CRANIAL ONTOGENY IN NEANDERTAL CHILDREN: EVIDENCE FROM NEUROCRANIUM, FACE AND MANDIBLE

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ABSTRACT

This study aims to integrate the child Neandertal craniofacial morphology of Dederiyeh 1 and 2 into the developmental context of Neandertals and modern humans, and check two inconsistent hypotheses on the postnatal developmental trajectories between the two groups, a common parallel pattern or a different directional pattern. Craniofacial morphology is considered as a complex of three anatomically separated modules of neurocranium, face and mandible. These modules roughly correspond to separate developmental units and thus convey different functional demands. We first compare growth profiles (changes in size) of each module, which discloses the general growth pattern of the cranium, and then investigate shape changes expressed in the form of ratio of the module sizes. Allometric relationship of the size describes the direction of the shape change, i.e. a major vector of developmental shifts. The general growth of the Neandertal cranium is categorized into two patterns; one is found in the neurocranium and the face, approximately parallel to that of modern humans, the other is found in the mandible, showing accelerated growth in two to four-year-old Neandertals. The accelerated growth of the mandible in Neandertals is confirmed in the shape changes and supported with the significant difference in the allometric slopes. Considering the mandibular measurements as those expressive of robustness, the accelerated pattern of mandibular growth may relate to masticatory function. Although the basic ontogenetic pattern of Neandertal cranium seems common with that in modern humans, the different developmental modules may indicate a minor shift in rate or timing of any developmental events and accumulation of these minor shifts would result into differences in adult morphology.

INTRODUCTION

When and how modern-human patterns of growth appeared in human evolution is one of the most intriguing issues in paleoanthropology. Recent expansion of research interests in this field has produced many studies concerning the growth of fossil hominids and proposed several hypotheses based on a variety of skeletal systems ranging from the tooth enamel structure to the gross morphology of craniofacial and postcranial bones (Ramirez-Rozzi and Bermudez de Castro, 2004; Lieberman et al, 2002; Dean et al., 2001; Lovejoy et al., 1999; McCollum, 1999). Among them, studies of craniofacial ontogeny have become popular with the application of geometric morphometric methods and have provided important data for postnatal changes in shape among closely related species or subspecies (Cobb and O'Higgins, 2004; Krovitz, 2003; Ackermann and Krovitz, 2002; O'Higgins and Collard, 2002; Strand Vidarsdottir et al., 2002; Williams et al., 2002, 2003; Ponce de Leon and Zollikofer, 2001).

These studies have produced two different interpretations for the patterns of postnatal craniofacial ontogeny between the closely related groups. One argues the presence of population specific facial shape trajectories during the postnatal period (Cobb and O'Higgins, 2004; O'Higgins and Collard, 2002; Strand Vidarsdottir et al., 2002) while the other emphasizes prenatal appearance of the difference and the maintenance of a common facial developmental trajectory during the postnatal period (Zollikofer and Ponce de Leon, 2004; Ackermann and Krovitz, 2002; Ponce de Leon and Zollikofer, 2001). Both scenarios are in agreement with each other in that a basic ontogenetic pattern is common among the groups and the group-specific differences detected in the adult form appear early in ontogeny, probably in the prenatal period. However, the former insists on the significant degree of difference in the directions of developmental shifts between the groups, while the latter considers it to be minimal and estimates a parallel postnatal developmental course.

This paper aims to check these inconsistent interpretations by comparisons of craniometric data between Neandertals and modern humans. We set three anatomically separated modules of neurocranium, face and mandible as separate developmental units, each of which can be considered to harmonize with a different functional demand. This is because the craniofacial morphology can be considered as a complex of modules, especially in the context of growth and development. We investigate changes of the size of each module, changes of the shape into the ratio of each module size, and also allometric relationships among them. Most of the above mentioned studies use a method of geometric morphometrics and thus tend to focus on changes of shape. However, all these steps are essential to a total understanding of growth and development in general and indispensable for visualizing the similarity or dissimilarity in craniofacial ontogeny between Neandertals and modern humans.

