

## ENAMEL HYPOPLASIA IN MIOCENE RHINOCEROSES (*TELEOCERAS*) FROM NEBRASKA: EVIDENCE OF SEVERE PHYSIOLOGICAL STRESS

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**ABSTRACT**—Quarry samples of lower cheek teeth of the Miocene rhinoceros *Teleoceras* are analyzed for the presence of enamel hypoplasia using macroscopic, thin-section, and scanning electron microscopic techniques. The presence of enamel pits, furrows, and grooves is noted predominantly on, but not limited to, the buccal side of dp4s. The enamel defect is not as common on permanent teeth, but does occur with decreasing frequency on p4s, m1s, m2s, and m3s.

Analysis of the formative sequence of deciduous cheek teeth in *Teleoceras* and the extant rhinoceros *Diceros bicornis* suggests that the *Teleoceras* dp4 was developing in the alveolus at the time of birth. Varying degrees of wear on the dp4s exhibiting enamel hypoplasia imply that the defect-producing stress did not result in immediate death. Isolation of the enamel hypoplasia to distinct bands on the *Teleoceras* dp4s suggests causes linked to non-lethal severe physiological stress due to metabolic disruption or nutritional deficiency occurring at or very near birth. The *Teleoceras* p4 was probably developing in the alveolus between three and five years of age. The observed p4-hypoplasias appear to reflect physiological stresses not related to weaning, but to some other stressful period such as cow-calf separation prior to the birth of the next offspring.

### INTRODUCTION

Physical anthropologists often study enamel defects in Recent human teeth to determine the prevalence of physiological stressors including mineral deficiencies, infectious diseases, premature births, and metabolic disruptions (Pindborg, 1982). Teeth exhibiting enamel defects are routinely “scored” against standardized tables allowing quantitative comparisons (Hillson, 1986). “The position of these defects, their width, and their depth can give information respectively on the age of occurrence, the duration, and the severity of the stressors that determined them” (Moggi-Cecchi et al., 1994:299). Studies of enamel defects in fossil (pre-Holocene) teeth are much less common. White (1978), for example, concluded that enamel defects in South African Plio-Pleistocene hominids were probably induced by weaning stress and may correlate with lowered fitness and an increased likelihood of death prior to sexual maturity. Although dental defects are known to occur in many other mammalian taxa, their potential use in paleoecological interpretations, as suggested by Hillson (1986), has not previously been explored by mammalian paleontologists.

The Miocene rhinocerotid *Teleoceras* is a common component of Barstovian, Clarendonian, and Hemphillian (North American Land Mammal Ages, Middle through Late Miocene) faunas of North America. I provisionally assign the Barstovian, Clarendonian, and Hemphillian specimens to *T. medicornutum*, *T. major*, and *T. fossiger*, respectively. As part of a systematic review of *Teleoceras* remains in the University of Nebraska State Museum (UNSM) collection, I observed a number of juvenile dentitions exhibiting pathologic enamel. The pathologic condition, known as enamel hypoplasia, is characterized by malformed enamel resulting from the disruption of amelogenesis (White, 1978). Enamel hypoplasias occur in distinct bands encircling the tooth crown, and two types are generally recognized (Hillson, 1986). M-hypoplasia is characterized by a furrow or groove (Fig. 1A), and G-hypoplasia is characterized by irregular pitting (Figs. 1B, 2B). The number of ameloblasts that experience disruption of matrix secretion appears to determine whether M- or G-hypoplasia occurs (Hillson, 1996). Dentine hypoplasia, distinguished by poorly mineralized dentine (Hillson, 1986), also occurs but can be studied only in thin sections, unlike enamel hypoplasia, which is evident externally.

The purpose of this paper is to: (1) describe the nature and location of enamel hypoplasias on the cheek teeth of the Miocene rhinocerotid *Teleoceras*; and (2) propose stressors that may account for the presence of enamel hypoplasia in *Teleoceras*.

### MATERIALS AND METHODS

More than 550 permanent and deciduous lower cheek teeth (isolated and within jaws) of *Teleoceras* from 33 quarry samples in the UNSM collection were macroscopically examined for the presence of enamel hypoplasia. Teeth were classified as “readable” or “unreadable”, and only “readable” teeth were used to calculate the frequency of enamel hypoplasia. “Unreadable” teeth included those that were: (1) highly fragmented or weathered; (2) covered in cement or dental calculus; (3) worn down to the cervix; or (4) in the case of erupting teeth, concealed in the alveolus to the extent that the lingual cervix was not visible. In cases where antimeric partners occurred (e.g., complete mandibles in the Poison Ivy Quarry), teeth on the more readable side were recorded. Upper teeth were also surveyed initially but, due to the scarcity of upper deciduous cheek teeth in the UNSM collection (only five readable dP4s from 20 localities containing at least one readable dp4 or p4, excluding the Poison Ivy Quarry sample), were not used in this analysis.

