

Tooth crown formation time in three Asian coryphodontids, and its implications for identifying living analogues

MAO Fang-Yuan^{1,2} WANG Yuan-Qing^{1*} MENG Jin^{1,3} JIN Xun¹

(1 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 * Corresponding author: wangyuanqing@ivpp.ac.cn)

(2 University of Chinese Academy of Sciences Beijing 100049 mfangyuan@gmail.com)

(3 American Museum of Natural History New York 10024)

Abstract Molar enamel samples of three Asian coryphodontid species, *Asiocoryphodon conicus* Xu, 1976, *Heterocoryphodon flerowi* (Chow, 1957) and *Eudinoceras mongoliensis* Osborn, 1924, were histologically studied in order to investigate the patterns of formation of their multi-cusped tooth crowns and estimate their tooth crown formation times. The third upper molar crown formation times of *A. conicus*, *H. flerowi* and *E. mongoliensis* were estimated to have been 2.99 ± 0.1 , 3.63 ± 0.11 and 3.68 ± 0.22 years, respectively, suggesting slow growth and a long life span. In combination with the inferred body sizes, the estimated crown formation times indicate that the life history of *H. flerowi* is most comparable to that of *Hippopotamus amphibius* among extant large herbivores, that the life history of *E. mongoliensis* is most properly compared with that of *Ceratotherium simum*, and that the life history of *A. conicus* was slightly shorter and faster-paced than that of *Hippopotamus amphibius*. Appropriate extant analogues for which data on intraspecific variation are available can be potentially helpful in better understanding the classification and phylogeny of coryphodontids, a highly diverse group of Cenozoic early mammals.

Key words Eocene, coryphodontids, incremental lines, tooth crown formation time

1 Introduction

Coryphodontids are a group of large, ungulate-like terrestrial herbivores that lived from the Late Paleocene until the Middle Eocene. The taxon is known from over 400 sites, distributed across all of the northern continents (Lucas, 1984; McGee, 2002). From the first skeleton unearthed in 1807 to the most recently named species (Dawson, 2012), about 59 coryphodontids have been described. Because of confusion in the early history of

中国科学院知识创新工程重要方向项目(编号:KZCX2-EW-106)、国家重点基础研究发展计划项目(编号:2012CB821900)、国家自然科学基金(批准号:40532010)、中国留学基金委留学基金和中国科学院化石发掘与修理特别支持费资助。

收稿日期:2013-04-25

research on this taxon and the considerable variation within the known sample of abundant, widely distributed specimens, coryphodontid classification has presented a challenge to paleontologists. Lucas (1984) discussed the validity of most of the species known at the time, and considered only 15 to be valid. However, his conclusions were questioned by Uhen and Gingerich (1995), mainly because these authors regarded many taxonomic differences among coryphodontids Lucas (1984) purported as the points of intraspecific variation (McGee, 2002). Coryphodontid classification has therefore remained unresolved at the alpha-taxonomic level, hindering research on the phylogeny and evolution of the group.

One practical way to investigate intraspecific variation in coryphodontids is to compare these extinct herbivores with relevant extant analogues. Ontogenetic development of the dentition can facilitate inferences about life history, which in turn can be helpful in identifying appropriate living analogues for extinct species (Smith, 1989, 1992; Smith et al., 1994). On the other hand, dental development represents an aspect of an individual's life history that can be preserved well in the fossil record (Kelley and Smith, 2003). Among the various methods of studying dental development, estimation of the tooth crown formation time (the time needed for the tooth enamel to undergo full development) based on measuring and counting the incremental growth lines of the enamel has been widely applied, because tooth crown formation time is closely related to several aspects of life history such as growth speed and longevity (Smith and Tompkins, 1995; Dean, 1997; Reid et al., 1998; Macho, 2001; Smith et al., 2004; Dirks and Bowman, 2007; Zhao et al., 2008).

We applied this approach by sampling the tooth enamel of the three most common Asian coryphodontid species: *Asiocoryphodon conicus* Xu, 1976, *Heterocoryphodon flerowi* (Chow, 1957) and *Eudiuoceras mongoliensis* Osborn, 1924. We used histological sections of the tooth enamel to estimate the crown formation time of each species. Moreover, estimates of crown formation time, and inferences about life history drawn from these estimates, will help to identify appropriate extant analogues for coryphodontids, based on the intraspecific data from various living species, and in turn to assess intraspecific variation of coryphodontids and clarify some problems regarding their classification.

2 Materials and methods

Dental specimens of *Asiocoryphodon conicus* and *Heterocoryphodon flerowi* were collected from a single quarry within the Lower Eocene Yuhuangding Formation at Dahupo locality in the Liguanqiao Basin, Henan Province, China (Xu, 1976; Lucas and Tong, 1987). The specimen of *Eudiuoceras mongoliensis* used in this study is from the Lower-Middle Eocene Arshanto Formation at the Nuhetingboerhe locality in the Erlian Basin, Nei Mongol (Inner Mongolia), China (Mao and Wang, 2012).

In the molars of coryphodontids, the height of the buccal side of the crown is usually

equal to that of the lingual side, suggesting that buccal and lingual crown formation times were equal and that the former can be interpreted as the time needed to form the crown as a whole. Given this fact and the rarity of fossil materials, we based our study entirely on longitudinal sections through the buccal part of the tooth. The completely longitudinal section along the buccal side of an M2 of *A. conicus* (IVPP V 18696) mesiodistally transected the parastyle, paracone, mesostyle and metastyle. An M3 (IVPP V 18697) of *A. conicus*, preserving the parastyle and paracone, was also sectioned. Because specimens of *H. flerowi* and *E. mongoliensis* suitable for destructive study are rare, these taxa were respectively represented only by IVPP V 18698 and V 18053, specimens that each comprise an M3 fragment with a paracone. All of the sectioned teeth are fully erupted but unworn, and are thus from adult individuals presumably at a similar maturity level. The decision to sample individuals of about the same age was taken to avoid the possibility of introducing ontogenetic discrepancies in crown formation time. The M3 of *H. flerowi* appears to be from a slightly more mature individual than are the other sectioned teeth, but the buccal part of the paracone of the M3 still remains unworn.

Studies of crown formation pattern and time rely on the fact that tooth enamel is formed in an accretional manner and contains microstructural features reflecting rhythmic processes, such as enamel prism cross-striations (circadian features) and Retzius lines (long period features) (Koenigswald and Clemens, 1992). Since the deposition of the lateral enamel is just after the cuspal enamel deposited, the total crown formation time is approximately equivalent to the cuspal enamel formation time (the time needed for the thickness of the cuspal enamel on the occlusal surface to become equal to the distance from a to a' in Fig. 1) plus the lateral enamel formation time (the time needed for all the lateral Retzius lines to form).

