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EVOLUTIONARY BIOLOGY

Early development of the Neanderthal ribcage reveals a different body shape at birth compared to modern humans

Daniel García-Martínez^{1,2,3*}, Markus Bastir², Asier Gómez-Olivencia^{4,5,6}, Bruno Maureille¹, Liubov Golovanova⁷, Vladimir Doronichev⁷, Takeru Akazawa⁸, Osamu Kondo⁹, Hajime Ishida¹⁰, Dominic Gascho¹¹, Christoph P. E. Zollikofer¹², Marcia Ponce de León¹², Yann Heuzé¹

Ontogenetic studies provide clues for understanding important paleobiological aspects of extinct species. When compared to that of modern humans, the adult Neanderthal thorax was shorter, deeper, and wider. This is related to the wide Neanderthal body and is consistent with their hypothetical large requirements for energy and oxygen. Whether these differences were already established at birth or appeared later during development is unknown. To delve into this question, we use virtual reconstruction tools and geometric morphometrics to recover the 3D morphology of the ribcages of four Neanderthal individuals from birth to around 3 years old: Mezmaiskaya 1, Le Moustier 2, Dederiyeh 1, and Roc de Marsal. Our results indicate that the comparatively deep and short ribcage of the Neanderthals was already present at birth, as were other skeletal species-specific traits. This morphology possibly represents the plesiomorphic condition shared with *Homo erectus*, and it is likely linked to large energetic requirements.

INTRODUCTION

Prenatal and early postnatal growth and development are crucial to understanding the adult size and shape of the different anatomical regions because of the large number and high rate of size and shape changes occurring in the human body during those phases (1–5). Also, from an evolutionary point of view, prenatal and early postnatal ontogeny are decisive because evolution happens via phylogenetic modification of the ontogenetic processes that occur mostly in those phases (3, 6, 7).

Adult morphologies can vary because of interspecific differences in the shape of an anatomical element at the moment of birth that are caused by differences in the prenatal ontogenetic trajectories or because of differences in the shape of an anatomical element that arise after birth that are caused by differences in the postnatal ontogenetic trajectories, either concerning their orientations, lengths, or a combination of both (1). Roughly speaking, if morphological differences are found at birth and the postnatal ontogenetic pattern is equal in the two species, their ontogenetic trajectories will be parallel. Conversely, if they have a similar morphology at birth but show differences in the postnatal ontogenetic pattern, their ontogenetic trajectories will be divergent (1–3). This distinction is important because

parallel postnatal ontogenetic trajectories between two closely related species could point to a consistency of genetic regulation of that anatomical element (1). In addition, the fact that a morphological feature is already present at birth will suggest that it is a relevant taxonomical characteristic not caused by developmental plasticity.

Ontogenetic trajectories in Neanderthals

Despite genetic similarities that allowed for admixture (8), there is a well-established consensus that Neanderthals showed significant morphological differences when compared to modern humans (MHs) in the cranium and postcranium (9, 10). Some of these differences are plesiomorphic inherited traits from their Early or Middle Pleistocene ancestors, while others are present exclusively in Neanderthals (autapomorphies) (11, 12). Neanderthals were highly encephalized (4, 13, 14) and heavy-bodied hominins (15, 16) requiring large amounts of energy (17–19). It has been proposed that to fulfill these energetic demands, the Neanderthal thorax had a large estimated total lung capacity (19) and a different thoracic shape that included a shorter, slightly deeper, and mediolaterally larger chest with more horizontally oriented ribs and a more invaginated thoracic spine, compared to MH (19–26).

The very specific Neanderthal traits found throughout the skeleton (i.e., those different in size and shape from MH) are the result of differences present at birth and/or differences in the postnatal ontogenetic pattern, which may vary in different skeletal regions. However, despite being the best-known extinct human species, there are only a few studies on the Neanderthal postnatal ontogeny due to the paucity of well-preserved subadult fossil remains, especially of the postcranium. Nonetheless, despite the limited record, some patterns have been proposed, providing evolutionary insights. For example, MH and Neanderthal femoral length followed similar growth patterns with no differences at birth (27). Other anatomical traits (e.g., general cranium shape, clavicle length, and femoral and tibial robusticity) seemed to be different at birth between the two species and followed parallel ontogenetic trajectories, resulting in different adult shapes (2, 27, 28). Last, in the case of the mandible (2, 29) and the

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brain (4, 13, 14), Neanderthals and MH had not only different shapes at birth but also divergent growth patterns. However, there are still many anatomical regions that are relatively well known in the Neanderthal adult record for which there are few ontogenetic studies, which is the case of the thorax (24, 25). Methodological improvements in virtual reconstruction and statistical missing data estimation have improved the knowledge of the adult Neanderthal thorax (26). However, ribs and vertebrae from perinates and infants are smaller and more fragile, which represents a major challenge during the study of the early postnatal ontogeny of the Neanderthal thorax. So far, only basic descriptions and inventories of fossil ribs and vertebrae have been available (30, 31), and artistic license was used when ribcage reconstructions of subadults were made (4).

