail body length to estimate body mass in *Coryphodon*, and Lucas described *Coryphodon armatus* as weighing 150 to 300 kg, depending on whether it was of 'normal' or 'heavy' habitus. Gingerich (1989b) estimated the mean body mass of small *Coryphodon eocaenus* ("*C. marginatus*") to be about 400 kg and the mean body mass of larger *C. radians* ("*C. subquadratus*") to be about 800 kg, based on molar tooth size. Long bone lengths and diameters suggested mean body masses of only 90 kg and 210 kg, respectively (Gingerich, 1990), with many consistent discrepancies between estimates from lengths and diameters indicating that *Coryphodon* is sufficiently unusual in proportions to require a broader comparison to extant mammals.

Here we estimated body mass using the ungulate regression of Legendre (1989): $\text{mass (g)} = \exp [(1.5133 \cdot \ln (L \times W) \text{ of } M_1) + 3.6515]$, where the length and width of M₁ are measured in mm. This yielded an estimate of about 340 kg mean body mass for *Coryphodon eocaenus* and about 600 kg mean body mass for *C. radians*. The mean body mass of *C. proterus* and *C. lobatus* might be as great as 700 kg. These are means for species, and it is important to note that the difference between masses calculated for *C. eocaenus* and *C. radians* is similar to the proportional difference that might be expected between the largest and smallest individuals in any homogeneous species population living at one time.

We do not have samples adequate to quantify dimorphism in overall body size, but the presence of canine dimorphism suggests that *Coryphodon* may well have been dimorphic in body size as well. Any effect of body size and cheek tooth size dimorphism on the patterns plotted in Figure 2 has been removed by normalization, but this does not mean there was no body size dimorphism.

SYSTEMATIC PALEONTOLOGY

The importance of quantifying the range of variation of molar size within species and finding that molar size is not dimorphic is that molar size can be used to recognize and distinguish species in the fossil record. Molar size can be used in conjunction with stratigraphic position to study patterns of change in tooth size, and by inference body size, through time. Patterns of change of individual specimens provide, in turn, a rational basis for species-level systematics and taxonomy.

Order PANTODONTA Cope, 1873a Family CORYPHODONTIDAE Marsh, 1876

Bathmodontidae Cope, 1873b, p. 102

Coryphodontidae Marsh, 1876, p. 428

Type genus.—*Coryphodon* Owen, 1845

Included genera.—*Coryphodon* Owen, 1845, in Europe and North America. *Asiocoryphodon* Xu, 1976; *Eudinoceras* Osborn, 1924; *Heterocoryphodon* Lucas and Tong, 1987; *Hypercoryphodon* Osborn and Granger, 1932; and *Metacoryphodon* Qi, 1987, in Asia.

Age and distribution.—Latest Paleocene (Clarkforkian) through earliest middle Eocene (early Bridgerian) in North America. Early Eocene in Europe. Early Eocene to middle Oligocene in Asia.

Discussion.—The familial name Bathmodontidae was coined by Cope in 1873 to include the genera *Bathmodon* and *Metalophodon* (Cope, 1873b), both of which have long been considered to be junior synonyms of *Coryphodon* (Cope, 1877; Osborn, 1898b). Bathmodontidae was dropped by subsequent authors in favor of Marsh's (1876) Coryphodontidae. We retain Coryphodontidae here because of its familiarity and its long and continuous use by others.

The exclusively Asian genera *Asiocoryphodon* (Xu, 1976), *Eudinoceras* (Osborn, 1924), and *Heterocoryphodon* (Chow and Tung, 1965; Lucas and Tong, 1987), are reported from the Eocene, and *Hypercoryphodon* (Osborn and Granger, 1932) is reported from the middle Oligocene. In a cladistic analysis of the genera within the Coryphodontidae, Lucas (1982) shows *Coryphodon* as the primitive sister taxon to the rest of the genera. The latest occurring species of *Coryphodon* also have bilophodont molars, a characteristic that all of the more derived genera share (Lucas, 1984a; this study). This, along with the fact that all of the other more-derived genera occur later in time, suggests that the lineage (or lineages) that gave rise to later genera probably originated somewhere within the genus *Coryphodon*.

Coryphodon Owen, 1845

Lophiodon (in part) Owen, 1843, p. 224

Coryphodon Owen, 1845, p. 607. Not Duméril and Bibron, 1854, p. 178

Bathmodon Cope, 1872a, p. 350

Metalophodon Cope, 1872b, p. 774

Manteodon Cope, 1882a, p. 73

Ectacodon Cope, 1882a, p. 73

Type species.—*Coryphodon eocaenus* Owen, 1846.

Included species.—Europe: *Coryphodon eocaenus* Owen (early Eocene), *C. oweni* Hébert (early Eocene), and *C. anthracoides* Blainville (early Eocene). North America: *Coryphodon proterus* Simons (Clarkforkian), *C. eocaenus* Owen (early-middle Wasatchian), *C. radians* Cope (middle Wasatchian), *C. armatus* Cope (middle-late Wasatchian), and *C. lobatus* Cope (middle-late Wasatchian). Asia: *C. tsaganensis* Reshetov (late Paleocene), and *C. eocaenus* Owen (early Eocene).

Diagnosis.—The following diagnosis of *Coryphodon* is taken from Lucas (1984b):

Coryphodon is a small- to medium-sized coryphodontid with long P²⁻⁴ ectolophs that are longer than those of *Eudinoceras* and *Asiocoryphodon*, about the same relative length as those of *Hypercoryphodon* and are relatively shorter than those of *Heterocoryphodon*. The P²⁻⁴ protocones of *Coryphodon* are not isolated and thus differ from those of *Asiocoryphodon* and *Eudinoceras*. M¹⁻³ of *Coryphodon* are the least bilophodont of any coryphodontid in that postprotocristae or metaconules are usually present, and the premetacristae are short relative to the protolophs. M³ of *Coryphodon* is an oval tooth with a distinct posterior crest and is less bilophodont than M³ of other coryphodontids. The lower canine of *Coryphodon* is only slightly curved outward and its incisors are very broad, unlike *Eudinoceras*. The P₂₋₄ trigonids of *Coryphodon* are relatively long (unlike *Eudinoceras*), and its M₁₋₃ paralophids and cristids obliquae are usually better developed than are those of other coryphodontids.

Age and distribution.—*Coryphodon* is known in North America from many specimens in the Clarkforkian and Wasatchian land-mammal ages (late Paleocene through early Eocene). *Coryphodon* is known in Europe from biochrons PE-I through PE-III (early Eocene) of Hooker (in press). *Coryphodon* is known in Asia from the late Paleocene Naran Bulak svita at Naran-Bulak and Tsagan Khushu in Mongolia (Reshetov, 1976) and from the early Eocene Dabu Formation of China (Zhai, 1978). Lucas (1984) synonymized Asian *C. tsaganensis* with European *C. anthracoides*.

Discussion.—Names of all species of North American *Coryphodon* are listed in Table 2 in the order in which they were described. Twenty-seven names have been proposed, of which five appear to be valid.

Coryphodon proterus Simons, 1960

Coryphodon sp. indet.(?), Jepsen, 1930, p. 493

Coryphodon sp. nov.(?), Van Houten, 1945, p. 425

Coryphodon sp. (in part), Dorr, 1952, p. 89

Coryphodon proterus Simons, 1960, p. 13, fig. 18

Coryphodon sp., Rose, 1981, p. 88, Pl. 4, fig. 3

Holotype.—YPM-PU 13400, with left and right I₁₋₃; left dentary with the lower canine and P₂-M₃; right P₁₋₄ and M₁; left and right premaxillary and maxillary fragments with I¹⁻³, P¹, and right P²; left and right P³-M³; partial basicranium; skull and mandible fragments, left and right zygomatic arches (see Simons, 1960, p. 13, fig. 18).

When originally described by Simons, YPM-PU 13400 consisted only of lower teeth. Additional collecting at the type locality produced upper teeth and skull material from the same individual (Lucas, 1984a). Another tooth, UM 68282, a left P₁ collected at the type locality, probably belongs to the type individual too.

Type locality.—The *Coryphodon proterus* type locality is three miles southwest of Bear Creek, in the Fort Union Formation (=Polecat Bench Formation), in the NW¼ of section 24, T8S, R20E, Carbon County, Montana (Simons, 1960).

Age and distribution.—*Coryphodon proterus* is the only species of *Coryphodon* known from the Clarkforkian land-mammal age (late Paleocene). It is known only from western North

America. Some very large specimens from the early Wasatchian (Wa-1) may belong in *C. proterus*. Figures 4-9 illustrate the relative size and stratigraphic position of *C. proterus* individuals.

Diagnosis.—*Coryphodon proterus* differs from the Wasatchian species *Coryphodon eoacaenus* in being much larger. The only other species of *Coryphodon* that is similar in size to *C. proterus* is *Coryphodon lobatus*. Figure 10 shows that *C. proterus* has a large entoconid on M_3 that distinguishes it from *C. lobatus* and *C. armatus*. In addition, the M_3 of *C. proterus* is elongate and is not bilophodont, in contrast to *C. lobatus*, which is not elongate and has a markedly bilophodont M_3 .

Description.— P^1 is very small and quite different in morphology from the other premolars. P^1 has a moderately deep V-shaped ectoloph. In addition, the protocone is represented only by a small cusp on the lingual edge of the tooth. P^{2-4} are similar to each other and to those of other *Coryphodon*. They increase in size from P^2 to P^4 . P^{2-4} bear narrow anterior and posterior cingula. P^{2-4} have deeply V-shaped ectolophs and high protocones.

M^{1-2} are similar to each other, with M^1 being smaller than M^2 . M^{1-2} are elongate labiolingually, especially in YPM-PU 13400. M^{1-2} lack complete lingual cingula. Preparacristae are lacking on M^{1-2} .

M^3 is labiolingually elongate and very large. M^3 area (length \times width) ranges from 1295 to 1588 mm². The M^3 has an incomplete lingual cingulum. It also has a very large posterolingual cingulum, upon which a cuspule is added to the posterior edge of the tooth in some individuals. M^3 lacks a preparacrista.

P_1 is very small and narrow. P_1 has a relatively smaller trigonid and smaller metaconid than P_{2-4} . P_{2-4} increase in size from P_2 to P_4 , with the premolars becoming relatively wider as well. The trigonid increases in size and the metaconid increases in height from P_{1-4} .