The methods used in this study to estimate cuspal and lateral enamel formation times were modified from Smith et al. (2010). Cuspal enamel formation time was estimated by dividing cuspal enamel thickness by cuspal daily secretion rate. Cuspal enamel thickness was measured along a line from the dentine horn tip (Fig. 1: a) to the position of the first lateral Retzius line at the tooth surface (a'). The measured cuspal enamel thickness was multiplied by a correction factor of 1.15 to compensate for the 3D spiral deviation of the cuspal prisms (Smith et al., 2003). The cuspal daily secretion rate was determined by averaging the length of the cross-striations in multiple randomly sampled areas of cuspal enamel (Martin, 1983). The lateral enamel formation time was determined by multiplying the total number of lateral Retzius lines by the Retzius line periodicity. The number of lateral Retzius lines was counted from the first lateral Retzius line (a'b) to the last Retzius line extending down the cervix of the crown (e), which represents the last enamel secreted. The Retzius line periodicity was determined by counting the number of cross-striations between successive Retzius lines.

For a multi-cusped tooth, the total crown formation time is usually longer than the time needed to form any individual cusp because cusps may begin and complete their development

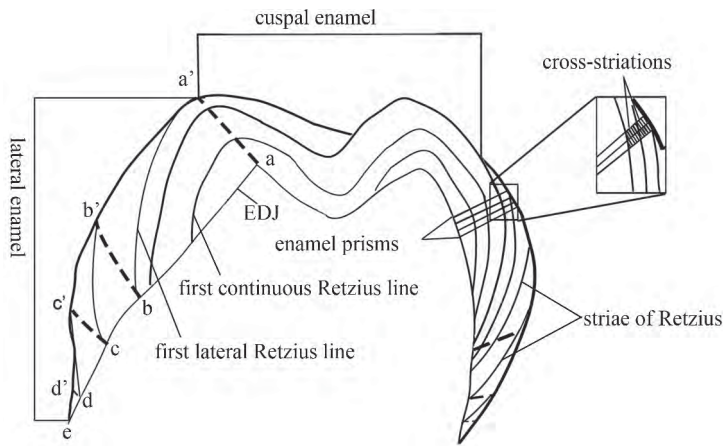


Fig. 1 Pattern of crown formation in a multi-cusped tooth
Modified from Risnes, 1986; EDJ, enamel-dentine junction

asynchronously (Smith et al., 2010). At the point of any two adjacent cusps begin coalescing, one continuous Retzius line will appear in the side of enamel the two cusps shared. After that, the two cusps will continue to grow through the overlaying of enamel on all sides of two cuspal bases. On the side of two cuspal base shared, rest of the Retzius lines become continuous, and all the continuous Retzius lines could be regarded as the isochrones of two cusps. By comparing the time needed to form the part of two cusps before the coalescing began, and the time needed to form the other side of the lateral enamel of two cusps after the part two cusps shared finished, we can deduce the whole time needed to form the two cusps. And so on, the whole crown formation time of multi-cusped tooth can be estimated by designing several sections to compare the crown formation time of all cusps by pairs.

Little relevant research has been carried out into mammalian dental development, except in primates. Since general patterns of tooth growth are similar across most mammals (Sherwood and Parsons, 1977), some results from the primate research should be informative regarding other mammals. In primates the initiation and development of M3 are regarded as highly variable, and this is generally true among mammals (Smith et al., 2010). However, the formation of the crown of a molar is much less variable than that of other parts of the tooth, such as the roots (Liversidge, 2008). Moreover, all molars of one individual, or even of different individuals of the same species, typically have a similar crown formation time on an annual scale (Smith et al., 2010). Variations in molar formation time on this scale should occur between species or even between whole clades, not within species. Therefore, variation in crown formation time among molars of one species should be small enough that the crown formation time of M3 can be used as a proxy for that of the molars in general. In coryphodontids it is usually difficult if not impossible to determine the formation time of M1-2, because these molars are heavily worn in most specimens. Therefore, most of the teeth sectioned in our analyses represent M3, although an M2 from *A. conicus* was also sectioned

to facilitate comparison between the crown formation patterns of M2 and M3 in a single individual.

To make thin sections, tooth samples were ultrasonically cleaned in water and submerged in liquid DPX mounting medium. After being exposed under a light curing instrument (EXAKT 530) for 12 hours, the embedded tooth samples were sectioned longitudinally through the highest cusps. Samples were mounted on glass slides and thin sections approximately 150 μm thick were made using a wire saw (EXAKT E300CP). Following grinding, polishing and acid pretreating (0.1 mol/L phosphoric acid for ~30 seconds) of the samples, cover slips were glued into place using DPX mounting media. The slides were observed using a binocular polarizing light microscope and digital images were captured with a Leica DMRX camera in the Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Incremental growth lines were measured and counted at magnifications ranging from $\times 50$ to $\times 600$.

Adult body size is affected by many factors, but correlates positively to some degree with such life history parameters as maturation time and lifespan (Ernest, 2003). Body size can also be estimated from fossils, using various proxies such as the tooth size and body length. Here we estimated body size using a regression introduced by Legendre (1989) for ungulates: $\text{mass (g)} = \exp [(1.5133 * \ln (L * W) \text{ of } m1) + 3.6515]$, where the length and width of $m1$ are measured in mm.

3 Results

3.1 Crown formation patterns

At $\times 50$ magnification, Retzius lines are very clear and can be traced along their entire courses (Fig. 2). The red line shown in Fig. 2A is a continuous, synchronic Retzius line connecting four cusps of the M2 of *A. conicus* (IVPP V 18696). Under the red line, the enamel of the mesostyle is the thickest in the tooth, and that of the metastyle is the thinnest. Because mean cuspal daily secretion rate should be invariant within a taxon (Smith et al., 2010), the mesostyle was probably the first cusp to emerge, and the initiation of mesostyle formation probably also represented the initiation of the formation of the crown as a whole. When the Retzius line (indicated in red) was formed, the apex of the paracone had already been deposited, but the other cusps continued to grow through the overlaying of additional enamel until their own external surfaces were in place. Above the red line, the thickest enamel is that of the metastyle, which indicates that this cusp was the last to form. When the cuspal enamel of metastyle was fully deposited, the lateral Retzius of metastyle began to secrete. Until the lateral Retzius line of the metastylar cervix was fully deposited, the crown formation was complete. Therefore, the total formation time estimated from the buccal section of M2 should be the sum of the formation time of the mesostyle cuspal enamel below the red line, the formation time of