Apart from this very basic knowledge, the little information we have about this issue comes from (i) descriptive anatomy of the prenatal (32) and early postnatal ontogeny of MH (33, 34) and (ii) late postnatal ontogeny of the Neanderthal first ribs (20). Research on prenatal ontogeny of the MH ribcage has found that all thoracic dimensions (anteroposterior, craniocaudal, and mediolateral) are modified during the fetal period to result in the newborn ribcage (32). All these dimensions develop differently in the different rib levels: For example, all levels have roughly the same anteroposterior relative length in early fetuses, whereas the upper and central ribs of late fetuses are much deeper, relatively, than the lower levels (32). This is consistent with research on later postnatal ontogeny of the human ribcage, which has found that, after birth, the upper and lower thorax have a differential development that gives rise to the adult ribcage of MH, which is relatively expanded in the cranial part and narrow in the caudal part (33, 34). This differential development, controlled by Hox gene expression (35), is crucial because it indicates that slight modifications during development at different rib levels would cause different ribcage morphologies. This could have evolutionary implications for understanding the adult thorax not only in our own species but also in other hominins such as Neanderthals. In addition, the only study that tackled the postnatal ontogeny of the thoracic skeleton in this species was carried out by Bastir *et al.* (20). They found divergent ontogenetic trajectories in the first ribs of MH and Neanderthals, the latter showing less curved first ribs in the youngest specimen (La Ferrassie 6) and along the entire postnatal ontogeny when compared to MH. However, we do not know to what extent this could be extrapolated to the entire thorax.

In this study, we used virtual and statistical methods to reconstruct the ribcage of four young Neanderthal specimens (Table 1), identifying potential differences with MH in thorax morphology affecting the evolution of body shape and influencing respiration. Specifically, we reconstructed the ribcages of perinatal individuals of Mezmaiskaya 1 [M1; 7 to 14 days (4)] and Le Moustier 2 [LM2; <120 days (36)] and infant individuals from Dederiyeh 1 [D1; 1.41 years (37)] and Roc de Marsal (RdM; 2.54 years (31)). We also provided the first three-dimensional (3D) morphological assessment of the early postnatal ontogeny of the MH ribcage during the decisive first 3 years of postnatal life to serve as a comparative baseline. Because of the differences in this anatomical region in adults, we tested whether Neanderthal thorax morphology was already different from that of MH at birth.

RESULTS

Final reconstructions of the four Neanderthal ribcages are shown in Fig. 1 and text S1.

Table 1. Centroid size and age-at-death estimation compared to previous age-at-death assessments.

	CS	Age at death (previous studies)	Age at death (this work)
M1	943.95*	7–14 days (4)	–
LM2	1115.28*	<120 days (36)	<75 days
D1	1675.93†	1 year and 4–6 months (37)	–
RdM	1971.49*	2.5–4 years (41)	ca. 3 years [due to the similar dental development compared to Engis (39)]

*Estimated using regression equations from TVC (text S1). †Directly measured.

MH and Neanderthal thorax size and growth patterns during early postnatal ontogeny

The ribcage of MH shows a rapid growth during the first ca. 100 days of life, which changes to a slower growth rate afterward (Fig. 2). For Neanderthals, we measured the centroid size (CS; see Materials and Methods) directly from the thorax reconstruction in D1 and using the costal size and thorax CS correlation (double-checked in the latter 3D reconstruction) in the rest of the individuals (Table 1 and text S1). When plotted with respect to their estimated age (or age ranges), the perinatal M1 individual fits well within MH size variation; the infant D1 is within this variation but above the MH regression line. For the two other Neanderthals, their current age-at-death ranges are wide but consistent with growth patterns observed for M1 and D1. The growth trajectory based on the mean Neanderthal age-at-death estimates roughly overlaps with that of MH during the first ca. 100 days but then diverges, with the Neanderthals' growth being slightly faster. This overall pattern, using CS as a proxy for thoracic size, is also present on the tubercle-ventral chord (TVC) of individual ribs (text S2), a classic measurement for evaluating costal size (22, 25).

When compared to MH of the same CS (as a proxy of volume), the four Neanderthal reconstructions showed metric differences that were consistent in all of them regardless of their age at death (text S3). All the Neanderthals had a craniocaudally shorter thoracic spine and a deeper thorax anterior-posteriorly when compared to MH of equivalent CS. However, the thorax width of the Neanderthals exceeded that of MH only in the oldest individuals (D1 and RdM), but not in the youngest ones (M1 and LM2; Table 2 and text S3).

