

Neanderthal brain size at birth provides insights into the evolution of human life history

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From birth to adulthood, the human brain expands by a factor of 3.3, compared with 2.5 in chimpanzees [DeSilva J and Lesnik J (2006) Chimpanzee neonatal brain size: Implications for brain growth in *Homo erectus*. *J Hum Evol* 51: 207–212]. How the required extra amount of human brain growth is achieved and what its implications are for human life history and cognitive development are still a matter of debate. Likewise, because comparative fossil evidence is scarce, when and how the modern human pattern of brain growth arose during evolution is largely unknown. Virtual reconstructions of a Neanderthal neonate from Mezmaiskaya Cave (Russia) and of two Neanderthal infant skeletons from Dederiyeh Cave (Syria) now provide new comparative insights: Neanderthal brain size at birth was similar to that in recent *Homo sapiens* and most likely subject to similar obstetric constraints. Neanderthal brain growth rates during early infancy were higher, however. This pattern of growth resulted in larger adult brain sizes but not in earlier completion of brain growth. Because large brains growing at high rates require large, late-maturing mothers [Leigh SR and Blomquist GE (2007) in Campbell CJ *et al.* *Primates in perspective*; pp 396–407], it is likely that Neanderthal life history was similarly slow, or even slower-paced, than in recent *H. sapiens*.

brain growth | endocranial volume | fossil hominins | obstetrics | virtual reconstruction

Human life history is typically characterized as exhibiting an extended period of developmental immaturity. This pattern of ontogeny is hypothesized to be essential for the development of higher cognitive capabilities, as during a prolonged period of childhood the slow-growing brain is exposed to a socially complex extramaternal environment (1). Recent studies, however, challenge this view, suggesting that contrasts between the human course of brain growth and that of our closest living relatives, the chimpanzees, are less evident than previously thought. Most notably, it appears that humans achieve their large adult brains primarily through higher growth rates early during ontogeny, rather than through a markedly extended period of growth (2–4).

Evidence from various primate species now provides a comparative framework to better understand how this pattern of brain growth is linked to various aspects of life history (5). Large adult brains are associated with slow life histories (2, 6). However, the pace of life history is not set by the duration of brain growth (2, 5). For example, the age at which brain growth is completed is not correlated with the age at reproductive maturation (2, 5, 7). Nevertheless, patterns of brain growth have indirect effects on life history variables via maternal energetic constraints, as the energetic costs of large, fast-growing brains must be sustained by large, late-maturing mothers (2, 5).

It is still unclear when and how the large neonate brains and high postnatal brain growth rates characteristic of modern humans evolved within the hominin clade (species more closely related to modern humans than to any other living species), notably because the decisive phases of birth and early infancy are

only scarcely represented in the fossil record. A recent analysis of the only well preserved *Homo erectus* infant neurocranium suggested that brain growth in *H. erectus* followed a chimpanzee-like rather than a modern human-like pattern (8). However, comprehensive comparative studies do not confirm this hypothesis; rather, they indicate that modern human-like ontogenetic traits such as increased neonate brain size and postnatal brain growth rates were already present in *H. erectus* (4, 9, 10).

Additional evidence for evolutionary changes in hominin growth patterns and life history comes from dental eruption schedules, especially from the time of eruption of the first permanent molar (M1), which has been associated with the cessation of brain growth (1, 11, 12). Compared with wild chimpanzees, in which M1 erupts at ≈ 4 years (13, 14), modern humans exhibit a later schedule, with population-specific mean M1 eruption times between 4.74 and 7.0 years (15), whereas the age at M1 eruption in *H. erectus* most probably was intermediate, at ≈ 4.5 years (13). Dental microstructure analysis in a late archaic *Homo sapiens* mandible from Jebel Irhoud, Morocco suggests a modern human-like schedule of dental development (16). Similar analyses of Neanderthal teeth remain contradictory (17–20), but overall, they indicate that Neanderthals were within the range of dental developmental schedules displayed by recent populations of anatomically modern *H. sapiens* (rAMHS). Microstructural data on the pace of dental development in early AMHS (eAMHS), e.g., in the Qafzeh–Skhul sample, are not yet available.