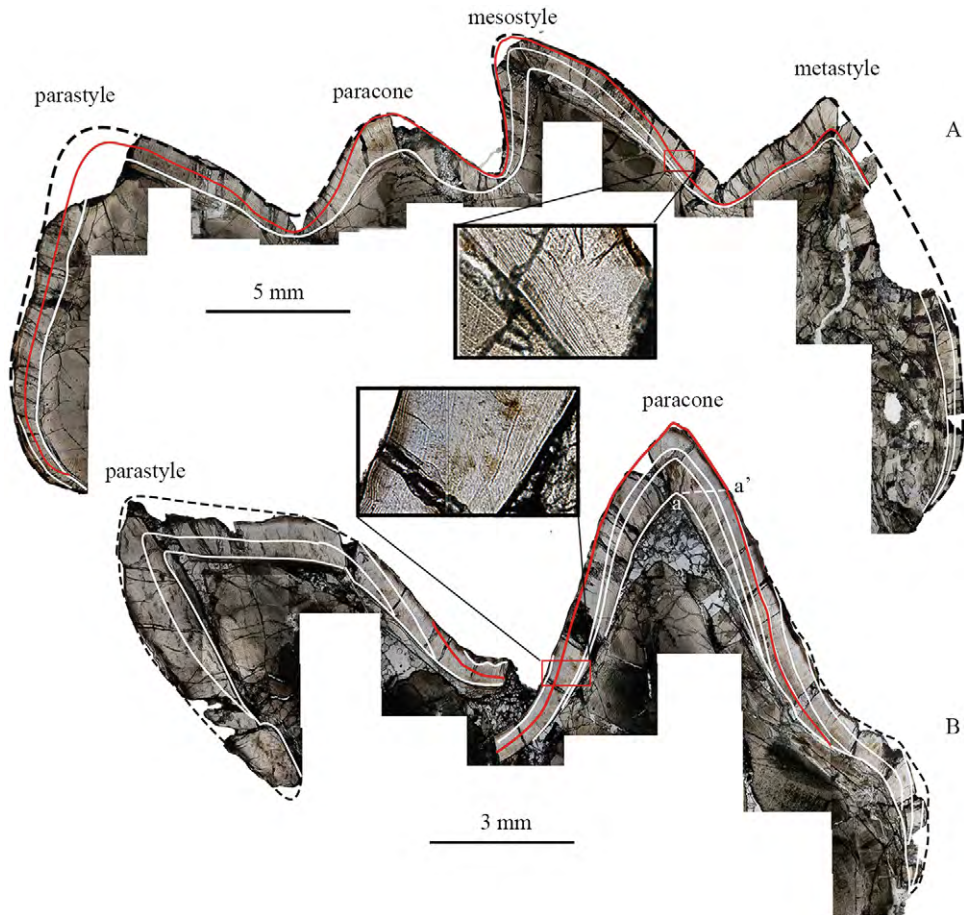


Fig 2 Mosaic images of sections through buccal side of M2 (IVPP V 18696) (A) and M3 (V 18697) of *Asiocoryphodon conicus* (B)

The solid white lines indicate the rough trend of the Retzius lines along with the entire courses; the detail of Retzius lines are showing in the black frame; the dashed black lines represent the reconstructed edge of the outer surface of the enamel, and the red lines are Retzius lines that are continuous across multiple cusps.

Both sections are longitudinal

the metastyle cuspal enamel above the red line, and the formation time of the metastyle lateral enamel.

No Retzius line is continuous across two cusps of the sectioned M3 of *A. conicus* (IVPP V 18697, Fig 2B), although some lateral Retzius lines of the parastyle are continuous with some cuspal Retzius lines of the paracone. The cuspal enamel of the paracone is thicker than that of the parastyle, suggesting that the paracone is the earlier of these structures to develop. At some point during the development of the paracone, the parastyle emerged, and completed the process of cuspal formation sooner than did the paracone. The parastyle continued to deposit lateral Retzius lines until the enamel of the paracone had been deposited up to the

red line, forming the paracone's cuspal outline. Lateral Retzius lines of the paracone continued to deposit for some time. Thus, the total formation time estimated from the buccal section of M3 should be the sum of the formation times of the cuspal and lateral enamel of the paracone.

This case study of buccal longitudinal sections through M2 and M3 of *A. conicus* demonstrates that interpreting Retzius lines that cross multiple cusps as isochronic can provide insights into the pattern of formation of a multi-cusped tooth. Furthermore, the total crown formation time of a tooth can be estimated by studying several sections. Because only limited fossil material was available, complete tooth sections could not be obtained for *H. flerowi* and *E. mongoliensis*. However, the tooth formation time of M3 in *A. conicus* is equal to the formation time of the paracone, and the paracone of a coryphodontid M3 is usually greater in crown height than the parastyle. Thus, we use time needed to form the paracone as proxy for total crown formation time in discussing the life histories of the three coryphodontid species included in our study.

3.2 Crown formation time

Cuspal daily secretion rate and lateral daily secretion rate were measured in the M3 paracone for three coryphodontid specimens representing different species. In each paracone, the rates were measured from some random areas of the outer, middle, and inner parts of the enamel, the outer enamel being close to the surface of the cusp and the inner enamel being close to the enamel-dentine junction (Fig. 1). Cuspal and lateral daily secretion rates vary within a given tooth depending on parts measured. This variation was obtained by using an optical microscope with the level of magnification at $\times 200$, or even higher. Mean cuspal and lateral daily secretion rates were determined by averaging the variations of the daily secretion rates in a single tooth (Table 1). In three coryphodontid species, cuspal and lateral daily secretion rates were positively correlated with tooth size. Other measured tooth parameters, in addition to estimated body masses and crown formation times, are listed for *A. conicus*, *H. flerowi* and *E. mongoliensis* in Table 2.

The results show that cuspal daily secretion rate was averagely slightly smaller in the middle enamel region in the teeth of *H. flerowi* and *E. mongoliensis* (Table 1). Respective mean cuspal daily secretion rates for *A. conicus*, *H. flerowi* and *E. mongoliensis* were 3.20, 3.94 and 4.04 $\mu\text{m}/\text{day}$, and respective mean lateral daily secretion rates for the same taxa were 3.21, 3.66 and 5.65 $\mu\text{m}/\text{day}$. Lateral daily secretion rate was higher than cuspal daily secretion rate in *A. conicus* and *E. mongoliensis*, indicating that in these two species the crown grew faster after cuspal formation was completed. In contrast, mean cuspal daily secretion rate was higher than mean lateral daily secretion rate in *H. flerowi*, indicating that crown growth slowed down following completion of cuspal formation.