For “readable” teeth, the occurrence of enamel hypoplasia, the severity of the defect if present, its height above the cervix, and the stage of tooth eruption and wear were recorded. Defect severity was qualitatively ranked and recorded as: (1) severe (type M-hypoplasia), a distinct furrow (Fig. 1A) present; (2) moderate (type G-hypoplasia), pits (Figs. 1B, 2B) or a shallow swale (Fig. 1C) present; and (3) slight, a textural change present (not figured), usually involving wavy enamel.

Inferred *Teleoceras* ages (Table 1) are based on the guidelines proposed by Goddard (1970:table 4) in his study of extant *Diceros bicornis* from Tsavo National Park, Kenya. I was able to examine one wild-shot male *D. bicornis* skull (ZM 05048) in the UNSM collection and found *Teleoceras* to be similar in skull and tooth morphology. Overall body size in the two taxa is also similar. A large series of skulls (70+) from the UNSM

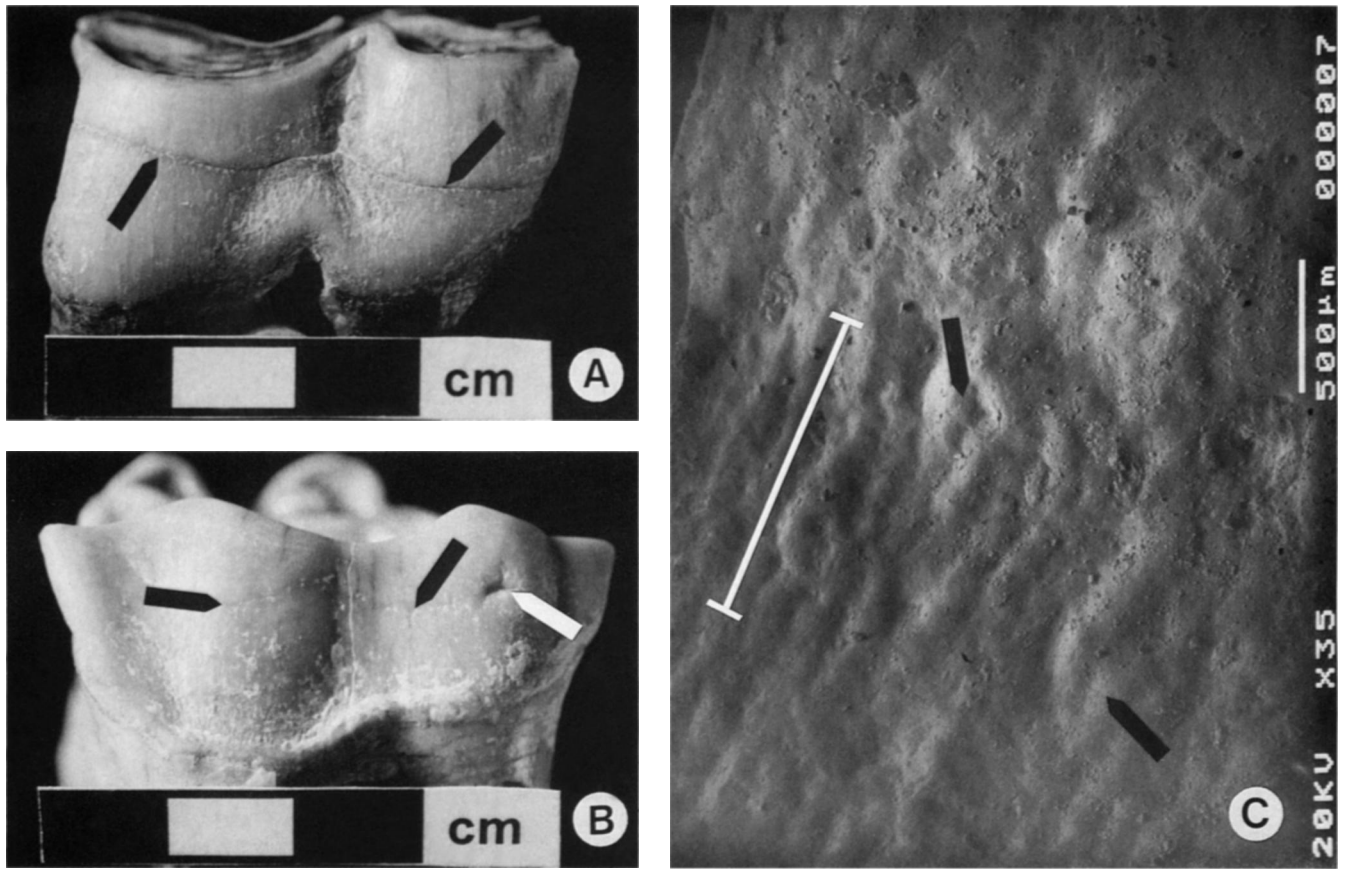


FIGURE 1. Surface expressions of enamel hypoplasia in *Teleoceras*. **A**, M-hypoplasia (arrows) on the buccal surface of a Clarendonian *T. major* dp4 (UNSM 121500) from the North Shore Quarry. **B**, M- (black arrows) and G-hypoplasia (white arrow) on the buccal surface of a Barstovian *T. medicornutum* dp4 (UNSM 84935) from Carrot Top Quarry. **C**, Swale hypoplasia (extent shown with white range bar) exhibiting wavy enamel (black arrows) on the buccal surface of a Barstovian *T. medicornutum* dp4 (UNSM 84965) from Carrot Top Quarry.