Neanderthals assume a key role in addressing comparative questions of how patterns of brain growth evolved, because comprehensive fossil evidence permitting direct association between dental, cranial, and postcranial developmental parameters from birth to adulthood is currently available only for this hominin taxon. It has long been known that on average, absolute adult brain size was larger in Neanderthals than in rAMHS (21), and several (mutually nonexclusive) hypotheses have been proposed to explain how this was attained: through larger-brained newborns (with possible implications for female pelvic morphology and the birth process), through higher brain growth rates during early infancy, and/or through an extended period of postnatal brain growth (21, 22).

To test these hypotheses, we examined the morphology of three well preserved Neanderthal specimens that document the crucial developmental phase from birth to the 2nd year of

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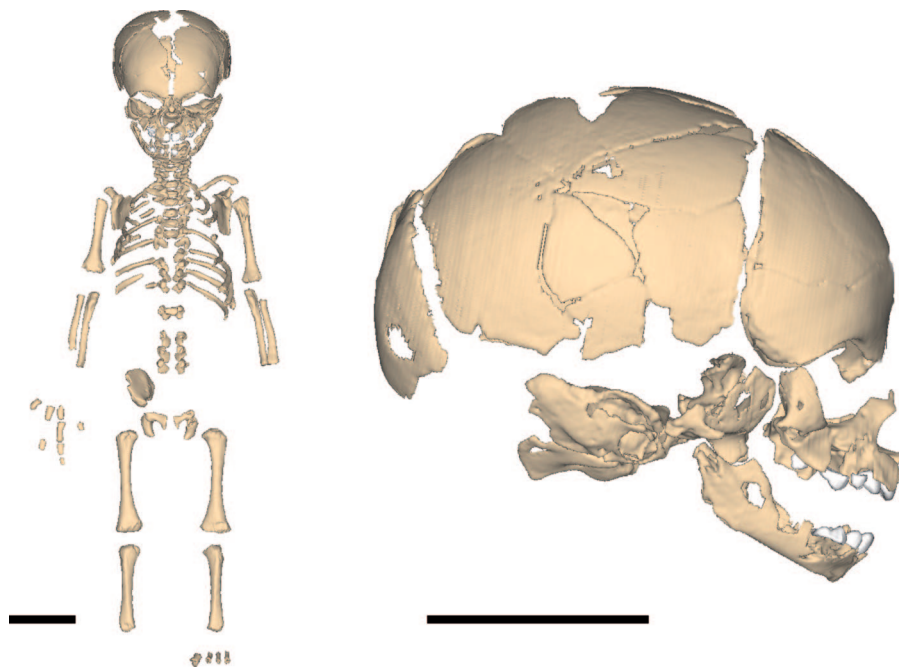


Fig. 1. Virtual reconstruction of the Mezmaiskaya Neanderthal. (A) Skeleton. (B) Skull in right lateral view. (Scale bars, 5 cm.)

postnatal life: a neonate specimen from Mezmaiskaya Cave, Russia (23, 24), and two specimens from Dederiyeh Cave, Syria with estimated individual ages of 1.6 and 2 years, respectively (25–27) [see [supporting information \(SI\) Tables 1–6](#)]. Using this evidence, we first reconstruct Neanderthal brain size at birth and adult female pelvic dimensions to assess whether Neanderthals would have been subject to similar obstetric constraints as rAMHS. Then, we search for commonalities and differences between Neanderthal and AMHS modes of early growth and development, which could hint at potential common ancestral versus novel, taxon-specific characteristics of brain growth.

Results

Virtual reconstruction (28) of the Mezmaiskaya specimen from 141 isolated but well preserved parts yielded an almost complete skull and a fairly complete postcranial skeleton (Fig. 1; [SI Text, Virtual Reconstruction of the Mezmaiskaya Specimen](#) and [Figs. S1 and S2](#)). Its morphology clearly indicates it is a Neanderthal, as does evidence from mtDNA analysis (24). Neanderthal apomorphies are a strongly projecting midface, a low position of the posterior semicircular canal of the inner ear relative to the lateral canal (high labyrinthine index), a low mandibular condyle, and a short tibial relative to femoral diaphyseal length (low crural index). Three-dimensional geometric morphometric analysis of the reconstructed cranial architecture also clearly groups the Mezmaiskaya individual with the Neanderthals (Fig. 2).