Developmental changes in the ribcage during early postnatal ontogeny in MH and Neanderthals

During early postnatal ontogeny, MH changes from a ribcage that is relatively narrow in the cranial part and extremely wide in the caudal part toward a ribcage that is volumetrically expanded in the cranial part and still wide in the caudal part (text S4). Perinatal Neanderthals (M1 and LM2) also have an upper ribcage that is relatively narrower than in older specimens (D1 and RdM), who have a more globular ribcage with similar widths at the upper and lower thorax (Fig. 1). In addition, the exploration of the 3D warps associated with standardized CS in Neanderthals and MH shows consistent interspecific

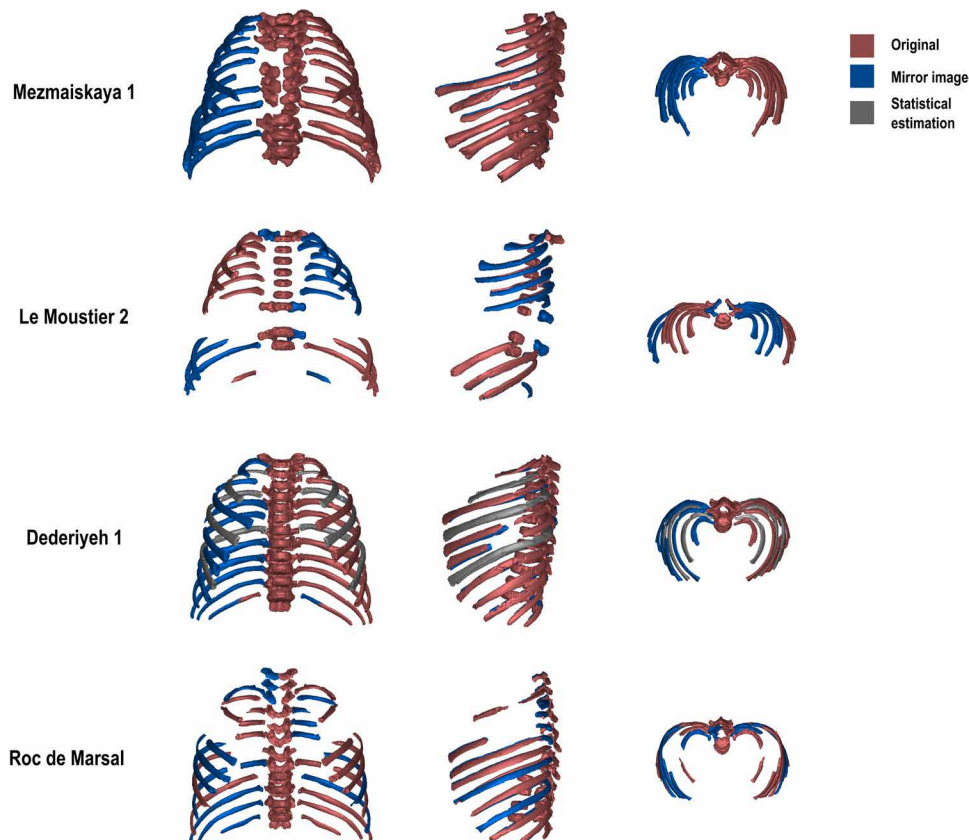


Fig. 1. Final virtual reconstruction of the four Neanderthal individuals studied here. Bones that are preserved in the original specimen are shown in red, whereas mirror images are shown in blue and statistical estimations in gray (only for D1 specimen).

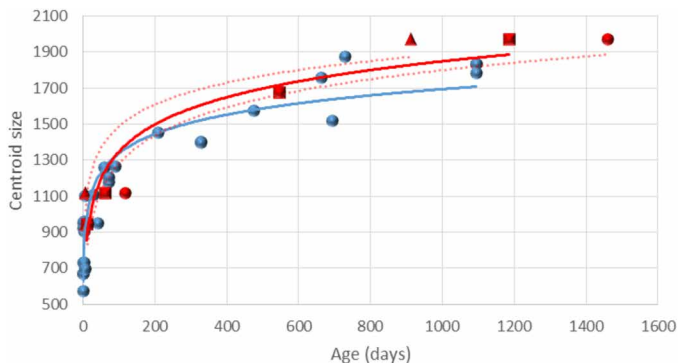


Fig. 2. Logarithmic growth trajectories for MH $y = 136.81 \ln(x) + 709.07$; $r^2 = 0.861$ and Neanderthals. For the latter, we plotted minimum (triangles), average (squares), and maximum (circles) ages proposed in the literature. The growth trajectories of MH and Neanderthals are displayed in blue and red color, respectively, and Neanderthal trajectories representing minimum and maximum ages are displayed as dotted lines. Note that individuals with very similar CS are overlapped, e.g., the case of Ind27 and Ind29.

morphological differences throughout the postnatal ontogeny studied here (Fig. 3). The Neanderthal thoracic spine is relatively shorter, and from the third rib onward, the ribcage of the Neanderthals is relatively deeper than in MH. In the most complete individual (D1), it is also possible to observe that its spine is more invaginated within

Table 2. Selected metric measurements (in millimeters) in the 3D reconstructed ribcages of fossil specimens compared with standardized MHs for the CS of each fossil specimen. Thorax width was quantified at the level of rib 7, thorax depth is at the level of T5 from the spinous process to the distal end of rib 5 (average of both sides), and anterior spine length is quantified as the distance between the anterior-superior-most point of T1 body and the anterior-inferior-most point of the T12 body. Standardized values of MHs were calculated on the basis of linear regression of classic measurements on full thorax CS (text S4). Smaller Neanderthal values are labeled with the symbol *, whereas larger values are labeled by the symbol #.

