The growth pattern of Neandertals, reconstructed from a juvenile skeleton from El Sidrón (Spain)

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Abstract:

Abstract: Ontogenetic studies help us understand the processes of evolutionary change. Previous studies on Neandertals have focussed mainly on dental development and inferred an accelerated pace of general growth. We report on a juvenile partial skeleton (El Sidrón J1) preserving cranio-dental and post cranial remains. Age at death was estimated at 7.7 years using dental histology. Maturation of most elements fell within the expected range of modern humans at this age. The exception was the atlas and mid-thoracic vertebrae, that remained at the 5-6-year stage. Furthermore, endocranial features suggest brain growth was not yet completed. The vertebral maturation pattern and extended brain growth most likely reflect Neandertal physiology and ontogenetic energy constraints, rather than any fundamental difference in the overall pace of growth in this extinct human.

Neandertals provide us with an important perspective on our own unique biology(*1*). Both modern humans and Neandertals arose from a recent common ancestor along independent evolutionary lines becoming large-brained hominins but with contrasting body forms. Developing a large brain is energetically expensive and places a constraint on somatic growth(*2*). The unusually high cost of modern human brain development is greatest during the infant and childhood periods and seems to require a compensatory slowing of childhood body growth(*2, 3*). Neandertals had larger average cranial capacity than modern humans, but little is known about the ontogenetic trajectories of brain and body underlying this difference.

Some studies have proposed that a larger brain in Neandertals can be explained through a faster rate of early postnatal growth(*4*), yet others have proposed a longer period of growth as an explanation(*5, 6*). However, in large brained hominins like modern humans and Neandertals, an accelerated pace of brain growth, coincident with accelerated somatic growth, would impose a high energetic cost(*2*). Yet, the trade-off between the different aspects of somatic and neural growth in Neandertals, particularly during the juvenile period, remains unclear.

Here, we describe a partial juvenile Neandertal skeleton from the 49 ky site of El Sidrón (Asturias, Spain). The specimen has a mixed dentition of deciduous and permanent teeth and preserves cranial, dental and postcranial remains (Fig. 1 and 2A, ST1 and 2), providing a rare opportunity to estimate an age at death from daily dental incremental markings preserved in teeth against to which compare many aspects of its dento-skeletal maturation. Chronological age is fundamental for assessing patterns of maturation in different dento-skeletal systems both within individuals and between species. This approach allowed us to ask what the probability is that this specimen would fit within or lie beyond the ranges of modern human variation and represent its own pattern of dental and skeletal maturation.

The El Sidrón cave system (Asturias, Spain) (Fig. 1C, ST1) has provided more than 2500 remains of 7 adults and 6 immature individuals belonging to a single Neandertal group(*7*) with close kinship relations(*8*). Among them, a partial immature skeleton was recovered with up to ~36% (left side) preserved. Virtually all the remains associated with this individual come from the 1 m^2 G-6 square grid of the archaeological site (ST2), importantly several of them were found in anatomical association. From the three mtDNA lineages detected within this Neandertal group, this individual belongs to the line A of the group, and was tentatively identified as the child of adult female 4 and the older sibling of infant 1(*8*).

A number of diagnostic Neandertal features are present throughout the skeleton (ST2). While ancient DNA failed to confirm the sex, group-specific evaluation of canine size and bone robusticity strongly suggests it was male (ST2). Dental development, with near-complete M1 root, would place him in the juvenile stage of hominin life history(*3*). Height and weight estimates indicate he was a sturdy individual, weighing ~26 kg and ~111 cm tall at the time of death (ST2). Bio-social markers indicate El Sidrón J1 was right-handed, with evidence that he was involved with, or learning, adult behaviors and economic activities(*9*). Apart from mild linear dental enamel hypoplasia around the age of 2-3 years, there is no other evidence of pathology. There are several post-mortem cut marks on some bones.

Age at death was first established by dental histology. Daily incremental markings in two sections of El Sidrón J1 LM^1 (see Methods, figs. S1 and S2, ST3) were used to estimate an average age at death of 7.69 years (range 7.61-7.78). Biological maturity was then assessed using modern human references for dental, skeletal and somatic maturation (ST4-7).