Comparative analysis of linear craniocentral and postcranial dimensions of the Mezmaiskaya specimen and of rAMHS perinatal samples (29) indicates that the Mezmaiskaya individual died between 1 and 2 weeks after birth (see [SI Text, Comparative Morphometrics of the Mezmaiskaya Specimen](#), [Table S2](#)). The reconstructed endocranial volume (ECV) of the specimen is between 422 ccm and 436 ccm. Assuming similar perinatal endocranial growth rates for Neanderthals as for modern humans [20 ccm per week (30)], the Mezmaiskaya ECV at birth was 20 ccm to 40 ccm lower than at death. Subtraction of the latter range of estimates from the former yielded an ECV at birth between 382 ccm and 416 ccm, with a mean value at 399 ccm ([SI Text, Comparative Morphometrics of the Mezmaiskaya Specimen](#)).

This figure corresponded to values obtained *in vivo* from modern human neonates [380–420 ccm (30)]. Our data thus confirm earlier hypotheses that the specific Neanderthal and AMHS morphologies developed during fetal life (31, 32) and suggest that the duration of Neanderthal pregnancy was similar as in rAMHS, assuming similar fetal growth rates.

Neonatal neurocranial size is a critical developmental and obstetric parameter in fossil and modern humans (33). To assess potential trade-offs between neonatal brain size and maternal pelvic dimensions in Neanderthals, we performed a virtual reconstruction of the fragmentary Tabun 1 female Neanderthal pelvis and simulated the Neanderthal birth process (Fig. 3; [SI Text, Virtual Reconstruction of a Female Neanderthal Pelvis](#)). Our data suggest that the Neanderthal female pelvic inlet was wider than in rAMHS, thus easily accommodating a full-term Neanderthal fetus. The reconstruction also indicates that female Neanderthal pelvic outlet dimensions might have been comparatively wide. However, due to the large neonate head, modern human-like rotational birth (in which the head of the neonate performs a quarter-turn from transverse to posteroanterior orientation during its passage through the birth canal) was the most probable option in Neanderthals. This would be in agreement with the hypothesis that rotational birth appeared during the Middle Pleistocene (34), probably in the last common ancestor of Neanderthals and AMHS.

To test whether early postnatal brain development was more rapid in Neanderthals than in rAMHS, we performed virtual cranial reconstructions of the Dederiyeh specimens ([SI Text, Virtual Reconstruction of the Dederiyeh 1 and 2 Neanderthal Infant Specimens](#) and [Fig. S3](#)). ECVs of Dederiyeh 1 and 2 are 1,096 ccm and 1,089 ccm, respectively. ECVs of the slightly older specimens from Pech de l'Azé (estimated individual age: 2.2 y) and Subalyuk 2 (3.2 y) (31) are 1,135 ccm and 1,187 ccm, respectively. Together, these data indicate that ECVs of very young Neanderthals are at the upper end of variation of rAMHS ECVs (2) at corresponding ages. Comparison of endocranial growth trajectories from birth to adulthood further indicates that on average, Neanderthal brains expanded at a higher rate and attained larger adult volumes than those of rAMHS (Fig. 4A).

