

## Research



**Cite this article:** Cofran Z, Walker CS. 2017  
Dental development in *Homo naledi*. *Biol. Lett.*  
**13:** 20170339.  
<http://dx.doi.org/10.1098/rsbl.2017.0339>

Received: 1 June 2017

Accepted: 7 August 2017

### Subject Areas:

evolution, palaeontology

### Keywords:

hominin, teeth, tooth eruption,  
life history, ontogeny

### Author for correspondence:

Zachary Cofran

e-mail: [zcofran@vassar.edu](mailto:zcofran@vassar.edu)

Electronic supplementary material is available  
online at [https://dx.doi.org/10.6084/m9.  
figshare.c.3854722](https://dx.doi.org/10.6084/m9.figshare.c.3854722).

## Evolutionary biology

# Dental development in *Homo naledi*

Zachary Cofran<sup>1,4</sup> and Christopher S. Walker<sup>2,3,4</sup>

<sup>1</sup>Anthropology Department, Vassar College, Poughkeepsie, NY, USA

<sup>2</sup>Department of Molecular Biomedical Sciences, College of Veterinary Medicine, North Carolina State University, Raleigh, NC, USA

<sup>3</sup>Department of Evolutionary Anthropology, Duke University, Durham, NC, USA

<sup>4</sup>Evolutionary Studies Institute and Centre for Excellence in Palaeosciences, University of the Witwatersrand, Johannesburg-Braamfontein, Gauteng, South Africa

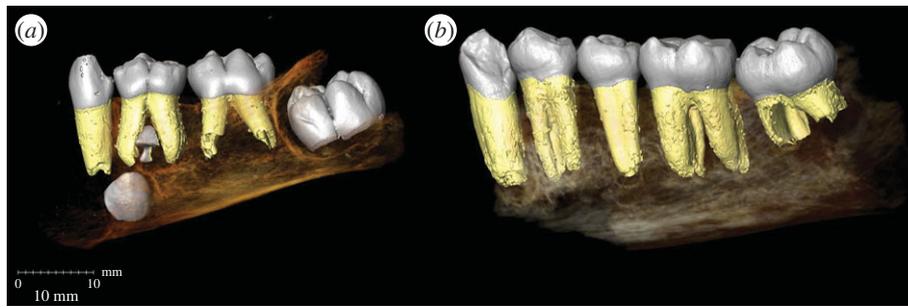
ZC, 0000-0002-8688-9976; CSW, 0000-0002-5173-2784

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  $\mu$ A current, with an isometric voxel size of 30.8  $\mu$ 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](http://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.

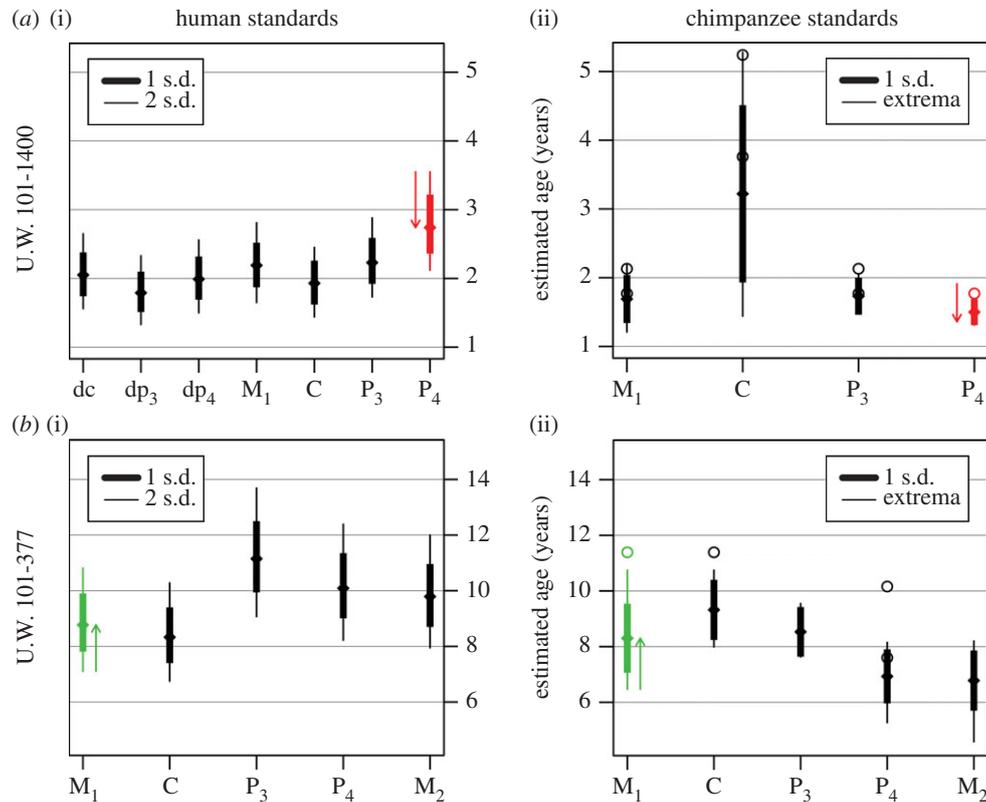
U.W. 101-377 tooth formation cannot be pigeonholed into 'human' or 'chimpanzee' categories. Compared with humans, C is underdeveloped relative to  $P_{3-4}$  and  $M_2$  (figure 2; electronic supplementary material, figure S3 and table S2). Compared with chimpanzees, all teeth are underdeveloped relative 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  $\pm 1$  s.d., and thin lines extend to  $\pm 2$  s.d. (humans) or sample extremes (chimpanzees). Open circles represent wild chimpanzees. Red bars indicate initiation of the P<sub>4</sub> that had not begun in U.W. 101-1400. Green bars indicate minimum age estimates for the M<sub>1</sub> 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 M<sub>2</sub> 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.

