



## Ontogenetic migration of the mental foramen in Neandertals and modern humans

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### Abstract

Since the nineteenth century, researchers have noted that Neandertal and modern human adults differ in mental foramen position, although the ontogenetic changes in the position of this feature have only recently come under the scrutiny of paleoanthropologists. Research on mental foramen position has focused on whether this feature is inferior to a particular tooth. However, tooth position may not be a reliable indicator of mental foramen position because of variability in tooth size within and between taxa and during eruption events. As opposed to observing the mental foramen with respect to the postcanine teeth, we examined linear distances from the mental foramen to other mandibular landmarks. Modern human adults may appear truncated, or paedomorphic, in mental foramen position with respect to Neandertal adults. However, infants of the two taxa differ substantially in anterior mandibular form. The initial differences in the shape of the mental region may be related to the embryological position of the mental foramen in modern humans and its role in the development of the mental trigone. The shape changes that accrue thereafter, possibly from faster mandibular growth rates in Neandertals, further distinguish the adults from one another. Although mandibular shape differences exist from early infancy onwards, adults of the two taxa are broadly similar in bi-mental foramen breadth with respect to mandibular size. For this reason, qualitative assessments of mental foramen position may provide less taxonomic information than previously thought.

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## Introduction

We explore the ontogeny of mental foramen position in Neandertals and modern humans to clarify how differences in the anterior mandible in adults of the two taxa arise. Our investigation differs from traditional nonmetric observations of mental foramen position because we compare the distances from the mental foramen to other mandibular landmarks for available life cycle stages of the two taxa. Mental foramen position in modern human adults appears to be more anterior with respect to its position in Neandertals, and we explore whether this is a truncation of similar developmental patterns, and if so, whether modern humans can be described as paedomorphic with respect to Neandertals. Furthermore, we explore how relative growth patterns capture differences in the position of the mental foramen with respect to the tooth row.

Nineteenth century researchers were the first to note the unusual position of the mental foramen in Neandertal mandibles (Dupont, 1866; Fraipont and Lohest, 1886). These researchers compared the position encountered in Neandertal mandibles, frequently located below the first mandibular molar ( $M_1$ ), to its position in modern humans, most often positioned inferior to the first or second premolar ( $P_3$  or  $P_4$ ), or under the interdental septum of  $P_3/P_4$  (Condemi, 1991; Trinkaus, 1993). During the twentieth century, this difference in position with respect to the tooth row was identified as a derived trait for Neandertals and was later used as evidence for their replacement in modern human origins scenarios (Stringer et al., 1984; Stringer, 1987; Condemi, 1991; Hublin, 1998; Quam and Smith, 1998). More recently, variation in mental foramen position in Neandertals and modern humans has been observed (Trinkaus, 1993), and the uniqueness of this trait to Neandertals has been questioned (Trinkaus, 1993; Franciscus and Trinkaus, 1995; Lebel et al., 2001; Rosas, 2001). Several authors have recently suggested that a more posteriorly placed mental foramen is an ancestral trait rather than uniquely derived in Neandertals, as several middle Pleistocene hominin populations also exhibit a mental

foramen below  $M_1$  (Coqueugniot, 2000; Rosas, 2001; Coqueugniot and Minugh-Purvis, 2003).

The posterior placement of the mental foramen in Neandertals and their purported ancestors has also been attributed to a scaling relationship—i.e., the mental foramen is more posteriorly positioned on larger mandibles (Rosas, 1997, 2001). Gorillas exhibit a similar scaling relationship (Robinson and Williams, 2003). Across hominoids, the position of the mental foramen relative to the tooth row appears to “migrate” posteriorly, although the cause of this “migration,” or the relative change in mental foramen position during ontogeny, is unknown. In addition to scaling, it is likely that mental foramen position is simply related to other ontogenetic changes in the mandible or dentition. For this reason, the position of the mental foramen may be a “spondyl” (Gould and Lewontin, 1979)—a structure that reflects relative growth in other regions of the mandible. For example, mental foramen position is said to be influenced by growth of the mandibular corpus and ramus (Trinkaus, 1993; Stefan and Trinkaus, 1998a, 1998b; Rosas, 2001), modification of the mandibular symphysis and condyle (Kjaer, 1989), changes in the alveolar process and dentition (El-Beheri, 1985; Kjaer, 1989; Trinkaus, 1993; Stefan and Trinkaus, 1998a, 1998b), expansion of the inferior alveolar nerve and blood vessels (Trinkaus, 1993; Kjaer, 1989; Stefan and Trinkaus, 1998a, 1998b; Coqueugniot and Minugh-Purvis, 2003), and/or mesial drift of the dentition (Green and Darvell, 1988; Kjaer, 1989; Trinkaus, 1993; Rosas, 2001).