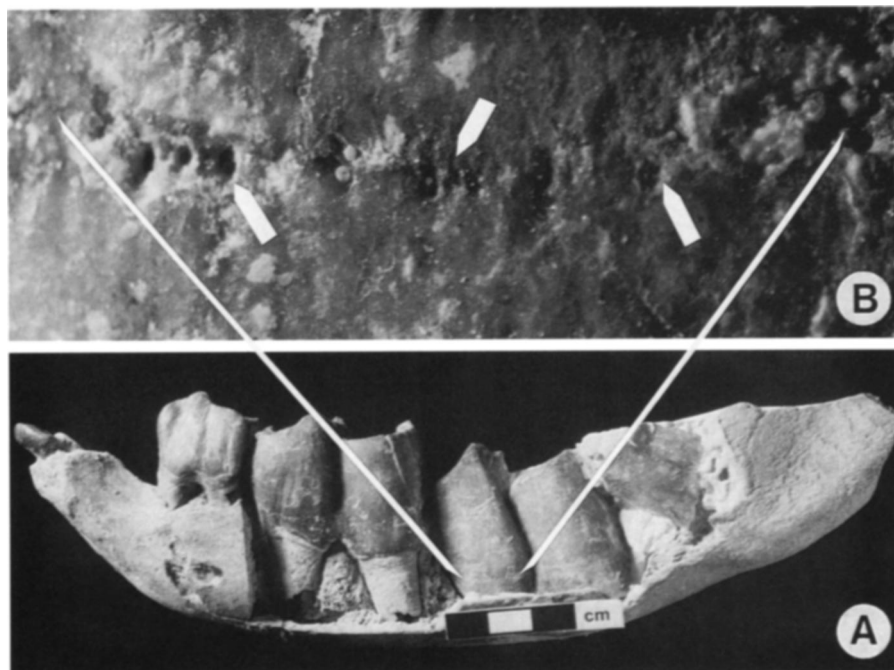


FIGURE 2. **A**, Dissected jaw (UNSM 121501) of a Clarendonian juvenile *T. major* from Creighton Quarry, dp2–3 in wear, dp4 erupting, developing m1 in the crypt. **B**, Enlarged view of the dp4 protolophid exhibiting G-hypoplasia (white arrows).

TABLE 1. Age classes assigned to *Teleoceras* lower cheek teeth. Adapted from Goddard's (1970:table 4) investigation of extant *Diceros bicornis*. \*Includes all adult dentitions showing moderate to advanced wear.

Goddard Class (GC)	Age (years)	Criteria
II	0.5	dp2–dp3 fully erupted, slight wear; dp4 partially erupted.
III	1	dp2 lophids confluent, dp3 in full wear; dp4 fully erupted, no wear.
IV	1.5	dp2 in heavy wear; dp3 lophids nearly confluent; dp4 in full wear; m1 protolophid emergent.
V	2	dp2 in heavy wear; dp3 lophids confluent; dp4 worn, lophids not confluent; m1 partially erupted, no wear.
VI	3	dp2–dp3 heavy wear; dp4 lophids usually confluent; m1 fully erupted, slight wear; m2 protolophid emergent.
VII	4	dp2–dp3 heavy wear; p2–p3 at bone level; dp4 lophids confluent; m1 full wear; m2 partially erupted, no wear.
VIII	5	p2–p3 partially erupted, displacing dp2–dp3; dp4 in heavy wear; m1 in full wear; m2 fully erupted, no wear.
IX	6	p2–p3 in light wear; p4 displacing dp4; m1 lophids confluent; m2 in slight wear; m3 protolophid emergent.
X	7	p2–p4 fully erupted, full wear; m1 in heavy wear; m2 in full wear; m3 fully erupted, no wear.
*X+	7+	permanent dentition fully erupted and progressively more worn.