**Funding.** This work was funded by grants from the National Geographic Society and the National Research Foundation of South Africa to Lee Berger.

**Acknowledgements.** We are grateful to Lee Berger and John Hawks for the invitation to work on the *Homo naledi* materials. For access to specimens, we thank Bernhard Zipfel (University of Witwatersrand), Stephany Potze and Lazarus Kagasi (Ditsong National Museum of Natural History). For CT scanning and technical assistance, we thank Kudakwashe Jakata, Matthew Skinner, Luke Delezene, Paul Klassen and Gabe Yapuncich. B. Holly Smith, Helen Liversidge, Paul Tafforreau and Adeline le Cabec gave advice in interpreting tooth formation in these fossils. Aaron Sandel commented and Matthew Skinner worked extensively on earlier drafts.

## References

- Schultz AH. 1960 Age changes in primates and their modification in man. In *Human growth* (ed. JM Tanner), pp. 1–20. Oxford, UK: Pergamon Press.
- Smith BH. 2000 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. In *Development, function and evolution of teeth* (eds MF Teaford, MM Smith, MW Ferguson), pp. 212–227. Cambridge, MA: Cambridge University Press.
- Smith TM *et al.* 2015 Dental ontogeny in pliocene and early pleistocene hominins. *PLoS ONE* **10**, e0118118. (doi:10.1371/journal.pone.0118118)
- Dean MC, Smith BH. 2009 Growth and development of the Nariokotome Youth, KNM-WT 15000. In *The first humans: origin and early evolution of the genus Homo* (eds FE Grine, JG Fleagle, RE Leakey), pp. 101–120. Dordrecht, The Netherlands: Springer.
- Kelley J, Schwartz GT. 2012 Life-history inference in the early hominins *Australopithecus* and *Paranthropus*. *Int. J. Primatol.* **33**, 1332–1363. (doi:10.1007/s10764-012-9607-2)
- Beynon AD, Dean MC. 1988 Distinct dental development patterns in early fossil