Coqueugniot (1999, 2000) recently investigated the position of the mental foramen in an ontogenetic series of Neandertals, early modern humans, and recent modern humans. She found that mental foramen position with respect to the postcanine teeth differs significantly between Neandertals and modern humans at all ages (Coqueugniot, 2000). However variation among young Neandertals must not be ignored, as small sample sizes and the idiosyncrasies of the fossilization process may affect the distribution of this trait. There are several young Neandertals—some of which are the only ones in a particular age class—that are identical in mental foramen position (with respect

to the tooth row) to their modern human counterparts. For example, the mental foramen of the 10-month-old Amud 7 infant (Rak et al., 1994) is inferior to the anterior root of the first deciduous molar ( $dm_1$ ), as it is in modern humans of a similar developmental age (Scheuer and Black, 2000). In Archi 1, aged at ca. 3 years (Minugh-Purvis, 1988; Mallegni and Trinkaus, 1997; Williams, 2001), the mental foramen lies inferior to the anterior root of  $dm_1$ , corresponding to the position exhibited by their modern human counterparts. However, the Barakai mandible, which is similar in developmental age to the Archi 1 mandible, exhibits a mental foramen inferior to the posterior root of  $dm_1$  (Faerman et al., 1994), and thus more posteriorly placed than is common among modern humans of comparable dental ages (Scheuer and Black, 2000). In similarly aged Neandertals, the mental foramen is inferior to either  $dm_1$  or the interdental septum between  $dm_1$  and  $dm_2$  (Akazawa et al., 1995; Tillier, 1996; Coqueugniot, 1999, 2000; Ishida et al., 2000). Neandertal fossils younger than two to three years are uncommon, and Neandertal neonates are nearly absent from the fossil record (Tillier, 1996). Whether the mental foramen was positioned similarly in Neandertal and modern human neonates (Figure 1) remains largely unknown.

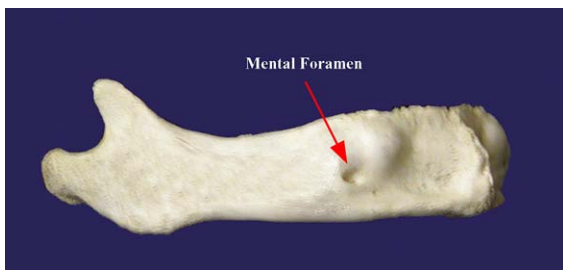


Figure 1. The mental foramen in modern humans “migrates” posteriorly (changes position relative to the tooth row) during ontogeny. The mental foramen generally forms prenatally under the anticipated anterior root of the developing crown of the first deciduous molar. This position is maintained at birth (shown above). The mental foramen position is generally stable during deciduous dental eruption. After  $M_1$  eruption, but during  $M_2$  eruption, the mental foramen most frequently migrates to a position inferior to  $P_4$  (FLW, unpublished data).

### *Mental foramen position and the dentition*

Most studies focusing on mental foramen position have characterized the position of this feature relative to the postcanine teeth. However, mental foramen position, and its migration during ontogeny, may be better explained by its relationship to mandibular size rather than the tooth under which it is observed. Sexual dimorphism in the dentition (Hillson, 1996), unequal amounts of attrition (Green and Darvell, 1988), variation in tooth size (Trinkaus, 1993), mesial drift, and the continuous shedding of the deciduous dentition during postnatal ontogeny all may obscure the relationship between mental foramen position and the tooth under which it appears. In addition, the mental foramen and the dentition have separate embryological origins (Trinkaus, 1993) and follow very different developmental trajectories throughout ontogeny. Although dental development seems to track mental foramen migration, the position of the mental foramen relative to the tooth row may reveal less information about evolutionary patterns than considering mental foramen position relative to some measure of size.

The ontogeny of Neandertal and modern human mental foramen position has not been previously explored within a morphometric context. This approach avoids using the dentition as a proxy to estimate the position of the mental foramen, and directly quantifies the ontogenetic change in mental foramen position from infancy to adulthood (cf. Coqueugniot, 2000). A morphometric treatment of ontogenetic changes in mental foramen position can yield estimates of developmental rates and durations that can be investigated under the rubric of heterochrony—a theoretical framework that seeks to describe evolutionary events as byproducts of perturbations in ancestral rates of growth, rates of development, and/or age at maturation in descendants (Gould, 1977; Shea, 1983, 1984, 1989; Godfrey and Sutherland, 1996; Godfrey et al., 1998; Ravosa and Vinyard, 2002; Williams et al., 2002, 2003; Leigh et al., 2003; cf. McKinney and McNamara, 1991). A heterochronic analysis of mental foramen position provides a better understanding of evolutionary processes than can be gained from simply

