

differs markedly from previous studies elsewhere^{5,14,18}. Our data support two possible mechanisms contributing to observed stream-water aluminium chemistry during these highly saturated periods. The decrease in $[Al_i]$ and increase in $[TOC]$, $[Al_0]$ and $[H^+]$ during rain events and melting episodes probably results in part from increased flow through upper organic soil horizons. It is important to realize that equilibrium conditions in organic soil layers could give lower $[Al_i]$ and pH than in mineral horizons because ion-exchange processes rather than mineral dissolution are operating. There is a tendency for $3pH - pAl^{3+}$ to increase with depth within each plot. A potentially important flow path is downward flow through well-drained soils on the steep hillslopes, followed by upward renewed contact with organic layers near the streams²¹. Saturated conditions can also lead to rain or melt water entering streams so rapidly that equilibrium with soils is not obtained, and runoff is therefore subject to kinetic controls.

The late winter and early spring phases of snow-melt (up to 15 April) merit separate consideration in view of the positive correlation between $[H^+]$ and $[Al^{3+}]$ during this period (Fig. 3). (Very recent results from autumn 1985 indicate a similar concentration pattern for an episode following a long dry period.) Initially $[H^+]$ in stream water is low and $[Al_i]$ moderate (Fig. 2). The substantial increase in $[Al_i]$ with the first minor melting episodes could be due to a piston effect, that is, the first melt water forcing 'old', aluminium-rich soil water into streams²².

A mathematical model simulating major ions in stream water in the Birkenes catchment has previously been developed⁶, and much of the current field work is aimed at improving this model. The model consists of two soil reservoirs (upper organic soils and deeper mineral soils), both incorporating the same gibbsite equilibrium assumption. This was based on earlier measurements of total aqueous aluminium in stream water⁶. Our data show that the aluminium sub-model needs revision. A reasonable modification of the current model structure would be to use different aluminium chemistry in the two soil reservoirs. Future field efforts will include new episode studies with the emphasis on lysimeter work, to model more accurately the soil-water interactions.

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Dental development in *Australopithecus* and early *Homo*

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Human ontogeny requires nearly twice the time as that of living apes¹. This extended period of maturation is usually regarded as a significant evolutionary advance enhancing the importance of learning¹⁻⁵. Mann⁶ suggested that alteration of the timing of growth and development occurred very early in hominid evolution, using evidence based on a human-like pattern of dental development identified in juvenile hominid dentitions from South African cave sites (primarily *Australopithecus robustus* from Swartkrans). He interpreted a human-like pattern to indicate a long human-like schedule of maturation. In contrast, recent study of incremental lines in tooth enamel⁷ suggests short developmental periods for *Australopithecus* and even for early members of the genus *Homo*. Here I report patterns of dental development for *A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, *H. habilis* and early *H. erectus*, indicating that *A. robustus* and *A. boisei* ('robust' australopithecines) differ from other hominid species. Most early hominids resemble pongids rather than modern humans in patterns of dental development.

Many new juvenile fossil hominids have been recovered^{8,9} since Mann's original study of australopithecine dental development⁶, and standards of human tooth formation have become more widely known¹⁰⁻¹⁵. Recent publication of a chronological

