Response to Comment on "The growth pattern of Neandertals, reconstructed from a juvenile skeleton from El Sidrón (Spain)"

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The comment by DeSilva challenges our suggestion that brain growth of the El Sidrón J1 Neandertal was still incomplete at 7.7 years of age. Evidence suggests that endocranial volume is likely to represent less than 90% adult size at El Sidrón as well as Neandertal male plus Krapina samples, in line with further evidence from endocranial surface histology and dural sinus groove size.

DeSilva (1) challenges one of several con- clusions we drew from the analysis of the El Sidrón J1 skeleton (2)—namely, the suggestion that the brain of this juvenile Neandertal was still growing at the time of his death (7.7 years old). The main objective of our research on the El Sidrón J1 skeleton was to present a study of growth and maturation of a Neandertal juvenile from an organismic per- spective, rather than focusing on one specific region or system such as the dentition or crani- um. DeSilva (1) seems to agree that we presented a "rich, whole-body treatment of El Sidrón J1," although he then writes that "an emphasis was made in the paper—and widely reported by the science media (2)—that at 7.7 years of age, this individual had only achieved 87.5% of its total brain volume, and was therefore still growing its brain."

We would prefer to limit our response to the findings and interpretations that we presented in the report, without reference to the remarks expressed and emphasized in the media. Basically, we do not agree that undue emphasis was made in the paper regarding an extended period of brain growth in Neandertals based on the es- timation of the endocranial volume (EV), which is the variable studied by DeSilva. We studied the pattern of growth and maturation of the teeth, postcranium, spine, body, and cranium. For the latter, we considered three types of information: surface histology, the size of the dural sinus grooves, and the EV. What we really emphasized were the following points: (i) The growth and maturation of the dentition and postcranium fell well within the modern human range, and thus we did not observe a fundamental difference in the overall pace of growth in comparison with modern hu- mans. (ii) One divergent aspect of ontogeny is the timing of maturation of the spine. (iii) On the basis of the three types of aforementioned ob- servations, the brain of El Sidrón J1 could still be growing. (iv) The maturation of the spine, together with ongoing brain growth, could point to an extended period of growth and maturation of the neuraxis.

The review of EV estimations in Neandertals by DeSilva contributes to the ongoing debate about the rate and duration of EV growth in Neandertal ontogeny (3, 4). Variation in sample size, accuracy, and comparability of different measurement techniques of EV remains an issue in all comparative studies of Neandertals. For the sake of clarity, we address the questions raised by DeSilva using only the values of EV provided by him (1). DeSilva presents successive different combinations of specimens in order to provide

Neandertal averages. It is interesting to note that as we restrict the initial Neandertal sample ac- cordingly to fit the characteristics of the El Sidrón sample, the percentage of adult EV attained by El Sidrón J1 decreases, as shown in Table 1. When the five male Würm Neandertal specimens are considered, the percentage of adult EV attained by El Sidrón J1 would be 81.79%. According to DeSilva, to restrict the comparison to adult male Neandertals is questionable because of problems with sex estimation, and although we agree with this general concern in paleoanthropology, we offer this comparison in order to present the whole range of possible estimations. We also agree with DeSilva that the Krapina fossils could be included in the reference sample for meth- odological reasons, and in this case (Würm males and Krapina adults), the percentage of adult EV attained by El Sidrón J1 would be 87.7%. If we consider all the comparisons included in Table 1, the average of percentage adult size attained by El Sidrón J1 is 90.67%.

In addition to this debate focused on direct estimations of EV, in our report we also included a second method for estimating the EV derived from the isolated occipital bone, which we briefly summarize here. A significant lineal relationship was found between the size of the occipital bone (geometric morphometric centroid size) and the endocranial volume in modern humans ($n = 20$; $y = 104.8581x – 243.6349$; $P = 0.0016$; $r = 0.6736$; $r2 = 0.4537$). The fitted lineal function in seven mostly male Würm Neandertals ($y = 153.56x – 953.5652$; $P = 0.0598$; $r = 0.7350$; $r2 = 0.5403$; table S33 in our report) yields a Neandertal adult mean ± 2SD of 1499 ± 270 cm3. The pre- dicted value of 1253.2 cm3 for El Sidrón J1 (spec- imen SD-2300) lies at the lower end of this interval (1228.6 to 1769.4 cm3), whereas the value of 1448 cm3 for El Sidrón adult occipital SD-1219 is close to the mean. The EV of El Sidrón J1 esti- mated by this method represents 86.5% of the adult occipital from El Sidrón (SD-1219). Withthe data used, the predicted value for J1 would be unlikely for an adult Neandertal male, al- though it is clear that predictions derived from this method must be considered as relative esti- mations of EV.

As mentioned, beyond the discussion on EV, we supported our suggestion of ongoing brain growth with other observations. The presence in El Sidrón J1 of inner occipital resorption areas, the smallest widths of the dural sinuses in a large hominin sample, and extremely fresh neural re- lieves are not conclusive by themselves, but they support our interpretation of potential continued brain growth. When considered together with the observations on spine maturation, we sug- gested that Neandertal neural growth and mat- uration might be extended in comparison with modern humans.

We agree that using isolated specimens and cross-sectional data is not the best methodology to infer growth and maturation—a problem that pervades paleoanthropology. Our study surely is a first step toward a more comprehensive understanding of the absence or presence of onto- genetic differences between two Homo species that successfully interbred. Detecting any potential differences with certainty will probably require the complete analysis of many Neandertal subadult skeletons, both known and yet to be discovered.

REFERENCES
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Table 1.

Neandertal endocranial volumes and percentage of adult size attained by El Sidrón J1. All values come from DeSilva (1).

Sample	EV (cm3)	Percentage of El Sidrón J1
DeSilva table 1,	1388	97.4
Rosas et al. table S32 with DeSilva values	1438	94
Würm	1459	92.5
Würm and Krapina	1437	93.9
Male Würm	1626	81.79
Male Würm and Krapina	1515	87.7