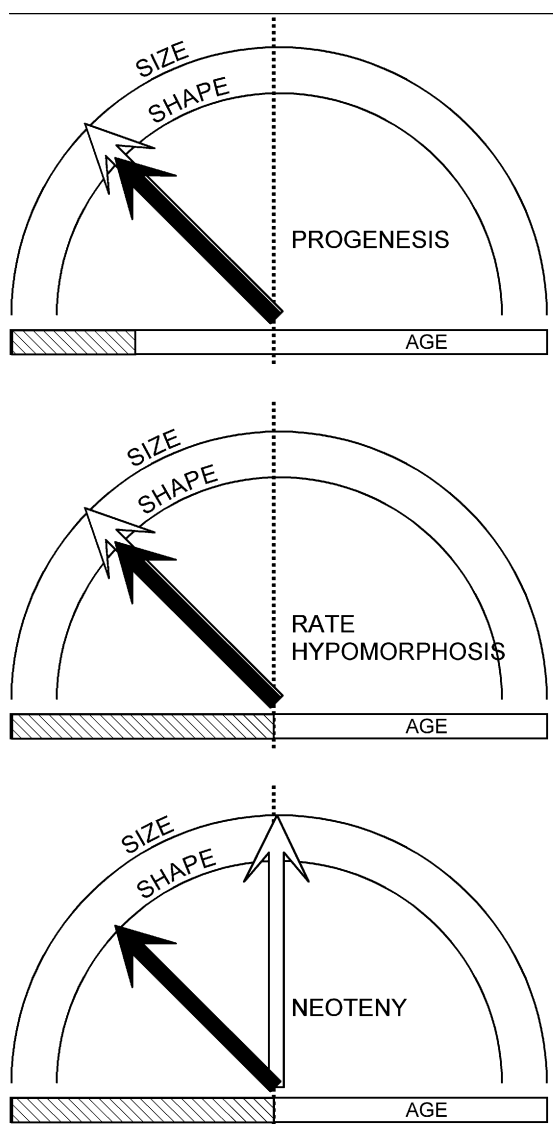


Figure 2. Three heterochronic processes, representing independent size, shape, and age trajectories, are illustrated on Gould's (1977) clock models: progenesis, rate hypomorphosis, and neoteny. The descendant's deviations from the ancestor's rates of size, shape, and maturation rates are depicted as perturbations away from the 12:00 position on the clocks. These three heterochronic processes theoretically yield paedomorphosis, but in different ways. Progenesis truncates ancestral rates of size and shape change via early maturation in descendants; rate hypomorphosis produces paedomorphosis, not by early maturation, but from a slower rate of coincident size and shape change from ancestor to descendant; neoteny truncates rates of ancestral shape change, but not ancestral rates of size increase (growth) or ancestral age at maturation. The descendant is

observing the position of the mental foramen relative the tooth row.

### Heterochrony

Traditional approaches to heterochrony explain how alterations in size, shape, and age from ancestor to descendant can account for much of evolutionary change in both the plant and animal kingdoms (Gould, 1977). Gould (1977) devised a clock model to demonstrate schematically the separation of size, shape, and age; on these clocks, one can perturb any one of these three parameters independently of the others (Figure 2). Gould (1977) also suggested that humans were neotenes via slowing the rate of shape change while maintaining ancestral rates of growth and maturation. Neoteny has historically been invoked to describe the origin of modern human adult morphology (Bolk, 1926; de Beer, 1958; Gould, 1977; Privratsky, 1981; Montagu, 1989; Verhulst, 1999). While theoretical arguments have been offered for and against the role of heterochrony in human evolution (Gould, 1977; Shea, 1989; McKinney and McNamara, 1991; McKinney, 1999; McNamara 2002), empirical data from the hominin fossil record remains the final arbiter of heterochronic scenarios. Ideally, we would be able to obtain sufficient ontogenetic data from unequivocal human ancestors. Unfortunately, it has proven difficult to extract ontogenetic series from the fossil record that are sufficiently complete to estimate rates of growth and rates of development from infancy to adulthood (Williams, 2000). For example, although Antón and Leigh (2003) do extract ontogenetic data from *Homo erectus* (sensu lato) to compare to modern humans, the sample size is small and the dental age for Mojokerto—the youngest *Homo erectus* fossil specimen known—is unavailable.

We utilize Neandertals here as a model “ancestor” without claiming that Neandertals are, or are

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mapped onto the “clock” or ontogenetic trajectory of the ancestor. For heterochrony to account for the differences between two taxa, the descendant is constrained to follow the ancestor's shape path (Godfrey and Sutherland, 1996; Williams et al., 2002, 2003). Figure modeled after Gould (1977) and Shea (1984).

not, ancestral to modern humans. This approach is not unlike that used by Shea (1983), who used common chimpanzees as a model for the ancestor of pygmy chimpanzees despite the fact that both species of *Pan* are living today and are thus unlikely to be ancestor and descendant, respectively. As long as one accepts the possibility of using Neandertals as a model ancestor, and in the absence of another taxon with a sufficiently dense ontogenetic sequence upon which to build such an argument, Neandertals remain the best possible comparative sample in any heterochronic analysis involving modern humans. Indeed, Stringer et al. (1990) stated: “In the absence of samples of immature archaic, but non-Neandertal, hominids of this period, we have no choice but to use the Neandertal sample as representative of (but not necessarily typical of) the evolutionary grade preceding that of modern humans, *whether or not they were actually ancestral to any living humans*” (p.116, italics added). Stringer et al. (1990:116) also noted that “in many aspects of their anatomy, the Neandertals also retained features from middle Pleistocene ancestors.” This may also be true of mental foramen position, as a posterior mental foramen position occurs in some middle Pleistocene archaic humans (Coqueugniot, 2000; Rosas, 2001; Coqueugniot and Minugh-Purvis, 2003), suggesting that Neandertals are plesiomorphic for the position of this feature, regardless of their evolutionary relationship to living humans.