MATERIALS AND METHODS

Neandertal children used in this study consist of 13 specimens with the age of about 2 to 10 years (Table 1). The specimens with the most initial stage of development are Dederiyeh 1 and 2 from Dederiyeh Cave, Syria (Akazawa and Muhesen, 2003) and this with the most advanced stage is Teshik-Tash 1 of the pre-adolescent stage (Weidenreich, 1945). Because of the small sample size of Neandertals, we should put aside considerations of the possible temporal and/or regional differences in the sample, as well as those between sexes. The age at death was recorded as given in the data in the original and many research papers, as listed in Table 1 (Dodo et al., 2003; Ishida and Kondo, 2003), which were largely based on the developmental stages of dental calcification and tooth formation. Difficulty of age estimation of fossil remains has been discussed elsewhere (Wolpoff, 1979; many others). Neandertals might have had different tooth formation pattern and relative timing from modern humans (Tompkins, 1996). In addition, age estimates inevitably have standard error because timing of dental formation and tooth eruption show a normal variation curve. We have always been mindful of the uncertainty and have paid attention to interpretation of the analysis when age estimates were used in growth study of fossil remains (Kondo and Ishida, 2003).

Table 1. Child Neandertal skulls used in this study

Specimen	Age(years)	Sources
Dederiyeh 1	2	Dodo et al. (1998, 2003)
Dederiyeh 2	2	Akazawa et al. (1999); Ishida and Kondo (2003)
Pech de l'Aze	2.5	Ferembach (1970); Faerman et al. (1994)
Roc de Marsal	3	Madre-Dupouy (1992); Tillier (1983a)
Subalyuk 2	3	Pap et al. (1996)
Barakai	3	Faereman et al. (1994)
Archi	3.5	Mallegni and Trinkaus (1997)
Molare	3.5	Mallegni and Ronchitelli (1989)
Devil's Tower	4	Tillier (1982)
Engis 2	4	Tillier (1983b)
La Chaise 13	4	Tillier and Genet-Varcin (1980)
La Quina 18	7	Martin (1926)
Teshik-Tash 1	10	Weidenreich (1945)

Comparative samples of modern humans included Japanese and European children of known sex and age. We collected original data of 69 modern Japanese samples from several Medical Schools in Tokyo, Sendai and other regions (Dodo et al., 2003; Wakebe, 1990). Modern European child samples were derived from the Spitalfileds collection in the Department of Palaeontology of the Natural History Museum in London.

Cranial and facial measurements were recorded using the methods of Bräuer (1988) and Dodo et al. (2003) in order to express major cranial, facial and mandibular morphology (Table 2). However, the selection of measurements was under restriction of availability in fossil specimens. The craniometric data of several fossil specimens including Dederiyeh 1 and 2, Pech de l'Azé, Roc de Marsal, and Devil's Tower, and the comparative modern samples were taken by us, while those of the other fossil specimens were cited from the previous reports (Table 1). In addition, estimated values, including Dederiyeh 2 (Ishida and Kondo, 2003) and Devil's Tower (Stringer et al., 1990), were used in order to increase sample sizes of Neandertal children.

Table 2. Craniofacial measurements used in this study.

	Abbreviation
Neurocranium	
maximum cranial length	GOL
maximum cranial breadth	MCB
basion-bregma height	BBH
$(GOL \times MCB \times BBH)^{1/3}$	geomCr
Face	
biorbital breadth	BOB
nasion-prosthion height	NPH
$(BOB \times NPH)^{1/2}$	geomF
Mandible	
symphysis height	symHT
symphysis thickness	symTH
corpus height	corHT
corpus thickness	corTH
$(symHT \times symTH \times corHT \times corTH)^{1/4}$	geomM

In order to consider a cranium as a complex of three developmental and functional modules, we investigated separately each of the neurocranium, face and mandible in terms of growth and development, and also explored the allometric relationships among them. The size of each module was defined as geometric means of several measurements (Table 2); the geometric mean of the neurocranium was calculated from maximum length and breadth, and basion-bregma height; that of the face from biorbital breadth and nasion-prosthion height; that of the mandible from symphysis height and thickness, and corpus height and thickness. The size of each module was then used as a unit of growth, and as a unit of standardization of size in analyses of shape changes. In other words, we considered the cranial growth in general as a combination of the growth of each unit (size vs. age), the cranial development as changes in proportion between the units (ratio vs. age), and the cranial allometry as it appeared in the relationship between the units (size vs. size).