M_{1-2} of *Coryphodon proterus* are bilophodont and lack an entoconid. They are similar to each other (with M_1 being smaller than M_2) and to M_{1-2} of other species of *Coryphodon*. Only their large size indicates that they belong to *C. proterus*.

M_3 area (length \times anterior width) ranges from 1070 to 1803 mm². M_3 has a prominent entoconid that is clearly separated from the hypoconulid. There is a prominent crest connecting the entoconid to the hypoconulid. In addition, the hypoconid-hypoconulid portion of the postcristid is at a high angle to the protolophid, thus the M_3 is not bilophodont (see Figure 10).

Measurements of the northwestern Wyoming sample of *Coryphodon proterus* are summarized in Table 3.

Discussion.—The description of *Coryphodon proterus* given by Simons (1960) is a clear and accurate description of the type specimen, but comparisons with other specimens of Clarkforkian *Coryphodon* show that some of the features in the type specimen are unique. The type specimen of *C. proterus* is one of the largest individuals known. The M_3 of the type specimen is extremely anteroposteriorly elongate when compared to other individuals. The M^3 is extremely labiolingually elongate as well. The crest between the hypoconulid and the entoconid is equal in length to the crest between the hypoconid and the hypoconulid in the type specimen. In other Clarkforkian *Coryphodon*, the entoconid-hypoconulid portion of the postcristid is shorter than the hypoconid-hypoconulid portion. This morphology is similar to that which is found in early Wasatchian *Coryphodon eoacaenus*. One specimen, UM 65650, has four cusps on the talonid of M_3 . The extra cusp is on the crest connecting the entoconid and hypoconulid. Despite these slight morphological differences, all Clarkforkian *Coryphodon* are included in *C. proterus*.

Referred specimens.—Clarkforkian strata of the Clarks Fork Basin, near Bear Creek, Montana: YPM-PU 13400, UM 68282. Clarkforkian strata of the Hoback Basin: UM 27255. Clarkforkian strata of the Clarks Fork Basin, Sand Coulee area: UM 65037, 65485, 65650, 65722, 66162, 68279, 69301, 69332, 71575, 73779, 80251, 82362, 83750, 83784, 85580, 87911, 88262, 88332, 95866. Clarkforkian strata of the northern Bighorn Basin, Foster Gulch area: UM 76148, 85436, 86801.

TABLE 2.—Systematic overview of the species of North American *Coryphodon*. Species are listed in the order in which they were described. Five species considered valid are numbered sequentially at left. Tooth crown areas (length \times width; measured in mm) of type specimens are listed, when available. Current taxonomic assignments, if different, are listed on second line of each entry.

Species	Type specimen	M ₃ (L \times W)	M ³ (L \times W)	Type locality
Current taxonomic assignment				
1. <i>Coryphodon eocaenus</i> Owen, 1846, p. 299 <i>Coryphodon eocaenus</i>	NHML M 27848	--	36.8 \times 23.9	Off Essex coast, of England, London Clay
2. <i>Bathimodon radians</i> Cope, 1872, p. 350 <i>Coryphodon radians</i>	AMNH 4300	32 \times 43	--	"Wahsatch beds" of western Wyoming
<i>Bathimodon semicinctus</i> Cope, 1872, p. 351 Nomen dubium	unknown	--	--	"Wahsatch beds" near Evanston, Wyoming
3. <i>Metatophodon armatus</i> Cope, 1872, p. 774 <i>Coryphodon armatus</i>	AMNH 4315	26.9 \times 37.8	--	"Green River division" of Wyoming
<i>Bathimodon latipes</i> Cope, 1873, p. 70 Nomen vanum (<i>Coryphodon radians</i> ?)	AMNH 4313	--	--	"Wahsatch beds" of western Wyoming
<i>Bathimodon brevipes</i> Cope, 1873, p. 103 Nomen nudum	unknown	--	--	unknown
<i>Bathimodon simus</i> Cope, 1874, p. 596 <i>Coryphodon armatus</i> (or <i>C. simus</i>)	USNM 2616	28.9 \times 35.4	32.7 \times 19.4	Arroyo Blanco, San Juan Basin, New Mexico
<i>Bathimodon molestus</i> Cope, 1874, p. 597 <i>Coryphodon armatus</i>	USNM 1119	28.2 \times 36.0	36.8 \times 22.8	Arroyo Blanco, San Juan Basin, New Mexico
<i>Bathimodon lomas</i> Cope, 1874, p. 597 <i>Coryphodon armatus</i>	type lost	--	--	San Juan Basin, New Mexico
<i>Bathimodon elephantopus</i> Cope, 1874, p. 597 <i>Coryphodon armatus</i>	USNM 111 (cotype)	27.8 \times 38.4	--	San Juan Basin, New Mexico
<i>Bathimodon latidens</i> Cope, 1875, p. 29 <i>Coryphodon armatus</i>	USNM 2614	--	35.5 \times 25.9	San Juan Basin, New Mexico
<i>Bathimodon cuspidatus</i> Cope, 1875, p. 30 <i>Coryphodon armatus</i>	USNM 1121	--	--	San Juan Basin, New Mexico
<i>Coryphodon armatus</i> <i>Coryphodon hamathus</i> Marsh, 1876, p. 423 <i>Coryphodon radians</i>	YPM 1330	--	--	Bighorn Basin, Wyoming

TABLE 2—continued.

Species Current taxonomic assignment	Type specimen	M ₃ (L×W)	M ³ (L×W)	Type locality
<i>Coryphodon obliquus</i> Cope, 1877, p. 207 <i>Coryphodon armatus</i>	unknown	--	32.0 × 23.0	San Juan Basin, New Mexico
4. <i>Coryphodon lobatus</i> Cope, 1877, p. 209 <i>Coryphodon lobatus</i>	USNM 6002	--	44.1 × 28.4	San Juan Basin, New Mexico
<i>Manteodon subquadratus</i> Cope, 1882, p. 166 <i>Coryphodon radians</i>	AMNH 4340	--	--	Wasatch beds of the Bighorn Basin, Wyoming
<i>Ectacodon cinctus</i> Cope, 1882, p. 167 <i>Coryphodon radians</i>	AMNH 4341	33.1 × 43.0	--	Wasatch beds of the Bighorn Basin, Wyoming
<i>Coryphodon anax</i> Cope, 1882, p. 168 <i>Coryphodon lobatus</i>	AMNH 4327	--	43.8 × 24.2	Wasatch beds of the Bighorn Basin, Wyoming
<i>Coryphodon repandus</i> Cope, 1882, p. 171 <i>Coryphodon radians</i>	AMNH 4309	--	38.5 × 27.9	Willwood Formation of the Bighorn Basin, Wyoming
<i>Coryphodon curvicristis</i> Cope, 1882, p. 172 <i>Coryphodon armatus</i>	AMNH 4326	--	35.4 × 27.9	Willwood Formation of the Bighorn Basin, Wyoming
<i>Coryphodon marginatus</i> Cope, 1882, p. 174 <i>Coryphodon eoacaenus</i>	AMNH 4337	25.1 × 38.3	--	Willwood Formation of the Bighorn Basin, Wyoming
<i>Metalophodon testis</i> Cope, 1882, p. 175 <i>Coryphodon radians</i>	AMNH 4317	29 × 41	--	Wasatch beds of the Bighorn Basin, Wyoming
<i>Baismodon pachypus</i> Cope, 1883 Nomen vanum	AMNH 4335	--	--	Bighorn Basin, Wyoming
<i>Coryphodon ventanus</i> Osborn, 1898b, p. 210 <i>Coryphodon lobatus</i>	AMNH 2976	--	42 × 30	Wind River Beds of the Wind River Basin, Wyoming
<i>Coryphodon wortmani</i> Osborn, 1898b, p. 212 <i>Coryphodon armatus</i>	AMNH 2977	27 × 39	42 × 31	Wind River Beds of the Wind River Basin, Wyoming
<i>Coryphodon singularis</i> Osborn, 1898b, p. 214 Nomen vanum (<i>Coryphodon armatus</i> ?)	AMNH 2980	--	--	Wind River Beds of the Wind River Basin, Wyoming
5. <i>Coryphodon proterus</i> Simons, 1960, p. 13 <i>Coryphodon proterus</i>	YPM-PU 13400	34.4 × 51.5	55.3 × 32.6	Southwest of Bear Creek, Carbon County, Montana

TABLE 3—Summary of molar measurements for *Coryphodon proterus* from northwestern Wyoming. N, number of individuals; SD, standard deviation, V, coefficient of variation (%). L, mesial-distal crown length; W, buccolingual crown width. All measurements in mm.

Measurement	N	Range	Mean	SD	V
Upper dentition					
M ¹ L	9	25.0 - 29.9	27.0x	1.5x	4.9
W	9	30.0 - 37.7	33.2x	2.6x	7.9
M ² L	4	32.6 - 35.5	33.9	1.2	3.7
W	4	36.1 - 44.0	40.0	3.2	8.1
M ³ L	7	30.9 - 38.0	33.2	2.5	7.5
W	7	41.9 - 51.5	46.2	3.9	8.4
Lower dentition					
M ₁ L	6	27.7 - 29.9	29.0	0.9	3.2
W	6	19.5 - 23.1	22.0	1.3	5.9
M ₂ L	5	33.7 - 40.0	36.7	2.8	7.6
W	5	23.3 - 27.7	26.1	1.7	6.4
M ₃ L	4	41.8 - 55.3	46.4	6.1	13.1
W	4	25.6 - 32.6	28.2	3.1	10.9

Coryphodon eocaenus Owen, 1846

Lophiodon isselensis (in part), Owen, 1843, p. 224

Coryphodon Owen, 1845, p. 607, Pl. 135, fig. 9

Coryphodon eocaenus Owen, 1846, p. 299, figs. 103, 104, 105, 107

Lophiodon eocaenum, Blainville, 1846, p. 107, Pl. 2

Coryphodon marginatus Cope, 1882b, p. 174

Coryphodon ?elephantopus, Patterson, 1939, p. 98, Pl. 6, 7, 8, 9

Coryphodon sp., Gingerich, 1989a, p. 29

Holotype.—NHML M 27848, right dentary fragment with an incomplete M₂ and complete M₃ (see Owen, 1846, figs. 103, 104, 107).