If mental foramen position does track dental development generally, and dental development parallels growth and shape changes in the jaws, an anterior location of the mental foramen in adult modern humans may signify a truncation of mandibular development compared to that of Neandertals. This could be interpreted as paedomorphosis in modern human adults. Paedomorphosis stems from at least three heterochronic processes: progenesis, rate hypomorphosis, and neoteny (Figure 2).

If it could be shown that modern humans exhibit truncated and coincident size and shape trajectories via an earlier maturation, then one could say that progenesis describes the differences in mental foramen position between Neandertals and modern humans. Progenesis is probably less likely of an

explanation of Neandertal and modern human differences than rate hypomorphosis or neoteny because modern human and Neandertal maturation ages seem to be broadly similar. Examination of incisal perikymata suggest that Neandertals and modern humans had similar rates of dental maturation compared to the rate of enamel accumulation characterizing *Homo erectus* (sensu lato) (Dean et al., 2001). Neandertal and modern human adult brain sizes also overlap significantly. Smith (1991) has shown that adult brain size is highly correlated with age at M<sub>1</sub> eruption in anthropoid primates. She suggested that Neandertal M<sub>1</sub>s erupted at 6.5 years of age, slightly later but within the range of modern human children (Scheuer and Black, 2000). Wolpoff (1979) suggested that Neandertal M<sub>3</sub>s erupted earlier than in their modern human counterparts, although M<sub>3</sub> eruption is highly variable across primates (Swindler, 2002). In short, Neandertals probably exhibited a maturation schedule similar to those observed among different populations of modern humans living today or in the recent past (Tillier, 1996; cf. Ramirez Rozzi and Bermudez de Castro, 2004). Progenesis as an explanation of truncated mental foramen position in modern humans compared to Neandertals is thus highly unlikely.

Shea (1984) described rate hypomorphosis as the reduction of allometrically associated size/shape trajectories. Rate hypomorphosis could be attributed to modern human adults with respect to Neandertal adults if age at maturation were similar (and this is likely), but mandibular size were smaller and the posterior migration of the mental foramen were truncated. Godfrey and Sutherland (1996) defined neoteny as a truncation, in the descendant, of ancestral developmental rates but without reduction of ancestral rates of growth and maturation ages. Neoteny describes a dissociation between size and shape changes (Shea, 1989; Godfrey et al., 1998; Leigh et al., 2003; Williams et al., 2003). Neoteny would describe mental foramen position in modern humans with respect to a Neandertal-like ancestor if the sizes of both adults were generally similar, and the posterior migration of mental foramen position with respect to size in modern human were truncated to some preadult stage of Neandertal development (Figure 2).

Neandertal morphology has previously been attributed to the converse of neoteny, the heterochronic process of acceleration. de Beer (1958) and Brothwell (1975) suggested that Neandertals are essentially peramorphic, or adultified humans (or conversely, that modern humans are neotenes). Although it is difficult to describe modern humans as global neotenes with respect to Neandertals (Williams et al., 2003), some aspects of modern human facial shape may be described as paedomorphic (Williams, 2000). In order to describe the mental foramen position of modern humans as the result of rate hypomorphosis or neoteny, it must be demonstrated that modern human adults are indeed paedomorphic in mental foramen position with respect to Neandertal adults. Modern human mental foramen position may be considered paedomorphic with respect to Neandertals if the position of the mental foramen in adult modern humans is similar to that of some preadult Neandertal life cycle stage. We define preadult as proportionally smaller bi-mental foramen breadth with respect to mandibular size.

In Gould's (1977) clock model, a descendant must follow the ancestral shape trajectory for heterochrony to describe the differences between two taxa (Godfrey and Sutherland, 1996; Godfrey et al., 1998; Williams et al., 2002, 2003). If the descendant is not on the ancestor's shape path, neomorphosis (novel shapes), rather than heterochrony, describes these differences (Godfrey et al., 1998). We examine ontogenetic series of Neandertal and modern human mandibles to explore whether heterochrony adequately describes the differences in mental foramen position exhibited between the two taxa.

## Materials and methods

Three-dimensional coordinates for nine mandibular landmarks were collected from ontogenetic sequences of Neandertal ( $n = 18$ ) and modern human ( $n = 291$ ) mandibles by one of us (GEK). The Neandertal sample derives from Europe and western Asia (Table 1). The modern human sample includes individuals from West Africa, Denmark, Hawaii, North America (the Indian

Knoll sample), England (the Spitalfields sample), Nubia, and Japan (Krovitz, 2000), as well as undocumented nonadults, mostly from the Bosma collection (Shapiro and Richtsmeier, 1997). The total modern human sample includes 173 nonadults and 118 adults. Each of the modern human populations used in this analysis includes both nonadults and adults. An individual was considered adult if the speno-occipital suture was obliterated, the third molar fully erupted, and, when available, the post-cranial epiphyses were fused.

