Revised estimates of Taung's brain size growth

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Cranial capacity, a proxy for the volume of the brain and associated cranial contents, is an important yardstick used to compare early hominin species because increasing brain size is a key characteristic of our lineage. In 1925, Raymond Dart claimed that a natural endocast found at the Buxton Limeworks near Taung, South Africa (which he named *Australopithecus africanus*), showed signs of neural reorganisation, but its juvenile status complicated comparison to other hominoid species. In an attempt to put its brain size and reorganisation into a comparative context, subsequent researchers have tried to estimate Taung's adult cranial capacity by comparison to coarse-grained hominoid growth data. In this study, we simulated brain growth in *A. africanus* using asymptotic growth models in known-age mountain gorillas, chimpanzees and modern humans, and show that, at just under 4 years old, Taung's brain had already finished or nearly finished growing according to hominoid developmental schedules. Percentage-growth remaining estimates are lower here than in previous studies using cross-sectional ontogenetic samples of unknown chronological age. Our new adult estimates (between 404 cm^3 and 430 cm^3 overall and 405–406 cm^3 for chimpanzee models) are smaller than previous estimates with a 'starting' cranial capacity of 404 cm^3, supporting the hypothesis that Taung's adult brain size would have fallen toward the lower end of the *A. africanus* range of variation and strengthening the case that Taung was female.

Significance:

- This is one of several recent studies to show that brain growth is completed in African apes and humans earlier than previously appreciated.
- New adult cranial capacity estimates for Taung are lower than previous estimates, supporting the hypothesis that Taung was female.
- Cessation of brain growth in hominoids at earlier ages than previously reported suggests that adult cranial capacities for hominin juvenile specimens have been overestimated.

Introduction

The type specimen of *Australopithecus africanus*, Taung, is a juvenile skull consisting of a partial face with fragmentary pieces of the basicranium attached, a mandible, and a natural hemi-endocast.[1] Taung has been the subject of intensive research focus because of its potential to resolve questions about hominin brain size and reorganisation[2-7] and *A. africanus* craniofacial growth[8-11], dental maturation[12-18] and brain ontogeny[19-21].

Raymond Dart originally estimated Taung's cranial capacity to be 520 cm^3 based on a reconstruction of the hemi-endocast.[2] Subsequent estimates have ranged between 382 cm^3 and 530 cm^3 (Tables 1–2). The most frequently cited estimate for Taung's cranial capacity – 404 cm^3 – was derived from an independent reconstruction of the hemi-endocast[22] and was recently corroborated by digital reconstruction of the endocast and endocranial cavity[23]. At 404 cm^3, Taung's cranial capacity is already at the lower end of the range of *A. africanus* variation (Table 2), even though the Taung juvenile died after gingival eruption of the first molars but before the they had moved into functional occlusion, and so still had several years remaining to reach adulthood.[12-19] Taung's importance to studies of hominin brain evolution and the scarcity of relatively complete crania and endocasts of adult *A. africanus* specimens have tempted researchers to estimate Taung's adult cranial capacity. Adult estimates range between 404 cm^3 and 785 cm^3 for 'starting' values ≥404 cm^3 (Table 1). Researchers working with different age estimates and differing ideas about *A. africanus* growth trajectories have sometimes modelled Taung with a large percentage-growth remaining, producing adult cranial capacity estimates >600 cm^3,[2,3,19,24-26] which are larger than any known adult *A. africanus* specimens. Uncertainty about brain growth parameters in fossil species makes it difficult to estimate how much growth Taung had already attained (and how much remained),[23,27-29] making it difficult to estimate adult cranial capacity. Size of the adult brain, which is approximated to some extent by cranial capacity, is an important parameter for understanding adaptive shifts in brain size and neural reorganisation early in human evolutionary history.