We assessed allometric relationships among the modules in terms of directions of the line fitting in the allometric space. After drawing reduced major axis (RMA) lines against each of the Neandertals and modern humans, we compared the directions (the slope values) of the lines and tested the difference by bootstrap resampling of the modern humans.

In order to compare growth and development between Neandertals and modern humans, we calculated a relative measure of individual variation from the average growth or developmental trajectories of modern humans. First, we applied locally weighted regression smoothing (LOESS) to modern human scatter plots and calculated the residuals, i.e., the deviations of all the data from the smoothed curve. After confirming the normal distribution of the modern residuals in the Shapiro-Wilk normality test, we calculated the deviations from the LOESS line for each fossil specimen and carried out t-test and Wilcoxson rank-sum test between Neandertals and modern humans.

RESULTS

We first present the results on the general growth (size change) of the skull, second the general development (shape change) of the skull, and in the last present the allometric relationship (size vs. size) between the modules.

General growth of the skull

The growth of the skull was presented in changes of the size of the three cranial modules of neurocranium, face and mandible (Figure 1). The growth trajectories of the neurocranium and the face show a sigmoid curve. Here the trajectory of Neandertals and modern humans seems almost parallel. The Neandertal specimens are always above the average of the modern humans, indicating a hypermorphic growth pattern, although the degree of difference is not consistent between the neurocranium and the face. Statistical results indicate that the difference in the neurocranium is significant with the level of 5% while that in the face is less than 1% level of significance (Table 3). The growth trajectory of the mandible shows a high linearity. The Neandertal trajectory looks steeper than that of modern humans with the highly statistically significant difference between the two (Table 3).