Poison Ivy Quarry appear to be assignable to discrete age classes (Voorhies, 1985) and the observed dental development in each age class corresponds closely to the classification scheme of Goddard (1970). A comparable timing of dental development for these taxa could not be supported on phylogenetic grounds alone. The most recent phylogenetic analyses of the Rhinocerotidae suggest that *Teleoceras* lies outside the ancestry of extant rhinoceroses (Prothero et al., 1986; Cerdano, 1995). Keeping this caveat in mind, for the purposes of this study, I assume that Goddard Classes (GC) I through X+ for *D. bicornis* have approximately the same chronological values in *Teleoceras*.

Two *Teleoceras* dp4s exhibiting enamel hypoplasia were chosen for radial thin section analysis. The teeth were encased in epoxy and then cut, mounted on glass slides, and polished. The polished radial thin sections were analyzed using plain and polarized light microscopy. Portions of hypoplastic enamel were cut from the remaining stumps and surface textures were examined using a scanning electron microscope (SEM).

## RESULTS

Enamel hypoplasia is present on medial Barstovian to late Hemphillian-aged *Teleoceras* lower cheek teeth from 18 of 21 UNSM localities containing at least one readable dp4 or p4 (Table 2). Enamel defects occur most frequently on dp4s (58/66), followed by p4s (20/54), m1s (4/52), m2s (3/39), and m3s (1/45).

On dp4s, moderate (Fig. 1C) and slight enamel hypoplasias are limited to the buccal tooth surface and often are most pronounced on the hypolophid. In severe cases (Fig. 1A), the defects are evident not only on the buccal surface, but also on the posterior and lingual surfaces of the dp4s. Abnormal (wavy) enamel surface texture (Fig. 1C) may occur cervically from the pronounced hypoplastic defect in both M- and swale hypopla-

TABLE 2. Incidence of enamel hypoplasia on *Teleoceras* lower cheek teeth from UNSM locality samples containing at least one readable dp4 or p4. NALMA=North American Land Mammal Age; P=permanent teeth; D=deciduous teeth; MNI=minimum number of individuals, determined by counting the highest number of duplicated dental elements (e.g., dp4s) in each assigned age class. \*Locality data for Stewart Quarry in Voorhies and Timperley (1997), for Grace Ranch in Tanner (1975), for June Quarry and Pratt Quarry in Skinner and Johnson (1984), and for all other localities in Voorhies (1990).

NALMA, species Locality*	# of teeth examined		# of teeth readable		MNI		Hypoplasia on readable teeth			
	P	D	P	D	P	D	Total	dp4	p4	others
Hemphillian, <i>T. fossiger</i>										
Devil's Nest	8	0	8	0	3	0	0/8	—	0/1	—
Uptegrove	4	3	4	3	2	1	0/7	0/1	0/1	—
Cambridge Q.	26	12	20	12	5	7	5/32	4/5	1/4	—
Borrow Pit	0	2	0	2	0	1	1/2	1/1	—	—
Graffhan-Richey	0	3	0	3	0	2	2/3	2/2	—	—
Clarendonian, <i>T. major</i>										
North Shore	29	40	27	33	7	11	15/60	11/16	3/6	m3, 1/3
Serendipity Q.	4	3	2	3	2	2	1/5	1/1	—	—
Grace Ranch	3	1	3	1	1	1	1/4	1/1	—	—
Pratt Slide	0	1	0	1	0	1	1/1	1/1	—	—
Bluejay Q.	6	2	6	2	3	1	1/8	—	1/2	—
Johndreau Q.	6	1	6	1	2	1	2/7	1/1	1/1	—
<i>Teleoceras</i> Bull Q.	5	3	2	3	1	1	1/5	1/1	—	—
Creighton Q.	5	16	5	16	2	5	7/21	5/5	1/1	m2, 1/1
Chokecherry Q.	14	20	8	17	4	8	3/25	3/3	0/2	—
Schlagel Ck.	13	5	13	5	5	3	5/18	2/3	2/4	m2, 1/1
Poison Ivy Q.	122	65	30	63	22	28	15/93	13/13	1/9	m1, 1/7
June Q.	5	0	5	0	1	0	0/5	—	0/1	—
Barstovian, <i>T. medicornutum</i>										
Hazzard Q.	5	0	5	0	1	0	1/5	—	1/1	—
Stewart Q.	17	4	17	4	4	3	3/21	2/2	1/4	—
Carrot Top Q.	68	17	67	17	9	5	15/84	8/8	4/9	m1, 3/14
Hottell Ranch	26	4	26	4	8	2	7/30	2/2	4/8	m2, 1/6
TOTAL	366	202	254	190	82	83	86/444	58/66	20/54	n/a