Table 1 Estimated daily secretion rates for molar teeth (measurements from M3) of *Asiocoryphodon conicus* (IVPP V 18697), *Heterocoryphodon flerowi* (V 18698) and *Eudinoceras mongoliensis* (V 18053) ($\mu\text{m}/\text{day}$)

Taxon	<i>A. conicus</i>		<i>H. flerowi</i>		<i>E. mongoliensis</i>	
Position	Cuspal	Lateral	Cuspal	Lateral	Cuspal	Lateral
Outside	2.51	3.43	3.33	3.51	3.97	6.42
	3.24	3.71	3.46	4.06	4.95	5.71
	2.89	2.97	4.35	4.46	4.33	5.03
	2.53	2.15	4.12	3.12	4.46	5.50
	3.46	2.88	4.29	3.75	3.96	5.83
Middle	3.64	3.75	4.09	3.33	3.75	5.24
	3.53	2.71	4.13	3.63	3.33	4.82
	3.82	3.02	3.76	3.70	3.63	5.99
	2.69	2.86	3.44	3.51	3.70	5.20
	3.24	2.50	3.89	3.24	3.51	5.36
Inside	3.33	3.33	4.29	4.17	3.24	5.62
	2.19	4.25	3.18	3.75	4.17	6.13
	3.50	3.11	4.55	3.19	5.22	6.25
	4.00	3.64	3.53	4.09	4.25	5.63
	3.43	3.88	3.57	3.41	4.19	6.04
Mean	3.20	3.21	3.94	3.66	4.04	5.65

Table 2 M3 crown formation times estimated from histological sections for *Asiocoryphodon conicus* (IVPP V 18697), *Heterocoryphodon flerowi* (V 18698) and *Eudinoceras mongoliensis* (V 18053)

Taxon	<i>A. conicus</i>	<i>H. flerowi</i>	<i>E. mongoliensis</i>
Cuspal daily secretion rate ($\mu\text{m}/\text{day}$)	3.20	3.94	4.04
Cuspal enamel thickness (μm)	1479	1795	2609
Number of Retzius lines	80 \pm 5	100 \pm 5	80 \pm 5
Retzius line periodicity (days)	7	8	7-8
Cuspal enamel formation time (days)	532	524	743
Body mass (kg)	600	1000	1400
Lateral enamel formation time (days)	560 \pm 35	800 \pm 40	600 \pm 80
Crown formation time (days)	1092 \pm 35	1324 \pm 40	1383 \pm 80
Crown formation time (years)	2.99 \pm 0.1	3.63 \pm 0.11	3.68 \pm 0.22

Cuspal enamel thickness was found to be 1479, 1795 and 2609 μm in *A. conicus*, *H. flerowi* and *E. mongoliensis*, respectively (Table 2). Although the paracone of the sectioned *H. flerowi* specimen is incomplete (Fig. 3B), the first lateral Retzius line is clearly observable in the section and the cuspal enamel thickness can be accurately measured. The cuspal enamel of *E. mongoliensis* is the thickest among the three species, and indeed is nearly twice as thick as the cuspal enamel of *A. conicus*. *A. conicus* and *H. flerowi* are nearly equal to each other in cuspal enamel thickness. In *H. flerowi*, tooth size (crown area) is normally nearly twice as large as in *A. conicus* and is slightly smaller than in *E. mongoliensis*. Although tooth size differs significantly among the three sampled species, this parameter does not appear to correlate with cuspal enamel thickness.

The number of cross-striations between pairs of successive Retzius lines was counted in the lateral enamel areas of the molars of the three coryphodontid species in order to accurately estimate Retzius line periodicity in each case (Fig 3; Table 2). The Retzius line periodicity of *H. flerowi* was found to be eight and that of *E. mongoliensis* was found to be seven to eight. In both M2 and M3 of *A. conicus*, the Retzius line periodicity was seven, a result consistent with the notion that Retzius line periodicity is constant in all teeth of a single individual (Smith et al., 2003). Despite the fact that all three species are assigned to different genera, their Retzius line periodicities were closely similar. This suggests that Retzius line periodicity, in coryphodontids, bears little significance for the classification and phylogeny of the group.

The number of Retzius lines was counted in the high-definition photomontages ($\times 200$ magnification), with some estimation (Table 2). In some areas of the tooth it proved impossible to determine the number of Retzius lines precisely, either because of damage to the enamel or because the lines were simply not clear enough to be countable. In this case, after confirming the orientation of the Retzius lines along with the course of them in the lower magnification ($\times 50$ magnification), the number of Retzius lines could be estimated with the help of the mean distance between successive Retzius lines. The data reveal that the number of Retzius lines was greater, at 100 ± 5 , in *H. flerowi* than in the other two species. The number of Retzius lines was 80 ± 5 in *A. conicus*, and a similar count was obtained in *E. mongoliensis*. These Retzius line counts indicate that the lateral enamel probably took longer to complete its development in *H. flerowi* than in the other species.

Taken together, the data show that cuspal enamel formation time was greater in *E. mongoliensis* than in *H. flerowi* or *A. conicus*, whereas lateral enamel formation time was the greatest in *H. flerowi* (Table 2). However, cuspal enamel formation time was still much longer in *E. mongoliensis* than in *H. flerowi*, so that total molar crown formation time was evidently similar in *H. flerowi* and *E. mongoliensis*, a conclusion consistent with the fact that fully developed molars of these taxa are similar in size.