	Anterior spine length	Thorax depth	Thorax width
M1	74.63*	69.17#	86.19*
MH CS = 943.95	79.08	66.81	86.61
LM2	87.82*	81.23#	102.86*
MH CS = 1115.28	92.94	78.77	103.22
D1	130.46*	120.79#	158.36#
MH CS = 1675.93	138.29	117.90	157.55
RdM	153.09*	141.03#	188.62#
MH CS = 1971.49	162.20	138.54	186.19

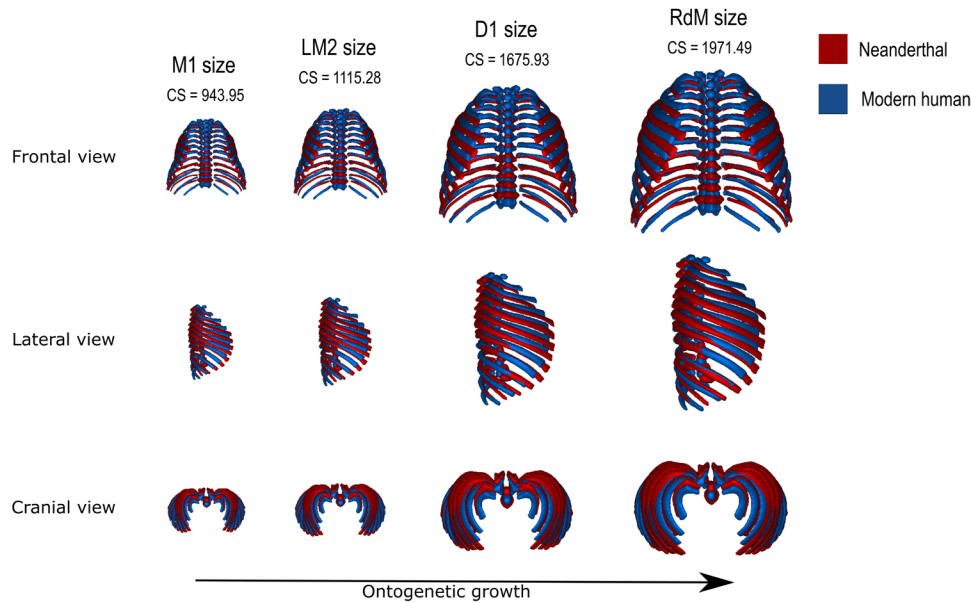


Fig. 3. Neanderthal ribcages (red) compared to MH (blue) of their respective same CS in Procrustes superimposition observed in different views. To better visualize the morphological differences between species, we warped a complete MH infant thorax 3D model into the coordinates of the fossil specimens using EVAN Toolbox software. Human standardizations were calculated using a multivariate regression of shape on the size of the 29 individuals from the comparative human sample. Perinatal Neanderthals (M1 and LM2) have an upper ribcage that is relatively narrower than in older specimens (D1 and RdM), who have a more globular ribcage, with similar widths at the upper and lower thorax (Fig. 1). Besides, the Neanderthal thoracic spine is relatively shorter, and from the third rib onward, the ribcage of the Neanderthals is relatively deeper than in MH. In the most complete individual (D1), it is possible to observe that this spine is more invaginated into the thorax than in MH. In this individual, it is also possible to assess that, when compared to MH of the same CS, the mid-lower ribs are relatively larger than the uppermost and lowermost ones. Regarding the orientation of the ribs in the sagittal plane, different declination can be observed at different rib levels, with the upper Neanderthal ribs (from 1st to 6th) more declined than in MH and the lower ribs (from 10th to 12th) more horizontally oriented. Rib torsion also contributes to interspecific differences because Neanderthal central ribs (from 6th to 8th) of early individuals have a stronger torsion (understood as spiraling) than in MH.

the thorax than in MH (text S5). In this individual, the mid-lower ribs are relatively longer than the uppermost and lowermost ones, when compared to MH of the same CS.