Dental maturity was assessed in two ways. Individuals from two reference samples of modern children of known age (n=4072 and n=6829) were assigned a radiographic stage of development for each tooth (ST4). Compared with the first sample, dental maturity of El Sidrón J1 was judged 71.7-72.1% complete. Probability density plots for mean age of transition entering each tooth stage were computed from the second sample, and El Sidrón J1 fell well within the modern human range for all tooth types represented (Fig. 2B). Skeletal maturity (SM) and skeletal age (SA) were assessed from six secondary ossification centers from the elbow, hand and wrist, and knee, applying established pediatric methods (figs. S3-S5, ST5). The SA interval ranged from 6 to 10 years, with an average of 7.62 ±2 years (Table S7). Maturity of each individual vertebra was assessed in two ways. Individuals from a sample of 106 immature modern human skeletons (of which 70 were of known age and sex) were assigned a stage of fusion of the neurocentral synchondrosis (NS) and a radiographic stage of development for the M_1 (see Methods). Probability density functions for mean age of transition entering fusion of the NS of C1 and T3-T11 were computed from the known age sample (Fig. 2C). The same procedure was applied to the total sample using mean age entering the respective M1 stage scored (Fig. 2D). Compared to chronological and dental age, maturation of each available vertebra of El Sidrón J1 fell at the extreme of the modern human range (fig. S6, ST6). Skeletal maturation (SM) of El Sidrón J1 vertebral column (fused C3-C5-C6, T1-T2 and L2-L3; unfused C1 and four middle thoracic vertebrae) fits the modern human observed sequence of NS vertebral fusion, but corresponds chronologically to younger individuals, between 4 to 6 years (Fig.2C). Percentage of adult size (PAS) attained(*10*) was calculated as a measure of somatic maturation for 53 measurements through the cranial, axial and appendicular skeleton (ST7). In comparison with a sample of 11 modern human skeletons with CA between 6.5 and 8.5 years, values of El Sidrón J1 fell within (49) or very close (4) to the modern human range (Fig. 3A). The height-for-age of El Sidrón J1 also fell within the range of modern humans(*11*) (Fig. 3B), with Neandertal body shape features already observable at 7.7 years(*12, 13*) (Fig. 3C).

Clearly visible bone resorption areas on the inner aspect of the occipital poles provide some evidence that brain expansion was still ongoing (Fig.4, ST8). Resorption activity is a characteristic of the period of brain growth in modern humans(*14*). These observations suggest that specific locations on the occipital lobe and cerebellum of El Sidrón J1 were still increasing in size. The extremely well defined imprints of the gyri and sinus impressions on the internal aspect of SD-2300, and narrow dural sinus grooves (ST8) further suggest that the encephalon was still exerting growing pressure on the neurocranium.

A consensus value for endocranial volume of ~1330 cm^3 (ST8) was computed, which represents ~87.5% of mean Neandertal adult endocranial volume (1520 cm^3). On average, modern humans achieve 90% of adult brain weight by 5 years old(*15*), and 95% by 7 years(*16*). This suggests further brain growth in El Sidrón J1 would likely have continued beyond the time expected in modern humans at 7.7 years.

The dental and skeletal maturity of El Sidrón J1 were compared with modern humans. Dental development is what one would expect for a child of his age. This contrasts with previous findings from isolated cranio-dental material that have reported a faster pace of dental development(*17, 18*). Compared with early *Homo* specimens at a comparable stage of dental development, El Sidrón J1 is at least 2.7 years older than a ~2 myr *Homo habilis* specimen, StW 151,(*19-22*) but almost identical in age (7.78 years) to a 315 kyr *Homo sapiens* specimen from Jebel Irhoud, Morocco(*23*), that shows a prolonged modern human-like period of dental developmental(*24*). At 7.7 years of age, El Sidrón J1 shows an I2 at the stage of alveolar eruption, an M2 at the stage of crown completion and an M3 crypt present in the mandible. It is, therefore, no longer possible to assume these events occurred earlier at ~6 years of age, or that M2 erupted at 8 years of age, in all Neandertals(*18*). As with El Sidrón J1, new ages at death(*18*) for younger Neandertal specimens (Engis 2, Gibraltar 2, Krapina B, Obi-Rakhmat 1) fall within modern ranges but two older specimens, Scladina and Le Moustier 1,(*18, 25*) now seem unexpectedly young. An assumed early age, 2155 days (see page 3 in (*18*)), of initial M3 mineralization(*18, 25*) or foreshortened estimates of root formation times(*26*) might explain this. Clearly, variation in Neandertal dental development would have been as great as today but may generally have tended towards the more advanced end of the modern human spectrum.