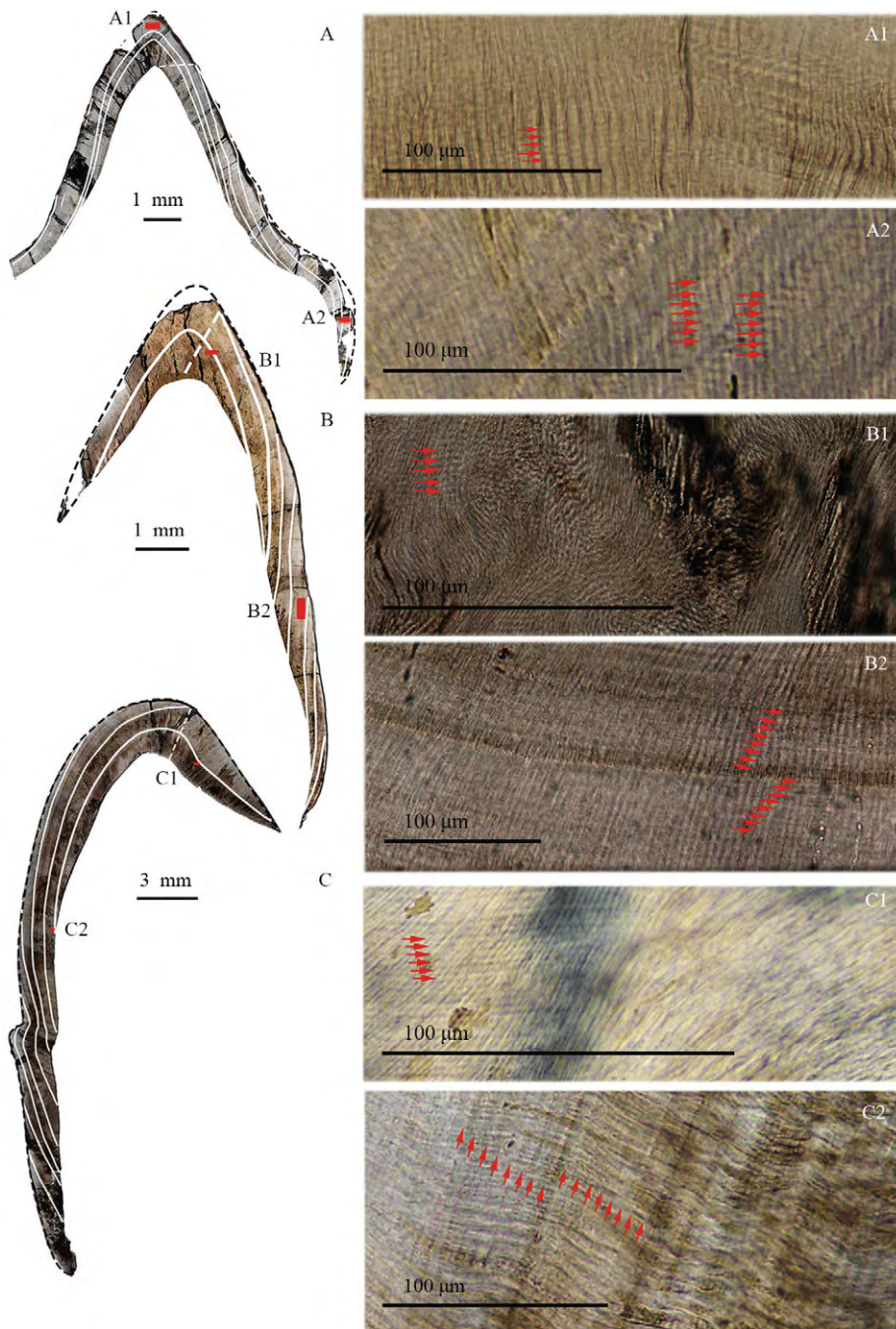


Fig. 3 Histological sections through teeth of *Asiocoryphodon conicus* (IVPP V 18697), *Heterocoryphodon flerowi* (V 18698) and *Eudinoceras mongoliensis* (V 18053), showing features indicative of tooth crown formation times

A, B, and C are longitudinal sections through the paracone of M3 in *A. conicus*, *H. flerowi* and *E. mongoliensis*, respectively, showing the cuspal enamel thickness and the Retzius lines; A1, B1, and C1 show the cross-striations that are used to estimate cuspal daily secretion rates, A2, B2, and C2 show the Retzius line periodicities. The solid white lines are Retzius lines, the white dashed lines indicate the cuspal enamel thicknesses, the black dashed lines are reconstructions of the sectioned enamel surfaces, and the red arrows show cross-striations

4 Discussion

Examining appropriate extant species that display intraspecific variation can be helpful in understanding intraspecific variation within mammalian species from the geological past. Thus, choosing suitable extant analogues and identifying methods that can facilitate this process become critical issues. Previously proposed criteria for choosing extant analogues for extinct species are mainly morphological and/or ecological. But in some cases, neither of them is sufficient enough to be used as possible tool for identifying analogues. For example, Lucas (1984) hypothesized that *Coryphodon molestus* was semiaquatic, and regarded *Hippopotamus amphibius* (the common hippo) as a functional and ecological analogue for *C. molestus* because of apparent similarities in functional morphology and habitat. But he also discussed *Tapirus* sp. (tapirs) and *Dicerorhinus sumatrensis* (the Sumatran rhinoceros) as dental functional analogues, and *Hexaprotodon liberiensis* (the pygmy hippopotamus) as a postcranial functional analogue of *C. molestus*. Clementz et al. (2008) found that $\delta^{18}\text{O}$ stable isotope values were significantly lower for some large species of *Coryphodon* in the Willwood Formation in the Clark Fork Basin, Wyoming than for other taxa within the same fauna. Because low $\delta^{18}\text{O}$ values are characteristic of semiaquatic mammals, the results of the study support the interpretation that coryphodontids were members of this ecological category. Combined with morphological comparisons, the isotope-based evidence for semiaquatic habits in large species of *Coryphodon* points to *Hippopotamus amphibius* as an appropriate analogue for these fossil taxa. However, the $\delta^{18}\text{O}$ values obtained for smaller species of *Coryphodon* were not low enough relative to those obtained for the associated fauna to support an inference of semiaquatic habits. It is therefore inappropriate to use *H. amphibius* as an analogue for small species of *Coryphodon*, and in fact $\delta^{18}\text{O}$ values are not helpful in identifying suitable analogues for these species. It is notable that $\delta^{13}\text{C}$ values in these species with different body masses are similar, suggesting that there is no signal to reflect ecological niche differences between these species. This makes the analogue comparison more complex. Therefore, neither functional morphology nor ecological methods can provide sufficient information to identify an appropriate analogue for coryphodontids.

Dental development in mammals is broadly correlated with many life history parameters, such as the ages associated with weaning, sexual maturity and longevity, and can therefore provide a means of drawing inferences about life history in both extant and fossil species (Smith, 1989, 2000). For extinct species, information about dental development is often available from fossils (Kelley and Smith, 2003), and provides a valuable basis for life history comparisons between extant and extinct species (Macho, 2001). For species without close modern relatives, the life historical resemblances to living species are based on similar

adaptations and ecological niches rather than shared phylogenetic history (Smith, 2000). Therefore, knowledge of dental development in an extinct species can be obtained from the fossil record and used to make inferences regarding the life history of that species. Comparisons with dental development in living mammals can provide the basis for these inferences, provided that the comparisons involve appropriate extant analogues. Two aspects of tooth development are commonly used to draw life history inferences: tooth eruption sequence and tooth crown formation time.