Regarding the orientation of the ribs in the sagittal plane, a different declination can be observed at different rib levels, with the upper Neanderthal ribs (from 1st to 6th) being more declined than in MH and the lower ribs (from 10th to 12th) more horizontally oriented. Rib torsion also contributes to interspecific differences because Neanderthal central ribs (from 6th to 8th) of early individuals have a stronger torsion (understood as spiraling along the rib axis) than in MH. Last, other minor differences can also be observed in Fig. 3. For example, both the upper (from 1st to 5th) and very lower (from 10th to 12th) regions of the Neanderthal ribcage are slightly wider than in MH, and their first ribs are less curved than in MH (see details in text S5).

When the morphological ontogenetic variation between species is explored in a Procrustes form space (size + shape; see Materials and Methods) principal components analysis (PCA; Fig. 4), we observe that the PC1 versus PC2 projection (96.57% of the variance of the sample) captures ontogenetic variation along the first PC and interspecific variation along the second PC. During postnatal ontogeny (from the PC1 negative values to the positive ones), the “pear-shaped” ribcage of newborns changes into a more globular ribcage in infancy. The main changes, which occur in the upper ribcage, are likely related to changes in the rib orientation at the costovertebral joint and the ossification at the distal end of the ribs. The morphological variation between humans and Neanderthals (observed along PC2 and

independent of ontogenetic state) shows that the latter present more caudally oriented ribs and spines that are shorter and more invaginated within the thorax than in MH. Last, the relative maximum depth is found in the central-upper thorax in MH, whereas in Neanderthals it is found in the central-lower thorax.

This clear ontogenetic and interspecific distribution along PC1 and PC2 allows us to evaluate a hypothetical ontogenetic linear regression for each species, which is almost parallel between humans and Neanderthals during early postnatal ontogeny. The slope of the Neanderthal linear regression ($a = -0.008$) is clearly within the confidence interval (CI) for their regression slope ($a = -0.031$; CI, -0.065 to 0.032). This implies that although Neanderthals and MH are different at birth, the morphological trend is similar in both species during early ontogeny, with each species undergoing a volumetric expansion of the ribcage and a lower thorax still relatively wider than the upper one but to a much lesser degree than in adults.

DISCUSSION

Most authors agree that prenatal ontogeny and the first years of postnatal ontogeny are key to understanding species-specific features of hominin anatomy that we find in adults because of the prominent growth and development during those phases (1, 3–5, 29). Our results allow us to explore this issue in the Neanderthal ribcage, shed light on their body shape evolution and bioenergetics, and have implications for understanding the evolution of the thorax in MH.

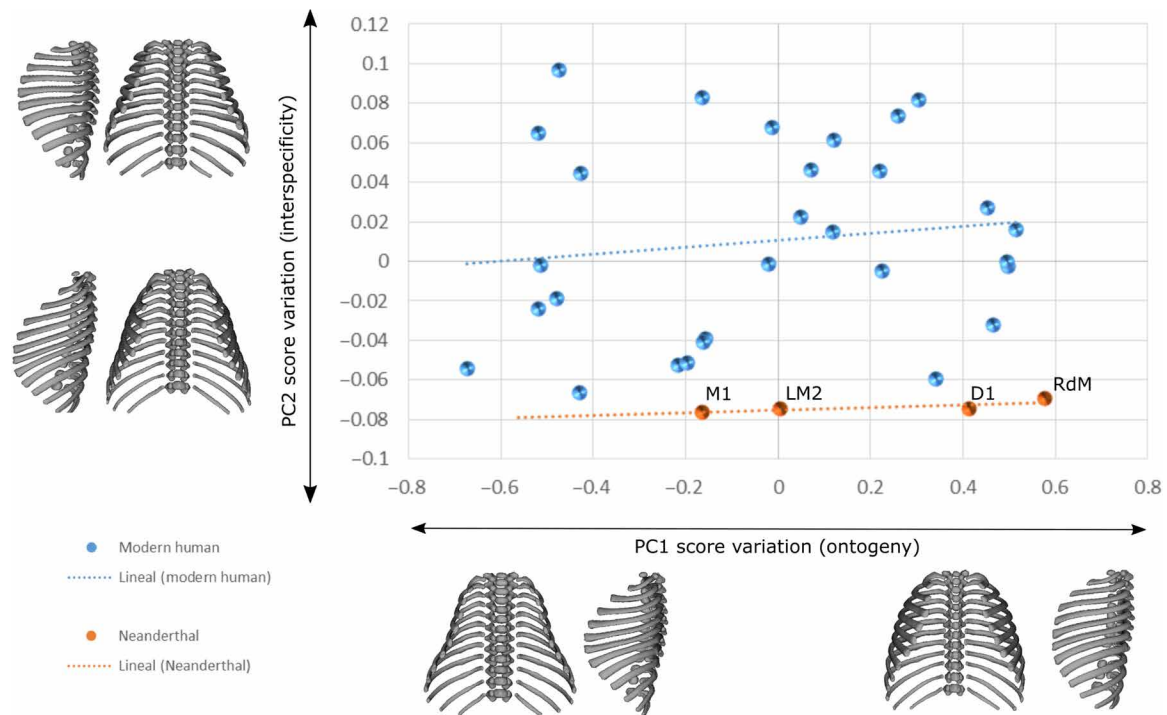


Fig. 4. PC1 versus PC2 scores (96.57% of the variation of the sample) representing ontogenetic variation in MH (blue dots and dashed line) and Neanderthals (orange dots and dashed line), as well as the 3D warps of the morphological variation associated to the variation in the PC scores. PC1 represents mainly ontogeny, whereas PC2 represents interspecific variation.