Type locality.—The type specimen of *Coryphodon eocaenus* was "dredged up from the bottom of the sea, between St. Osyth and Harwich on the Essex coast." (Owen, 1846). Its mode of preservation and associated sediment indicates that it is from the early Eocene London Clay (Owen, 1846). Hooker (in press) suggests that the type of *C. eocaenus* is from the Harwich Stone Band within the Harwich Member of the London Clay.

Age and distribution.—*Coryphodon eocaenus* is known from Europe and western North America. In Europe, the earliest reported *C. eocaenus* specimens are from lower Eocene deposits. These specimens are from the Suffolk Pebble bed, Blackheath beds, and Harwich Member of the London Clay in England (Hooker, in press); the *Sables d' Erquelinnes* in Belgium; the *Argiles à Lignites*, *Argiles Plastique*, and *Sables de Sinceny* in France (Lucas, 1984b). In North America, *C. eocaenus* ranges in age from Wasatchian biochron Wa-0 to

Wa-2 (earliest Eocene). Figures 4–9 illustrate the relative size and stratigraphic position of *C. eocaenus* individuals.

Coryphodon daubensis described by Zhai (1978) were placed in *C. eocaenus* by Lucas (1984b), but retained as a distinct species by Russell and Zhai (1987).

Diagnosis.—*Coryphodon eocaenus* is a medium-to small-sized *Coryphodon*. The M_3 of *C. eocaenus* has a well-developed entoconid, and it is not bilophodont, which distinguishes it from *C. armatus*, and *C. lobatus*. The average size of *C. eocaenus* smaller than that of *C. radians*, but the size distribution of *C. eocaenus* considerably overlaps with *C. radians*. *C. eocaenus* can be distinguished from *C. radians* by the presence of a well-developed entoconid on M_3 that *C. radians* lacks (Fig. 10). *C. eocaenus* is distinctly smaller than *C. proterus*.

Description.— P^1 is very small and different in morphology from P^{2-4} , possessing a moderately deep V-shaped ectoloph and a small protocone. P^{2-4} increase in size from P^2 to P^4 and bear well-developed anterior and posterior cingula. P^{2-4} have deeply V-shaped ectolophs and high protocones.

M^{1-2} are similar to each other (with M^1 being smaller than M^2) and to M^{1-2} of other species of *Coryphodon*. M^{1-2} have narrow anterior and posterior cingula. Presence of lingual cingula on M^{1-2} is variable.

M^3 is ovate and lacks a preparacrista. The posterolingual cingulum is well developed. M^3 area (length \times width) ranges from 730 to 1412 mm². The M^3 has a complete lingual cingulum.

P_1 is very small and narrow. P_{2-4} increase in size from P_2 to P_4 , with the premolars becoming relatively wider as well. The trigonid increases in size and the metaconid increases in height from P_{1-4} .

M_{1-2} of *Coryphodon eocaenus* are bilophodont and lack an entoconid. They are similar to each other (with M_1 being slightly smaller than M_2) and to M_{1-2} of other species of *Coryphodon*. Only their moderate to small size indicates that they belong to *C. eocaenus*.

M_3 area (length \times anterior width) ranges from 750 to 1166 mm². The talonid of M_3 has three cusps, including a prominent entoconid that is clearly separated from the hypoconulid. There is a prominent crest connecting the entoconid to the hypoconulid, thus the M_3 is not bilophodont. In addition, the hypoconid-hypoconulid portion of the postcristid is at a high angle to the protolophid. The paraconid is strongly developed as a crest and sometimes as a distinct cusp (see Figure 10).

Measurements of the northwestern Wyoming sample of *Coryphodon eocaenus* are summarized in Table 4.

Discussion.—Patterson's specimen of *Coryphodon eocaenus* is a relatively complete skeleton that is mounted and on display in the Museum of Comparative Zoology, Harvard. It was collected from the Graybull beds at South Elk Creek by Dr. E. L. Troxell in 1929 (Patterson, 1939). Patterson did not refer this specimen to *C. eocaenus*, partly due to taxonomic confusion caused by the large proliferation of species that had been named at that time, but its size, morphology, and stratigraphic position place it precisely in *C. eocaenus*.

In an early version of this manuscript, we used the name *Coryphodon ryani* for late, small *C. eocaenus*—*C. ryani* as used in Morgan et al. (1995) is a nomen nudum, and we do not now think it warrants separation from *C. eocaenus*.

Referred specimens.—From Wasatchian-age strata of the Clarks Fork Basin, Sand Coulee area: UM 64895, 64915, 64932, 65306, 65308, 65360, 67045, 69403, 69448, 69519, 69569, 69745, 69993, 71215, 73829, 78967, 79469, 79809, 80018, 80235, 82177, 82753, 82759, 82764, 83389, 83557, 85742, 85748, 88318, 92867, 98331, 101917. From Wasatchian-age strata of the Clarks Fork Basin, McCullough Peaks area: UM 87508, 87509, 87772, 92225,

TABLE 4—Summary of molar measurements for *Coryphodon eocaenus* from northwestern Wyoming. N, number of individuals; SD, standard deviation, V, coefficient of variation (%). L, mesial-distal crown length; W, buccolingual crown width. All measurements in mm.

Measurement	N	Range	Mean	SD	V
Upper dentition					
M ¹ L	14	21.6 - 29.0	25.7	2.2	8.7
W	14	24.5 - 35.5	29.6	3.1	10.3
M ² L	14	26.0 - 35.0	29.3	2.7	9.4
W	14	31.0 - 43.3	35.4	3.4	9.5
M ³ L	17	24.1 - 36.7	27.1	3.2	12.0
W	17	24.6 - 44.0	35.1	4.5	12.9
Lower dentition					
M ₁ L	14	20.1 - 27.6	24.4	1.8	7.3
W	14	15.0 - 20.0	17.8	1.5	8.5
M ₂ L	14	29.7 - 37.2	32.3	2.0	6.2
W	14	20.1 - 26.5	22.8	1.9	8.5
M ₃ L	19	32.6 - 40.0	36.8	2.0	5.4
W	19	23.0 - 29.6	25.4	1.5	6.0

94998, 95876, 95983, 96181, 96291, 96471, 96517, 96759, 97270, 97319. From Wasatchian-age strata of the Clarks Fork Basin, Foster Gulch area: UM 76369, 77109, 77208, 77220, 77230, 77231, 77232, 82005, 85240, 85317, 85847, 85936, 85939, 85940, 86847, 86864, 86894, 86898, 86971, 87055, 87166, 87329. From Wasatchian-age strata of the Bighorn Basin, Greybull River area: UM 87271. From Wasatchian-age strata of the central Bighorn Basin: UM 63582, 63802.

Coryphodon radians Cope, 1872

Fig. 3

- Bathmodon radians* Cope, 1872a, p. 351; 1884, Pl. 44e, fig. 14
Coryphodon hamatus Marsh, 1876, p. 426, figs. 1-2
Coryphodon radians, Cope, 1877, p. 211
Manteodon subquadratus Cope, 1882a, p. 73
Ectacodon cinctus Cope, 1882a, p. 73. Osborn, 1898b, p. 203
Metalophodon testis Cope, 1882a, p. 73. Osborn, 1898b, p. 203
Coryphodon repandus Cope, 1882b, p. 171
Coryphodon cinctus, Osborn, 1898b, p. 203
Coryphodon testis, Osborn, 1898b, p. 203

Lectotype.—AMNH 4300, left M² - M³.

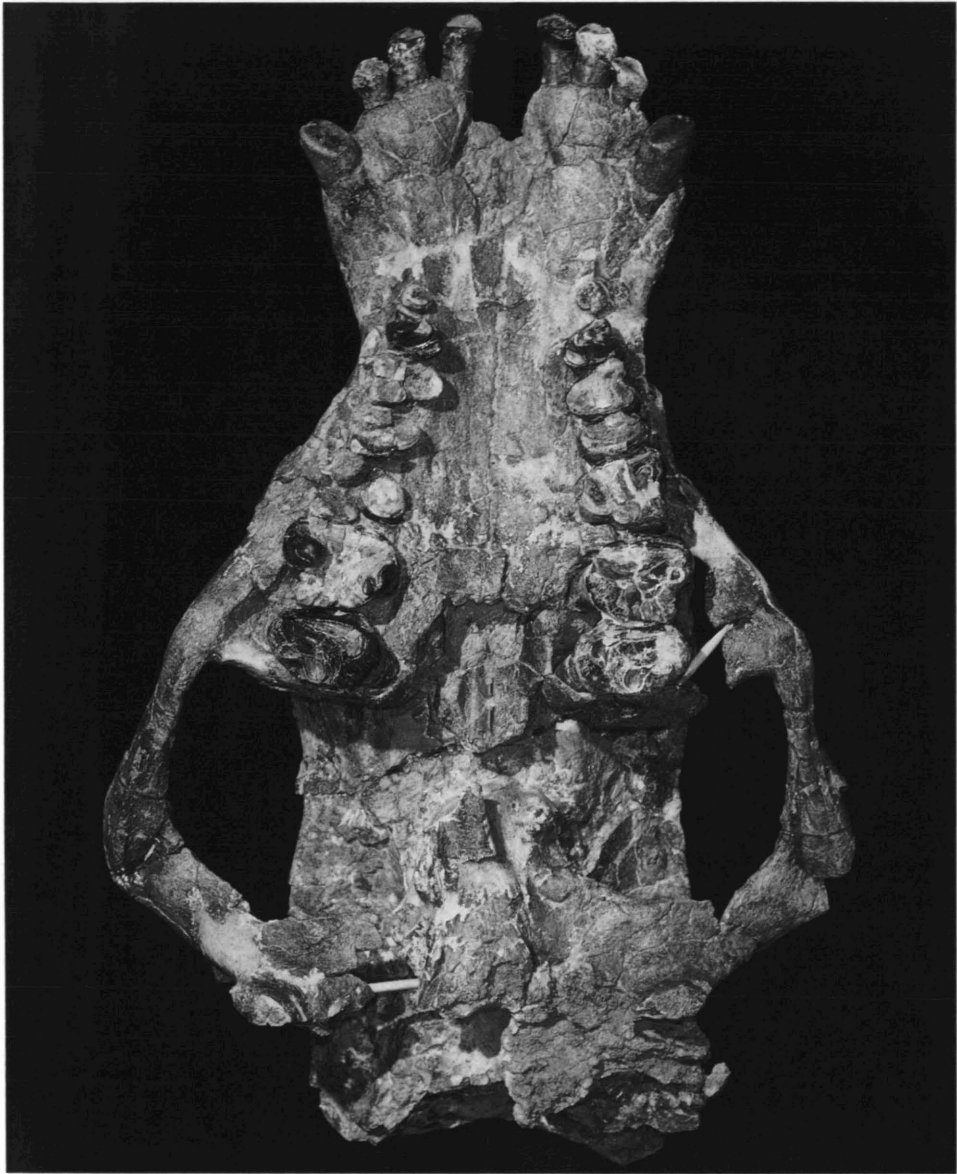


FIG. 3—Cranium of *Coryphodon radians*, UM 98530 (UM locality MP-122, Wa-4), in palatal view. Note the small size of upper canines indicating that specimen is female, and heavy wear on all teeth indicating that individual died in old age. Scale is in cm.