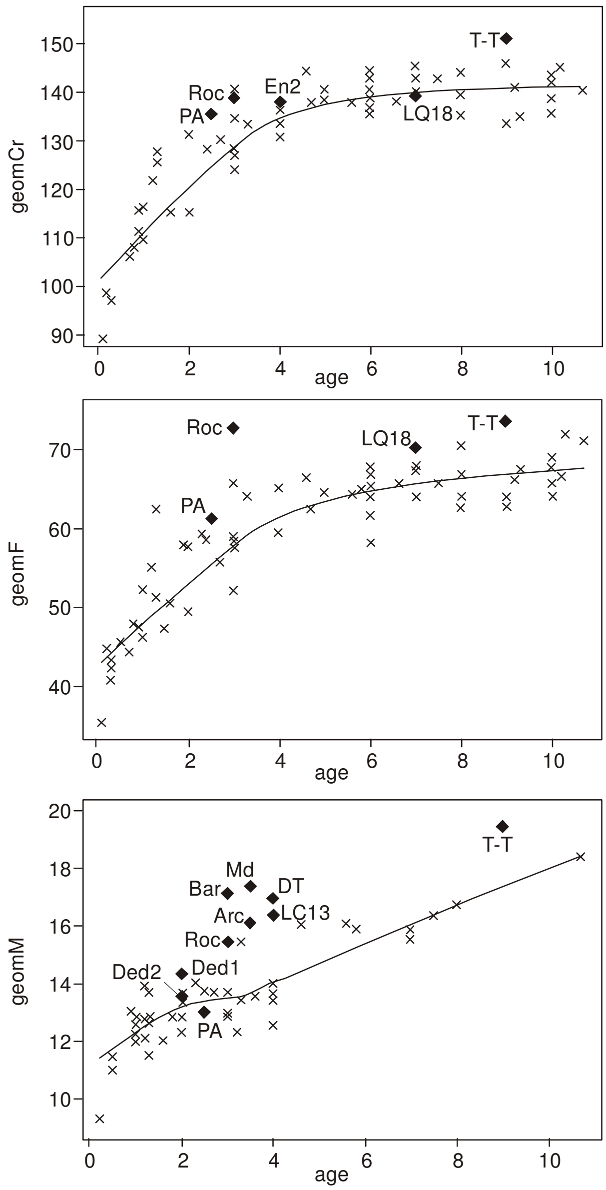

Figure 1. Growth trajectories (changes in size) of the neurocranium (geomCr, top), the face (geomF, middle), and the mandible (geomM, bottom). Abbreviations: Ded1 and Ded2, Dederiyeh 1 and 2; PA, Pech de l'Azé; Roc, Roc du Marsal; En2, Engis 2; LQ18, La Quina 18; T-T, Teshik-Tash 2; Bar, Barakai; Mol, Molare; Arc, Arcy; LC13, La Chaise 13; DT, Devil's Tower

Table 3. Statistics for growth trajectories (size changes) of neurocranium, face and mandible

	Shapiro-Wilk Normality test	Neandertals vs. modern humans		
		T-test		Wilcoxon rank-sum
		df	t	
geomCr	0.987 ns	68	–2.40 *	–2.19 *
geomF	0.969 ns	71	–4.24 ***	–3.14 **
geomM	0.980 ns	59	–6.64 ***	–3.89 ***

Significant level: ns – not significant; * < 0.05; ** < 0.01; *** < 0.001

General development of the skull

The general development of the skull was presented as changes in proportion of the three modules (Figure 2 in the left column). The proportion of the face and the neurocranium (geomF/geomCr, Figure 2, top left) linearly increases with age, being indicative of the faster growth of the face than the brain during the postnatal period. The supposed trajectory of Neandertals looks parallel to, and always greater than, the modern humans in the proportional value with the significant difference (Table 4). This means that a characteristics of the big face relative to the neurocranium develops early in ontogeny, at least prior to the age of two, and the difference keeps its degree during the postnatal period. In other words, it is plausible that the postnatal developmental course of the face/neurocranium proportion is common between Neandertals and modern humans.

Table 4. Statistics for developmental trajectories (shape changes) of neurocranium, face and mandible

	Shapiro-Wilk Normality test	Neandertals vs. modern humans		
		T-test		Wilcoxon rank-sum
		df	t	
geomF/geomCr	0.984 ns	64	–4.27 ***	–2.79 **
geomM/geomCr	0.988 ns	22	–0.77 ns	ns
geomM/geomF	0.877 *	22	2.27 *	ns

Significant level: ns – not significant; * < 0.05; ** < 0.01; *** < 0.001

The proportion between the mandible and the neurocranium gradually increases with age (geomM/geomCr, Figure 2 middle left). The Neandertal values widely scatter over the variation of the modern humans and thus show no significant difference (Table 4), while the rate of the change in Neandertals seems greater.

The relationship between the mandible and the face is roughly stable with age in the modern humans (geomM/geomF, Figure 2 bottom left). The Neandertal specimens exhibit two extreme positions; younger three are below the modern average while the older one is beyond it. A hypothetical developmental trajectory of the Neandertals is steep, although the group-averaged difference is not statistically significant (Table 4).