Neanderthal early thoracic growth

Previous research on Neanderthal adult thorax size found that the upper Neanderthal ribs were similar (25) or even smaller than in MH (20, 24), whereas the central-lower ribs were significantly larger (22, 24, 25). While the Neanderthal costal skeleton as a whole was large, relative to the humeral length (25), the general volume (using CS as a proxy) was similar to MH due to both the shorter thoracic spine and the morphology resulting from the articulation of the costal skeleton with the spine (24, 26).

In general terms, and when compared to MH, our study shows that Neanderthals had similar general thorax sizes around birth but reached slightly larger thorax sizes in infancy (D1 and RdM), suggesting a higher thorax growth rate during the first few years of postnatal life. This would be consistent with the notion of a more rapid life history for Neanderthals based on evidence of dental histology (38–40) and also dental development in individual D1, thought to be a 2-year-old because of the development of their incisors (41) despite the estimated histological age at death of ca. 1 year and 5 to 7 months (37). On one hand, we can hypothesize that because the overall adult Neanderthal ribcage was similar to that in MHs, if this rapid growth rate was not limited only to the early postnatal ontogeny and occurred later, the adult size in Neanderthal thoraces would have been reached earlier than in MH. On the other hand, other researchers have proposed that juvenile Neanderthals had a slower fusion of some elements of the thoracic spine compared to MH (27), which could suggest a slowdown of the thoracic growth or a dissociation of the ribcage size increase and the fusion of some spinal elements in Neanderthals. Dissociations of dental development, somatic growth, and life history variables are not infrequent (42), and a more comprehensive approach would include the study of the den-

tal development along with the development of other anatomical elements such as the ribcage or the brain from the same individuals.

In our study, we built a growth trajectory based on the studied individuals (Fig. 2) using an accurate age-at-death estimate for M1 and D1 individuals and a relatively large range for LM2 and RdM. For these individuals, we have used the mean value of the upper and lower limits of the age range. In the case of RdM, the value used (1186 days; i.e., 3.24 years) was similar to the estimated histological age of Engis [3 years (39)], which shows a similar pattern of development to RdM (43). In addition, on the basis of the MH growth trajectory (Fig. 2), we consider it likely that LM2 was less than 75 days old. Other researchers found that for some skeletal values such as humeral length or femoral length, this specimen had slightly lower values than M1 (44), so a slightly younger age for LM2 could be attributed compared to M1.

Neanderthal early thoracic development

Once the M1, LM2, D1, and RdM ribcages were reconstructed, the form space PCA assessment still yielded an almost parallel growth trajectory. This is consistent with the parallel growth trajectories from other Neanderthal anatomical traits, such as the general cranium shape, clavicle length, or the femoral and tibial robusticity, features that present interspecific differences already at birth (2, 27, 45).

Our size results based on linear measurements of the ribcage show that shorter and deeper thoraces in Neanderthals are very constant throughout the early postnatal ontogeny, but absolute thorax width changes early in postnatal ontogeny. This is based on the perinatal M1 and LM2 individuals, whose ribcages are absolutely narrower than those of their MH counterparts of the same CS (M1 < MH by 0.5%, LM2 < MH by 0.3%), and on infant D1 and RdM individuals,

whose ribcages are absolutely wider than those of their MH counterparts (D1 > MH by 0.5% and RdM > MH by 1.3%). The most complete individual, D1, provides us with two additional features also observed in Neanderthal adults: the relatively longer mid-thoracic ribs compared to the uppermost and lowermost ribs and the presence of a more invaginated spine within the thorax than in MH. The latter feature is also suggested by the more dorsally oriented transverse processes of the lowermost thoracic vertebrae of RdM.

Apart from the traditional measurements, the size based on CS confirms that perinatal Neanderthals already exhibited significant differences in thorax morphology when compared to MH (Figs. 1 to 4). Not only the best-preserved Neanderthal (D1) but also the rest of the individuals that were estimated using an MH reference had several features that are species-specific and distinguish them from MH: the relatively shorter thoracic spine, the deeper thorax, and the (slightly) wider ribcage, features that are also observed in adults (21, 24, 26). The relatively short thoracic spine, which is related to relatively shorter vertebral bodies, was already noticed in the D1 individual (45), and despite the limited adult Neanderthal fossil record, it has been proposed as a specific feature of the adult thoracic vertebrae (21) or the thoracic spine as a whole (26). Our results are also consistent with previous research on body form of LM2, M1 (44), and D1 (45) that hypothesized that perinatal Neanderthals already had a wide body, with a long pubis and robust long bones. Last, this is in concert with the results from the Neanderthal La Ferrassie 6, where the authors hypothesized that the elongation of the Neanderthal pubis was a feature expressed early in ontogeny (46). These features, present at birth and constant in early postnatal ontogeny, would make the trunks of very young Neanderthals volumetrically larger compared to MH, which would underline the presence of different body shapes in Neanderthals throughout their entire ontogeny (15–17).