TABLE 3. Severity of enamel hypoplasia on readable *Teleoceras* dp4s from UNSM locality samples containing at least five individuals exhibiting deciduous dentition.

Locality	Surface expression of enamel hypoplasia on dp4s			
	Severe	Moderate	Slight	Absent
Cambridge Q.	1/5	3/5	0/5	1/5
North Shore Q.	1/16	4/16	6/16	5/16
Creighton Q.	2/5	1/5	2/5	0/5
Chokecherry Q.	0/3	2/3	1/3	0/3
Poison Ivy Q.	3/13	2/13	8/13	0/13
Carrot Top Q.	6/8	2/8	0/8	0/8

sia. No apparent difference exists in the occurrence of enamel defects on antimeric dp4s in the only sample (Poison Ivy Quarry) in which multiple associated mandibles occur. Variability in dp4 defect-severity is evident within and between localities (Table 3). However, the position of the buccal enamel defect on dp4s is consistent, ranging from 5.3–13.9 mm (mean=9.1 mm) above the cervix on the protolophid and 6.0–15.9 mm (mean=11.6 mm) above the cervix on the hypolophid.

In extant *D. bicornis*, the enamel crown of dp4 is contained within the alveolus at birth. A radiograph (Goddard, 1970:plate 2a) of the mandible of a 5.5 month old calf shows that the dp4 crown is fully formed, suggesting that amelogenesis ceased within a few months following birth. Based on this timing of crown formation in *D. bicornis*, it appears that the position of the enamel defect observed on *Teleoceras* dp4s corresponds approximately to that portion of the crown developing at the time of birth. One of the Creighton *T. major* specimens that died prior to the full eruption of dp4 (approximately 6 months old, GC II) was dissected to expose the dp4 in the alveolus (Fig. 2A). The tooth (Fig. 2B) exhibits pitting (G-hypoplasia) on the buccal enamel surface approximately 9.5 mm above the developmental front, suggesting that the hypoplastic region corresponds to that portion of the tooth actively developing at birth.

Analysis of radial thin-sections of *Teleoceras* dp4s demonstrates that the anomalies observed macroscopically are not merely superficial. The defects appear (Figs. 3A–D) to be associated with an axially (towards the pulp cavity) directed bend in the enamel dentine junction (EDJ) above the enamel hypoplastic lesion. In the dentine, dentinal tubules bend cervically at the defect (Fig. 3D). The enamel hypoplasia may parallel the bend in the EDJ (Fig. 3A) or show a marked difference (Fig. 3C) in the depth of the hypoplastic lesion. Both enamel and dentine hypoplasias may occur on the buccal (Fig. 3A) and lingual (Fig. 3B) sides of the same dp4 in *Teleoceras*.

Approximately one-third of the readable *Teleoceras* p4s show enamel hypoplasia, usually, as in dp4s, on the buccal side near the base of the crown. The defect occurs from 3.7–12.4 mm (mean=6.9 mm) above the cervix on the protolophid, and 4.6–11.5 mm (mean=7.2 mm) above the cervix on the hypolophid. The GC XI male *D. bicornis* skull (UNSM, ZM 05048) mentioned above exhibits p4 enamel G-hypoplasia at approximately 13 mm above the cervix on the protolophid and 16 mm above the cervix on the hypolophid, somewhat higher on the tooth than seen in *Teleoceras*. In *D. bicornis*, p4 begins development during GC V and displaces dp4 by GC IX. A radiograph (Goddard, 1970:plate 2b) of the lower jaw of a 3 year old (GC VI) female *D. bicornis* illustrates that the cervix of the p4 has not yet formed at this age. An additional radiograph (Goddard, 1970:plate 1a) of the mandible of a 5 year old (GC VIII) female indicates that p4 amelogenesis is probably complete. The portion of the p4 crown showing the defect in *Teleoceras* is judged to form between GC VI and GC VIII.