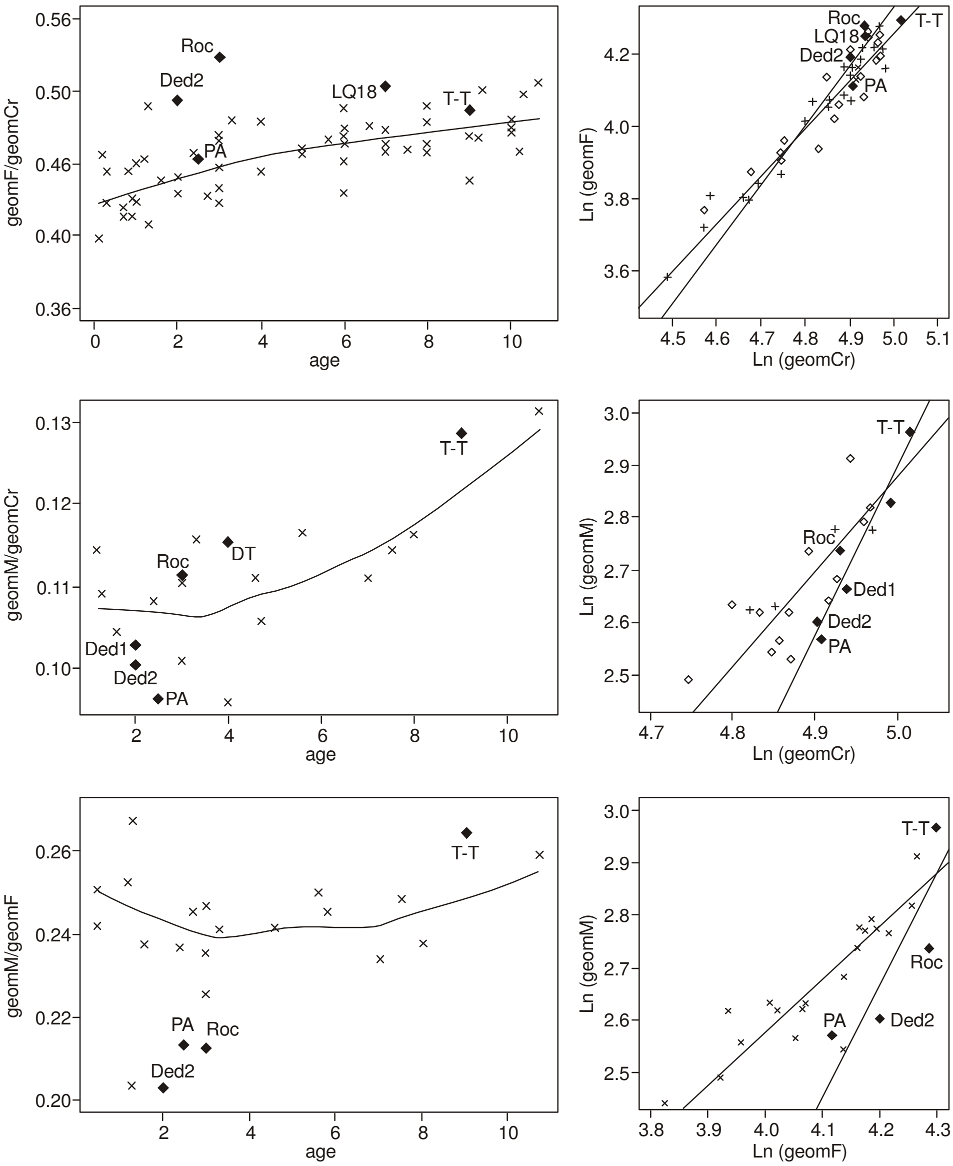

Figure 2. Shape trajectories (proportion of the module size, left column) and allometric relationship; top (right): face vs. neurocranium, middle (right): mandible vs. neurocranium, bottom (right): mandible vs. face. Abbreviations are the same in Figure 1

Allometric relationship

In order to clarify the growth and developmental patterns between the modules, we observed the allometric relationships (Figure 2, right column). We can see here a relative growth between the selected modules, and thus we can check the difference in the growth pattern between Neandertals and modern humans. The different growth pattern of the modules is synonymous with the different developmental trajectories in the shape space (the proportion of the modules).

The different combination of the modules exhibits different degrees of dissimilarity in the allometric space. In the case of the neurocranium vs. the face, the Neandertal specimens occupy a larger end but fall within the range of variation of the modern humans. The directions of the RMA lines are almost parallel. Although the slope value for the Neandertals exceeds the bootstrap derived confidence limit (Table 5), it is probably due to the small range of distribution as well as the small sample size of the Neandertal specimens. The allometric relationship between Neandertals and modern humans should be considered similar in the combination of the neurocranium and the face.