Ontogenetic trajectories of the Neanderthal and MH ribcage

Our results support that, for the very early postnatal ontogeny (0 to 3 years), Neanderthal and MH thoraces followed an almost parallel ontogenetic trajectory, which is in agreement with research on the skull and clavicle (2, 4, 5, 27, 47). However, when looking at other anatomical regions, previous authors suggested divergent trajectories for anatomical traits such as the shape of the brain and mandible (1, 13, 14).

In our specific case, it could be argued that Neanderthals and MH followed parallel or just slightly divergent (not statistically significant) trajectories because we used an MH reference for the Neanderthal growth simulations. The inclusion of older subadult Neanderthal individuals [e.g., El Sidrón J1 (27) and Teshik-Tash 1 (48)] will complement our current understanding of their postnatal thorax growth. For the moment, our ontogenetic interpretations should be restricted to these very early stages. It is possible to find stronger morphological differences in later postnatal ontogeny of the thorax because it is a structure influenced by body composition and energy requirements, which are strongly modified during adolescence, at least in MH (49).

Implications and conclusions

Together, the current evidence indicates that most of the skeletal differences between the Neanderthal and MH thorax are already largely established at birth, the Neanderthal thorax being deeper and shorter than that of MH and showing a strongly invaginated spine at a young age. This is consistent with research on the Neanderthal

postcranium of M1 and LM2 that found that, with some exceptions (e.g., radius/humerus proportions), the skeletal differences between Neanderthals and MH were largely established by the time of birth. The fact that the characteristic differences between Neanderthal and MH thoracic morphologies are already present at birth indicates species-specific differences in the prenatal developmental trajectories and their genetic underpinnings. This early determination of shape might fit with paleogenetic studies proposing a selective sweep of RUNX2, a genetic fixation of genes somehow related to ribcage morphology (8).

Note that the thoracic differences between adult Neanderthals and MH were already noted by some 20th century anthropologists, who referred to adult Neanderthals as “barrel-chested.” However, this is confusing because the ribcages of *Homo erectus* from Nariokotome and the MH ribcage have also been called “barrel-shaped” [see references in the work by Franciscus and Churchill (22)]. Thus, while the term barrel-shaped may be useful for differentiating the thoracic bauplan of the late members of the genus *Homo* from that of great apes [traditionally described as having “funnel-shaped” ribcages (50)], it is limited when differentiating between taxa such as MH, *H. erectus/ergaster*, or Neanderthals. We consider the ribcage of the latter two species to be characterized by a “short and deep barrel” shape, whereas the MH thorax is characterized by a “tall and flattened barrel” shape (46), consistent with their respective somatypes (15).

In addition, the fact that morphological differences in the ribcage are already present at birth confirms that these are relevant taxonomical characteristics that are not caused by developmental plasticity. This is consistent with the idea that the Neanderthal body plan is likely plesiomorphic in the genus *Homo*, inherited at least from their Middle Pleistocene ancestors from Sima de los Huesos (11, 12, 51) if not already from *H. erectus* (46). Stocky bodies (high body mass index, combined with nonmodern body proportions) have been proposed for some Early Pleistocene hominins, based on the information from the Gona pelvis (52) and supported by recent estimations of Kenia National Museum-West Turkana (KNM-WT) 15,000 body size (53). Previous researchers also noticed in Neanderthal ribs and vertebrae some plesiomorphic features likely inherited from *H. erectus*, such as the rounder cross section, the lack of torsion of the lower ribs (22, 54, 55), and the more dorsal orientation of the transverse processes (21, 55). A recent reconstruction of the Nariokotome ribcage shows that thoracic features such as the deep and short thorax of Neanderthals are already found in *H. erectus/ergaster* (55). This evidence supports the hypothesis that the Neanderthal thorax, linked to a massive body, is (at least partially) inherited from their Early Pleistocene ancestors (text S6). As a consequence, the MH thorax, narrow and shallow with twisted ribs and narrow rib cross sections (12, 22, 54), would be derived within the *Homo* clade (text S6), suggesting that the Neanderthal ribcage morphology is a phylogenetically informative feature and not caused by developmental plasticity.