Only a few molars exhibit enamel hypoplasia. The positions are apparently random and represent isolated occurrences of disruption of amelogenesis. In *D. bicornis*, m1 is developing in the alveolus at 5.5 months (Goddard, 1970:plate 2a). The developing m1 protolophid is evident also in the alveolus of the Creighton *T. major* GC II specimen (Fig. 2A). However, no hypoplastic defect was observed on the Creighton m1 protolophid that would suggest that the m1 had begun development prior to the development of the hypoplasia on the dp4. In *D. bicornis*, m2 is fully formed prior to the formation of the lower third of the p4 crown (Goddard, 1970:plate 2b). It appears that the stressor causing the hypoplastic defect on the *Teleoceras* p4 occurs after m2 is fully formed. In *D. bicornis*, the m3 begins forming while the lower third of p4 is developing (Goddard, 1970:plate 2b). The degree of *Teleoceras* m3 formation at the time of p4 hypoplasia development is unresolved, but enamel hypoplasia was not observed near the occlusal surface of the unworn m3s.

## DISCUSSION

A literature review reveals that enamel hypoplasia in Miocene rhinocerotids (or any rhinocerotid) is previously undescribed. Enamel defects have been reported for a variety of mammals and associated with various causative agents. In humans, enamel hypoplasia has been linked to weaning stress (Moggi-Cecchi et al., 1994), very low birth weights (Seow et al., 1989), and varying degrees of malnutrition (reviewed by Hillson, 1996). In North American wild ungulates (*Odocoileus* sp., *Cervus elaphus*, *Bison bison*, *Alces alces*, *Antilocapra americana*) and hares (*Lepus* sp.), fluoride toxicosis is believed to be a primary causative agent (Shupe et al., 1984). Similarly, fluoride ingestion by the European Roe Deer (*Capreolus capreolus*) is suspected to result in enamel hypoplasia (Kierdorf et al., 1993). Additional studies have documented enamel hypoplasia in cattle (*Bos taurus*, Shearer et al., 1978), pigs (*Sus scrofa*, Limeback et al., 1992), and Sprague-Dawley rats (*Rattus* sp., Nordlund and Lindskog, 1985).

The diffuse macroscopic appearance of fluoride-induced hypoplasia (Shupe et al., 1984:figs. 2, 3) seems to reflect long-term exposure to the toxin, and differs greatly from the well-defined (Fig. 1A) hypoplasia observed in *Teleoceras*, which appears to represent a short-term event. It is unlikely that the defect in *Teleoceras* resulted from fluoride toxicosis.

The high frequency (58/66) of enamel hypoplasia at a relatively constant height above the cervix on the buccal surface of dp4s implies a stressor acting at a common ontogenetic stage in *Teleoceras* juveniles. The position of the hypoplasia is not only relatively constant for spatially and temporally disjunct members of one species, but is similar among the three species of *Teleoceras* examined. A common stressor that should remain constant in timing for congenic species is birth. The developmental sequence for *D. bicornis* and the position of the hypoplastic defect on the dp4 in the *T. major* GC II jaw (Fig. 2A, B) from Creighton Quarry indicate that the dp4 hypoplasia-inducing stressor occurred at or very near birth.

The presence of the defect and continued development after its formation on dp4 indicates that the hypoplasia-producing stress did not cause immediate death in these rhinoceroses. Tooth development quickly returned to normal in some cases (Fig. 1A), but may have continued in a sub-optimal state for some time in others. The occurrence of abnormal (wavy) enamel surface texture cervical (towards the root) to the main hypoplastic defect in both M- and swale hypoplasia (Fig. 1C) suggests continued dysfunctional amelogenesis after the formation of the initial defect.

In humans, a visible defect in both the enamel and dentine, the neonatal line, is known to occur in teeth that are in the

