

Research



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Evolutionary biology

Dental development in *Homo naledi*

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Humans' prolonged somatic development and life history are unique among primates, yet their evolutionary origins remain unclear. Dental development has been used as a proxy to reconstruct life history evolution in the hominin clade and indicates a recent emergence of the human developmental pattern. Here, we analyse tooth formation and eruption in two developing dentitions of *Homo naledi*, a late-surviving, morphologically mosaic hominin species. Deciduous dental development is more similar to humans than to chimpanzees, probably reflecting hominin symplesiomorphy rather than bearing life history significance. The later stages of permanent tooth development present a mix of human- and chimpanzee-like patterns. Surprisingly, the M_2 of *H. naledi* emerges late in the eruption sequence, a pattern previously unknown in fossil hominins and common in modern humans. This pattern has been argued to reflect a slow life history and is unexpected in a small-brained hominin. The geological age of *H. naledi* (approx. 300 kya), coupled with its small brain size and the dental development data presented here, raise questions about the relationship between dental development and other variables associated with life history.

1. Introduction

Patterns and sequences of dental development are intimately connected to species' life history. Schultz noted that primates differ from many other mammals in having relatively accelerated replacement of the deciduous teeth and delayed addition of the permanent molars [1,2]. As humans are the most extreme example of this pattern, with the permanent molars M_{2-3} usually emerging last of all, he linked humans' tooth emergence sequence with our prolonged period of growth. In the contexts of hominin evolution, dental development has been a key source of inference about life history of extinct species. Members of *Australopithecus* and early *Homo* generally display faster permanent tooth crown formation and earlier ages of tooth emergence than is observed in recent humans [3–6], and their greater conformity to chimpanzee patterns of dental development suggests that slow life history appeared relatively late in human evolution.

The recently discovered species *H. naledi* displays many primitive features (e.g. australopith-sized brain [7]) at an unexpectedly recent date (236–335 kya [8]). This presents a unique opportunity to evaluate life history patterns in a primitive hominin that temporally overlapped with much larger-brained *Homo* species, and to elucidate our understanding of life history evolution in the human lineage. Two immature mandibles with securely associated dentitions allow reconstruction of dental development in *H. naledi* (figure 1; electronic supplementary material, text S1), which we compare to dental ontogeny in chimpanzees (*Pan troglodytes*) and hominins.

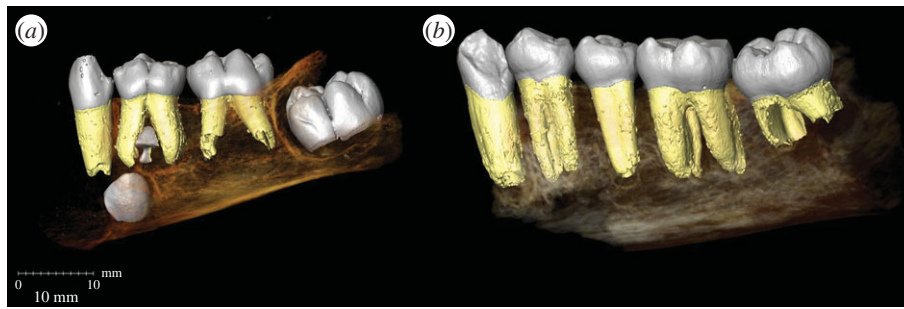


Figure 1. Tooth emergence and formation in U.W. 101-1400 (a) and U.W. 101-377 (b). (Online version in colour.)

2. Material and methods

Tooth emergence was observed on original specimens. Tooth formation was assessed from microCT scans, produced at the University of Witwatersrand microCT facility on a Nikon Metrology XTH 225/320 LC dual-source scanner. Scans were conducted with 95 kV energy and 95 μ A current, with an isometric voxel size of 30.8 μ m. CT images were processed in Avizo 6.3 (VSG, Burlington MA, USA). Developing crown heights and root lengths were measured from CT images with IMAGEJ (<http://rsb.info.nih.gov/ij/>), and from three-dimensional surface renderings in Geomagic Studio (www.geomagic.com). Stages of crown and root formation were scored according to published standards for comparison with other studies [9–13] (electronic supplementary material, text S2 and table S3). To determine whether the overall pattern of tooth formation is more similar to humans or chimpanzees, we used these standards to obtain age estimates of individual teeth for each specimen (figure 2). The purpose is not to estimate the specimens' chronological ages, but to see whether all of an individual's teeth provide the same signal (e.g. if *H. naledi* followed a human-like pattern then each tooth should produce similar age estimates by human standards, but different estimates by chimpanzee standards).