Last, the ontogenetic evidence presented here lends further support to the hypothesis that Neanderthals had high metabolic demands: Their distinctive thoracic morphology was already present at birth, and thoracic growth was faster than in MHs (10, 17, 19). Large piriform aperture/nasal bones in the RdM, LM2, D1, and D2 individuals have been observed (14, 31, 41, 56), which would be in concert with a high airflow into the respiratory system through a more projecting face in Neanderthal perinates compared to MH (14) and the hypothetical functional integration between the cranial and postcranial

respiratory system (57). In addition, the morphological differences in the Neanderthal thorax found at birth, paralleling their adult state, would show a body shape characterized by shorter, deeper, and (slightly) wider trunks compared to MH of the same size. This would be consistent with previous authors on Neanderthal postcranial anatomy that proposed that perinatal individuals such as M1, LM2, or La Ferrassie 6 would be characterized by a very large ilium relative to femur length, similar to what is observed in adults (44–46).

MATERIALS AND METHODS

Background information regarding the Neanderthals studied here can be found in the corresponding literature (31, 36, 58, 59). Data acquisition of original thoracic material from the Neanderthals D1 and M1 was performed with helical computed tomography (CT; beam collimation, 1 mm; pitch, 1; slice reconstruction increment, 0.3 to 0.5 mm). The LM2 specimen was scanned at the Musée National de Préhistoire in Les Eyzies-de-Tayac-Sireuil using the portable industrial μ CT scanner (BIR ACTIS 225/300) of the Max Planck Institute for Evolutionary Anthropology Leipzig (MPI-EVA), with an isotropic voxel resolution of 70 μ m. The RdM Neanderthal axial skeleton was scanned with an Artec Spider 3D scanner (www.artec3d.com/). The comparative human sample comprises 29 forensic individuals whose ages comprised from birth to 3 years old that were scanned at the Institute of Forensic Medicine of the University of Zurich (text S7). All individuals were scanned in the supine position for postmortem virtual autopsy. Individuals with obvious pathologies affecting skeletal thoracic form were excluded. Because individuals were cadavers, any uncertainty caused by kinematic status while scanning was automatically ruled out. Before analysis, all CT data were anonymized to comply with the Helsinki declaration, and the approval to use these preexisting CT scans for our research was obtained from the Ethical Committee of the Canton of Zurich (BASEC-Nr. Req-2019-00987).

Ribcages were segmented through a semi-automatic protocol for Digital Imaging and Communication On Medicine (DICOM) images using the 3D Slicer software (www.slicer.org/) and subsequently reconstructed as 3D models. These 3D models were imported into Viewbox4 software (www.dhal.com) for (semi-) landmarking using existing protocols (60). Thoracic morphology was quantified through 20 homologous 3D landmarks and semilandmarks on ribs 1 to 10 and 19 3D landmarks and semilandmarks on ribs 11 and 12. Four landmarks were measured on each thoracic vertebra, and two on the sternal manubrium. The thoracic morphology was described by 524 landmarks and sliding semilandmarks (60). Semilandmarks were slid along their corresponding curves concerning the fixed landmarks to minimize bending energy from each individual to the consensus of the sample (61). Missing data in both the MH and the Neanderthals were estimated following a thin-plate spline approach (62). In the reference Neanderthal for the developmental simulations, D1, only 17% of landmarks or semilandmarks were missing, and they were estimated using MH as a reference. Once the whole set of coordinates was obtained, the landmarks were submitted to the Procrustes superimposition and analyzed following standard procedures for size and shape analysis (61). The size was studied through the CS, calculated as the square root of the sum of squared distances of all the landmarks from their centroid (61).

The TVC was used to address differences in linear measurements at different levels of the ribcage. Specifically, we studied the TVC of

the 1st, 8th, and 10th ribs of the sample, because those levels were the best represented in the Neanderthal sample. Also, because the 8th and 10th levels are used for full thorax CS estimations of M1, LM2, and RdM, it is important to know whether we are under- or overestimating those sizes using costal size versus full thorax size correlations. These differences were assessed using a biplot of the log-transformed distributions of TVC versus age with the 95% confidence ellipse and the convex hull distribution for the MH. In the case of the M1, LM2, and RdM Neanderthals, we plotted their estimated range of maximum and minimum age from the literature (4, 36, 37, 43). Virtual reconstruction of the thoracic elements and ribcage of the D1 subadult ribcage was done in the first place because it was the best-preserved individual of the four Neanderthals studied here. The reconstruction was done through virtual (e.g., mirror image) and statistical methods (text S1), previously validated and published (26, 63). Once the ribcage of this individual was reconstructed, we carried out forward/backward developmental simulations (64) using D1 as a reference for reconstructing the other three ribcages (LM2, M1, and RdM), based on the ontogenetic trajectory of our comparative sample of 29 recent humans from birth to 3 years (text S7).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/41/eabb4377/DC1>

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Early development of the Neanderthal ribcage reveals a different body shape at birth compared to modern humans

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