We chose nine mandibular landmarks to represent the symphysis, corpus, and alveolus. These are listed in Table 2 and depicted in Figure 3. These landmarks were shown to have diagnostic value in a previously conducted measurement error study (Williams and Richtsmeier, 2003). Landmarks from the left side of the mandible were used for all modern human individuals and most Neandertals, except for St. Césaire and Tabūn 1, which preserve only the right side. The distance between the left and right mental foramen (bi-mental foramen breadth) was also measured. Euclidean distances between the left mental foramen and the other eight mandibular landmarks, as well as the length of the dental arcade, were

Table 1  
List of Neandertals examined

Specimen	Original fossil or cast	Dental age*
Roc de Marsal	cast	3
Châteauneuf 1	original	3
Le Chaise	cast	4.5
Devil's Tower	original	4.75
Teshik-Tash	cast	9.5
Malarnaud	cast	16
Le Petit Puymoyen	original	17
La Naulette	original	17.5
Amud 1	cast	30
Kebara 2	cast	30
La Ferrassie	cast	25
La Quina 5	original	25
Regourdou	original	25
Shanidar 1	cast	35
Spy 1	original	25
St. Césaire	original	25
Tabūn 1	original	30
Zaffaraya	cast	25

\* See text for discussion of dental age.

Table 2  
List of landmarks

IDI	Infradentale inferior (between central incisors, most anterior point on the alveolar margin)
POG	Pogonion (most anterior projection of the mental symphysis, taken in midline)
GNA	Gnathion (middle point on the lower border of the mandible)
GET	Genial tubercles (between genial tubercles in midline)
LI <sub>2</sub> C	Left junction of I <sub>2</sub> and C at alveolar border
LRAM	Left anterior root of ramus (where anterior edge of mandibular ramus and corpus intersect)
LGON	Left gonion
LMF	Left mental foramen (marked inferolaterally, most superior if several)
RMF	Right mental foramen (marked inferolaterally, most superior if several)

obtained from digitized three-dimensional coordinates (Lele and Richtsmeier, 2001). Raw linear distances for eight unique mandibular dimensions were then compared to dental age for each individual. These measurements are not independent, as they all relate the position of the mental foramen relative to other landmarks. While certain distances are probably highly correlated—such as those involving the mandibular symphysis—these distances provide localized information about mandibular morphology. For example, interlandmark distances between the mental foramen and gnathion (LMF-GNA) and between the mental foramen and pogonion (LMF-POG) may increase in size at different rates if a mental eminence develops.

### Dental aging

Ages for both adult and nonadult Neandertal mandibles were taken from the literature (Minugh-Purvis, 1988; Williams, 2001). Minugh-Purvis (1988) used calcification scores to estimate the age of Neandertal nonadults. Calcification scores have been shown to provide excellent age estimates in numerous studies (see Kuykendall, 1996; Krovitz, 2000, and references therein). Williams (2001) estimated ages for adult Neandertals based on patterns of tooth wear and suture closure for modern humans (Ubelaker, 1978; Buikstra and Ubelaker, 1994).

Dental ages for most modern human nonadults were based on tooth calcification scores. A calcification score for each tooth was determined from lateral radiographs and dental age was assessed using referenced standards specifically designed to predict age from an observed stage of dental development (Smith, 1991). Age estimates for all teeth were averaged to provide a minimum age for each individual. Although known age was available for some Spitalfields nonadults ( $n = 5$ ), the unknowns ( $n = 25$ ) are preserved better than the known individuals (GEK, personal observation); when age was unknown, individuals were assigned a dental age on the basis of tooth calcification scores. To estimate how different the known ages are from those obtained from calcification scores, one of us (GEK) compared the ages of the five known Spitalfields specimens with those obtained from

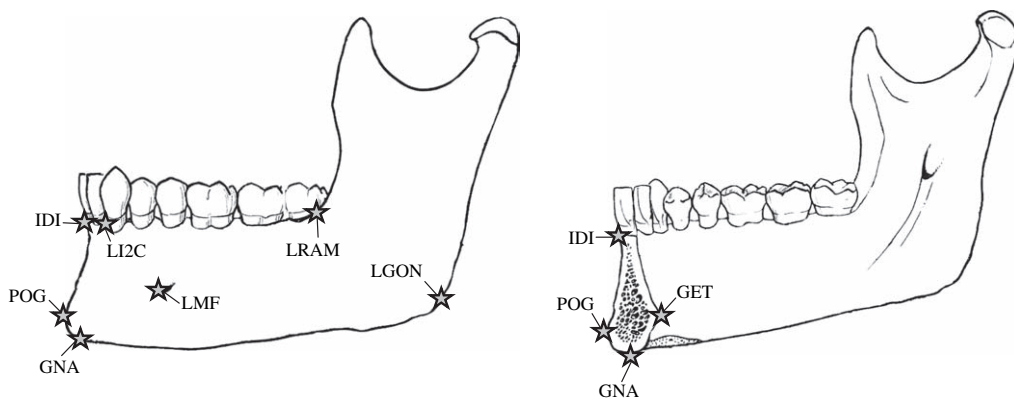


Figure 3. Landmarks used in this study.

the calcification scoring procedure detailed above. Although the age of one of these individuals was overestimated by 0.75 years, ages based on calcification scores tended to fall below known age by 0.1–0.7 years (mean = 0.2 years). This is not surprising as dental and skeletal age estimates frequently underestimate known chronological age (Molleson et al., 1993; Lampl and Johnston, 1996).