In studying relative eruption sequences in some extant primates, Schultz (1935) found that eruption of deciduous teeth and molars, and replacement of teeth (permanent incisors, canines, and premolars), could be used to predict the tempo of life history in primates. Schultz (1960) reported that, in slow-growing, long-lived species of primates, the eruption of molars is interspersed with the eruption of replacement teeth. In rapidly growing species, by contrast, the molars typically erupt first and are followed sequentially by the permanent incisors, canines, and finally premolars. An interspersed pattern of tooth eruption appears to represent a strategy for prolonging postnatal growth, because long life places an extra load on deciduous teeth and that species adapt by replacing them relatively early. Smith (2000) examined eruption sequences in a wider variety of mammalian taxa, including insectivorans, archontans, and ungulates, and documented the same overall pattern in a broad range of mammals. In general, tooth replacement begins relatively early in slow growing, long-lived species. Because the eruption of the molars was interspersed with that of the replacement teeth of *Coryphodon molestus* (Lucas, 1984; Lucas and Schoch, 1990), this taxon was clearly characterized by gradual and prolonged postnatal growth, and Smith (2000) concluded that *C. molestus* conformed to a slow-growing, long-lived life pattern. She also used the relative eruption times of i1 and p3 as a proxy, which show that *C. molestus* is most similar to extant mammals in which M1 emerges between the ages of 0.34 and 0.8 years and the total lifespan is about 21-35 years. This result shows that the tempo of life history was considerably faster in *C. molestus* than in hippos, in which M1 erupts at an age of around two years and the life span is about sixty years. In fact, the life history of *C. molestus* is more comparable to that of a large deer or pig.

As more assemblages of *Coryphodon* were recovered, McGee and Turnbull (2010) reexamined previously described assemblages and reassessed the dental eruption sequence in *Coryphodon*. These authors argued that the relative timing of the eruption of i1 and p3 could not be confirmed in known specimens of *Coryphodon*, and accordingly rejected the i1-p3 eruption sequence as a basis for life history inferences in *Coryphodon*. Instead, they proposed to use the timing of the eruption of p3 relative to that of the molars as a proxy, and found that *Coryphodon* shared an eruption pattern as m1m2p3m3 seen today in *Equus burchelli*, *Tayassu tajacu*, *Sus scrofa*, *Hippopotamus amphibius*, *Ceratotherium simum*, and *Procapra capensis*. The first molar formation time, adult body mass and maximum life span in each of these species are as follows: *E. burchelli*, 0.88 yr, 257 kg and 40 yr; *T. tajacu*, 0.40 yr, 19.2 kg

and 24.7 yr; *S. scrofa*, 0.47 yr, 100.9 kg and 21 yr; *H. amphibius*, ~2 yr, 1258 kg and 61 yr; *C. simum*, 2.75 yr, 2233 kg and 50 yr; and *P. capensis*, 0.54 yr, 3.6 kg and 11 yr (Ernest, 2003). These data show that the maximum life span of each of these species exceeds 10 years, consistent a life pattern characterized by slow growth and considerable longevity. Therefore, it can be concluded that coryphodontids also had a relatively long lifespan. To achieve greater specificity, it is reasonable to assume that the maximum life span of each species of coryphodontids would be most similar to that of herbivores of similar body mass and mode of life. Because body size and longevity correlate only imperfectly with tooth eruption sequence, it will also be useful to look at other factors such as crown formation in order to more confidently designate a particular extant species as the appropriate life history analogue for coryphodontids.

Among the various aspects of dental development, the timing of molar crown formation is more stable than the dental eruption sequence. The latter may be affected by factors such as root growth, which is itself subject to the influence of sex hormones and is therefore highly variable (Kelley and Smith, 2003). As noted previously, M1 is often so heavily worn in adult coryphodontid specimens that it is difficult to obtain growth-related information from this tooth. For this reason, M3 was chosen as the focus of the present study. A drawback, however, is that data on the formation time of M3 in extant large herbivores are sparse. Given that reported crown formation times for all of the molars in a given mammalian species are typically similar and that the crown formation time of M1 is usually only slightly shorter than that of M3 (Smith et al., 2010; Dirks et al., 2009; Tafforeau et al., 2007), it is likely that M1 formation times in *A. conicus*, *H. flerowi* and *E. mongoliensis* correspond well to M3 formation times in the same taxa. In other words, actual M1 formation times should be slightly shorter than 2.99, 3.63 and 3.68 years (Table 2), respectively, in the three coryphodontid species. However, these annual-scale differences should have little effect on life history inferences. Our data on M3 formation time should also approximate M1 formation time, and suggest that *A. conicus*, *H. flerowi* and *E. mongoliensis* were similar to *Hippopotamus amphibius* (~2 yr) and *Ceratotherium simum* (2.75 yr) in the timing of molar eruption (Smith, 2000).

Life history comprises many events and processes, only a few of which are aspects of dental development such as eruption sequence and crown formation time (Smith and Tompkins, 1995). Although dental development gives insight into other aspects of life history (Macho, 2001), a rigorous interpretation of life history requires data on other relevant factors such as body size, environmental settings and social complexity (Smith, 2000).

Adult body size is roughly positively correlated with maturation time and lifespan (Ernest, 2003). According to the body size regression of ungulates introduced by Legendre (1989), the body masses of *A. conicus*, *H. flerowi* and *E. mongoliensis* are inferred to have been about 600, 1000, and 1400 kg, respectively. Thus, based on the combined evidence from tooth crown

formation time and body size, the life history of *H. flerowi* was probably most comparable with that of *Hippopotamus amphibius*; the life history of *E. mongoliensis* was probably most comparable with that of *Ceratotherium simum*; and the life history of *A. conicus* probably unfolded somewhat more slowly than that of *Hippopotamus amphibius*.

Having identified a particular extant species as the most appropriate analogue for each coryphodontid considered in the study, we might now be in a position to clarify the classification of coryphodontids by using data on intraspecific variation in the extant species in question. A size-independent variance metric that is widely used for evaluating intraspecific variation is the coefficient of variation, a statistic for assessing the consequences of group-based demographic differences. Simpson et al. (1960) stated that, for linear dimensions, the coefficient of variation for a monospecific sample should fall within the range 4 to 10. For a fossil assemblage that may contain two closely related sympatric species, with reference to an extant analogue, the span of coefficient of variation for body size existing within a single species can be used to test whether or not multiple species are in fact present.