Table 5. Slope values of RMA lines in allometric relationships of neurocranium, face and mandible

	Neandertals	Modern humans	Bootstrap derived 95% confidence limits
geomF vs. geomCr	1.626	1.326	1.236–1.416
geomM vs. geomCr	3.243	1.783	1.377–2.967
geomM vs. geomF	2.118	1.016	0.899–1.226

The other two comparisons of the mandible against the neurocranium and the face exhibit clear differences in the directions of RMA lines between Neandertals and modern humans (middle and bottom right in Figure 2). The respective slope values signify the differences (Table 5). They are beyond the bootstrap derived 95% confidence limits of the modern humans. These indicate that the mandibular growth of Neandertals is more accelerated than that of modern humans at least during the postnatal-to-preadolescent (the age of 2 to 10) period.

DISCUSSION AND CONCLUSION

This study discloses both similarity and dissimilarity in growth and developmental patterns in the cranium between Neandertals and modern humans. Different results occur depending on the combination of the modules considered. Considering the neurocranium and the face, the growth trajectories are parallel and the allometric relationships are comparable between Neandertals and modern humans, thus producing similar pattern of change in the proportion (shape trajectory). The other two cases, taking the mandible into consideration, exhibit significant differences in the allometric relationships between Neandertals and modern humans. This leads to the different trajectories of the proportions (shape trajectory).

These results indicate a possible accelerated growth in the mandible of Neandertals during the postnatal period. In order to understand this finding, the measurement selection in calculation of each hypothetical module's size is worth considering. Based on the definition for each module, the sizes of the neurocranium (geomCr) and of the face (geomF) literally represent global dimensions of the brain volume and of the facial area. On the other hand, the measurements for the mandibular size, the height and thickness of the symphysis and the corpus, are not representative of its global size, rather indicative of the structural robustness. Therefore, the mandibular value (geomM) should be understandable from a functional aspect, i.e. in terms of adaptation in the masticatory system. It seems reasonable that this kind of functional adaptation appears later in ontogenetic time scale compared to those controlled by genetic or epigenetic systems.

Does this finding support the proposed idea of species-specific or population-specific postnatal trajectory of the face or the cranium? This question is not easy to answer simply in affirmative, because the analytical design of this study is not strictly identical to the previous ones. This study considers the craniofacial ontogeny as a complex of interrelated modules of neurocranium, face and the mandible, while many of the previous studies have been designed to find a major transform vector of the total cranium or a particular part of it. As already mentioned, the general ontogenetic pattern should be common in terms of the craniofacial systems among closely-related species or subspecies. However, morphological differences in adult forms among these taxa should appear through any shifts in rate or timing of developmental events during ontogeny. These shifts might be too small to detect in a global shape transformation of the cranium. In this context, the idea of the cranial ontogeny as a complex of developmental modules is noteworthy. In this study, one aspect of the mandibular morphology, the mandibular body size, can be interpreted as an example to show different developmental trajectories between Neandertals and modern humans. However, it is premature to consider it as species-specific. We should notice a wide variation in growth profiles among living populations, and even in the growth of neurocranial and facial dimensions there are clear differences in some prehistoric/historic populations (Okazaki, 2004; Steyn and

Henneberg, 1997). If this mandibular morphology were largely affected by functional demands, the growth profile of it would depend on the subsistence patterns such as hunter-gatherers vs. sedentary farmers. As our modern samples consist of industrialized cultural peoples, we must check the difference based on the subsistence or ecological patterns among modern humans and then compare the degree of difference among modern humans with those of Neandertals.

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REFERENCES

Ackermann R. R., Krovitz G. E. (2002) Common patterns of facial ontogeny in the hominid lineage. *The Anatomical Record* (*New Anat.*), **269**, 142–147.

Akazawa T., Muhesen S. (eds) (2003). *Neanderthal Burials. Excavations of the Dederiyeh Cave, Afrin, Syria*. Roma, L'erma di Bretschneider.