Dental eruption schedules were used to estimate dental ages for the West Africa and Hawaii samples (Eveleth and Tanner, 1976, 1991), as it was not possible to obtain radiographs for these two populations. To ascertain the difference between the ages based on eruption schedules and those obtained from calcification scores, one of us (GEK) compared the ages estimated for 24 Danish nonadults using both techniques. Although the age estimates provided by the two methods differed slightly, particularly for individuals peri-M<sub>1</sub> eruption, the ages from calcification scores were neither uniformly higher nor lower than those obtained from eruption schedules. A paired samples t-test yielded nonsignificant differences between the two aging techniques ( $p = 0.543$ ), and 79.2% of the age estimates differed by less than one year. Although the estimated ages for these West Africa and Hawaii samples may differ somewhat depending on whether eruption schedules or radiographs are used, the value of including these populations outweighed the potential risks of error from differences in dental ages.

Modern human adult mandibles were not assigned an age in years during data collection. For the purposes of this study, adult mandibles were randomly assigned ages between 25 and 35 years. Since the algorithm we used models the maturation phase of growth trajectories as flat lines, these assigned ages for adults did not substantially affect the growth curve analysis (see Williams et al., 2003).

### *Modeling growth*

Estimating growth requires choosing a model that most accurately interpolates the ontogenetic variation within a sample. Many previous

researchers who have investigated growth in the context of heterochrony have relied on log-transformed growth allometries following the influential work of Shea (1983, 1984). Coincident growth allometries (ontogenetic scaling) are thought to reveal heterochronic process (Shea, 1984), but there are problems with this procedure that may obscure the actual heterochronic relationship between taxa (Godfrey et al., 1998; cf. Ravosa and Vinyard, 2002). Although growth allometries do show the extent to which adults depart from infant morphologies, and we explore them here, log-transformation of growth trajectories can linearize an inherently curvilinear pattern. It is currently possible to apply nonlinear growth models to ontogenetic datasets (Godfrey and Sutherland, 1995).

We chose to examine nonlinear approximations of Neandertal and modern human growth patterns. There are several popular growth models in the literature to choose from (see de Bruin, 1993), although each one entails limitations and assumptions. A major limitation of many growth models, such as Gompertz, von Bertalanffy's, and negative exponent, among others, lies in the difficulty in approximating the growth signature from the limited ontogenetic data available from fossil taxa. Growth models that utilize third- or higher order polynomials contain a number of assumptions about the shape of growth trajectories that may be unrealistic with small cross-sectional samples (Williams et al., 2003). Complex growth models are most successful when the density of the data is not constrained (de Bruin, 1993). One particular disadvantage of quadratic-based growth models that is often ignored is that they continue to increase asymptotically beyond known maturation times (Williams, 2001).

### *Piecewise regression*

We used a second-order version of piecewise regression to estimate growth trajectories from our Neandertal and modern human samples. This version of piecewise regression can capture the growth signal for limited ontogenetic series. Piecewise regression is composed of a simple quadratic and a breakpoint value that signals

maturation. The flat line behavior of the second component of piecewise regression signifies adult values for a given trait so that the growth model does not asymptotically continue after maturation. Leigh and Terranova (1998) successfully used a second-order version of piecewise regression to capture growth trajectories for various strepsirrhines. Williams (2001) utilized the same algorithm to model growth in *Homo* and *Pan*. We used this algorithm to estimate Neandertal and modern human growth of mandibular traits: **Trait =  $\{(\beta_0 + \beta_1 * \text{age} + \beta_2 * \text{age}^2)$  if  $\text{age} < \beta_3$ , or  $(\beta_0 + \beta_1 * \beta_3 + \beta_2 * \beta_3^2)$  if  $\text{age} \geq \beta_3\}$ .**

Leigh and Terranova (1998) interpreted these four coefficients in the following way:  $\beta_0$  = the initial, or infant, size,  $\beta_1$  = initial growth rate,  $\beta_2$  = decline in the pace of growth, and  $\beta_3$  = the age at which growth ceases. These interpretations are also used here. While modeling the data, the same constraints and starting values were assigned to both the Neandertal and modern human samples. Minimum and maximum constraints

for each of the estimated coefficients were constructed to estimate patterns of growth for this least-squares likelihood surface (Williams et al., 2003). The least-squares solutions proved to be nearly equivalent to those obtained from maximum likelihood (Model II), but were preferred because the maximum likelihood solutions failed to solve certain cases in which the density, or distribution, of the data was idiosyncratic. Starting values for each of the coefficients allowed the iteration process to solve without exceeding the specified limits (up to 50 iterations with 20 half-steps were specified for all calculations). From the iterative process, the four coefficients were estimated for all eight linear distances for both taxa. Figure 4 shows an example of these growth models superimposed on a scatter plot of raw data points. Growth curves were calculated separately for Neandertals and modern humans and are presented separately for linear distances of the mandibular alveolus and corpus. The modeled growth curves reveal rates and durations of the growth of traits.