The high diversity of coryphodontids during the Eocene has often posed a problem for attempt to evaluate phylogenetic interrelationships within this clade. Fossil assemblages that contain coryphodontids occur at various places. Of these known coryphodontid assemblages, some are known to contain two sympatric species, e.g. the Early Eocene Dahupo Locality in the Liguangqiao Basin, Henan Province, China (Xu, 1976; Lucas, 1984; Lucas and Tong, 1987). At some other sites, such as the Deardorff Hill *Coryphodon* Quarry in the Piceance Creek Basin of Colorado, USA, the number of species present is a matter of controversy (Lucas, 1984; McGee and Turnbull, 2010). At this point, discriminating between intraspecific and interspecific variation becomes an important issue in trying to determine whether multiple species are present at a given locality. Because of varying opinions on the amount of intraspecific variation that is present within the samples from the Deardorff Hill *Coryphodon* Quarry, the number of species present remains uncertain. Lucas (1984) divided the specimens from the quarry between two *Coryphodon* species, *C. lobatus* and *C. anthracoides*, because the coefficient of variation based on molar sizes obtained from the sample (4-11) exceeded the range (4-10) that would be expected for a single species. In contrast, McGee and Turnbull (2010) assigned all the specimens from the Deardorff Hill Quarry to a single species, *C. lobatus*, and regarded their high coefficient of variation as an indication of sexual dimorphism.

Coryphodon lobatus and *Heterocoryphodon flerowi* resemble each other in tooth morphology, crown height and crown area, indicating that they are closely related and had similar body masses and life histories. Therefore, *C. lobatus* probably resembled *H. flerowi* in being comparable to *Hippopotamus amphibius* in life history. Under this assumption, the coefficient of variation present in *Hippopotamus amphibius* may shed light on how to determine the boundary for the coefficient of variation of *C. lobatus*.

In general, age range would be wide in the populations characterized by high

longevity, such as the wild hippos. Another characteristic of hippos populations which is worth mentioning here is that male hippos appear to continue growing throughout their lives in the wild (Marshall and Sayer, 1976), implying that within a population the size range of individuals with different age is wide and that variation among individuals and between males and females may be large. Even under such conditions, coefficients of variation for linear dental measurements of individual molars of *H. amphibius* range only from 4 to 9 (Hooijer, 1950; Lucas, 1984). Although the coefficient may exceed this range for some teeth, even within a species, first molars usually have smaller tooth size coefficients of variation than other molars in both living and fossil species (Gingerich, 1974).

Thus, the high coefficient of variation (11) calculated from the first lower molars of the Deardorff Hill *Coryphodon* Quarry specimens appears to be too large for the sample to contain only one species. Qualitative variations in form, such as the presence in some specimens of a postero-lingual cingulum and a very small metastyle on M3 (Lucas, 1984), cannot conclusively indicate whether the sample represents one species or two. However, the coefficient of variation, interpreted in the light of comparisons with an extant analogue, strongly favors division of the available specimens into two species.

5 Conclusions

This study examined only four coryphodontid molars, and was therefore limited to providing preliminary data on how the molar cusps developed, how long the crown took to form, and which living mammal is the most suitable analogue for each extinct species considered. However, the study demonstrates that estimates of crown formation time based on molar sectioning can be used to draw inferences about the life histories of both extant and extinct species. However, the relationship between dental development and life history is complex. Inferences about life histories of extinct species should not be made until sufficient data about crown formation time and other aspects of life histories from living animals for comparison are available, and the result should be synthesized with factors that can affect life histories as basis. Such studies can highlight the classification of early mammals and help to solve some problems associated with their diversification.

Acknowledgments We thank Bai Bin, Li Qian, Li Ping, Xing Hai, Daniel L. Gebo, K. Christopher Beard, Zhou Wei, Li Shijie, Li Qi, Guo Zhenguang and Wang Yongxing for assistance in the field; Zhao Lingxia, Hu Rong and Zhang Lizhao for discussion; and Zhang Wending, Zhang Shukang and Beth Goldoff for assistance in the lab; and Corwin Sullivan for English improvement and suggestions.

亚洲三种冠齿兽类的齿冠形成时间及其对选取现生类似种的参考意义

毛方园^{1,2} 王元青^{1*} 孟津^{1,3} 金迅¹

(1 中国科学院古脊椎动物与古人类研究所, 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044
* 通讯作者)

(2 中国科学院大学 北京 100049)

(3 美国自然历史博物馆 纽约 10024)

摘要: 选取了亚洲常见的三种冠齿兽类 *Asiocoryphodon conicus* Xu, 1976, *Heterocoryphodon flerowi* (Chow, 1957) 和 *Eudinoceras mongoliensis* Osborn, 1924, 对其臼齿材料进行组织学切片研究, 以讨论多尖牙齿齿冠形成模式和估算它们的齿冠形成时间。结果显示, *A. conicus*, *H. flerowi* 和 *E. mongoliensis* 上第三臼齿齿冠的形成时间分别为 2.99 ± 0.1 , 3.63 ± 0.11 和 3.68 ± 0.22 yr, 三种冠齿兽类的生活史均符合慢生长、长生命型模式。综合考虑体型的影响, 相较其他大型植食性动物, *H. flerowi* 的生活史更适合与现生河马 (*Hippopotamus amphibius*) 进行类比, *E. mongoliensis* 的生活史更适合与白犀 (*Ceratotherium simum*) 进行类比, 而 *A. conicus* 的生活史则稍快稍短于现生河马。这些现生类似种的种内变化数据可为冠齿兽类的部分分类学问题提供参考。