- hominids. *Nature* **335**, 509–514. (doi:10.1038/335509a0)
7. Berger LR *et al.* 2015 *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife* **4**, e09560. (doi:10.7554/eLife.09560)
  8. Dirks PHGM *et al.* 2017 The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa. *eLife* **6**, e24231. (doi:10.7554/eLife.24231)
  9. Moorrees CF, Fanning EA, Hunt EE. 1963 Age variation of formation stages for ten permanent teeth. *J. Dent. Res.* **42**, 1490–1502. (doi:10.1177/00220345630420062701)
  10. Demirjian A, Goldstein H, Tanner JM. 1973 A new system of dental age assessment. *Hum. Biol.* **45**, 211–227. (doi:10.2307/41459864)
  11. Shackelford LL, Harris AES, Konigsberg LW. 2012 Estimating the distribution of probable age-at-death from dental remains of immature human fossils. *Am. J. Phys. Anthropol.* **147**, 227–253. (doi:10.1002/ajpa.21639)
  12. Kuykendall KL. 1996 Dental development in chimpanzees (*Pan troglodytes*): the timing of tooth calcification stages. *Am. J. Phys. Anthropol.* **99**, 135–157. (doi:10.1002/(SICI)1096-8644(199601)99:1<135::AID-AJPA8>3.0.CO;2-#)
  13. Liversidge HM, Molleson T. 2004 Variation in crown and root formation and eruption of human deciduous teeth. *Am. J. Phys. Anthropol.* **123**, 172–180. (doi:10.1002/ajpa.10318)
  14. Machanda Z, Brazeau NF, Bernard AB, Donovan RM, Papakyrikos AM, Wrangham R, Smith TM. 2015 Dental eruption in East African wild chimpanzees. *J. Hum. Evol.* **82**, 137–144. (doi:10.1016/j.jhevol.2015.02.010)
  15. Kuykendall KL, Mahoney CJ, Conroy GC. 1992 Probit and survival analysis of tooth emergence ages in a mixed- longitudinal sample of chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **89**, 379–399. (doi:10.1002/ajpa.1330890310)
  16. Smith TM, Smith BH, Reid DJ, Siedel H, Vigilant L, Hublin JJ, Boesch C. 2010 Dental development of the Taï Forest chimpanzees revisited. *J. Hum. Evol.* **58**, 363–373. (doi:10.1016/j.jhevol.2010.02.008)
  17. Boughner JC, Dean MC, Wilgenbusch CS. 2012 Permanent tooth mineralization in bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*). *Am. J. Phys. Anthropol.* **149**, 560–571. (doi:10.1002/ajpa.22166)
  18. Smith BH. 1994 Sequence of emergence of the permanent teeth in *Macaca*, *Pan*, *Homo*, and *Australopithecus*: its evolutionary significance. *Am. J. Hum. Biol.* **6**, 61–76. (doi:10.1002/ajhb.1310060110)
  19. Kelley J, Dean MC, Ross S. 2009 Root growth during molar eruption in extant great apes. *Front. Oral Biol.* **13**, 128–133. (doi:10.1159/000242404)
  20. Liversidge H. 2003 Variation in modern human dental development. In *Patterns of growth and development in the genus homo* (eds JL Thompson, GE Krovitz, AJ Nelson), pp. 73–113. Cambridge, MA: Cambridge University Press.
  21. Conroy GC, Vannier MW. 1991 Dental development in South African australopithecines. Part II: dental stage assessment. *Am. J. Phys. Anthropol.* **86**, 137–156. (doi:10.1002/ajpa.1330860205)
  22. Bermúdez de Castro JM, Martínón-Torres M, Prado L, Gómez-Robles A, Rosell J, López-Polín L, Arsuaga JL, Carbonell E. 2010 New immature hominin fossil from European Lower Pleistocene shows the earliest evidence of a modern human dental development pattern. *Proc. Natl Acad. Sci. USA* **107**, 11 739–11 744. (doi:10.1073/pnas.1006772107)
  23. Dean MC, Liversidge HM. 2015 Age estimation in fossil hominins: comparing dental development in early *Homo* with modern humans. *Ann. Hum. Biol.* **42**, 415–429. (doi:10.3109/03014460.2015.1046488)
  24. Smith TM, Toussaint M, Reid DJ, Olejniczak AJ, Hublin J-J. 2007 Rapid dental development in a Middle Paleolithic Belgian Neanderthal. *Proc. Natl Acad. Sci. USA* **104**, 20 220–20 225. (doi:10.1073/pnas.0707051104)
  25. Berger LR, de Ruiter DJ, Churchill SE, Schmid P, Carlson KJ, Dirks PHGM, Kibii JM. 2010 *Australopithecus sediba*: a new species of *Homo*-like australopithecine from South Africa. *Science* **328**, 195–204. (doi:10.1126/science.1184944)
  26. Schwartz GT. 2012 Growth, development, and life history throughout the evolution of *Homo*. *Curr. Anthropol.* **53**, S395–S408. (doi:10.1086/667591)