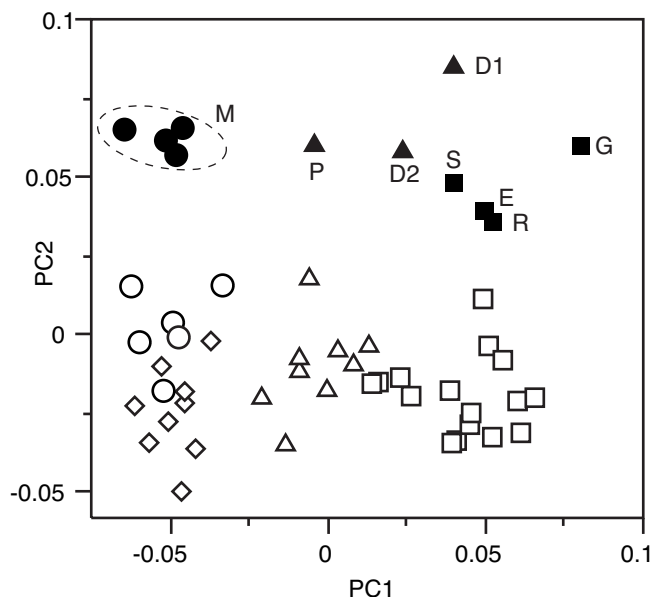


Fig. 2. Geometric morphometric analysis of shape variability in a sample of immature Neanderthal and rAMHS crania. PC1 and PC2 are the first two shape components, which account for 27% and 13% of the total shape variability in the sample, respectively. PC1 captures shape change during cranial development in both Neanderthals and rAMHS, whereas PC2 captures major differences in cranial morphology between Neanderthals and AMHS. Filled symbols: Neanderthal specimens [M, Mezmaiskaya (four reconstructive variants enclosed in 95% density ellipse); P, Pech de l’Azé; D1 and D2, Dederiyeh 1 and 2; S, Subalyuk 2; E, Engis 2; R, Roc de Marsal; G, Gibraltar 2]. Open symbols: rAMHS (mixed European/African/Asian sample). Diamonds: fetuses; circles: neonates; triangles: 0.5 to <3 years; squares: 3 years to ≤ 5.5 years.

However, Neanderthal and rAMHS trajectories coincide when related to taxon-specific adult mean ECVs (Fig. 4B), indicating that both taxa reached adult sizes within the same time period, and along equivalent trajectories. Together, these graphs show that compared with rAMHS, Neanderthals attained their larger adult brains via higher growth rates rather than via an extended growth period. The graphs also show that higher growth rates do not imply faster completion of brain growth.

Discussion

These findings permit several inferences regarding the evolution of brain growth patterns and of human life history. A neonate brain size of ≈ 400 ccm is most likely a feature of the last common ancestor of Neanderthals and AMHS, and it might represent the

upper physiological and obstetrical limit that can be attained in hominins, irrespective of the course of postnatal brain expansion. Various studies have proposed that a large neonatal brain size (≈ 300 ccm) and secondary altriciality were features already present in *H. erectus* (4, 9, 35) (estimates are summarized in *SI Text, Estimates of Homo erectus Neonatal Brain Size*). Because fetal brain growth requires substantial maternal energy investment (36), a large neonatal brain size must have represented a significant selective advantage in *H. erectus*, possibly by providing the primary substrate for complex learning tasks during childhood (4). Likewise, the high early postnatal brain growth rates of Neanderthals and AMHS compared with chimpanzees, which imply a more than twofold increase of ECV during the 1st year of life, might be a feature of their last common ancestor, and there is evidence that high postnatal brain growth rates might already have evolved in *H. erectus* (4, 9). Overall, therefore, our data support the hypothesis (4, 9) that the origins of “modern” human-like patterns of brain growth and life history must be sought relatively early during the evolution of the genus *Homo*.

High postnatal brain growth rates have been interpreted as an evolutionary extension of fetal modes of growth into early infancy (36), and this is thought to be the main ontogenetic mechanism to attain an exceptionally high degree of encephalization during adulthood (2). What are the implications of this pattern of brain growth for life history evolution? Recent analyses suggest that the correlation between brain growth patterns, adult brain size, and life history is indirect and results from maternal energetic constraints (2, 5, 7): The additional energetic costs of the fast-growing infant brain are mainly sustained by the mother, such that species investing in large infant brains that grow at high rates to reach large adult sizes require large, late-maturing mothers (2, 5).

In this context, the higher early brain growth rates and larger adult brains of the Neanderthals compared with rAMHS have interesting implications. The pattern of Neanderthal brain growth fits into the general pattern of rate hypermorphosis in this species: Compared with rAMHS, Neanderthals have been shown to attain larger adult cranial sizes and more advanced (peramorphic) shapes within a given period of ontogenetic time (31). Rate hypermorphosis might be a correlate of greater average body size in Neanderthals compared with rAMHS (21, 22). However, it does not imply earlier cessation of brain growth (Fig. 4B), nor does it imply a faster pace of life history (as was suggested in refs. 18 and 19): In light of the maternal energetic constraints hypothesis (2, 5), our results suggest that Neanderthal life history had a similarly slow pace as that of rAMHS, and probably was even somewhat slower.