Type locality.—The type specimen was collected by F. V. Hayden in Wasatch group beds near Evanston, Wyoming (Cope, 1872a).

Age and distribution.—*C. radians* first occurs in North America in Wasatchian biochron Wa-3 (early Eocene). *C. radians* persists through Wasatchian biochron Wa-3b land-mammal biochron. Figures 4-9 illustrate the relative size and stratigraphic position of *C. radians* individuals.

TABLE 5—Summary of molar measurements for *Coryphodon radians* from northwestern Wyoming. N, number of individuals; SD, standard deviation, V, coefficient of variation (%). L, mesial-distal crown length; W, buccolingual crown width. All measurements in mm.

Measurement	N	Range	Mean	SD	V
Upper dentition					
M ¹ L	8	21.5 - 28.4	25.7	2.7	10.1
W	8	24.0 - 32.9	30.3	3.4	10.1
M ² L	7	27.0 - 36.8	32.2	3.6	11.3
W	7	31.8 - 44.0	38.5	4.8	12.5
M ³ L	7	24.8 - 33.9	29.2	3.0	10.3
W	7	33.5 - 42.6	38.1	3.2	8.5
Lower dentition					
M ₁ L	4	27.3 - 29.3	28.5	0.9	3.2
W	4	16.6 - 21.3	19.8	2.2	11.2
M ₂ L	6	29.4 - 35.5	32.6	3.0	9.1
W	6	18.5 - 24.8	22.1	2.1	9.7
M ₃ L	4	31.8 - 40.1	37.0	3.6	9.8
W	4	23.3 - 28.8	25.8	2.4	9.4

Diagnosis.—*Coryphodon radians* can be recognized based on its size, the absence of an entoconid on M₃, and the shape of the trigonid of M₃. *C. radians* is a moderate-sized *Coryphodon*. The average size of *C. radians* is smaller than both *Coryphodon proterus* and *Coryphodon lobatus*, and larger than *Coryphodon eocaenus*, and *C. armatus*. In addition, *C. radians* lacks a well-defined entoconid. A crest is often present connected to the hypoconulid, but there is no cusp on the crest. Also, the M₃ is not bilophodont (Fig. 10). The hypoconid-hypoconulid portion of the posteristid is at a high angle to the protolophid, which distinguishes it from *Coryphodon armatus*. The upper molars of *C. radians* have anterior and posterior cingula, but they are not as broad as those found on the upper molars of *C. armatus*. The M³ posterior cingulid is less prominent than those found in *C. eocaenus* and *C. proterus*.

Description.—P¹ of *Coryphodon radians* is very small and has a moderately deep V-shaped ectoloph and a small protocone. P²⁻⁴ increase in size from P² to P⁴ bearing well-developed anterior and posterior cingula, deeply V-shaped ectolophs and high protocones.

M¹⁻² are similar to each other (with M¹ being smaller than M²) and to M¹⁻² of other species of *Coryphodon*. Some M¹⁻² are more quadrate, while others are more labiolingually elongate. M¹⁻² have narrow anterior and posterior cingula. M¹⁻³ have complete postprotocristae.

M³ is about the same size (crown area) or smaller than M². M³ area (length × width) ranges from 830 to 1363 mm². M³ has a complete lingual cingulum along with a posterolingual cingulum. Some individuals have preparacristae as well, but this character is variably present.

P₁ has a relatively smaller trigonid and smaller metaconid than P_{2,4}. P_{2,4} increase in size from P₂ to P₄, with the premolars becoming relatively wider as well.

M₁₋₂ of *Coryphodon radians* are bilophodont and lack an entoconid. They are similar to each other (with M₁ being slightly smaller than M₂) and to M₁₋₂ of other species of *Coryphodon*. Only their moderate to large size indicates that they belong to *C. radians*.

CLARKS FORK BASIN *CORYPHODON*

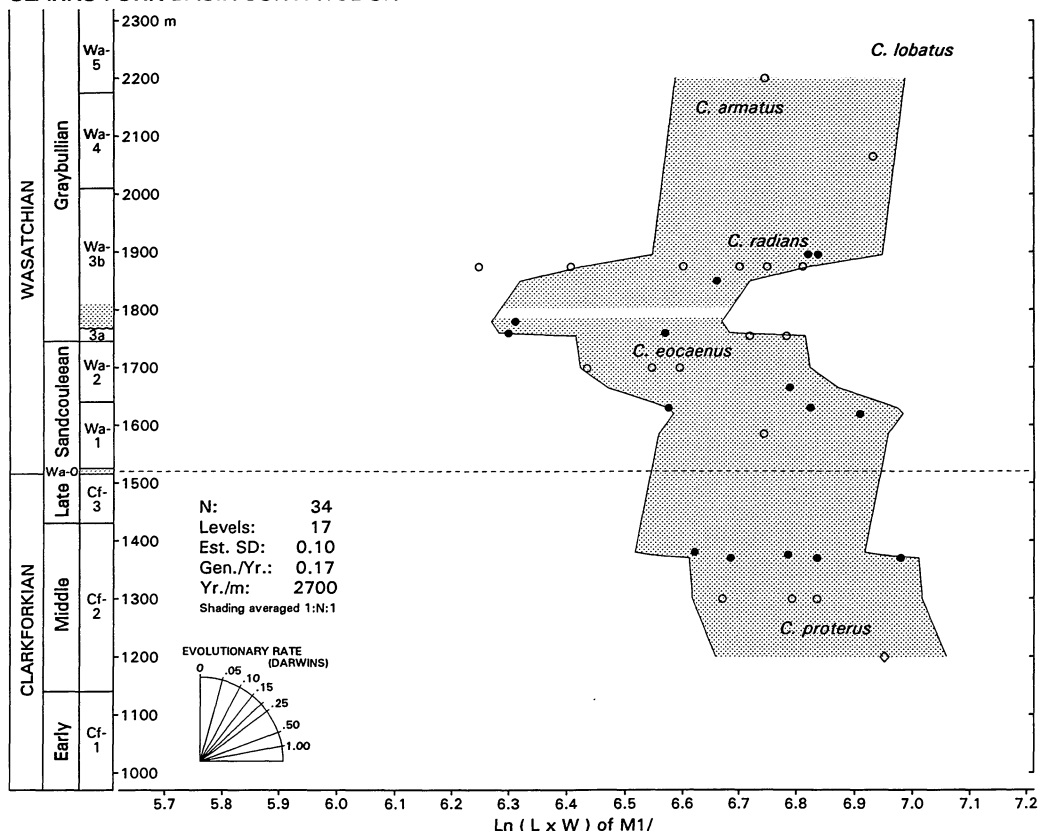


FIG. 4—Pattern of change of tooth size in early Eocene *Coryphodon* in northwestern Wyoming. Measure plotted is natural logarithm of M^1 area. Solid circles represent specimens known to meter level, as measured in the Polecat Bench–Sand Coulee section, while open circles represent specimens known only to land-mammal biochron. Specimens from localities not in the Polecat Bench–Sand Coulee section were correlated faunally. Rates of change shown here, both between samples and along lineages, are well within the range of rates calculated on the same scale of time in other studies.

M_3 area (length \times anterior width) ranges from 878 to 1155 mm². M_3 lacks a prominent entoconid but a crest connected to the hypoconulid is present in the position of the entoconid. The hypoconid-hypoconulid portion of the postcristid is at a high angle to the protolophid. The posteristid forms an angle with the hypoconulid at its posteriorly pointing apex; thus the M_3 is not bilophodont. In addition, the paraconid (which is represented by a crest rather than a distinct cusp) is well developed (see Figure 10).

Measurements of the northwestern Wyoming sample of *Coryphodon radians* are summarized in Table 5.

Discussion.—*Coryphodon radians* includes the first described specimen of *Coryphodon* from North America, originally named *Bathmodon radians* (Cope, 1872).

Referred specimens.—From Wasatchian-age strata of the Bighorn Basin, Sand Coulee area: UM 66684, 66774, 67033, 67287, 71697, 83033, 98205. From Wasatchian-age strata of the Bighorn Basin, McCullough Peaks area: UM 82516, 87720, 92219, 93560, 94655, 95220, 96219, 96262, 99271, 101955. From Wasatchian-age strata of the Clarks Fork Basin, Foster