3. Results

(a) U.W. 101-1400

Tooth wear indicates a deciduous emergence sequence of $[di_1-di_2]-dp_3-dc-dp_4$ (brackets mean the sequence is unknown or variable). This sequence is usually seen in humans and other primates [1], whereas dc is usually last to emerge in chimpanzees [14,15]. The state of deciduous and permanent tooth formation (electronic supplementary material, figure S1 and table S1) corresponds to an age of around 2 years based on either chimpanzee or human standards, although there is greater similarity with humans (figure 2). In contrast to U.W. 101-1400 and humans, chimpanzees at a comparable stage of M_1 formation have some of the P_4 crown formed and less developed canines [12,16,17].

(b) U.W. 101-377

Premolars and M_1 are in occlusion, while C and M_2 have attained only gingival emergence. Greater apical wear on the canine indicates an emergence sequence of $[M_1-I_1-I_2]-[P_3-P_4]-[C-M_2]-M_3$ (electronic supplementary material, figure S2). The premolar– M_2 sequence matches the most common pattern among humans, which is much less common in chimpanzees and unknown in Early–Middle Pleistocene hominins [18]. By contrast, relatively late canine

emergence is most common among chimpanzees and Plio-Pleistocene hominins, but rarer in humans.

U.W. 101-377 tooth formation cannot be pigeonholed into 'human' or 'chimpanzee' categories. Compared with humans, C is underdeveloped relative to P_{3-4} and M_2 (figure 2; electronic supplementary material, figure S3 and table S2). Compared with chimpanzees, all teeth are underdeveloped relative to M_1 , while C and P_3 are advanced over P_4 and M_2 . M_2 development at gingival emergence, with about half the root formed, is similar to apes [19], whereas human M_2 s usually attain gingival emergence with around 75% root length [20]. Thus, U.W. 101-377 juxtaposes human-like M_2 emergence sequence with chimpanzee-like root development.

4. Discussion

These mandibles capture two snapshots in the dynamic processes of dental development in *H. naledi*. Although many other immature dental specimens are known for this species, U.W. 101-1400 and -377 provide the only secure associations of multiple teeth. Future discoveries in Rising Star Cave will demonstrate whether these are representative of the species. As with the rest of the species' skeleton, tooth formation and emergence show a mix of primitive and derived features. Many features are probably plesiomorphies at various levels. For instance, because dc emergence usually precedes dp_4 among anthropoids [1] including early hominins [20], this may be the ancestral condition for all apes and monkeys. The relatively underdeveloped M_2 roots at emergence are also seen in apes and fossil hominins [21], implying a hominine symplesiomorphy. Underdeveloped C crowns compared to chimpanzees at the same state of M_1 formation as U.W. 101-1400 may reflect hominins' reduced canine size [6].

The similarity in development of U.W. 101-1400 to humans may be a function of its young age. This infant shows comparable states of permanent tooth formation to *A. robustus* infants SK 64, -438 and -3978 [6,21], and is only slightly less mature than *H. antecessor* specimen ATD6-112 [22]. The significance of this similarity among morphologically distinct hominins is unclear: *A. robustus* shows a prolonged period of deciduous tooth emergence similar to humans [23], but also formed its permanent teeth more rapidly than humans [3]. By contrast, developing M_1 s from ATD6 provide the earliest evidence of a human-like delayed M_1 emergence. The state of tooth formation in the *H. naledi* infant may therefore reflect its being an infant hominin rather than bear any life history significance.

