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 M2 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 M2–3 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.

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estimates by chimpanzee standards). To produce similar age estimates by human standards, but different
H. naledi
all of an individual's teeth provide the same signal (e.g. if individual teeth for each specimen (figure 2). The purpose is not
to compare with other studies [9–13] (electronic supplementary
material, figure S2). The premolar–M 2 sequence matches the most
canine emergence shows a mix of primitive and derived features. As with the rest of the species' skeleton, tooth formation and
growth at gingival emergence, with about half the root
formation was assessed from microCT scans, produced at the
University of Witwatersrand microCT facility on a Nikon Metrol-
ysis XTH 225/320 LC dual-source scanner. Scans were conducted
with 95 kV energy and 95 μA current, with an isometric voxel
size of 30.8 μm. CT images were processed in Avizo 6.3 (VSG, Bur-
lington 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
humans, C is underdeveloped relative to P3 and M2 (figure 2;
electronic supplementary material, figure S3 and table S2). Com-
pared with chimpanzees, all teeth are underdeveloped relative
to M2, while C and P3 are advanced over P4 and M2. M2 develop-
ment at gingival emergence, with about half the root
formed, is similar to apes [19], whereas human Ms usually
attain gingival emergence with around 75% root length [20].
Thus, U.W. 101-377 juxtaposes human-like M2 emergence
sequence with chimpanzee-like root development.

3. Results

(a) U.W. 101-1400
Tooth wear indicates a deciduous emergence sequence of
d1–d2–dp3–dc–dp4 (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 stan-
dards, although there is greater similarity with humans
(figure 2). In contrast to U.W. 101-1400 and humans, chim-
panzees at a comparable stage of M1 formation have some of the P4 crown formed and less developed canines [12,16,17].

(b) U.W. 101-377
Premolars and M1 are in occlusion, while C and M2 have
attained only gingival emergence. Greater apical wear on
the canine indicates an emergence sequence of [M1–I1–I2]–
[P3–P4]–[C–M2]–M3 (electronic supplementary material,
figure S2). The premolar–M2 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 P3 and M2 (figure 2;
electronic supplementary material, figure S3 and table S2). Com-
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4. Discussion

These mandibles capture two snapshots in the dynamic pro-
cesses 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 d2 emergence usually precedes dp4
among anthropoids [1] including early hominins [20], this
may be the ancestral condition for all apes and monkeys. The
relatively underdeveloped M2 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 M1 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 ATD-6-112
[22]. The significance of this similarity among morphologi-
cally 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 M1s from
ATD6 provide the earliest evidence of a human-like delayed
M1 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 M3 and fully emerged premolars. All
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].

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.)

References

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