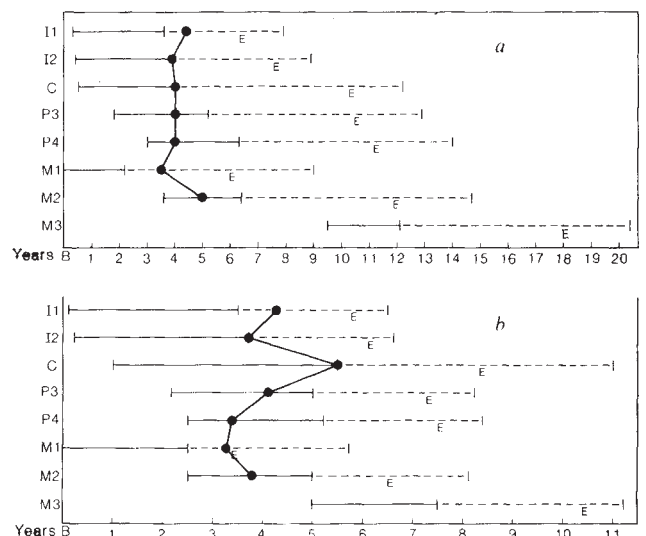


Fig. 1 Mandibular teeth of the Gibraltar 2 Neanderthal child plotted on a, human and b, pongid charts of permanent tooth formation. Charts modified from Dean and Wood¹⁶. Solid lines, crown formation; dashed lines, root formation; E, eruption. The pongid chart is magnified by a factor of 1.8 to equalize periods of pongid and human tooth formation. Gibraltar 2 shows simultaneous events that fit expectations for a human child (that is, plotted points approach a vertical line). The same events are out of synchrony on the pongid chart. Modern human standards are based on longitudinal radiographic studies of mandibular teeth of US caucasian schoolchildren¹⁰ (male-female averages of stages 'crown initialization', 'crown complete' and 'apical closure' shown above differ slightly from Dean and Wood¹⁶). Pongid standards based on cross-sectional study of mandibular and maxillary radiographs of skeletal samples of chimpanzees and gorillas combined with eruption ages drawn from other studies¹⁶. Direct observations are supplemented with radiographs¹⁹ for Gibraltar 2.

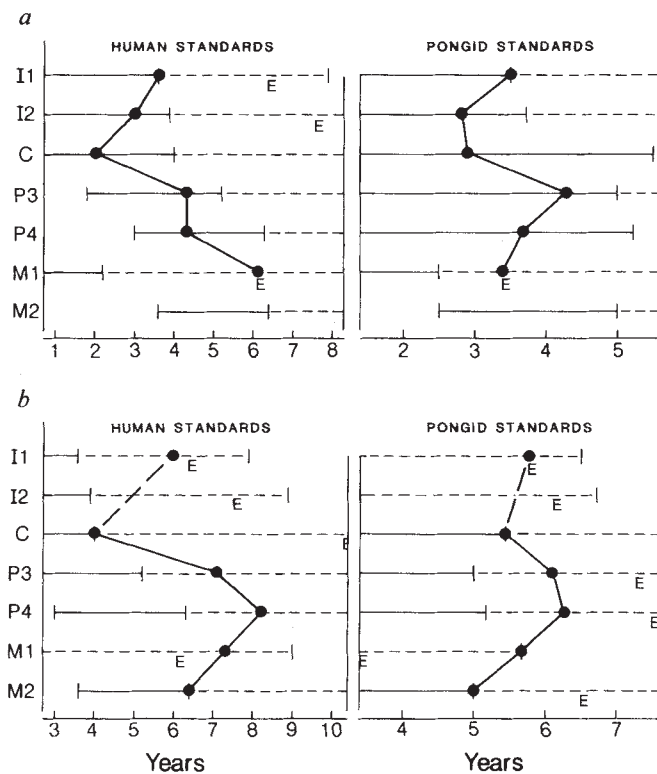


Fig. 2 Maxillary tooth formation of two fossil hominids plotted as humans (left) and as pongids (right), using standards shown in Fig. 1. *a*, STS 24 (Sterkfontein *A. africanus*); *b*, ER 1590 (East Turkana *H. habilis*), both showing such large deviations that it is difficult to assign age at death using human standards. Dashed line indicates missing data for an intervening tooth. Note the delay of anterior teeth relative to M1, characteristic of pongids. Dispersion is lessened when cases are plotted as pongids, particularly for anterior teeth and the first molar.

scale for pongid dental development¹⁶ allows the reassessment of patterns of early hominid dental development with an explicit comparison to living pongids as well as humans. Teeth provide the principal source of developmental information in fossil hominids; there is only one substantial juvenile skeleton of an early hominid with associated skull and dentition identifying it¹⁷.

Dean and Wood¹⁶ presented tooth-crown and root formation of the human and pongid dentition in a summary (Fig. 1). The pongid scale is based on many less data than the human scale and contains some extrapolation, but represents an improvement over information previously available.