More intriguing is the developmental status of U.W. 101-377, with an emerging M_2 and fully emerged premolars. All

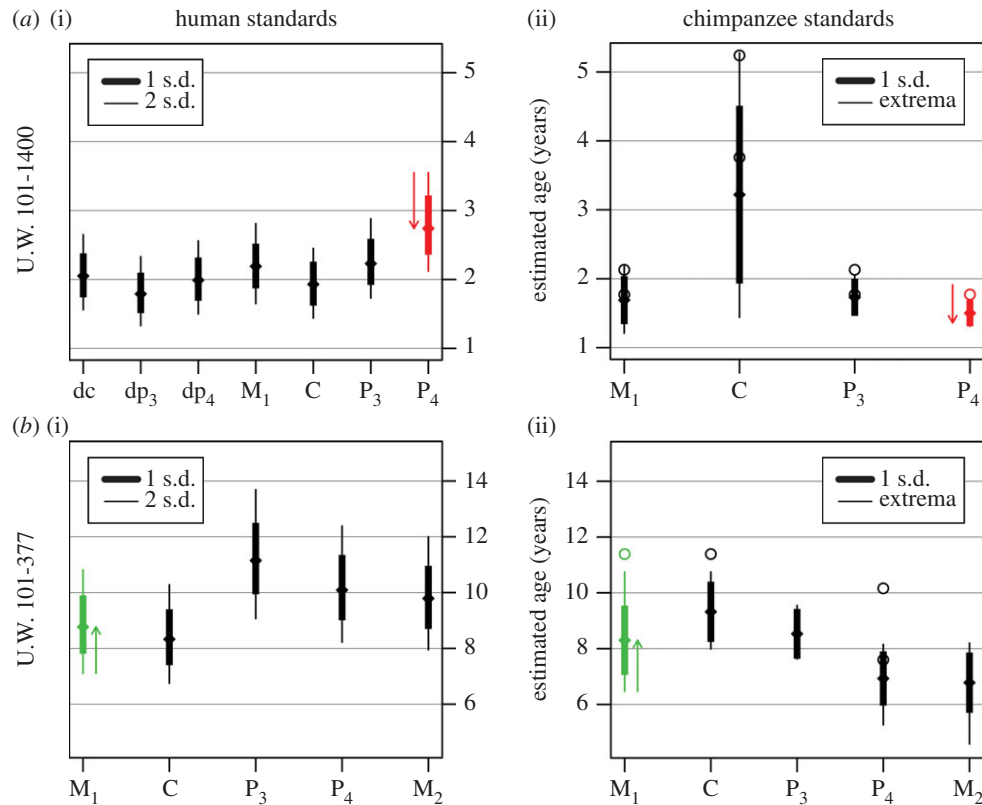


Figure 2. Estimated age at death from each tooth of U.W. 101-1400 (a) and 101-377 (b), based on human (i) and chimpanzee (ii) formation standards. Tick marks indicate mean estimates, thick lines extend to ± 1 s.d., and thin lines extend to ± 2 s.d. (humans) or sample extremes (chimpanzees). Open circles represent wild chimpanzees. Red bars indicate initiation of the P₄ that had not begun in U.W. 101-1400. Green bars indicate minimum age estimates for the M₁ that had completed formation in U.W. 101-377. Note deciduous formation standards are not available for chimpanzees. (Online version in colour.)

other Plio-Pleistocene hominin taxa for which this sequence can be discerned (South African australopiths, *H. erectus* and Neandertals) emerged M₂ before one or both of the premolars [4,18,24,25]. This sequence also characterizes apes, and may reflect relatively rapid craniofacial and somatic growth [1,2,6,26]. That *H. naledi* displays the pattern most common among humans may indicate slower growth in this species. Brain size as small as that of *H. naledi* [7], however, is associated with more rapid growth and maturation among primates [26]. The occurrence of the human-like sequence in *H. naledi* and a primitive sequence in other hominins raises questions about the adaptive significance of tooth emergence sequences. Future research may shed light on these questions: tooth histological data may yield accurate chronological estimates of age at death for these specimens (e.g. [4]), demonstrating the actual pace of life history in *H. naledi*. Further work should also examine the degree to which posterior molar emergence is constrained by facial size and growth [2,26].

Data accessibility. Tooth formation states and original images are in the electronic supplementary material.

Authors' contributions. Z.C. and C.S.W. conceived the project. Z.C. designed the research and measured developing crowns and roots. Z.C. and C.S.W. assessed stages of tooth formation, wrote the paper, gave final approval for publication and are accountable for all aspects of the work.

Competing interests. We have no competing interests.

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