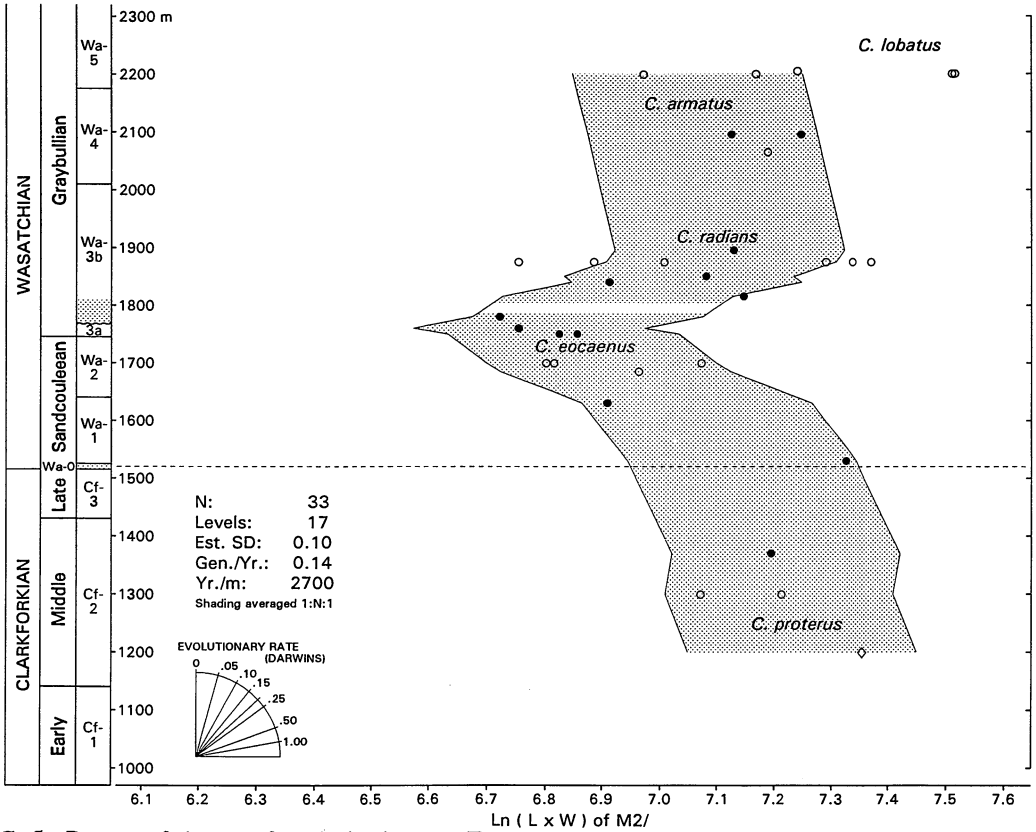
CLARKS FORK BASIN *CORYPHODON*

FIG. 5—Pattern of change of tooth size in early Eocene *Coryphodon* in northwestern Wyoming. Measure plotted is natural logarithm of M^2 area. Solid circles represent specimens known to meter level, as measured in the Polecat Bench–Sand Coulee section, while open circles represent specimens known only to land-mammal biochron. Specimens from localities not in the Polecat Bench–Sand Coulee section were correlated faunally. Rates of change shown here, both between samples and along lineages, are well within the range of rates calculated on the same scale of time in other studies.

Gulch area: UM 85958, 86866, 87319. From Wasatchian-age strata of the central Bighorn Basin: UM 61791, 63575, 63744, 63753, 63811, 63849, 63929, 64308.

Coryphodon armatus Cope, 1872

Metalophodon armatus Cope, 1872b, p. 774

Bathmodon molestus Cope, 1874, p. 597

Bathmodon lomas Cope, 1874, p. 597

Bathmodon elephantopus Cope, 1874, p. 598

Bathmodon latidens Cope, 1875, p. 29

Bathmodon cuspidatus Cope, 1875, p. 30

Coryphodon cuspidatus, Cope, 1877, p. 206, Pl. 46, fig. 1

Coryphodon obliquus Cope, 1877, p. 207, Pl. 47, fig. 7

Coryphodon latidens, Cope, 1877, p. 214; Pl. 48, figs. 1-2; Pl. 49, figs. 1-3

Coryphodon elephantopus, Cope, 1877, p. 217, Pl. 50, figs. 5-6; Pl. 51, figs. 1-6; Pl. 52, fig. 1; Pl. 53, fig. 1; Pl. 54, fig. 1

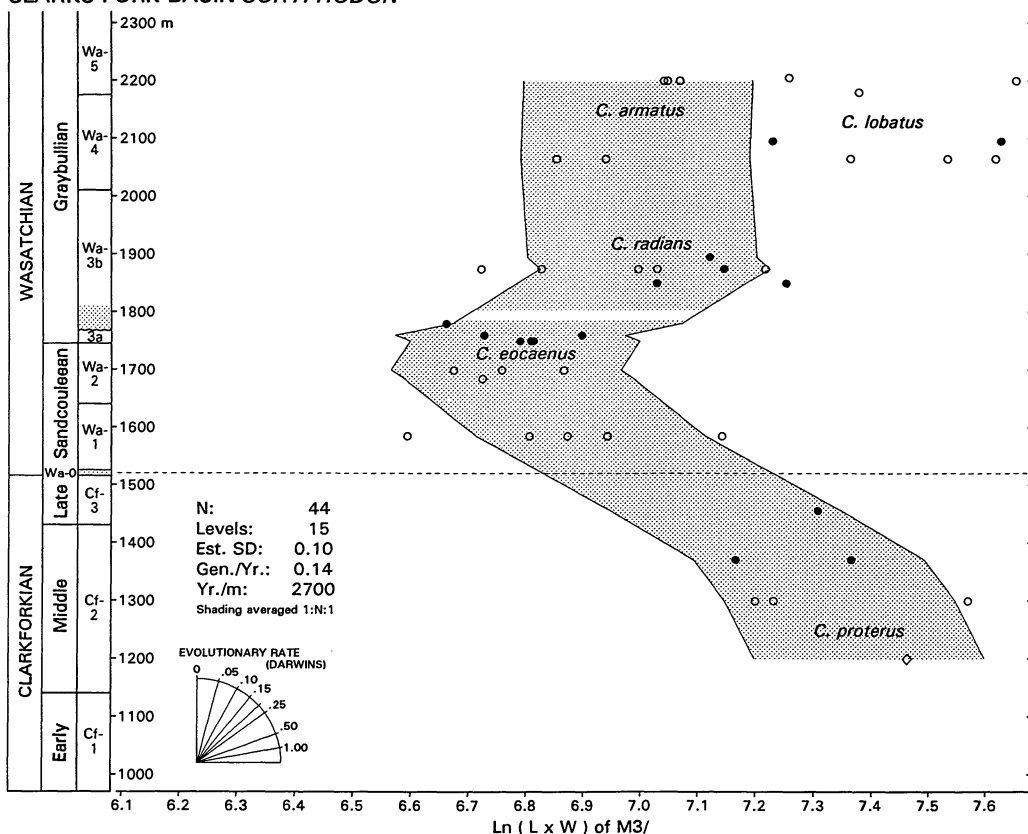
CLARKS FORK BASIN *CORYPHODON*

FIG. 6.—Pattern of change of tooth size in early Eocene *Coryphodon* in northwestern Wyoming. Measure plotted is natural logarithm of M^3 area. Solid circles represent specimens known to meter level, as measured in the Polecat Bench–Sand Coulee section, while open circles represent specimens known only to land-mammal biochron. Specimens from localities not in the Polecat Bench–Sand Coulee section were correlated faunally. Rates of change shown here, both between samples and along lineages, are well within the range of rates calculated on the same scale of time in other studies.

Bathmodon molestus, Cope, 1877, p. 229, Pl. 54, fig. 2; Pl. 56, figs. 1-7; Pl. 57, figs. 1-2

Coryphodon curvicristis Cope, 1882b, p. 172

Coryphodon armatus, Osborn, 1898b, p. 208, figs. 15, 16, 25

Coryphodon wormani Osborn, 1898b, p. 212, figs. 18, 27

Coryphodon radians (in part), Gazin, 1962, p. 70, Pl. 12, figs. 1-2

Holotype.—AMNH 4315, M^3 , M^2 , upper premolars, upper canine and incisors, probably mixed from two adult individuals (Osborn, 1898b).

Type locality.—The type specimen was collected by E. D. Cope from the Wasatch Formation of the Eocene of Wyoming. The type specimen was located south of Bitter Creek Station.

Age and distribution.—*Coryphodon armatus* is known only from the late early Eocene of North America. *C. armatus* is found in beds ranging in age from Wasatchian biochron Wa-4 through Wa-6 in the Bighorn Basin of Wyoming (Figs. 4–9). In the San Juan Basin of New Mexico, *C. armatus* is found in the Almagre and Largo local faunas of the Regina Member of

TABLE 6—Summary of molar measurements for *Coryphodon armatus* from northwestern Wyoming. N, number of individuals; SD, standard deviation, V, coefficient of variation (%). L, mesial-distal crown length; W, buccolingual crown width. All measurements in mm.

Measurement	N	Range	Mean	SD	V
Upper dentition					
M ¹ L	2	27.2 - 28.5	27.9	0.9	3.3
W	2	31.2 - 32.5	31.9	0.9	2.9
M ² L	3	30.1 - 34.5	32.7	2.3	7.0
W	3	35.4 - 37.6	36.7	1.2	3.2
M ³ L	5	26.3 - 32.0	29.3	2.0	7.0
W	5	34.5 - 40.1	37.2	2.6	6.9
Lower dentition					
M ₁ L	9	23.1 - 28.9	26.1	2.2	8.2
W	9	15.6 - 19.7	18.2	1.2	6.8
M ₂ L	11	30.3 - 35.9	32.9	1.6	4.9
W	11	22.2 - 25.5	23.8	1.0	4.3
M ₃ L	11	36.6 - 41.2	39.3	1.5	3.7
W	11	25.7 - 30.7	27.8	1.5	5.6

the San José Formation, which are correlated with Bighorn Basin faunas of biochron Wa-5 or later.

Diagnosis.—*Coryphodon armatus* differs from the contemporaneous *Coryphodon lobatus* in being considerably smaller. In addition, the upper molars of *C. armatus* have broad anterior and posterior cingula, in contrast to those of *C. lobatus* that bear narrow cingula. *C. armatus* lower third molars are bilophodont and lack entoconids. *C. armatus* is much smaller than the Clarkforkian *C. proterus*. The size range of *C. armatus* overlaps with those of *Coryphodon eoacenus*, and *Coryphodon radians*. *C. armatus* can be distinguished from each of these species by the absence of an entoconid and the absence of an entoconid-hypoconulid portion of the posteristid on the M₃. The posteristid of *C. armatus* is linear, lacking the hypoconulid-entoconid portion entirely. This crest is parallel to the protolophid, making M₃ distinctly bilophodont, in contrast to *C. eoacenus* and *C. radians* (Fig. 10).

Description.—P¹ is small and has a moderately deep V-shaped ectoloph. P²⁻⁴ are similar to each other, increasing in size from P² to P⁴. P²⁻⁴ bear anterior and posterior cingula. P²⁻⁴ have deeply V-shaped ectolophs and high protocones.

M¹⁻² are quadrate in shape. M¹⁻² are similar to each other with M¹ being smaller than M². M¹⁻² have incomplete lingual cingula. M¹⁻² have very wide anterior and posterior cingula. M¹⁻³ have complete postprotocristae.

M³ is small and ovate. M³ of *C. armatus* lacks a preparacrista and the presence of a posterolingual cingulum is variable. M³ also lacks a complete lingual cingulum. M³ area (length × width) ranges from 947 to 1175 mm².

P₁ is very small and narrow. P₂₋₄ increase in size from P₂ to P₄, with the premolars becoming relatively wider as well. P₁ has a relatively smaller trigonid and smaller metaconid than P₂₋₄.