Previous adult predictions are based on overestimates of the amount of brain growth remaining in hominoids. At the time Taung was discovered in 1924, there were several misconceptions in the scientific literature about great ape growth and development. For example, it was thought that brain growth continued throughout the entire juvenile growth period until eruption of the third molars, or even beyond[19(and references therein),25,34,37,38], with humans reaching 81–88%[24,25,38] and great apes 85–92%[19,24] of adult brain size in the period just prior to eruption of the first molars; and that chimpanzees followed a tooth eruption schedule similar to that of modern humans, with the first permanent molar erupting at the end of the sixth year[19] or early in the fifth year[25]. Based in part on these misconceptions, Keith[24,25] and Dart[2,3] increased Taung's juvenile cranial capacity by 15–20% to produce adult cranial capacity estimates of 520–625 cm^3. Zuckerman[19] increased Taung's juvenile cranial capacity by 3% to as much as 57% based on the supposed amount of growth expected in chimpanzees and gorillas between eruption of the first molars and adulthood (Table 1). More recent estimates, while lower, have mostly relied on data from Ashton and Spence[33] who found that 92.5% of adult cranial capacity is attained on average prior to eruption of the first molar in cross-sectional samples of hominoids (including orangutans, gorillas, chimpanzees and modern humans).

Table 1: Previous juvenile and adult cranial capacity estimates for Taung presented in numerical order of adult cranial capacity. Table references are noted below or can be found in references[30,34]. C = chimpanzee; G = gorilla; H = modern human; A = australopith; gc = growth curve.

Reference	Year	Juv	Adult	% increase	Model
Falk and Clarke[28]	2007	382	390	2.1	C gc (98%)
Falk and Clarke[28]	2007	382	406	6.3	C gc (94%)
Falk[31]	1987	404[22]	412 (404–420)	2.0 (0–4.0)	C gc (96–100%)
Conroy et al.[32]	2000	405[22]	422	4.2	C (%, female)
Wolpoff	1996–1997	405[22]	425	4.9	95%
Neubauer et al.[23]	2012	403	428	6.2	A (Sts 71)
Conroy et al.[32]	2000	405[22]	431	6.4	C (94%, combined sex)
Holloway[22], Holloway et al.[27]	1970, 2004	405[22]	440[a]	8.6	C (92%)[33]
Conroy et al.[32]	2000	405[22]	455	12.4	C (%, male)
Keith[24]	1925	<450	≤520	15.6[b]	G, C (~86%)
Zuckerman[19]	1928	500	540 (515–566)	8.0 (3.0–13.2)	C
Tobias[34]	1971	500[19]	540	8.0	O, G, C, H (92.5%)[33]
Coon	1962	494	543	9.9	H ('unlikely')
Zuckerman[19]	1928	500	550	10.0	C, G ('likely')
Tobias	1965, 1967	520[2]	562	8.1	O, G, C, H (92.5%)[33]
Miller	1991	–	563	–	Mid-range estimate
Le Gros Clark	1947	500[19]–520[2]	570	9.6–14.0	C
Keith[22]	1931	500[19]	600	20.0	G
Le Gros Clark, Tobias	1955, 1963	520[2]	600	15.4	?
Zuckerman[19]	1928	500[19]	605[c]–638	21.0–27.5	C (max starting size/age; 'extremely unlikely')
Dart[3]	1956	520[2]	624	20.0	NR
Dart[2]	1926	520[2]	625	20.2[d]	NR
Schepers	1950	510–530	650	22.6–27.5	NR
Elliot Smith[26]	1925	520[2]	>650	>25[e]	NR
Zuckerman[19]	1928	520[2]	728	40.0	C (min starting size/age; 'extreme, ridiculously high')
Zuckerman[19]	1928	500[19]	769–785	54.0–57.0	C (min size/age; 'obviously ridiculous')

[a]Computed so that 405 cm^3 is 92% of adult cm^3.[33]
[b]Keith[24(p.234)] used somewhat imprecise language ('volume of the brain in the juvenile … must be less than 450 cc, and if we allow a 15 per cent. increase for the remaining stages of growth, the size of the adult brain will not exceed 520 cc.'), and so rounded this value to 15%.
[c]Miscalculated as 603 cm^3 in Zuckerman[19].
[d]Dart[2] reported this value as 20%.
[e]Elliot Smith[26(p.235)] reported this as a 20% increase: '… brain would probably have increased in volume to the extent of a fifth had it attained the adult status.' He obtained this value by calculating per cent complete (520 x 100/650=80%) rather than percentage change ([650–520] x 100/520=25%).

Table 2: Cranial capacity values for *Australopithecus africanus* specimens. More information about ranges of estimates can be found in references[23,30,34]. Sex attributions follow Grine[35]. 3DR = three-dimensional digital reconstruction, including correcting distortion and reconstructing broken portions using chimpanzees and Sts 5 as models[23]; PERM = partial endocast reconstruction method[27].