Fractional stages of crown development (such as crown one-half complete) can be plotted directly because formation proceeds linearly^{10,11}. Root formation is less simple¹¹, here approximated by allotting the first three-quarters of formation to root elongation and the last one-quarter to apical closure (pongid root formation is plotted directly because standards seem to refer to root elongation¹⁶). Any individual, living or fossil, with developing crowns and roots can be plotted on both human and pongid charts, allowing one to judge which standard provides the best fit by the dispersion of dental ages predicted by individual teeth.

Three methodological points should be noted in Fig. 1: (1) the pongid scale is stretched to make the duration of pongid dental development equal to that of humans, with 10 pongid years equalling 18 human years. This scales dispersion of events in pongids to that of humans in the absence of standard deviations for pongids. (2) the most distinctive feature of pongid dental development, compared with that of humans, is a delay of canines and, to a lesser extent, incisors relative to first molars. (3) charts in Fig. 1 can be applied to both maxillary and mandibular teeth as differences are reportedly small¹².

The example plotted in Fig. 1 is the Gibraltar 2 child, a Neanderthal. Gibraltar 2 shows events that are out of synchrony on a pongid scale (note the canine) but are expected for a human child of four years of age. The fact that a Neanderthal approaches standards based on US caucasian schoolchildren helps illustrate that sex differences¹⁰ and population differences^{15,18} (and judgemental errors of plus or minus one stage¹⁰),

although real, are small on the present scale. Whereas these factors can shift mean values by about one standard deviation, my study is concerned with differences of four to six standard deviation units. Finally, results for the Neanderthal child suggest that one must look farther back in human evolutionary history to find significant developmental differences from living humans.

Formation stages assigned to fossil specimens are based on direct observation of crowns and roots exposed by breakage (radiographs of these heavily mineralized specimens are often poor⁶, and published formation stages¹⁹ are too broad for the present study). Tooth eruption is used as a marker only if slight wear indicates recent eruption before death. Sixteen specimens representing 15 individuals have two more more teeth in diagnostic stages.

Two specimens are plotted on human and pongid charts in Fig. 2. First (*a*), STS 24, a specimen of *A. africanus* from Sterkfontein, is thought to represent a six-year-old child because M1 erupted just before death⁶. All other teeth give far younger ages, ranging as low as two years for the canine. Dispersion is lessened on the pongid chart, where the same developmental events suggest an age of three to four years. Second (*b*), ER1590, a specimen of *H. habilis* from East Turkana, exhibits major deviations from a human pattern: suggested ages range from four years for the canine to more than eight years for the last premolar (P4), a nearly impossible combination for a human child. Standard deviations for events at four years old are about six months in humans, gradually increasing to about one year at ten years of age^{10,14}. If ER 1590 is assigned a mean age of 6.5 years, P4 is $+2.3\sigma$ and C is -5.4σ (if aged on M1, as fossils usually are, C is -6.6σ). By comparison, the pongid scale suggests an age of between five and six years. The magnification of 1.8 for the pongid chart makes these specimens imperfect pongids, but there is an improvement in fit (a factor of 1.8 is the maximum and most conservative that can be used; any smaller factor improves fit to pongid standards).

Dental ages of all specimens are given in Table 1. Numerical measures of fit to standards are based on the dispersion of dental ages interpolated for each tooth.

Table 1 begins with the Neanderthal child and proceeds back

Table 1 Dental ages for juvenile fossil hominids interpolated from human and pongid standards of tooth formation