Akazawa T., Muhesen S., Ishida H., Kondo O., Griggo C. (1999). New discovery of a Neanderthal child burial from the Dederiyeh cave in Syria. *Paleorient*, **25**, 127–140.

Bräuer G. (1988). Osteometry. In *Anthropologie*. R. Martin and K. Knussman (eds.), pp.160–232. Stuttgart: Gustav Fischer.

Cobb S. N., O'Higgins P. (2004) Hominins do not share a common postnatal facial ontogenetic shape trajectory. *J. Exp. Zool*. (Mol. Dev. Evol.), **302B**, 302–321

Dean C., Leakey M. G., Reid D., Schrenk F., Schwartz G. T., Stringer C., Walker A. (2001) Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature*, **414**, 628–631.

Dodo Y., Kondo O., Nara T. (2003). The skull of the Neanderthal child of burial No.1. In *Neanderthal Burials. Excavations of the Dederiyeh Cave, Afrin, Syria*. Akazawa T., Muhesen S.,(eds.), pp. 93–137. Roma, L'erma di Bretschneider.

Dodo Y., Kondo O., Muhesen S., Akazawa T. (1998). Anatomy of the Neandertal infant skeleton from Dederiyeh Cave, Syria. In *Neandertals and Modern Humans in Western Asia*. T. Akazawa, K. Aoki and O. Bar-Yosef (eds.), pp. 323–338. New York: Plenum Press.

Faerman M., Zilberman U., Smith P., Kharitonov V., Batsevitz V. (1994). A Neanderthal infant from the Barakai Cave, western Caucasus. *J. Hum. Evol.*, **27**, 405–415.

Ferembach D. (1970). Le crane de l'enfant du Pech de l'Azé. In *L'enfant du Pech de l'Azé*. D. Ferembach, P. Legoux, R. Fenart, R. Empereur Buisson and E. Vlček (eds.), Archives de l'Institute de Paleontologie Humaine Mémoire 33, 13–51. Paris: Masson.

Ishida H., Kondo O. (2003). The skull of the Neanderthal child of burial No.2. In *Neanderthal Burials. Excavations of the Dederiyeh Cave, Afrin, Syria*. T. Akazawa and S. Muhesen (eds.), pp. 271–297. Roma, L'erma di Bretschneider.

Kondo O., Ishida H. (2003). Ontogenetic variation in the Dederiyeh Neandertal infants: postcranial evidence. In *Growth and Development in the Genus Homo*. J. Thompson, A. J. Nelson and G. Krovitz (eds.), pp. 386–411. Cambridge: Cambridge University Press.

Krovitz G. E. (2003) Shape and growth differences between Neandertals and modern humans: Grounds for a species-level distinction? In *Growth and Development in the Genus Homo*. J. Thompson, A. J. Nelson and G. Krovitz (eds.), pp. 320–342. Cambridge: Cambridge University Press.

Lieberman D. E., McBratney B. M., Krovitz G. (2002) The evolution and development of cranial form in Homo sapiens. *Proc. Nat. Acad. Sci*., **99**, 1134–1139.

Loveloy C. O., Cohn M. J., White T. D. (1999) Morphological analysis of the mammalian postcranium: A developmental perspective. *Proc. Nat. Acad. Sci*., **96**, 13247–13252.

Madre-Dupouy M. (1992). *L'enfant de Roc de Marsal. Etude analytique et comparative*. Paris: Editions du C.N.R.S.

Mallegni F., Ronchitelli A. T. (1989). Deciduous teeth of the Neanderthal mandible from Molare Shelter, near Scario (Salerno, Italy). *Am. J. Phys. Anthropol*., 79, 475–482.

Mallegni F., Trinkaus E. (1997). A reconsideration of the Archi 1 Neandertal mandible. *J. Hum. Evol*., 33, 651–668.

Martin H. (1926). *L'Enfant Mousterien de 8 Ans: Station de La Quina (Charente)*. Angouleme: Imprimerie Ouvriere.