Specimen	Sex	Cranial capacity	Range of estimates	Methods/notes
MLD 1	M	510[27]	500–650[3]	Missing frontal and temporal lobes; reconstructed via PERM[27]
MLD 37/38	F	440[23]	425–480	Undistorted posterior cranium filled with matrix, required reconstruction in rostral part of frontal lobes; 3DR
Sts 5 (skull no. 5)	F[a]	475[23]	473[23]–485[20]	Complete cranium with broken calotte that fits back on; 3DR
Sts 19/58 (skull no. 8)	F	436[5,27]	436–570	Posterior cranium, endocast made by hand, reconstructed via PERM[27]
Sts 25[b]	F	363[30,c]	350–375[30]	Estimated using regression on vault variables
Sts 60 (TM 1511)	M?	391[23]	384[23]–428	Natural endocast; 3DR
Sts 71 (skull no. 7)	F	412[23]	370–430[32]	Nearly complete but distorted cranium; 3DR
StW 505	M	568[23]	515–625	Relatively complete but distorted cranium; 3DR
Taung	F[d]	403[23]–404[22]	382[28]–525	Natural hemi-endocast, missing part estimated, mirror-imaged; 3DR
Type 2 (TM 1512)	F	457[27]	457–580	Distorted natural endocast missing basal portion

[a]Sts 5 in particular has been attributed as female and male at different times (see Grine[35] and Tawane and Thackeray[36] for references).
[b]We also considered a 400–425-cm^3 estimate for Sts 17,[30] a partial face and associated cranial vault pieces that do not fit together perfectly; we followed Wolpoff's recommendation to exclude this specimen from consideration (Wolpoff M 2018, personal communication).
[c]Mid-point of range of estimated values.
[d]See discussion

Here we reconsider evidence for Taung's adult cranial capacity, taking into account the most up-to-date estimates of chronological age, cranial capacity and brain growth trajectories in African apes and modern humans; and use these new estimates to reassess brain size variability in *A. africanus*.

Materials and methods

We used mountain gorilla (*Gorilla beringei*), chimpanzee (*Pan troglodytes*) and modern human (*Homo sapiens*) cranial capacity growth curves to produce developmental simulations[10,11,23] of Taung's brain growth trajectory and to calculate the per cent changes that would have occurred between a given set of 'starting' ages and brain growth completion (Figure 1). We used starting age estimates of 3.73, 3.83 and 3.93 years based on a comparison of Taung's root length and crown development to *A. africanus* specimen Stw 402[17], but also considered 3.3-year[8,9,12] and 3.5-year[13,15] estimates (based on patterns of root and crown development) and 4-year[24,39], 4.5–5.5-year[40] and 5–7-year[41] estimates (based on varying interpretations of dental development and tooth eruption timing) in order to assess the impact of different starting ages on adult cranial capacity estimates.

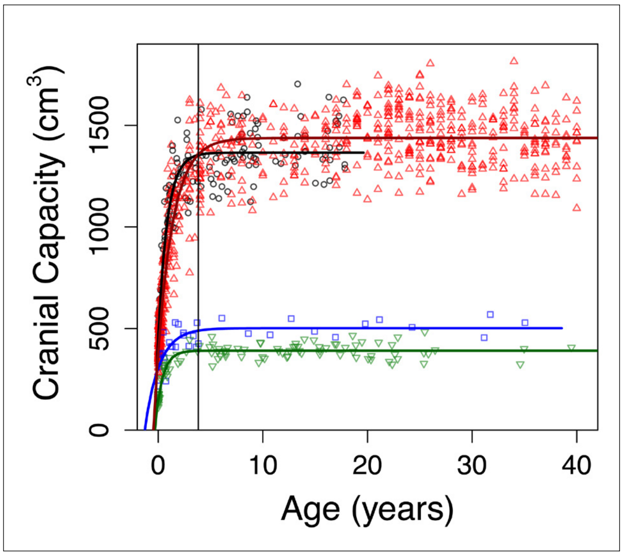

Figure 1: Distance growth curves for two samples of modern humans (black open circles, red triangles), chimpanzees (green triangles) and gorillas (blue squares) used to model Taung's cranial capacity growth. The vertical line indicates Taung's estimated age of 3.83 years.