What are the potential developmental, cognitive, and phyletic implications of these subtle developmental differences between



Fig. 3. Reconstruction of Neanderthal birth (crossed stereo pictures). The pelvic reconstruction combines elements of the Tabun 1 specimen (ilium, ischium, pubis) with their mirror-imaged counterparts (transparent), and replacement parts (violet) from a modern human female pelvis (sacrum, ischial spines). The Mezmaiskaya skull is visualized during its passage through the pelvic inlet. (Scale bar, 10 cm.) (See also *SI Text, Virtual Reconstruction of a Female Neanderthal Pelvis* and Figs. S4 and S5).

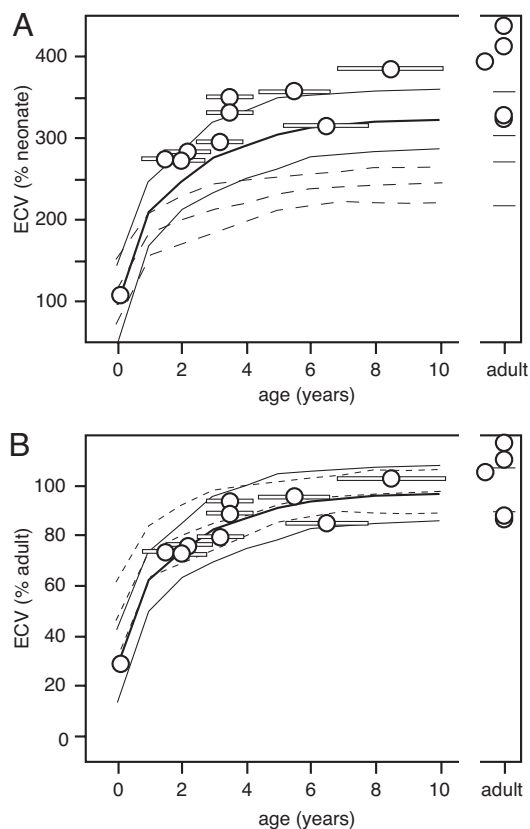


Fig. 4. Postnatal endocranial volume (ECV) growth in Neanderthals, rAMHS, and chimpanzees. (A) Growth as a percentage of neonate taxon-specific mean ECV values (Neanderthals: 400 ccm, rAMHS: 400 ccm, chimpanzees: 155 ccm). (B) Growth as a percentage of adult taxon-specific mean ECV values (1,500 ccm, 1,350 ccm, 386 ccm). Solid lines: rAMHS mean \pm SD; dashed lines: chimpanzee mean \pm SD (data from refs. 2, 48, and 49). Circles: Neanderthal individuals (from left to right and bottom to top: Mezmaiskaya, Dederiyeh 1 and 2, Pech de l'Azé, Subalyuk 2, Roc de Marsal, Gibraltar 2, Engis 2, La Quina 18, Teshik Tash, Le Moustier 1, Tabun 1, Gibraltar 1, La Ferrassie 1, Amud 1); horizontal bars: estimated range of individual age. In A, note that Neanderthals are at the upper range of the rAMHS distribution. In B, note complete overlap between Neanderthal and rAMHS trajectories, and overlap between chimpanzee and hominin trajectories after an age of 2 years.

the brains of Neanderthals and rAMHS? In recent humans, the temporal course of endocranial volume expansion is only loosely correlated with the temporal course of brain maturation (37), such that hypotheses regarding differences in cognitive development cannot be substantiated with fossil evidence. Nevertheless, several hypotheses can be proposed to explain how differences in brain growth rates between Neanderthals and AMHS evolved. High brain growth rates in the Neanderthals could represent a derived feature. This hypothesis would be in concert with the notion that Neanderthal morphology is derived in many respects. As an alternative hypothesis, high rates in the Neanderthals might represent an ancestral condition, probably shared with eAMHS as opposed to rAMHS, whose lower brain growth rates would represent a derived condition. Support for this hypothesis comes from the observation that adult brain size of eAMHS was similar in range to that of the Neanderthals (38, 39), such that it is likely that brain growth rates were similar as well.