关键词: 始新世, 冠齿兽类, 增长线, 齿冠形成时间

中图法分类号: Q915.873 文献标识码: A 文章编号: 1000-3118(2014)02-0152-18

References

- Chow M C, 1957. A new *Coryphodon* from Sintai, Shantung. *Vert Palasiat*, 1(4): 301–304
- Clementz M T, Holroyd P A, Koch P L, 2008. Identifying aquatic habits of herbivorous mammals through stable isotope analysis. *Palaios*, 23(9): 574–585
- Dawson M R, 2012. *Coryphodon*, the northernmost Holarctic Paleogene pantodont (Mammalia), and its global wanderings. *Swiss J Palaeont*, 131: 11–22
- Dean M C, 1997. A comparative study of cross striation spacings in cuspal enamel and of four methods of estimating the time taken to grow molar cuspal enamel in *Pan*, *Pongo* and *Homo*. *J Hum Evol*, 35(4-5): 307–329
- Dirks W, Anemone R L, Holroyd P A et al., 2009. Phylogeny, life history and the timing of molar crown formation in two archaic ungulates, *Meniscotherium* and *Phenacodus* (Mammalia, 'Condylarthra'). In: Koppe T, Meyer G, Alt K W eds. *Comparative Dental Morphology. Frontiers of Oral Biology*. Basel: Karger Press. 3–8
- Dirks W, Bowman J E, 2007. Life history theory and dental development in four species of catarrhine primates. *J Hum Evol*, 53(3): 309–320
- Ernest S K M, 2003. Life history characteristics of placental nonvolant mammals. *Ecology*, 84(12): 3402
- Gingerich P D, 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *J Paleont*, 48(5): 895–903

- Hooijer D A, 1950. The fossil Hippopotamidae of Asia, with notes on the recent species. *Zool Verhand*, 8(1): 1–124
- Kelley J, Smith T M, 2003. Age at first molar emergence in early Miocene *Afropithecus turkanensis* and life-history evolution in the Hominoidea. *J Hum Evol*, 44: 307–329
- Koenigswald W von, Clemens W, 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. *Scan Microsc*, 6(1): 195–217
- Legendre S, 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. *Münchner Geowiss Abh*, 16(A): 1–110
- Liversidge H, 2008. Timing of human mandibular third molar formation. *Ann Hum Biol*, 35(3): 294–321
- Lucas S G, 1984. Systematics, biostratigraphy and evolution of early Cenozoic *Coryphodon* (Mammalia, Pantodonta). PhD dissertation. New Haven: Yale University Press. 1–649
- Lucas S G, Schoch R M, 1990. Ontogenetic studies of early Cenozoic *Coryphodon* (Mammalia, Pantodonta). *J Paleont*, 64(5): 831–841
- Lucas S G, Tong Y S, 1987. A new coryphodontid (Mammalia, Pantodonta) from the Eocene of China. *J Vert Paleont*, 7: 362–372
- Macho G A, 2001. Primate molar crown formation times and life history evolution revisited. *Am J Primat*, 55(4): 449–462
- Mao F Y, Wang Y Q, 2012. Coryphodontids (Mammalia: Pantodonta) from the Erlian Basin of Nei Mongol, China, and their biostratigraphic implications. *Vert PalAsiat*, 50(3): 258–280
- Marshall P J, Sayer J A, 1976. Population ecology and response to cropping of a *Hippopotamus* population in eastern Zambia. *J Appl Ecol*, 13(2): 391–403
- Martin L B, 1983. The relationships of the later Miocene Hominoidea. PhD dissertation. London: University of London Press. 1–440
- McGee E M, 2002. Intraspecific dental variability in cf. *Coryphodon anthracoides* (Mammalia: Pantodonta) from Roehler's *Coryphodon* Catastrophe Quarry, Washakie Basin, Wyoming. *Rocky Mt Geol*, 37(1): 61–73
- McGee E M, Turnbull W D, 2010. A paleopopulation of *Coryphodon lobatus* (Mammalia: Pantodonta) from Deardorff Hill *Coryphodon* Quarry, Piceance Creek Basin, Colorado. *Fieldiana Geol*, 52: 1–12
- Osborn H F, 1924. *Eudinoceras*, upper Eocene amblypod of Mongolia. *Am Mus Novit*, 145: 1–5
- Reid D J, Beynon D A, Ramirez Rozzi F V, 1998. Histological reconstruction of dental development in four individuals in a medieval site in Picardie, France. *J Hum Evol*, 35: 463–477
- Risnes S, 1986. A study of certain growth-related structural features of mature rat and human dental enamel. PhD dissertation. Oslo: University of Oslo Press. 1–39
- Schultz A H, 1935. Eruption and decay of the permanent teeth in primates. *Am J Phys Anthropol*, 19(4): 489–581
- Schultz A H, 1960. Age changes in primates and their modification in man. In: Tanner J M ed. *Human Growth*. Oxford, UK: Pergamon Press. 1–20
- Sherwood R A, Parsons T S, 1977. *The Vertebrate Body*. Philadelphia: Holt-Saunders International Press. 300–310
- Simpson G G, Roe A, Lewontin R C, 1960. *Quantitative Zoology*, revised ed. New York: Harcourt, Brace and World Press. 1–440
- Smith B H, 1989. Dental development as a measure of life history in primates. *Evolution*, 43(3): 683–688
- Smith B H, 1992. Life history and the evolution of human maturation. *Evol Anthropol: Issues, News, Rev*, 1(4): 134–142
- Smith B H, 2000. 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates.

- In: Teaford M F, Smith M M, Ferguson M W J eds. Development, Function and Evolution of Teeth. New York: Cambridge University Press. 212–227
- Smith B H, Crummett T L, Brandt K L, 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *Am J Phys Anthropol*, 37(S19): 177–231
- Smith B H, Tompkins R L, 1995. Toward a life history of the Hominidae. *Annu Rev Anthropol*, 24: 257–279
- Smith T M, Martin L B, Leakey M G, 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *J Hum Evol*, 44: 283–306
- Smith T M, Martin L B, Reid D J et al., 2004. An examination of dental development in *Graecopithecus freybergi* (= *Ouranopithecus macedoniensis*). *J Hum Evol*, 46: 551–577
- Smith T M, Tafforeau P, Reid D J et al., 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proc Natl Acad Sci USA*, 107: 20923–20928
- Tafforeau P, Bentaleb I, Jean-Jacques J et al., 2007. Nature of laminations and mineralization in rhinoceros enamel using histology and X ray synchrotron microtomography potential implications for palaeoenvironmental isotopic studies. *Palaeogeogr, Palaeoclimatol, Palaeoecol*, 246(2-4): 206–227
- Uhen M D, Gingerich P D, 1995. Evolution of *Coryphodon* (Mammalia, Pantodonta) in the late Paleocene and early Eocene of northwestern Wyoming. *Contrib Mus Paleont Univ Mich*, 29(10): 259–289
- Xu Y X, 1976. Some new forms of the Coryphodontidae from the Eocene of Xichuan, Henan. *Vert PalAsiat*, 14(3): 185–193
- Zhao L X, Lu Q W, Zhang W D, 2008. Age at first molar emergence in *Lufengpithecus lufengensis* and its implications for life-history evolution. *J Hum Evol*, 44: 307–329