We collated cranial capacities and/or brain masses for mountain gorilla, chimpanzee and modern human comparative samples from the literature[42-47] and set up each data set – including deleting outliers – following previously determined criteria[42,44,48,49]. Because raw data were not available in one instance[47], we digitised axes and data points from the original paper using WebPlotDigitizer[50]. We transformed brain mass data from previous studies[42-46] into cranial capacities following equations in Cofran and DeSilva[51]. As we are modelling the amount of growth that occurs between a given 'starting' age and asymptotic growth cessation, results would differ minimally (if at all) based on different methods for adjusting between brain mass (in grams) and cranial capacity (in cubic centimetres or millilitres). In this case, we prioritised maintaining all the data in the same units as the fossil data (cm^3) over leaving each data set in its original units. After visually examining growth curves for modern humans, chimpanzees and mountain gorillas, we decided to cap three data sets at 40 years of age in order to limit the known impact that brain shrinkage at older ages can have on curve-fitting.[43,46,48,52] The fourth (modern human) data set included only individuals up to 18 years.[47]

We fit the data in R (R Core Development) using a non-linear asymptotic regression model with a vertical offset (SSasymp), which is a 'self-starting' function that iteratively fits a model using initial estimates of the horizontal asymptote ('Asym'), the natural logarithm of the rate constant ('lrc'), and a numeric parameter corresponding to the response value when the input is zero ('R0'). We estimated cranial capacities from the regression fit at given starting ages for Taung and calculated percentage-change values for cranial capacities between each starting age and the maximum age for each data set (in each case the growth curve had reached asymptotic stability). We then estimated adult values for Taung by increasing Taung's juvenile cranial capacity by these percentage-change values. The R code for each of these operations is presented in the supplementary material. As noted above, we produced estimates for the most realistic 3.73–3.93-year-old starting values (Table 3), but also tested the effects of different juvenile starting cranial capacity estimates (Supplementary table 1) and different starting ages (Supplementary table 2). In this study, we prioritised testing the effects of different starting juvenile cranial capacity and age estimates over fitting confidence intervals, which adds a layer of complexity that will be addressed in a follow-up study.

To assess variability in the *A. africanus* sample, we calculated coefficients of variation (CV)[53] for the *A. africanus* hypodigm with different adult estimates for Taung (Table 4), and compared these values to bootstrapped samples of adult *Gorilla gorilla* + *G. berengei*, *P. troglodytes*, and *H. sapiens* matching the sample size of the *A. africanus* sample ($n=10$ including Sts 25, $n=9$ excluding Sts 25; see explanation below), as well as to historical CV values for *A. africanus* (Supplementary table 3). We did not include cranial capacity data for the recently published specimen StW 573 from the Silberberg Grotto at Sterkfontein because its taxonomic status is still under debate, and its endocast has not yet been virtually reconstructed to correct for distortion during the fossilisation process.[54]

We also simulated *A. africanus* cranial capacity growth by looking at per cent changes necessary to grow Taung to different *A. africanus* 'target' adults, thereby simulating different models for growth increases in Taung's cranial capacity[10,11] (Table 5). We compared these percentages to values for comparative samples to assess the likelihood that Taung's remaining brain growth would be sufficient to produce target adult cranial capacity values.

Results

Adult cranial capacity estimates for Taung fall within a relatively narrow range regardless of narrowly defined starting age and choice of species- or sex-specific models (Table 3). By 3.83 years of age, cranial capacity has reached 97.5% of adult size in gorillas (100% in males, 97.8% in females), 99.8% in chimpanzees (99.5% in males, 99.8% in females), and 94.0–99.3% in modern humans (94.4–99.0% in males, 95.2–99.0% in females). Because there is so little growth remaining between 3.73–3.93 years of age and adulthood (Figures 1–2), juvenile estimates increase by only 0–26 cm^3 (Table 3) – a maximum increase of ~6.5%. There is a 3–26 cm^3 (0.75–6.48%) increase according to modern human growth curves, but chimpanzees and gorillas have, respectively, <1% and <3% growth remaining (Table 3, Figure 2, Supplementary table 1). Adult cranial capacity estimates range between 404 cm^3 and 415 cm^3 according to the gorilla curve, 405 cm^3 and 406 cm^3 according to the chimpanzee curve, and 407 cm^3 and 430 cm^3 according to the two human curves (Table 3). The two modern human growth curves differ from each other in terms of percentage-growth change and estimated adult cranial capacities, with a more prolonged growth trajectory in brains derived from 19th-century German autopsy material[46] than in a 20th-century sample of cranial capacities from an Australian research hospital[47] (Table 3, Figures 1–2). Adult cranial capacity estimates for different starting cranial capacities and ages are presented in Supplementary tables 1 and 2.