Taxon	Specimen	Tooth	Dental ages of all teeth (years)														Fit to standards (σ)		
			Human standards				Pongid standards				Dental ages of all teeth (years)						Human	Pongid†	Best‡
			I1	I2	C	P3	P4	M1	M2	I1	I2	C	P3	P4	M1	M2			
Homo																			
<i>H. sapiens</i>																			
	Gibraltar 2	md	4.4	3.9	4.0	4.0	4.0	3.5	5.0	4.3	3.7	5.5	4.1	3.4	3.3	3.8	0.47	1.34	H
<i>H. erectus</i>																			
	ER 820*	md	—	7.5	5.5	—	—	—	—	—	6.1	6.9	—	—	—	—	1.41	1.02	P?
	ER 1507	md	—	—	4.0	5.4	6.0	—	6.1	—	—	5.5	5.2	5.0	—	4.8	0.97	0.54	P?
<i>H. habilis</i>																			
	ER 1590	mx	6.0	—	4.0	7.1	8.2	7.3	6.4	5.8	—	5.5	6.1	6.3	5.7	5.0	1.44	0.83	P
Australopithecus																			
<i>A. boisei</i>																			
	OH 30*	mx	—	—	2.9	3.5	4.6	2.2	—	—	—	4.0	3.6	3.9	2.5	—	1.02	1.24	H
	OH 30	md	3.4	—	2.6	—	—	2.2	—	3.3	—	3.7	—	—	2.5	—	0.61	1.10	H
	ER 1171	md	—	—	—	—	6.3	—	6.4	—	—	—	—	5.2	—	5.0	0.07	0.25	H?
	ER 1477	md	3.4	—	2.3	3.5	—	—	—	3.3	—	3.3	3.6	—	—	—	0.67	0.31	P?
	ER 1820	md	3.6	—	—	—	—	2.5	—	3.5	—	—	—	—	2.7	—	0.78	1.02	H
<i>A. robustus</i>																			
	SK 63*	md	—	—	4.3	—	—	6.0	5.4	—	—	5.7	—	—	3.3	4.2	0.86	2.18	H
	SK 839	mx	2.8	3.0	—	—	—	1.7	—	2.7	2.8	—	—	—	1.9	—	0.70	0.89	H
	SK 852	md	3.6	3.6	2.9	—	—	2.5	—	3.5	3.5	4.0	—	—	2.7	—	0.54	0.97	H
<i>A. africanus</i>																			
	STS 24*	mx	3.6	3.0	2.0	4.3	4.3	6.1	—	3.5	2.8	2.9	4.3	3.7	3.4	—	1.39	0.99	P
	STS 24	md	3.6	3.6	—	—	—	6.1	—	3.5	3.5	—	—	—	3.4	—	1.44	0.10	P
	STS 57	mx	—	—	—	4.9	6.0	6.1	4.5	—	—	—	4.8	5.0	3.4	3.3	0.80	1.62	H?
	STW 151*	mx	6.4	5.8	3.8	5.2	—	7.3	6.4	5.8	5.2	5.3	5.0	—	5.7	5.0	1.21	0.72	P
	STW 151	md	6.4	—	4.0	4.9	6.3	7.3	6.4	5.8	—	5.5	4.8	5.2	5.7	5.0	1.20	0.70	P
<i>A. afarensis</i>																			
	LH 2*§	md	3.6	—	3.1	4.0	—	6.1	—	3.5	—	4.4	4.1	—	3.6	—	1.32	0.76	P
	LH 3§	mx	3.9	3.9	2.9	4.3	6.0	6.1	—	3.7	3.7	4.0	4.3	5.0	4.6	—	1.28	0.93	P
	LH 3§	md	—	3.9	3.1	4.3	5.4	6.1	—	—	3.7	4.4	4.3	4.5	4.6	—	1.20	0.64	P
	LH 6	mx	—	5.0	3.8	5.4	—	6.1	—	—	4.6	5.3	5.2	—	4.9	—	0.96	0.57	P

* Abbreviations, mx, maxilla; md, mandible; ER, East Rudolph (= East Turkana); LH, Laetoli hominid; STS, Sterkfontein; STW, Sterkfontein Witwatersrand; SK, Swartkrans; OH, Olduvai hominid.

† Pongid dental ages multiplied by 1.8 to compute σ , scaling human and pongid development to the same length of time. Pongid dental ages shown above are not multiplied.

‡ The standard (H, human, P, pongid) yielding the lower standard deviation of dental age is judged as the better fit. Query denotes equivocal cases lacking data for the crucial contrast between M1 and the anterior teeth (I1, I2, C).