M_{1-2} are bilophodont and similar to each other. M_1 is smaller than M_2 , which is smaller than M_3 . M_{1-2} lack entoconids.

M_3 is bilophodont and the hypoconid-hypoconulid portion of the posteristid is parallel to the protolophid. Most specimens lack an entoconid entirely, but a small cusplule is present in some specimens. The paraconid is represented by a prominent ridge on the M_3 , rather than a distinct cusp (see Figure 10). M_3 area (length \times width) ranges from 941 to 1216 mm².

Measurements of the northwestern Wyoming sample of *Coryphodon armatus* are summarized in Table 6.

Discussion.—*Coryphodon molestus* was synonymized with *Coryphodon armatus* by Osborn (1898b), but Lucas (1984a) pointed out that type of *Metalophodon armatus* was actually an M_3 of *Coryphodon eocaenus*, thus the specific name was not available. Since these individuals were found together it is unlikely that they are from different species. Also, it is not clear that the two upper third molars in the original holotype of *C. armatus* belong to *C. eocaenus*. Osborn's (1898b) synonymy of *C. molestus* with *C. armatus* is followed here. The M_3 of the cotype of *Coryphodon armatus* (AMNH 4316) figured in Osborn (1898b) and shown here in Figure 10 as *C. armatus*, clearly lacks an entoconid and it is distinctly bilophodont. These two characters, along with its small size clearly place it in *C. armatus*.

Referred specimens.—From Wasatchian-age strata of the Bighorn Basin, Sand Coulee area: UM 73490, 88190. From Wasatchian-age strata of the Bighorn Basin, McCullough Peaks area: UM 91253, 91935, 92511, 92623, 93293, 93733, 93755, 93804, 94041, 94233, 94667, 94760, 95010, 97008, 97142, 98538, 99476, 99542. From Wasatchian-age strata of the Bighorn Basin, Greybull River area: UM 75493. From Wasatchian-age strata of the central Bighorn Basin: UM 63753. University of Michigan specimens from Wasatchian-age strata of the San Juan Basin include: UM 21179, 21691, and UNM J-157 (cast), all from the Regina area, and UM 3480 from Laguna Colorado.

Coryphodon lobatus Cope, 1877

Coryphodon lobatus Cope, 1877, p. 209, Pl. 46, figs. 2-10

Coryphodon anax Cope, 1882a, p. 73; 1884, p. 537, Pl. 44a, figs. 7-12; Pl. 44b, figs. 1-5; Pl. 44e, fig. 6; p. 44f, figs. 1-11

Coryphodon lobatus (in part), Osborn, 1898b, p. 204, figs. 15, 16

Coryphodon ventanus Osborn, 1898b, p. 210, fig. 16

Lectotype.—USNM 6002, right P_3 - M_3 (Cope, 1877, Pl. 46, figs. 9-10; designated by Lucas, 1984a).

Type locality.—The type specimen was collected by E. D. Cope in September of 1874 (Lucas, 1984a) from the Regina Member of the San José Formation, Arroyo Blanco, San Juan Basin, New Mexico. See Lucas (1981), p. 954, fig. 3 for the location of Arroyo Blanco.

Age and distribution.—*Coryphodon lobatus* is known only from the Eocene of North America. In the Bighorn Basin of Wyoming, *C. lobatus* is found in strata of Wasatchian biochron Wa-4 through Wa-6 (Figs. 4-9). In the San Juan Basin of New Mexico, *C. lobatus* is found in strata that have been correlated with Bighorn Basin strata that are Wasatchian biochron Wa-5 or later in age.

Diagnosis.—*Coryphodon lobatus* is a very large *Coryphodon*, comparable in size only to *Coryphodon proterus*. *C. lobatus* is easily distinguished from *C. proterus* by the morphology of M_3 . *C. lobatus* is bilophodont and usually lacks an entoconid. A few individuals retain a small entoconid, but the hypoconid-hypoconulid portion of the posteristid is almost parallel to the protolophid in *C. lobatus*. *C. lobatus* is considerably larger than the morphologically similar contemporaneous species, *C. armatus*. *C. lobatus* can be distinguished from *C. eocaenus* and *C. radians* by its larger size and by its bilophodont M_3 (Fig. 10).

TABLE 7—Summary of molar measurements for *Coryphodon lobatus* from northwestern Wyoming. N, number of individuals; SD, standard deviation, V, coefficient of variation (%). L, mesial-distal crown length; W, buccolingual crown width. All measurements in mm.

Measurement	N	Range	Mean	SD	V
Upper dentition					
M ¹ L	1	31.2 - 31.2	31.2		
W	1	32.8 - 32.8	32.8		
M ² L	6	33.5 - 40.8	36.5	3.1	8.6
W	6	39.5 - 46.0	42.3	2.6	6.1
M ³ L	7	30.6 - 39.1	35.6	3.2	8.9
W	7	43.0 - 54.0	47.9	4.4	9.3
Lower dentition					
M ₁ L	3	29.1 - 32.8	31.0	1.9	6.0
W	3	20.9 - 22.8	22.0	1.0	4.5
M ₂ L	6	30.9 - 38.5	36.2	2.7	7.4
W	6	24.6 - 33.3	27.5	3.2	11.6
M ₃ L	4	42.4 - 51.4	46.9	3.8	8.2
W					

Description.—P¹ is very small and different in morphology from P²⁻⁴. P¹ has a moderately deep V-shaped ectoloph and a small protocone. P²⁻⁴ are similar to each other and to those of other *Coryphodon*. They increase in size from P² to P⁴. P²⁻⁴ bear narrow anterior and posterior cingula, deeply V-shaped ectolophs, and high protocones.

M¹⁻² are quadrate in shape and similar to each other. Anterior and posterior cingula are present, but not strongly developed. M¹⁻² lack complete lingual cingula.

M³ is large and somewhat labiolingually elongate, but not as much so as in *C. proterus*. Preparacrista are occasionally present. M³ also lacks a large, posterolingual cingulum. M³ area (length × width) ranges from 1380 to 2108 mm².

P₁₋₄ resemble those of other *Coryphodon*, but are relatively larger. P₁ has a relatively smaller trigonid and smaller metaconid than P₂₋₄.

M₁₋₂ are bilophodont and lack an entoconid. The lower molars increase in size from M₁ to M₃.

M₃ is very large, in both width and length. M₃ area (length × anterior width) ranges from 1344 to 1763 mm². It is more bilophodont than most *Coryphodon* (the exception being *C. armatus*) but the hypoconid-hypoconulid portion of the postcrisid is not quite parallel to the protolophid. In addition an entoconid crest or a small entoconid is sometimes present on M₃ (see Figure 10).

Measurements of the northwestern Wyoming sample of *Coryphodon lobatus* are summarized in Table 7.

Discussion.—Osborn (1898b) named a new species, *Coryphodon ventanus* for a collection of specimens from the "Wind River beds" of the Wind River Basin. The Wind River Forma-

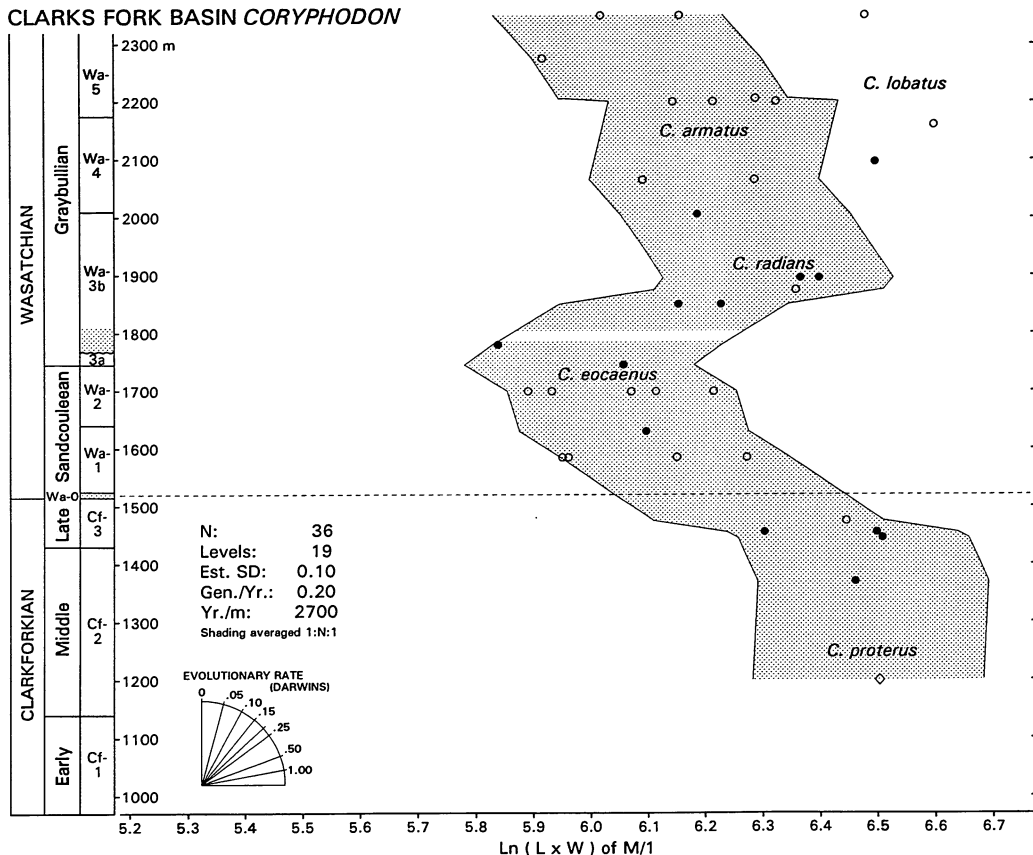
CLARKS FORK BASIN *CORYPHODON*

FIG. 7—Pattern of change of tooth size in early Eocene *Coryphodon* in northwestern Wyoming. Measure plotted is natural logarithm of M_1 area. Solid circles represent specimens known to meter level, as measured in the Polecat Bench–Sand Coulee section, while open circles represent specimens known only to land-mammal biochron. Specimens from localities not in the Polecat Bench–Sand Coulee section were correlated faunally. Rates of change shown here, both between samples and along lineages, are well within the range of rates calculated on the same scale of time in other studies.

tion is regarded as middle Wasatchian to early Bridgerian in age (Krishtalka et al., 1987). The M_3 that Osborn figured (his figure 16) is virtually identical to that of *Coryphodon anax*, which he synonymized with *C. lobatus*. The morphology of M_3 and the stratigraphic occurrence of *C. ventanus* are consistent with its placement in *C. lobatus*.