Regardless of which growth curve is used, all the adult estimates noted above place Taung at the low end of the range of adult *A. africanus* variation. Original estimates for *A. africanus* cranial capacities were fairly large (>500 cm^3 in several cases), whereas revised estimates tend to be smaller. One cranium in particular, Sts 25 (350–375 cm^3), does not appear in many comparative analyses of *A. africanus* cranial variation because it is fragmentary and still partially embedded in matrix, so its cranial capacity has been estimated by regression[30] (Wolpoff M 2018, personal communication). We tested the effect of including Sts 25 in the *A. africanus* hypodigm on CV values by running analyses with and without this specimen. Table 4 shows CV values for the *A. africanus* hypodigm. Including new adult estimates for Taung in the *A. africanus* sample produces CV values that range between 11.8% and 13.6%, which are similar to values for the sample including Holloway's[22] 440-cm^3 adult estimate but lower than CV values for samples that included larger adult estimates (Supplementary table 3). Coefficient of variation values for 404–440 cm^3 estimates in this study and others[22,28,32] can be accommodated within the range of variation for all extant samples, but larger adult estimates (>550 cm^3 and >600 cm^3 for samples that include and exclude Sts 25, respectively) fall outside the 95% confidence intervals for modern humans (Figure 3).

Table 3: Adult cranial capacity estimates for Taung produced using narrowly defined starting ages

Species	Sex	Adult estimates for starting age (years)			
		3.83		3.73–3.93	
		% Increase	Adult estimate	% Increase	Adult estimate(s)
Gorilla[42]	M	0.000	404	0.000	404
	F	2.248	413	2.087–2.421	412–414
	Comb	2.492	414	2.314–2.685	413–415
Chimp[43-44]	M	0.442	406	0.388–0.503	406
	F	0.178	405	0.153–0.207	405
	Comb	0.250	405	0.217–0.289	405
Human1[47]	M	0.978	408	0.874–1.094	408
	F	1.111	408	0.997–1.238	408–409
	Comb	0.845	407	0.753–0.949	407–408
Human2[46]	M	6.038	428	5.625–6.483	427–430
	F	4.848	424	4.498–5.227	422–425
	Comb	5.971	428	5.563–6.411	426–430

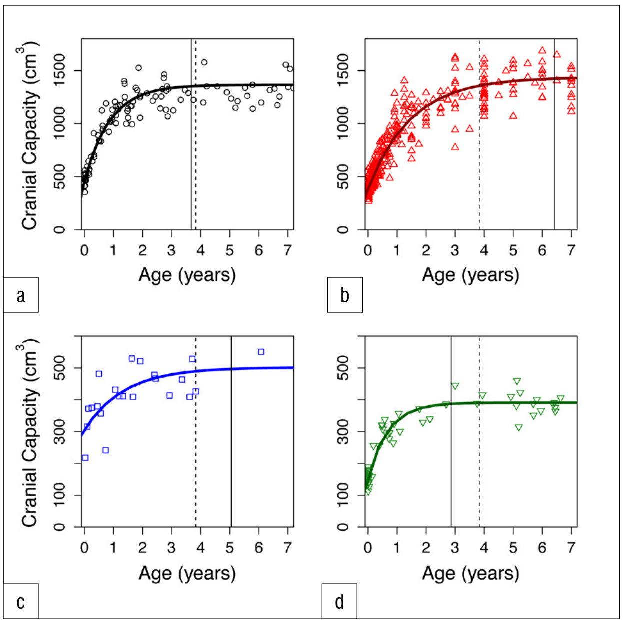

Figure 2: Close-up views showing the first 7 years of cranial capacity growth in (a,b) modern humans, (c) mountain gorillas and (d) chimpanzees. In each panel, the dashed vertical line indicates the 'starting age' for Taung and the solid vertical line indicates the point of 99% growth completion.