A *Homo erectus* juvenile aged between 7.6 to 8.8 years (KNM WT 15000) shows evidence of both advanced dental development and earlier attainment of body mass and stature than is typical of modern humans of a similar age(*22, 27*). However, SA and PAS are also within the modern range, given the limited level of biological resolution of SA and PAS estimation.. Growth and development in this juvenile Neandertal fits the typical features of human ontogeny, where there is slow somatic growth between weaning and puberty (*3, 28*) that may offset the cost of growing a large brain. Moreover, a slower pace of growth provides an opportunity for shifts in both the rate and timing of brain growth(*4-6, 15*). Even so, divergent morphogenetic trajectories underlying shape differences, such as brain development(*29-31*) and cranio-facial morphology(*32, 33*) can exist within this broadly human growth pattern.

The one divergent aspect of ontogeny is the timing of maturation within the vertebral column. In all hominoids the NS of the middle thoracic vertebrae and the atlas are the last to fuse, but in this Neandertal it appears that fusion occurs around 2 years later than in modern humans (or closer to M1 root closure than M1 root a quarter to half formed).

At 1.5-2 years old, the state of maturation of the complete spine of the Dederiyeh 1 child (*34, 35*) suggests that, earlier in ontogeny, when the posterior synchondroses fuse, Neandertals followed a vertebral maturation schedule similar to modern humans. The later fusion of the NS could reflect a decoupling of certain smaller scale aspects of growth and maturation in these extinct humans in the transition from the childhood to the juvenile stage. While the implications of this are unknown, it may be related to the characteristically expanded Neandertal torso(*36, 37*) or to ongoing growth of the neuraxis. Altogether these findings suggest that late Neandertal neural growth pattern exhibits a degree of modularity relative to dental development, something also detected in gorillas(*38*).

Clarifying differences and similarities in growth patterns between extincts humans, especially Neandertals, and modern humans helps us better define our own phylogenetic history. The unique pattern of vertebral maturation and extended brain growth might reflect the Neandertal physiology and ontogenetic energy constraints, rather than defining a fundamental difference in the overall pace of growth in this species of *Homo*.

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Fig. 1. El Sidrón J1 Neandertal skeleton. A: The 138 specimens, 30 of which are deciduous and permanent teeth, that compose El Sidrón J1 skeleton. Cranial, axial and appendicular elements are well represented, but the legs (especially the right one) are less represented. **B**: Virtual reconstruction of El Sidrón J1 skull and endocast based on the same cranial bone specimens shown in A. **C**: Localization of El Sidrón site in the Iberian Peninsula (Asturias, Spain), with a map of the karst system with the 25 m long Osario Gallery shadowed, and the excavated area of this Gallery. Most of the specimens of El Sidrón J1 were recovered from the G-6 1m^2grid of the excavation.