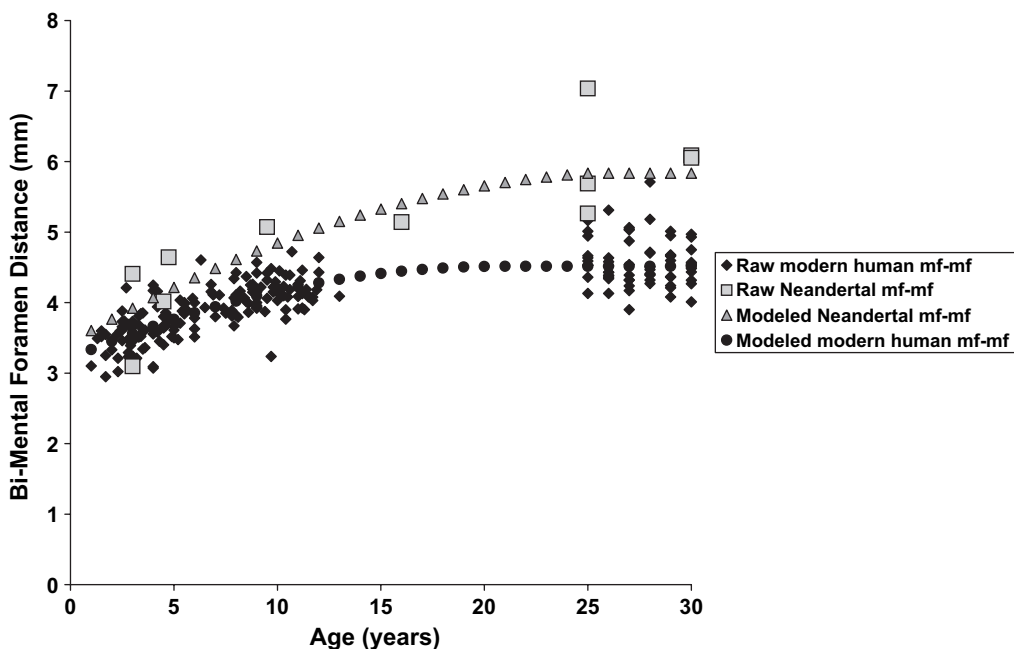


Figure 4. Bi-mental foramen breadth by age in Neandertals and modern humans. Modeled growth curves are superimposed on raw scatter plots to show the interpolation of the data.

### Shape indices

Following Gould's clock model, we isolated shape from size to identify heterochronic products such as paedomorphosis (juvenilized) and peramorphosis (adultified). Shape can be isolated in many ways. Thompson (1961) depicted shape as ratios of  $y$  and  $x$  coordinates, and shape change as deformations of these coordinates. Gould constructed shape as a ratio of  $y$  (trait) over  $x$  (some measure of size) and shape change as a vector of changing  $y/x$  ratios (see also Alberch et al., 1979; Godfrey and Sutherland, 1995, 1996; Williams et al., 2002). Bookstein (1984) defined shape as a collection of landmarks arranged uniformly in triangles, and shape change as the mean deformation (or dilations of the lengths) between landmarks for the triangle sets. Darroch and Mosimann (1985) used canonical and principal components to define aspects of shape. A classical definition of shape (Jolicoeur and Mosimann, 1960) as the second principal component, and thus a residual of size (usually corresponding to the first principal component), is misleading as all principal components contain both size and shape information (Corruccini, 1987). Some authors argue that size and shape parameters must be completely uncorrelated (e.g., Gelvin and Albrecht, 1985), although the biological significance of this "zero correlation" is unclear (Corruccini, 1987).

We define shape here as a ratio of  $y$  over  $x$ , where  $y$  is a given interlandmark linear distance and  $x$  is a measure of mandibular size. While some authors may find such a definition of shape to be problematic (e.g., Corruccini, 1987), there are appropriate justifications for using this treatment. First, no definition of shape enjoys universal support. Second, most definitions of shape employ a construction of ratios at some level [e.g., Mosimann's (1970) classical approach of dividing a vector of measurements by the geometric mean, or size vector].

Shape trajectories were constructed for Neandertals and modern humans by dividing each modeled growth curve by a modeled mandibular size (MMS) variable that consisted of all the raw linear distances summed and then modeled via

piecewise regression. This procedure was conducted separately for each taxon. Modeling this summary size variable was necessary to provide compatibility to the suite of modeled growth curves for each trait under investigation. Figure 5 represents one of these shape trajectories and shows modeled bi-mental foramen breadth (LMF-RMF) divided by mandibular size MMS ( $y$ ) compared to age ( $x$ ). Eight of these shape trajectories were subjected to principal components analysis (PCA) to explore mandibular shape change within a multivariate context.