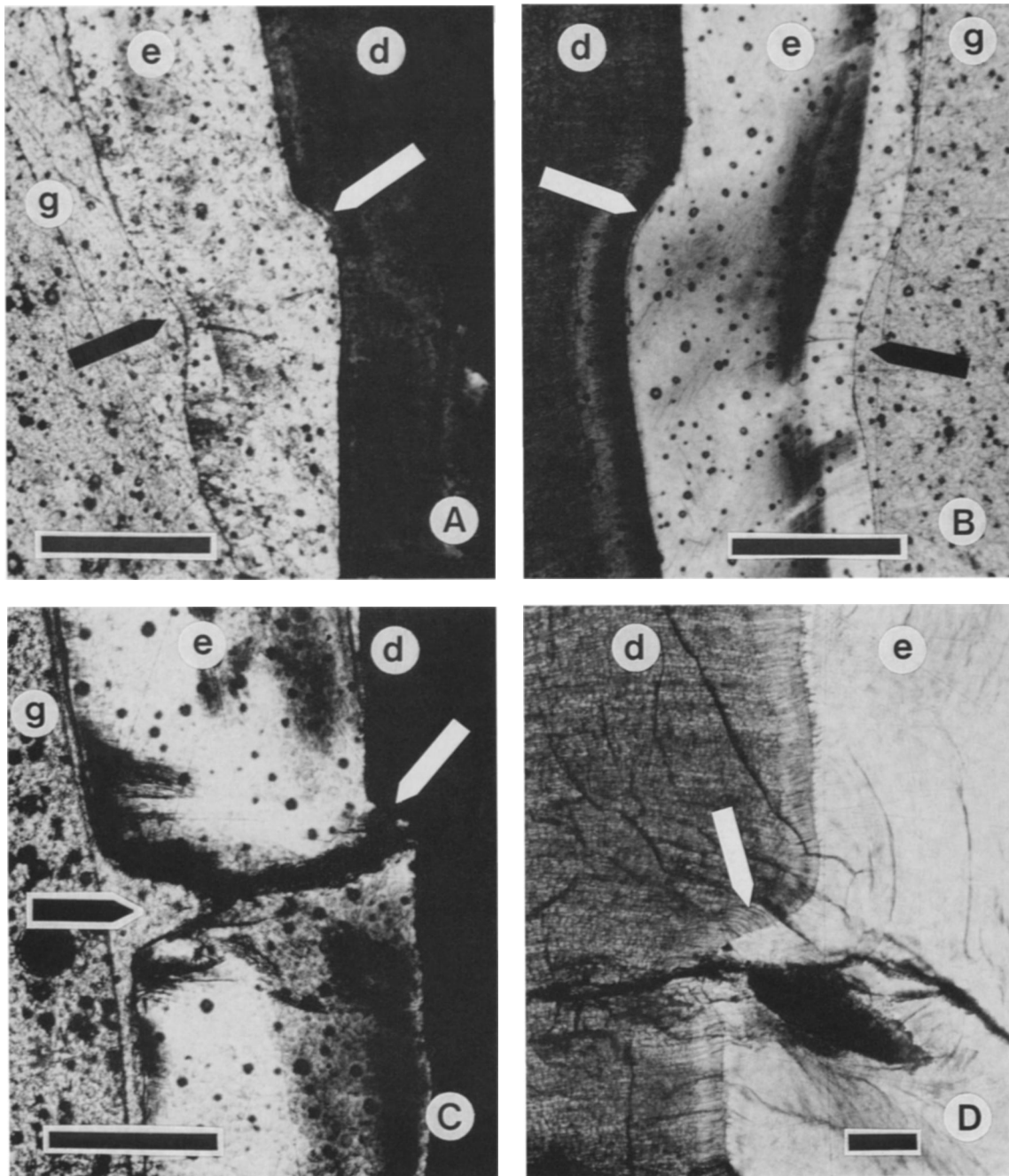


FIGURE 3. Radial thin-section micrographs of two Barstovian *T. medicornutum* dp4s from Carrot Top Quarry. Lingual (A) and buccal (B) sides of a dp4 (UNSM 84965) illustrating dentine hypoplasia (white arrows) and enamel hypoplasia (black arrows). C, A deep hypoplastic lesion (black arrow) on the buccal surface of a dp4 (UNSM 84968). D, Bending of the dentinal tubules (white arrows) at the dentine hypoplastic defect on a dp4 (enlargement, reversed, of area shown by white arrow in C, UNSM 84968). **Abbreviations:** g, groundmass (epoxy); e, enamel; d, dentine. In A, B, and C, scale bar=1 mm. In D, scale bar=100  $\mu$ m.

formative stage at birth. In enamel, the neonatal line is manifested as an enhanced Retzius band and appears to reflect an interruption in prism formation (Hillson, 1996:fig. 6.7). The morphology of the deep hypoplastic lesions (Figs. 1A, 3C) in *Teleoceras* indicates that the observed hypoplasias are not over-developed neonatal lines as they are described in human examples.

The occurrence of enamel hypoplasia on adult teeth suggests stressors unrelated to those that induced the defects on dp4s.

The relatively high frequency (20/54) of enamel hypoplasia on p4s implies an additional stressor occurring at another ontogenetic stage. Based on extant *D. bicornis* and the Poison Ivy Quarry sample of *Teleoceras*, the estimated age at which the p4 crown would be developing is 3 to 5 years, likely closer to 4 years old.