Fig. 2. Dental and vertebral maturation of El Sidrón J1. A: CT scan image of the mandible of El Sidrón J1, with the enamel in green. **B**: Probability density plots (PDP) for mean age of transition entering each mandibular tooth stage scored for El Sidrón J1 in a radiographic sample (n=6829) of modern children of known chronological age (CA). Red vertical lines represent CA of EL Sidrón J1 from dental histology(7.69 years, range 7.61-7.78). **C**: Maturation of the spine relative to CA in El Sidrón J1 and modern humans. The vertical axis represents the presacral vertebral column and age in years is represented in the horizontal axis. For each vertebra the three successive maturation stages are represented (see vertebral diagrams in the figure): stage 1, unfused posterior synchondrosis (PS) and neurocentral synchondrosis (AS); stage 2, fused PS and unfused NS; stage 3, fused PS and NS. A sample of 70 known CA skeletons was used to develop PDP for mean age of transition entering fusion of the NS for each vertebra (from stage 2 to 3). El Sidrón J1 is displayed in red, and the two oldest modern human cases (4.83 and 5.6 years) with a spine maturation similar to El Sidrón J1 (unfused C1 and middle thoracic vertebrae) are represented in black. The C1 falls within the p=0.01 shaded area of the PDP, while the four thoracic vertebrae would fall outside (T3-T4), in the p=0.05 shaded area (T5, T6, T7, T9), or under the PDP (T8). **D**: Maturation of the spine relative to dental maturation in El Sidrón J1 and in modern humans. The vertical axis represents C1 and the thoracic vertebrae, while stages of formation of the first permanent mandibular molar are represented in the horizontal axis. A sample of 106 modern human skeletons of diverse origins was

used to develop PDP for mean first molar formation stage entering fusion of the NS for each vertebra (from stage 2 to 3). The vertical red line, representing complete root formation of the first permanent molar of El Sidrón J1, falls in the p=0.05 area in all PDP.

Fig. 3. Somatic maturation and size-by-age of El Sidrón J1.**A**: The percentage of adult size (PAS) of El Sidrón J1 in comparison with 11 modern human skeletons with CA between 6.5 and 8.5 years (ST7). L: Length variables, including bones from the appendicular and axial skeleton contributing to stature (i.e. vertebral body height). W: Width variables, including diaphysis and epiphysis from the appendicular and axial (articular widths, diaphyseal circumferences, vertebral body widths). C: Craniofacial and Central Nervous System-associated variables from cranial bones, mandible and vertebrae. Variables listed in ST7. **B**: Femoral lengths of El Sidrón J1 and a Neandertal ontogenetic series(*17*), with 80 modern human skeletons with CA 0-9 years, with fitted quadratic models (Neandertals, R^2=0.968; modern humans, R^2=0.952). **C**: Clavicle length of El Sidrón J1 and a Neandertal ontogenetic series(*18*), with 51 modern human skeletons with CA 0-9 years, with fitted quadratic models (Neandertals, R^2=1; modern humans, R^2=0.889). 1: La Ferrassie 4/Le Moustier 2, 2: La Ferrassie 4b/La Ferrassie 4, 3: Mezmaiskaya, 4: Kiik-Koba 2, 5: Shanidar 10, 6: Dederiyeh 2, 7: Dederiyeh 1, 8: Roc de Marsal 1, 9: La Ferrassie 6, 10: Cova Negra, 11: Amud 7.

Fig. 4. Occipital bone of El Sidrón J1 with reference grid and color coded remodeling activity map superimposed. All pictures were taken with light reflected microscope at 20x magnification. Each image is framed with its corresponding color code of histological activity (blue: bone deposition; pink: bone resting deposition; green: bone resorption; orange: erosion/abrasion of taphonomic origin) and connected to its anatomical location. Alphanumeric legend indicates grid reference.During the process of growth remodeling, osteoblastic activity (formation: blue color) usually exceeds osteoclastic activity (resorption: green color), resulting in

differential growth of the bone. Deposition areas are characterized by the presence of collagen fiber bundles and insertion of Sharpey's fibers, while resorption areas are recognized as anisotropic resorption bays (Howship's lacunae). Bone deposition (blue) is easily appreciated by collagen fiber bundles, at times changing direction forming a wavy impression (1B, 4A). Resting deposition can be identified by dense and uniform bright surface in which deposition of bone matrix masks other histological features, including collagen fiber and Sharpey's fibers (4D, 5D). Insertions of Sharpey's fibers are quite spread in the deposition surfaces (2B, 5D). A well-defined reversal line can be seen in 3C, and an example of taphonomic alteration (e.g. scratches) is appreciated in 3B.