Table 4: Coefficient of variation (CV) estimates for the *Australopithecus africanus* hypodigm computed using different values for Taung's adult cranial capacity

Adult value	Reference/model	w/Sts 25	w/o Sts 25
		CV (%)	CV (%)
405–406	C[this study]	13.5–13.6	12.3
404–415	G[this study]; C[28]	13.4–13.6	12.1–12.4
423–430	H[this study]	13.2–13.3	11.8–11.9
440	C[22,27]	13.1	11.6
520	G,C[24]	13.7	12.1
540	C[19]	14.2	12.6
550	C,G[19]	14.5	12.9
562	H,C,G,O	14.8	13.3
570	C[Table 1]	15.1	13.6
600	G[25]	16.2	14.8
625	NR[2]	17.2	15.9
650	NR[26]	18.3	17.1
728	C (min–max size/age)[19]	22.1	21.1

C, chimpanzee; G, gorilla; H, human; O, orangutan; NR, not reported

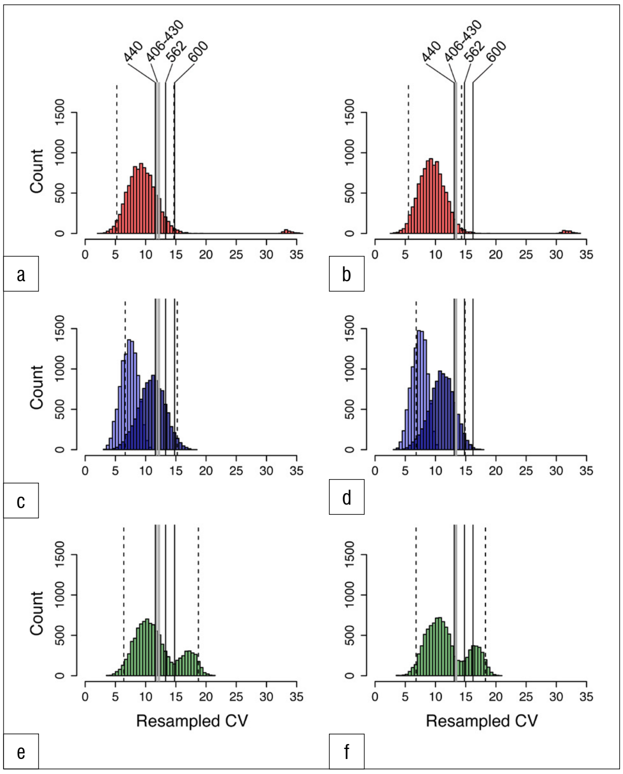

Figure 3: Resampled coefficients of variation (CVs) for (a,b) modern humans (red), (c,d) lowland gorillas (dark blue), mountain gorillas (light blue) and (e,f), chimpanzees (green) for sample sizes $n=9$ (left, excluding Sts 25) and $n=10$ (right, including Sts 25). Solid vertical lines indicate CVs for the *Australopithecus africanus* sample with different adult estimates for Taung – from left to right in each panel: 440 cm^3,[22] estimates from this study (404–430 cm^3), 562 cm^3,[34] and 600 cm^3.[25] Dashed lines indicate 95% confidence intervals for each distribution.

Discussion

Adult cranial capacities estimated for Taung with starting ages between 3.73 and 3.93 years (Table 3) ranged between 404 cm^3 (no increase) and

430 cm^3 (6.4% increase). These values are at the lower end of the adult *A. africanus* range of variation (Table 2). As expected, the largest of these adult estimates are produced by modern human growth curves. Estimates calculated using chimpanzee and gorilla growth curves ranged between 404 cm^3 and 415 cm^3 (Table 3). If *A. africanus* brain growth followed a chimpanzee trajectory as previously suggested[12,13,15,16,18,19,24,25,31,32,39], then Taung had <1% growth remaining, so 405–406 cm^3 may be the most reasonable estimate of adult cranial capacity.