McCollum M. A. (1999) The robust Australopithecine face: a morphogenetic perspective. *Science*, **284**, 301–305.

O'Higgins P., Collard M. (2002) Sexual dimorphism and facial growth in papionin monkeys. *J. Zool.*, **257**, 255-272.

Okazaki K. (2004) A morphological study on the growth patterns of ancient people in the northern Kyushu-Yamaguchi region, Japan. *Anthropological Science*, **112**, 219–234.

Pap I., Tillier A.-M., Arensburg B., Chech M. (1996). The Subalyuk Neanderthal remains (Hungary): a re-examination. *Annales Historico-Naturales Musei Nationalis Hungarici*, **88**, 233–270.

Ponce de Leon M. S., Zollikofer C. P. E. (2001) Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature*, **412**, 534–538.

Ramirez Rozzi F. V., Bermudez de Castro J. M. (2004) Surprisingly rapid growth in Neanderthals. *Nature*, **428**, 936–939.

Steyn M., Henneberg M. (1997) Cranial growth in the prehistoric sample from K2 at Mapungubwe (South Africa) is population specific. *Homo*, **48**, 62–71.

Strand Vidarsdottir U., O'Higgins P., Stringer C. (2002) A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *J. Anat*., **201**, 211 –229.

Stringer C. B., Dean M. C., Martin R. D. (1990). A comparative study of cranial and dental development within a recent British sample and among Neandertals. In *Primate Life History and Evolution*. C. J. DeRousseau (ed.), pp. 115–152. New York: Wiley-Liss, Inc.

Tillier A. M. (1982). Les enfants neanderthaliens de Devil's Tower (Gibraltar). *Z. Morph. Anthropol.*, **73**, 125–148.

Tillier A. M. (1983a). L'enfant Neanderthalien du Roc de Marsal (Campagne du Bugue, Dordogne). *Annles de Paleontologie*, **69**, 137–149.

Tillier A. M. (1983b). Le crane d'enfant d'Engis 2: un exemple de distribution des caracteres juveniles, primitifs et neanderthaliens. *Bull. Soc. roy. belge Anthropol. Prehist.*, **94**, 51–75.

Tillier A. M., Genet-Varcin E. (1980). La plus ancienne mandibule d'enfant decouverte en France dans le gisement de la Chaise de Vouthon (Abri Suard) en Charente. *Z. Morph. Anthropol.*, **72**, 196–214.

Tompkins R. L. (1996) Relative dental development of Upper Pleistocene hominids compared to human population variation. *Am. J. Phys. Anthropol.*, **99**, 103–118.

Wakebe T. (1990). A morphological study of cranium of infants and children in the Japanese. *Nagasaki Igakkai Zasshi*, **65**, 805–824.

Weidenreich F. (1945) The Paleolithic child from the Teshik-Tash cave in southern Uzbekistan (Central Asia). *Am. J. Phys. Anthropol.*, **3**, 151–162.

Williams F. L., Godfrey L. R., Sutherland M. R. (2002) Heterochrony and the evolution of Neandertal and modern human craniofacial form. In *Human Evolution through Developmental Change*. N. Minugh-Purvis and K. J. McNamara (eds.), pp. 405–441. Baltimore: The John Hopkins University Press.

Williams F. L., Godfrey L. R., Sutherland M. R. (2003) Diagnosing heterochronic perturbations in the craniofacial evolution of *Homo* (Neandertals and modern humans) and *Pan* (*P. troglodytes* and *P. paniscus*). In *Growth and Development in the Genus Homo*. J. Thompson, A. J. Nelson and G. Krovitz (eds.), pp. 295–319. Cambridge: Cambridge University Press.

Wolpoff M. H. (1979) The Krapina dental remains. *Am. J. Phys. Anthropol.*, **50**, 67–114.

Zollikofer C. P. E., Ponce de Leon M. S. (2004) Kinematics of cranial ontogeny: heterotopy, heterochrony, and geometric morphometric analysis of growth models. *J. Exp. Zool*. (*Mol. Dev. Evol.*), **302B**, 322–340.