Referred specimens.—From Wasatchian-age strata of the Clarks Fork Basin, Sand Coulee area: UM 73563, 73648. From Wasatchian-age strata of the Bighorn Basin, McCullough Peaks area: UM 91129, 92003, 92075, 93753, 94016, 94065, 94071, 94593, 96713, 96753, 98530, 99306. From Wasatchian-age strata of the Bighorn Basin, Greybull River area: UM 75552. From Wasatchian-age strata of the central Bighorn Basin: UM 64130, 64268, 72645. From Wasatchian-age strata of the Washakie Basin: UM 17597. In addition, one University of Michigan specimens comes from Wasatchian-age strata of the Daniel area, Green River Basin: UM 56657.

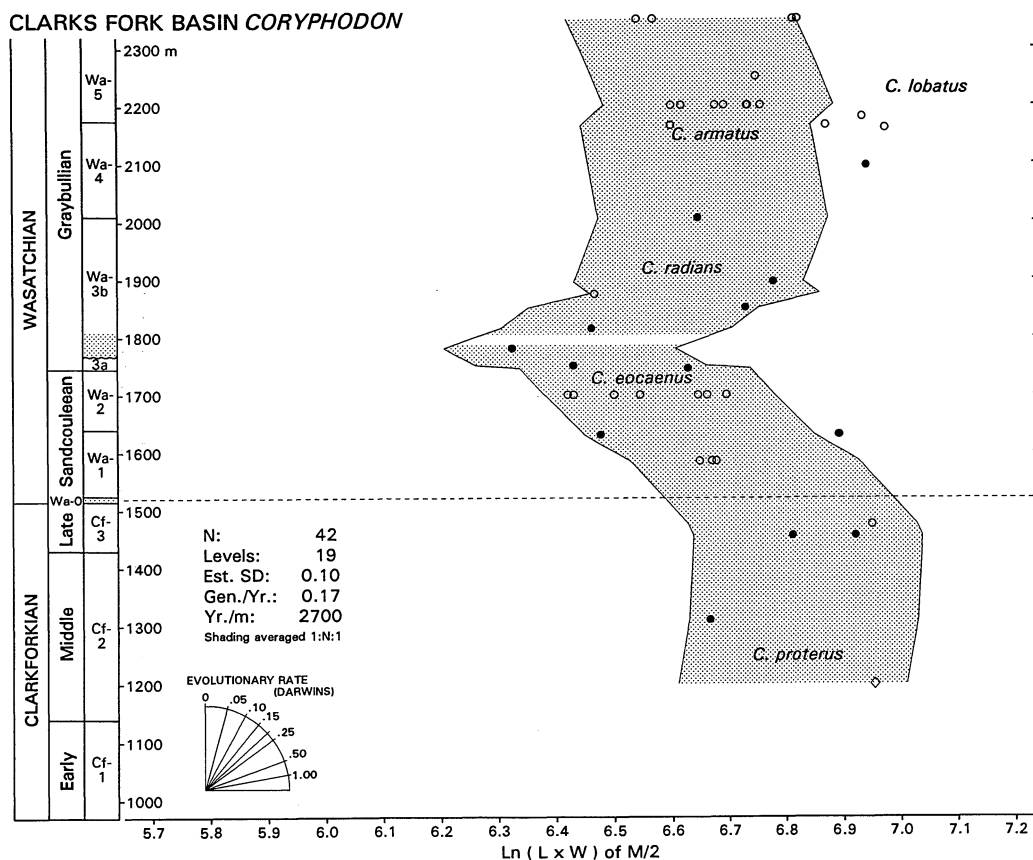


FIG. 8—Pattern of change of tooth size in early Eocene *Coryphodon* in northwestern Wyoming. Measure plotted is natural logarithm of M_2 area. Solid circles represent specimens known to meter level, as measured in the Polecat Bench–Sand Coulee section, while open circles represent specimens known only to land-mammal biochron. Specimens from localities not in the Polecat Bench–Sand Coulee section were correlated faunally. Rates of change shown here, both between samples and along lineages, are well within the range of rates calculated on the same scale of time in other studies.

LUCAS' CLADISTIC ANALYSIS OF *CORYPHODON* SPECIES

Lucas (1984a,b) reviewed the taxonomy of *Coryphodon* and reduced the number of species within the genus, which had been subdivided to the point of confusion in North America. However, Lucas' cladistic analysis could not resolve the sister group relationships among species of *Coryphodon* because the data matrix used to analyze relationships does not contain enough characters to fully resolve a phylogeny. The minimum number of binary characters needed to yield a fully-dichotomous cladogram is $t-1$, where t is equal to the number of taxa. Lucas' matrix (see Lucas, 1984a, p. 423, table 32) contains eight taxa with nine characters. One of the characters has two derived character states and is thus counted twice to account for two possible character state transitions. This brings the number of characters to ten, which seems to be sufficient, but some of the characters in the matrix are uninformative. Two (presence of a metaconule on M^{1-2} and a ridge on the posterolingual cingulum) are autapomorphies of "*Coryphodon subquadratus*", while another (cheek teeth broad relative to

CLARKS FORK BASIN *CORYPHODON*

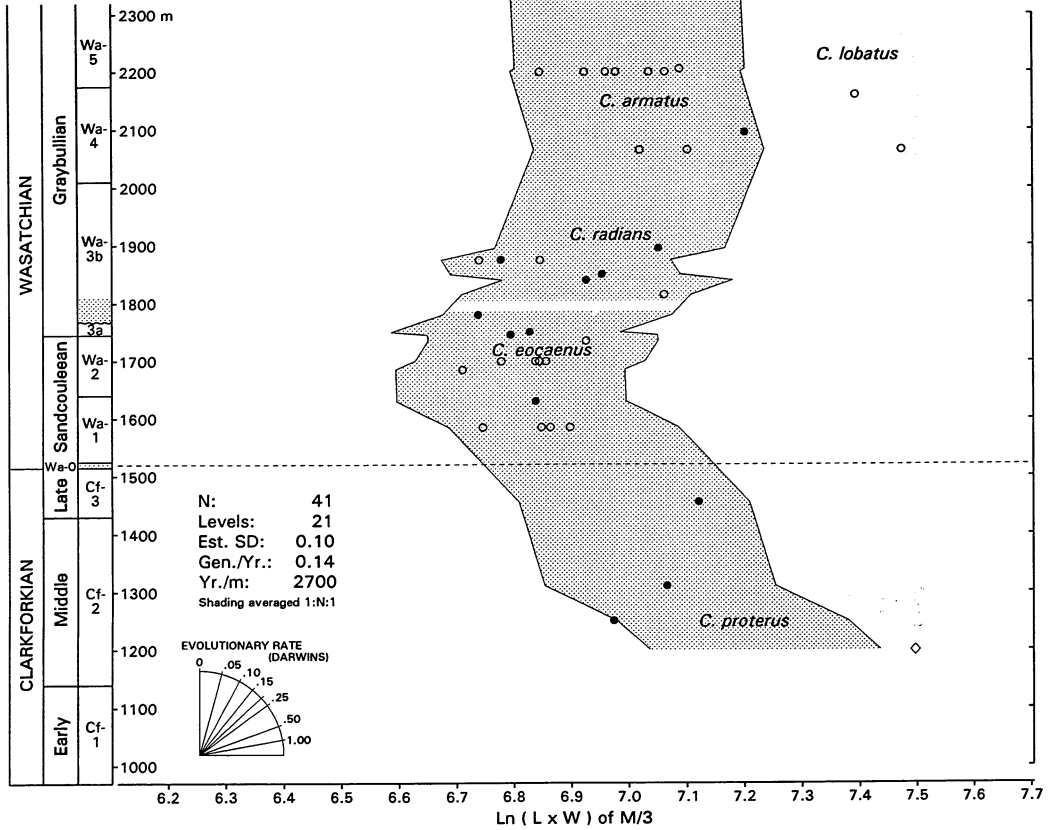


FIG. 9—Pattern of change of tooth size in early Eocene *Coryphodon* in northwestern Wyoming. Measure plotted is natural logarithm of M_3 area. Solid circles represent specimens known to meter level, as measured in the Polecat Bench–Sand Coulee section, while open circles represent specimens known only to land-mammal biochron. Specimens from localities not in the Polecat Bench–Sand Coulee section were correlated faunally. Rates of change shown here, both between samples and along lineages, are well within the range of rates calculated on the same scale of time in other studies.

length) is autapomorphic for *Coryphodon lobatus*. Also, if "*Coryphodon subquadratus*" is not a valid taxon, another character, presence of a postprotocrista on M^{1-3} becomes autapomorphic for *Coryphodon simus*, a taxon whose validity is in question as well. While autapomorphic characters can be useful for recognizing species, they do not contribute to the resolution of relationships in a cladistic analysis. Thus, they cannot be counted toward the number of characters that will determine sister group relationships. With this in mind, the number of cladistically-useful characters drops from ten to six. Clearly the six remaining characters are not sufficient to determine phylogenetic relationships among *Coryphodon* species.

One morphological feature of *Coryphodon* evolution that was not utilized in Lucas' cladistic analysis is body size. Lucas (1984a) stated that the trend in size through time displayed by *Coryphodon* does not follow the morphocline of any of the other characters. While it is true that size does not follow a unidirectional morphocline through time, we here document a recognizable pattern of size change through time (see Figures 4-9). Characters should not be discarded from a phylogenetic analysis simply because they are not concordant with other characters. In fact, size is one of the most (if not *the* most) important character for delimiting

species and for studying evolutionary trends in the fossil record (Gingerich and Simons, 1977; Gingerich, 1983).

STRATOPHENETIC ANALYSIS OF SPECIES-LEVEL PHYLOGENY IN *CORYPHODON*

A stratophenetic approach was used to analyze *Coryphodon* phylogeny because (1) species are groupings with temporal as well as morphological and geographical components, (2) the temporal distribution of species furnishes an important constraint on phylogeny, and (3) a previous attempt at a cladistic analysis showed that there are not enough morphological characters available to produce a dichotomous cladogram based on morphology alone (Lucas, 1984a,b; see above). *Coryphodon* is well-sampled stratigraphically in the Bighorn and Clarks Fork basins, which is a prerequisite for species-level stratophenetic analysis of phylogeny.