Five modern estimates of Taung's adult cranial capacity are available for comparison. Based on an average value of 92% for brain growth completion prior to eruption of the first molar in hominoids[19,33,34], Holloway[22] added 35 cm^3 to Taung's juvenile cranial capacity to predict an adult value of 440 cm^3. Following the same logic we followed here, Falk[31] increased Taung's juvenile estimate using a chimpanzee brain development curve, producing estimates ranging between 404 cm^3 and 420 cm^3. Somewhat presciently, Falk[31(p.19)] wrote: ''If Taung was as old as 3.7 years, … (the) curve suggests that its adult cranial capacity had already been achieved!'' Falk and Clarke[28] estimated a juvenile cranial capacity of 382 cm^3 based on a different reconstruction of Taung's endocast, then increased this value to 406 cm^3 based on a chimpanzee growth curve. Holloway and Broadfield[29] updated Falk and Clarke's[28]adult estimate (to 390 cm^3) by setting their juvenile value to 98% growth-complete. Conroy et al.[32] replaced the averaged value for hominoid brain growth completion prior to eruption of the first molar[33] used by Holloway[22] with a different set of values based on growth in chimpanzees, increasing Holloway's 404/405-cm^3 juvenile estimate to 431 cm^3 based on a mixed-sex sample, 422 cm^3 based on a female sample, and 455 cm^3 based on a male sample. Our new estimates for Taung based on chimpanzee growth curves – 405–406 cm^3 – corroborate Falk's[31] estimates using a different data set and are similar to estimates from Holloway and Broadfield[29], but are lower than estimates from Holloway[22], Conroy et al.[32] and Falk and Clarke[28].

The range of *A. africanus* cranial capacity variation in this study, 205 cm^3 (363–568 cm^3), is fairly large compared to older studies (Supplementary table 3) because of the inclusion of two small crania: Sts 25[30] (350–375 cm^3), a small specimen which preserves the left half of the cranial base and a partial vault still covered with breccia; and a new, smaller estimate of 391 cm^3 for Sts 60[23]. If Sts 25 is excluded from the sample, the range drops to 177 cm^3, with end-points of the range defined by crania that have been digitally reconstructed with a high degree of confidence.[23] Coefficients of variation range between 11.8% and 13.6% for different iterations of the sample (Table 4), which are on par with recent studies but higher than in earlier work (Supplementary table 3).[22,27,31,34] It has been recognised previously that variability between specimens can be underestimated when regression formulae are used to estimate cranial capacities as well as when complete fossil crania like Sts 5 are used as 'templates' to reconstruct less complete crania.[34,55] Both of these conditions apply historically (Supplementary table 3). Coefficient of variation values for *A. africanus* cranial capacity (Table 4) generated in this study fall within the ranges of lowland gorilla, chimpanzee and modern human variation, but fall outside the range of mountain gorilla variation derived from limited samples (Figure 3). Adult estimates for Taung >550–600 cm^3 yield CV values outside the range of modern human variation and estimates >565 cm^3 yield CV values outside the range of gorilla variation (Figure 3). High CV values (>10%) support results based on craniofacial linear measurements.[56]

As noted above, another way to approach this problem is to estimate how much the brain would have had to grow to reach target adult *A. africanus* cranial capacities and to compare these values to growth data for hominoid comparative samples. Starting at 3.83 years of age with a 404 cm^3 cranial capacity, Taung would have needed to grow ~2% to match Sts 71's cranial capacity (Figure 4, Table 5) – a value that falls within the range of variation of two of the comparative samples (Figure 4). Setting aside for a moment Sts 25 and Sts 60 (two small specimens with adult cranial capacities smaller than Taung's juvenile cranial capacity), Taung's cranial capacity would otherwise have had to increase 7.9–40.6% to match any of the other *A. africanus* specimens and 17.6% or 26.2–40.6% to match growth in male specimens. This amount of brain growth remaining at 3.83 years of age is unlikely. In fact, to match these values, Taung would have had to have been between 1.19 and 2.63 years old based on human growth curves and 0.51 and 1.45 years old based on chimpanzee curves (Table 5) – values outside the range of ages previously suggested for Taung. If Taung grew more like a chimpanzee[12,13,15,16,18,19,24,25,31,39], then it would not have been possible to reach the upper echelons of *A. africanus* adult variation. Another line of evidence supports a small adult cranial capacity estimate for Taung. According to developmental simulations of craniofacial growth[11], Taung would have grown up to resemble Sts 71, a small-brained putative female, more closely than Sts 5 (which is either a large-brained female[35] or a small-brained male[36]) and other early hominin specimens. It is reassuring that different types of data from the brain and craniofacial region point to the same specimen as an adult target. If Taung grew according to an ape-like brain growth trajectory, then its estimated adult size and similarity to Sts 71, both in the face and neurocranium, support interpretations that Taung is a small female.[24,25,57,58]