§ First molars of Laetoli hominids 2 and 3 show stages that do not usually coincide in humans: root is one-third on LH 2 (age 3.9) and two-thirds on LH 3 (age 5.6) yet M1s were erupted with some wear (age 6.1). No discrepancy results using the pongid scale.

in time. The clear fit to human standards shown by Gibraltar 2 shifts to better fit by pongid standards, equivocally for early *H. erectus* and more strongly for *H. habilis*. The human pattern emerges as dominant in robust australopithecines, in both cases of *A. robustus* from Swartkrans (SK 839 and 852 count as one as they are the same individual²⁰), and in three of four cases in hyper-robust *A. boisei* from Olduvai and East Turkana. *A. africanus*, a species near the nexus of the two lineages, shows the pongid pattern in two of three cases. The oldest known species, *A. afarensis*, fits pongid standards. Several important specimens are questionable (queries in Table 1) because they lack data for the combination of teeth that usually contributes most to dispersion, M1 versus the anterior teeth. There are insufficient data to resolve the pattern of early *H. erectus*. Cases that disagree with other conspecifics (the sole 'H' in *A. africanus*, the sole 'P' in *A. boisei*) also lack these crucial teeth.

Patterns are clearer when the four specimens lacking data for M1 are discarded. All human charts are superimposed on M1 development in Fig. 3, with remaining teeth scored only in terms of years of advance or delay relative to M1. A clear S-shaped pattern emerges for a 'primitive' group (top) made up of *A. afarensis*, *A. africanus* and *H. habilis*. Incisors and canines are delayed relative to M1 as expected for a pongid. All three species are similar at this scale of resolution. The 'robust' group (Fig. 3, bottom) has diverged from other hominids in dental development. Mann⁶ identified the development pattern of *A. robustus* as human, but the resemblance is probably superficial. Points in Fig. 3 do not fall evenly about the line representing human

development; 11 of 13 teeth are advanced relative to human M1. *A. robustus* and *A. boisei* thus share a unique pattern that is neither human nor pongid.

The strong patterning of *A. afarensis*, *A. africanus* and *H. habilis* dental development relative to human standards does not support the use of a human schedule to assign age at death (it is unclear how one would do so in any case as individual teeth disagree by three and four years). The case for applying a human schedule to *A. robustus* and *A. boisei* is lessened because their dental development appears to be unique and not shared with humans. Mean dental ages assigned using a pongid scale of dental development for LH 2 (3.9 years), STS 24 (3.4), SK 63 (4.4) and ER 820 (6.5) are similar to ages assigned the same specimens by Bromage and Dean⁷ using a completely independent method (compare 3.3, 3.3, 3.2 and 5.3, respectively).

Attribution of a human pattern of dental development to South African fossils⁶ was the sole evidence supporting extended maturation in early hominids, supported by theoretical predictions. Prolonged infant and child dependency appears consistently in theories of early cultural evolution, especially in the origin of a home base, food sharing, division of labour and evolution of mating patterns^{4,21-24}. The assumption that all early hominid species had lengthened periods of development has probably influenced interpretation of the archaeological record, particularly in the level of 'humanness' ascribed to early ancestors^{25,26}. Evidence of dental development presented here, taken together with that of incremental lines⁷, suggests that early hominids had not yet achieved this advanced grade. A human-