The Bighorn and Clarks Fork basins provide a long and well-sampled stratigraphic section that has yielded numerous specimens of *Coryphodon*. Figures 4-9 show the distribution of the natural logarithm of upper and lower molar areas through strata and time in the Clarks Fork and Bighorn basins for all *Coryphodon* specimens for which stratigraphic level is known to land-mammal biochron or better. Many are known to meter level, as measured in the Polecat Bench-Sand Coulee area of the northern Bighorn and Clarks Fork basins. Individuals that are known only to land-mammal biochron have been placed in the center of the land-mammal biochron to which they belong.

The *Coryphodon* lineage is first represented in the Bighorn and Clarks Fork basins (and the world) by early Clarkforkian *Coryphodon proterus*. Groups that are possibly ancestral to *Coryphodon* include members of the family Pantolambdidae (sensu lato; Gingerich and Childress, 1983). However, none of the genera in North American Pantolambdidae (nor any other known Paleocene pantodont) shares any special features with *Coryphodon*. The appearance of *Coryphodon* in the Clarkforkian of North America with no identifiable North American ancestry, suggests that *Coryphodon* may have immigrated from another continent at this time.

From the early to late Clarkforkian, *Coryphodon proterus* decreased in size while retaining the same basic morphology. Figures 4 to 9 show the pattern of evolution of *Coryphodon* molar tooth size through time, and Figure 10 shows how M_3 shape changed through time. *C. proterus*, being both older and very similar (and the only Clarkforkian *Coryphodon* known), was probably the immediate ancestor of *Coryphodon eocaenus*, the earliest Wasatchian *Coryphodon*. The morphology of *C. eocaenus* is very similar to that of late Clarkforkian *C. proterus*, but *C. eocaenus* is somewhat smaller. The trend toward decreasing size continued in *C. eocaenus* until middle Wasatchian biochron Wa-3a. The time of the size minimum in the *Coryphodon* lineage corresponds to Gingerich's (1991) Wasatchian biochron Wa-3a, and evidently preceded Schankler's (1980) Biohorizon A. Biohorizon A was poorly defined when it was first proposed, the stratigraphic sections and systematic interpretations on which it was based were never published, and it is thus difficult to recognize in the central Bighorn Basin or elsewhere (Badgley and Gingerich, 1988; Badgley, 1990).

By Wasatchian biochron Wa-3b, the size of the *Coryphodon* lineage had increased again, the entoconid that was present in *C. proterus* and *C. eocaenus* is found on fewer individuals, and it is often less prominent when present. The evolution of *Coryphodon radians* from *C. eocaenus* was accompanied by the loss of the M_3 entoconid. In Wasatchian biochron Wa-4 there is evidence of two *Coryphodon* lineages. While both lineages are characterized by having relatively bilophodont molars, the *Coryphodon armatus* lineage was smaller, while the *Coryphodon lobatus* lineage was larger than *C. radians*. *C. lobatus* was as large as Clarkforkian *C. proterus*.

BIGHORN BASIN CORYPHODON

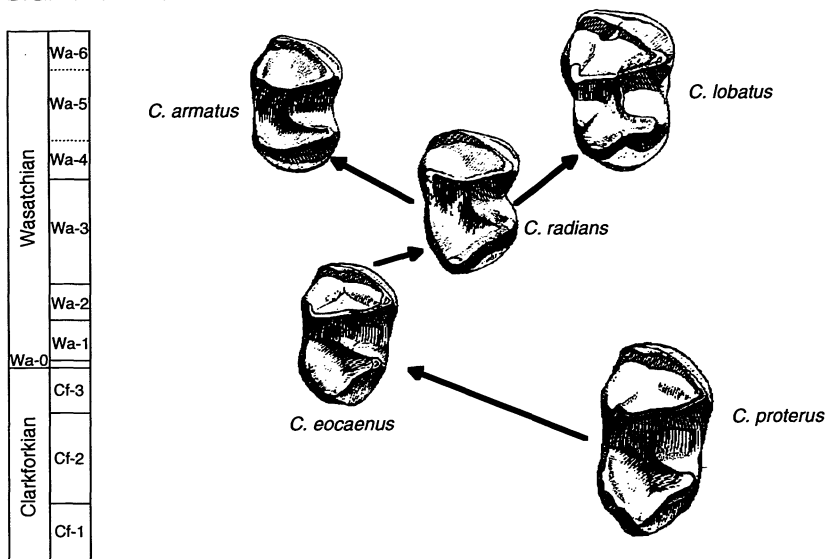


FIG. 10—Evolution of *Coryphodon* lower third molars through early Eocene time in northwestern Wyoming. The M_3 of *Coryphodon proterus* is large, elongate, and has a prominent entoconid. The M_3 of *Coryphodon eocaenus* is smaller than *C. proterus*, but retains a well developed entoconid while the M_3 of *Coryphodon radians* has lost the entoconid and is larger than *C. eocaenus*. The M_3 of *Coryphodon armatus* has lost the entoconid completely and is distinctly bilophodont. The M_3 of *Coryphodon lobatus* is also bilophodont, but is much larger than the M_3 of *C. armatus*.

OTHER NORTH AMERICAN CORYPHODON

Lucas (1984b) recognized three species of North American *Coryphodon* that are omitted here: *Coryphodon subquadratus*, *C. oweni*, and *C. simus*. Each of these taxa was omitted for a different reason. *Coryphodon subquadratus*, as described by Lucas, may not be a valid taxon. The presence of metaconules on the M^{1-2} , which Lucas described as an autapomorphy of *C. subquadratus*, is variably present throughout the entire genus *Coryphodon*. There is no evidence of a coherent group of individuals from the Bighorn Basin representing a separate species that corresponds in size and morphology to the previously described *C. subquadratus*.

Coryphodon eocaenus as described here includes specimens from North America previously identified as *Coryphodon oweni* (Lucas, 1984a). *C. oweni* is still a valid taxon for small *Coryphodon* in Europe. The type sample of *C. oweni* is composed of individuals smaller than any North American *Coryphodon* (while small individuals of *C. eocaenus* approach this small size in Wasatchian biochron Wa-2 and 3a, the mean size of samples as a whole is larger).

No individuals were assigned to *Coryphodon simus*. From the description of the species in Lucas (1984b), it appears that *C. simus* is very similar to *C. armatus*, but a little smaller. In addition, the stratigraphic position of all the specimens indicate that they occur in the middle or late Wasatchian (all are from the San José Formation, San Juan Basin, New Mexico). These specimens may represent continuation of a trend toward decreasing size. If this is the case, these specimens may be included in *C. armatus* if they fall within an acceptable range of variation, as suggested by Osborn (1898b). If they do not, they may represent a distinct species and should be recognized as *C. simus*.

DISCUSSION

The pattern of size change in *Coryphodon* through time in the Bighorn Basin can be seen readily in any of the upper or lower molars, as is illustrated in Figures 4–9. The general pattern is similar in each of the plots. Differences are due, at least in part, to the small number of data points, and the lack of precise stratigraphic control on localities that are not from the measured Polecat Bench–Sand Coulee section. For example, most of the plots show a wide variation in the molar size of *Coryphodon radians* during Wasatchian biochron Wa-3b, but most of those specimens included in the range of variation are not measured into the Sand Coulee section. Since the lineage was changing through the time period (which is rather long relative to earlier Wasatchian biochrons) and all of the specimens are shown at the midpoint of the biochron, variation in the *Coryphodon* lineage over the entire biochron is shown at a single point in time. The observed range is certainly an overestimate of the true variation at any time in the Wa-3b biochron since some of the specimens are from early Wa-3b, and some are from late Wa-3b.

The *Coryphodon* lineage begins in western North America at a very large body size. *Coryphodon proterus* is one of the largest of all species of *Coryphodon* (equaled only by the later *Coryphodon lobatus*) and the type specimen (shown in Figures 4–9 as an open diamond low in Clarkforkian biochron Cf-2) is the largest of the *C. proterus* individuals. The body size of the *Coryphodon* lineage decreased at a moderate rate (around 0.2–0.3 darwins, net) from *C. proterus* to *Coryphodon eocaenus* from the late Clarkforkian through the early Wasatchian. *C. eocaenus* then evolved, becoming larger at similar net rates, into *Coryphodon radians*.

The total range of variation in Bighorn Basin *Coryphodon* increased greatly from Wasatchian Wa-3b to Wa-5 time. This is interpreted here as indicating an increase from one to two species, with two sister species, *Coryphodon armatus* and *Coryphodon lobatus*, being derived from ancestral *Coryphodon radians*. It is unclear precisely when this speciation event took place. It seems that by Wasatchian-4 time the total range of variation had increased, but since most of the specimens in Wasatchian-3b and Wasatchian-4 do not come from localities for which precise stratigraphic levels are known, the speciation event can only be said to have occurred late in biochron Wa-3b or early in Wa-4. *Coryphodon radians* includes specimens that are later in time than the very smallest *Coryphodon eocaenus* in Wa-3a but precede division of *Coryphodon* into two separate lineages.

Rea et al. (1990) suggested that size change in *Coryphodon* was linked to global climate change at the marine Paleocene-Eocene boundary. The small size of *Coryphodon* in biochron Wa-3a was thought possibly to be a correlated response to the sharp negative isotopic excursion in $\delta^{18}\text{O}$ found in planktonic foraminifera and reflecting a 4–5° warming in sea-surface temperatures at the marine Paleocene-Eocene boundary. The theory was that, while mammals of intermediate sizes are subject to many complex constraints, mammals at extremes of body size might be sensitive in some simple way to changes in global mean annual temperature. Decrease in *Coryphodon* body size through Wa-2 and Wa-3a time was interpreted as a possible response to warming continental climate (Gingerich, 1989b). This seemed to support the idea that the marine Paleocene-Eocene boundary was correlative with the mid-Wasatchian land-mammal age in North America. New correlations of the terrestrial and marine records show that the Paleocene-Eocene boundary marked by a short-term carbon isotopic shift in the marine record is at the Clarkforkian-Wasatchian boundary in the Bighorn Basin, where there is a similar isotopic shift in carbon in soil carbonates (Koch et al., 1992). Thus the size minimum in the *Coryphodon* lineage is now thought to have occurred later than the isotopic shift in the marine record (Uhen, 1992; Clyde et al., 1994, 1995).

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