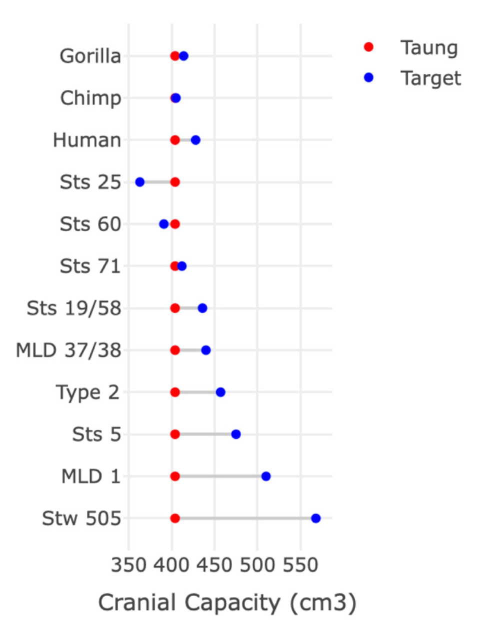

Figure 4: Dumbbell plot showing developmental trajectories necessary to grow a 404-cm^3 Taung cranial capacity to target *Australopithecus africanus* adult specimens starting at 3.83 years of age. Comparative data for cranial capacity growth in gorillas, chimpanzees and modern humans are presented at the top of the graph.

Table 5: Results for growth simulations

Specimen	Cranial capacity (cm^3)		% Change	% Target	Predicted starting age (years)	
	Target adult	Change			Chimpanzee model	Human model
Sts 25	363	-41	-10.148	111.3	–	–
Sts 60	391	-13	-3.218	103.3	–	–
Sts 71	412	+8	+1.980	98.1	2.32	3.41
Sts 19/58	436	+32	+7.921	92.7	1.45	2.63
MLD 37/38	440	+36	+8.911	91.8	1.37	2.54
Type 2	457	+53	+13.119	88.4	1.14	2.22
Sts 5	475	+71	+17.574	85.1	0.96	1.96
MLD 1	510	+106	+26.238	79.2	0.74	1.59
Stw 505	568	+164	+40.594	71.1	0.51	1.19

In this study, we followed the logic of previous studies by using modern human and African ape growth curves to estimate Taung's adult brain size. However, Taung is one of only a few *Australopithecus* juveniles with a fairly secure developmental age that can be used to test hypotheses about how the pattern and rate of hominin growth compare to growth in African apes and modern humans.[45,59,60] The results presented here rely on the assumption that brain growth in *Australopithecus* can be modelled accurately with reference to these comparative samples. We acknowledge that this does not necessarily have to be the case. It will take a combination of new fossil discoveries of juvenile specimens, new comparative data[43-47], innovative analyses[44,45,59,60], and reinterpretations of previous data and analyses[48,49,51] to test this assumption about growth and development in the genus *Australopithecus*.

Conclusions

Our results support the hypothesis that Taung was female and help to clarify the lower end of the *A. africanus* range of variation. This study focused on brain ontogeny in Taung, which is important not only in an historical sense but also because Taung is one of only a few juvenile specimens that can shed light on brain growth in *Australopithecus*. It is possible to extend this type of developmental simulation to other juvenile fossil endocasts and crania, including specimens of *Australopithecus afarensis*, *Paranthropus boisei*, *P. robustus*, *Australopithecus sediba*, *Homo habilis*, *Homo erectus* and *Homo neanderthalensis*. Evidence for early cessation of brain growth in hominoid comparative samples published here and elsewhere[42,48,49,51,59,60] brings to light the intriguing possibility that previous adult cranial capacity predictions from juvenile specimens might be overestimates.

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Authors' contributions

R.C.M. conceptualised the study, designed the methodology, validated data, performed some of the data analyses, and wrote and revised all drafts of the paper. E.Z. collated and curated data, performed data analysis, and helped revise early drafts of the paper.

Data availability

Data in this article are available as an open data set.[61]

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