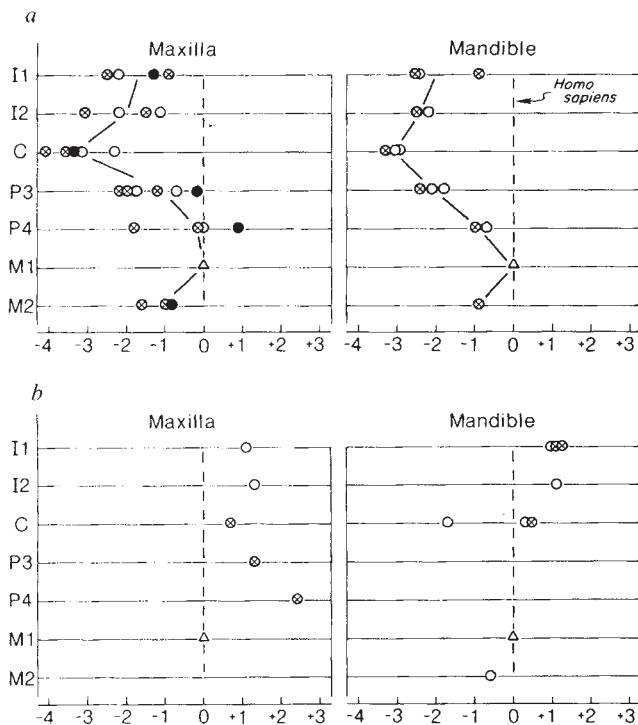


Fig. 3 Pattern of deviation of eleven fossil hominins (cases with data for M1) from human standards of tooth formation. *a*, Primitive group; *b*, robust group. Human charts are superimposed on M1 for the maxilla (left) and mandible (right). Remaining teeth are scored as years of advance (+) or delay (-) relative to M1. Dashed line at zero, position of modern humans. All fossils fall into two groups that do not overlap: *a*, *A. afarensis* (open circles), *A. africanus* (crossed circles) and *H. habilis* (solid circles); *b*, *A. robustus* (open circles) and *A. boisei* (crossed circles). Note that the primitive group shows an S-shaped pattern with most teeth delayed relative to human standards, although the data are insufficient to define a clear pattern. The lower canine of SK 63 is an outlier; roots of anterior teeth of SK 63 are slightly damaged¹⁹, which may cause underestimation of age.

like pattern of extended maturation may be a relatively late acquisition in human evolution²⁷. Little is known of ontogeny during the million-year interval encompassed by *H. erectus*. Every juvenile fossil recovered and each new line of evidence is important.

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Suspended clay concentration controlled by filter-feeding zooplankton in a tropical reservoir

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Clay suspended in lake water may be an important factor in limiting primary production by decreasing availability of light¹⁻³ and of nutrients^{4,5}. Seasonal changes in the concentration of suspended clay in a lake or a reservoir are usually attributed to the periodicity in hydrological events such as flooding, stratification and mixing⁶⁻⁹. From data presented here it is evident that filter-feeding zooplankton are also important in determining the seasonality of clay abundance. I show that monthly, predator-induced periodicities in the density of zooplankton are synchronized with the periodicities in the rate of decrease in the clay-induced turbidity of the surface waters of a tropical reservoir.

The concentration of suspended clay or silt particles frequently exceeds 1 mg l^{-1} in lakes fed from glaciers and in artificial reservoirs in semi-arid regions. The seasonal fluctuations in clay concentration are in the range of two to three orders of magnitude. The maxima appear suddenly as an effect of floods carrying a large quantity of clay into the lake^{2,6,7}, or as an effect of resuspending clay particles from the sediments during lake overturn^{3,8,9}. The subsequent minima are always more gradual because a long time is needed for fine clay particles to settle. Whereas there is no doubt that any increase in suspended clay concentration must originate from physical processes, I believe it is unlikely that the decreases also result from the purely physical processes of particle sedimentation.

My doubts came from an accidental observation of natural lake water from Cahora Bassa, a large reservoir on the lower Zambezi River, Mozambique, in south eastern Africa ($15^{\circ} 30' \text{ S}$, $30^{\circ} 20' - 32^{\circ} 40' \text{ E}$). The reservoir (volume 30.5 km^3 ; area $1,902 \text{ km}^2$; maximum depth 127 m) is heavily loaded with particles of clays such as montmorillonites, kaolinites and illities (identified by X-ray diffraction), most of which (97%) are $1-2 \mu\text{m}$ long in the largest linear dimension. I observed the maximum concentration of these particles in the surface waters (10^9 particles per litre) during and after the lake overturn from May to September, when the turbidity of water determined on a HATCH turbidimeter was $>20 \text{ JTU}$ (Jackson turbidity units) and Secchi disk transparency $<0.9 \text{ m}$ (Fig. 1). The lowest concentration (10^6 particles per litre) was observed at the end of the stratification period from January to March when the turbidity was $<3 \text{ JTU}$ and transparency $>2.5 \text{ m}$ despite an increase in the phytoplankton standing crop at that time (Fig. 1). The correlation between the Secchi disk transparency and turbidity