Moggi-Cecchi et al. (1994) suggested that weaning produces the highest metabolic stress in human offspring, often leading to hypoplastic defects. However, the stressor that induced the

enamel hypoplasia on the *Teleoceras* p4s does not appear to be weaning. In extant rhinoceroses, calves experience a protracted period (6 to 12 months) of gradual weaning from the dam's milk (Owen-Smith, 1988) and probably suffer a less stressful nutritional transition than that experienced by human offspring. In extant *Ceratotherium simum*, calves normally suckle up to 18 months and have been recorded suckling at 24 months (Owen-Smith, 1988). The young of extant *Rhinoceros unicornis* rarely suckle longer than 18 months (Laurie et al., 1983). The calves of *D. bicornis* suckle for approximately 19 months (Owen-Smith, 1988). Based on similar adult body sizes, the assignment of a comparable timing for weaning in *Teleoceras* is reasonable and thus it would have occurred prior to 4 years of age.

Without knowledge of *Teleoceras* behavior, I can only speculate as to the p4 hypoplasia-inducing stressor. Cow-calf separation is one possibility. In extant rhinoceroses, the young are driven away prior to the birth of the next calf (Owen-Smith, 1988). In extant *R. unicornis*, the calf is forced to leave the dam approximately 3 years after birth (Laurie et al., 1983). *C. simum* and *D. bicornis* exhibit mean intercalf intervals of 2.5 years (Owen-Smith, 1988). However, approximately 25% of the Madlozi, Umfolozi Game Reserve (South Africa), *C. simum* cows (N=35) tallied by Owen-Smith (1988:fig 8.4) exhibit intercalf intervals between 3 and 4 years. In *C. simum* cows (N=23) from the Kyle Game Park (Zimbabwe), the birth interval is 3.45 years (Owen-Smith, 1988:table 8.6). For *D. bicornis* in Ngorongoro and Olduvai (Tanzania) and Amboseli (Kenya) the mean intercalf interval is approximately 4 years (Owen-Smith, 1988). The position of the p4 G-hypoplasia on the wild-shot *D. bicornis* skull in the UNSM collection suggests a stressor occurring between 3.0 and 3.5 years of age. Hillman-Smith and Groves (1994) suggested that intercalf intervals tend to increase as population density increases in *D. bicornis*. *T. major* likely spent more time in herds than any of the extant rhinoceroses and, unlike the extant African species, appears to have had a seasonally restricted calving period (Voorhies, 1985). It is unknown whether increased local densities and a restricted calving period could have increased the intercalf interval to a relatively constant 4 years in *Teleoceras*.

Other possible stressors for *Teleoceras* include puberty and the ostracism of young males by the herd. The lowest estimated mean ages at puberty for male *R. unicornis*, *C. simum*, and *D. bicornis* are 6.0, 5.5, and 6.0 years, respectively. Onset of female puberty ranges from 4 to 7 years (Owen-Smith, 1988). Puberty would appear to occur too late in life in *Teleoceras* to account for the p4 hypoplasia, but male ostracism remains a possibility.

### CONCLUSION

Two episodes of enamel hypoplasia formation are recorded on the lower cheek teeth of the Miocene rhinoceros *Teleoceras* in collections spanning 14 Ma to 5 Ma. The enamel defect occurs on 87% of the readable *Teleoceras* dp4s in the UNSM collection. The relatively constant position of the defect on the buccal side of dp4s implies a stressor occurring at a common ontogenetic stage in temporally and spatially disjunct groups of rhinoceroses. Using inferred ages based on tooth development in the extant rhinoceros *D. bicornis*, the timing of the dp4 enamel hypoplasia-inducing stressor in *Teleoceras* is determined to be birth. The enamel defect also occurs on 37% of the observable *Teleoceras* p4s examined. The enamel hypoplasia-inducing stressor on this tooth is likely some physiological stress other than weaning, possibly the abandonment of the calf by the dam prior to the birth of a new offspring, and thus may reflect the intercalf interval in *Teleoceras*.

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## CORRECTION

### DEVONIAN PLACODERM SCALES FROM AUSTRALIA

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Scales referred to *Buchanosteus confertituberculatus* specimen NMV P159895 (Burrow and Turner, 1998:678, Figs. 4B, 6A–H) are actually from *Buchanosteus confertituberculatus* specimen NMV P159896. The latter specimen comprises the trunk shield, several head plates, and associated scales, and was collected by K. Orth in 1982. The former specimen, NMV 159895, is a headshield and braincase, and was collected by B. Munro in 1983.