According to this second hypothesis, the high ancestral rates of brain growth were probably reduced only relatively recently during AMHS evolution. Brain size reduction in AMHS during the late Pleistocene is well documented, and it went in parallel with body size reduction (39). We can only speculate on potential

selective constraints driving this evolutionary trend toward rate *hypomorphosis*. Evidence from recent human populations indicates that size reduction is correlated with faster life histories and higher mortality risks (40). Alternatively, brain size reduction during the Late Pleistocene could be the result of an evolutionary performance optimization. Evidence for substantial cerebral reorganization comes from Late Pleistocene AMHS (Cro-Magnon 1) and Neanderthals (La Chapelle-aux-Saints 1, La Ferrassie 1, and Forbes' Quarry 1), which had larger cerebral hemispheres relative to cerebellum volume than modern humans (41). It could be argued that growing smaller—but similarly efficient—brains required less energy investment and might ultimately have led to higher net reproduction rates. Such an evolutionary shift might have contributed to the rapid expansion of Upper Paleolithic AMHS populations into Eurasia.

The notion that genes down-regulating rates of early brain growth might have contributed to the fitness of our own species is an intriguing, but testable, hypothesis. Genes involved in the regulation of brain growth that show evidence of recent selective sweeps are of special interest (42, 43), but their known normal variants do not account for variation in brain size (44). Further research is thus necessary to clarify the genetic basis of brain and body size variation in modern humans and its relationship to life history variation.

Overall, integrating neurocranial, dentognathic, and postcranial data on Neanderthal and AMHS development reveals a complex pattern of between-taxon and within-taxon variability of life history-related variables, and indicates that hominin life history evolution was a modular (5), mosaic-like, rather than a linear, process. Inferences on the evolution of hominin life history and cognitive development must be drawn with caution, especially when drawn from isolated aspects of fossil morphology.

Materials and Methods

Data acquisition from original fossil specimens was performed with helical computed tomography (beam collimation: 1 mm, pitch: 1; slice reconstruction increment: 0.3–0.5 mm). All CT data were transferred to a high-performance graphics workstation, and virtual reconstructions were carried out according to standard procedures (28). Details are given in *SI Text*.

The taxonomic status of the Mezmaiskaya specimen was assessed with two methods: three-dimensional geometric–morphometric analysis of cranial shape (Fig. 2 and *SI Text*, *Virtual Reconstruction of the Mezmaiskaya Specimen*), and identification of autapomorphic characters (*SI Text*, *Comparative Morphometrics of the Mezmaiskaya Specimen*, Table S2). The developmental status of the specimen was assessed with comparative craniodental and postcranial data from modern human perinatal specimens of mostly European origin (29, 45), taking advantage of the fact that perinatal dental and skeletal dimensions are closely correlated with chronological age (46).

The ontogenetic series of Neanderthals comprises 15 specimens (immatures: Mezmaiskaya, Dederiyeh 1 and 2, Pech de l'Azé, Subalyuk 2, Engis 2, Roc de Marsal, Gibraltar 2, La Quina 18, Teshik Tash, Le Moustier 1; adults: Gibraltar 1, Tabun 1, La Ferrassie 1, Amud 1). Three-dimensional cranial landmark coordinate data and estimates of ECVs were obtained from virtual reconstructions of these specimens (28, 31). Individual ages at death were estimated by using modern human dental eruption scores (15, 47). All Neanderthal age estimates are given as ranges ($\pm 30\%$ for estimated ages < 2 years, and $\pm 20\%$ for estimates above that age). These ranges were evaluated by considering within-population and among-population variation of dental eruption ages in extant humans (15, 47): Eruption ages of the deciduous teeth exhibit coefficients of variation of $\pm 30\%$ around population-specific mean values, whereas population-specific mean values themselves exhibit a range of variation of $\pm 15\%$ around the interpopulation mean. For the permanent teeth, both values reach $\approx \pm 20\%$. The lower range of Neanderthal age estimates takes into account studies suggesting a fast pace of Neanderthal dental eruption ($\approx 20\%$ faster than the average rAMHS schedule, according to refs. 18 and 19). The mean to upper range of Neanderthal age estimates corresponds to the assumption of similar Neanderthal and rAMHS dental eruption schedules (20). Data for age-related modern human brain size variation are from various sources (2, 48, 49) representing European and African populations.

Geometric morphometric analysis of three-dimensional cranial shape variability in immature Neanderthals and rAMHS (Fig. 2) followed standard

procedures of shape analysis described in ref 50. (See *SI Text*, *Virtual Reconstruction of the Mezmaiskaya Specimen* for sample composition and *Table S1* for cranial landmark definitions).

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