In addition to our analysis of modeled mandibular shape change, we also compared mandibular shape at different stages of Neandertal and modern human life cycles (Williams et al., 2002). Mandibular shape indices were constructed by dividing the mean value of each linear distance for each available life cycle stage by mandibular size (MS), defined as the sum of all eight traits per taxon. This approach is similar to Gould's (1977) and is logically consistent with shape as a dimensionless value, because each shape index is a proportion of MS. To increase the number of fossils available, we omitted one of the linear distances (LMF-LGON) that is preserved in only a few Neandertals. We matched modern human life cycle stages to those available for Neandertals. These life cycle stages corresponded to infants (pre-M<sub>1</sub> eruption) and adults (post-M<sub>3</sub> eruption). Specifically, we compared the linear distances for 65 modern human infants, aged 2.6 to 5.9 years (mean = 3.97 years), to two Neandertal infants (Roc de Marsal and Châteauneuf), and 112 modern human adults to five adult Neandertals (La Ferrassie, Kebara 2, Shanidar 1, Amud 1, and Spy 1). The mandibular shape indices for Neandertal and modern human life cycle stages were also subjected to PCA. The two multivariate analyses of shape (one from modeled data, the other from life cycle stages) determined whether heterochrony can account for the evolutionary differences between Neandertals and modern humans. If modern human modeled ages, or mean life cycle stages, overlap those of Neandertals on PC axes, one can infer paedomorphosis (or peramorphosis). If the shape paths differ, one can infer neomorphosis (novel shapes).

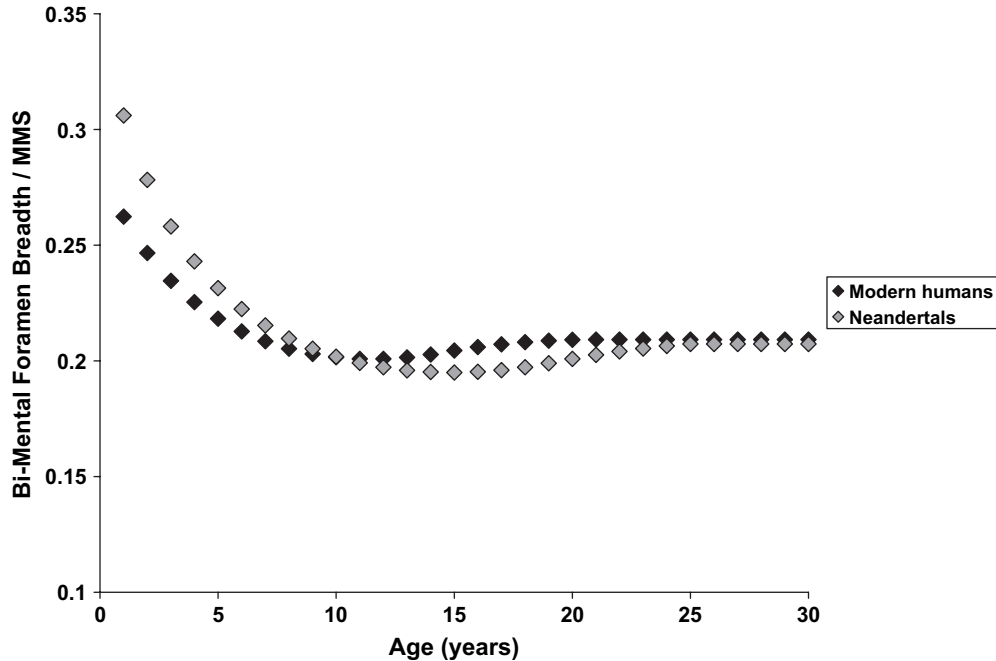


Figure 5. Neandertal and modern human postnatal shape change in bi-mental foramen breadth with respect to mandibular size. Modeled growth curves show much overlap between the two taxa.

### *Growth allometries*

Growth allometries that approximate changes in the anterior-posterior placement of the mental foramen (LMF-IDI compared to MS) and the tooth row (IDI-LRAM compared to MS) as the mandible increases in size provide an alternate means to evaluate differences in mental foramen position characterizing Neandertals and modern humans. The null hypothesis of isometry was evaluated using 95% confidence limits. These log-transformed growth allometries capture patterns of relative growth that characterize the placement of the mental foramen with respect to the tooth row.

## **Results**

### *Modeled growth*

The estimated Neandertal and modern human growth coefficients for initial size ( $\beta_0$ ), initial

growth rate ( $\beta_1$ ), decline in the pace of growth ( $\beta_2$ ), and the age at which growth ceases ( $\beta_3$ ) are provided in Table 3. Statistical tests of the significance of the differences between the Neandertal and modern human coefficients were not possible due to small sample sizes, and the resulting large confidence intervals that characterize the Neandertal data.

Table 3 shows that the initial growth rate ( $\beta_1$ ) is faster in Neandertals compared to modern humans. The decline in the pace of growth ( $\beta_2$ ) was fairly consistent across all linear distances for both taxa. Initial size, or infant size ( $\beta_0$ ), and age at maturation (duration of growth,  $\beta_3$ ) differ between the two taxa, with Neandertal infants larger in some distances and modern human infants larger in others. In general, Neandertals continued growing for a longer period of time than do modern humans, although the linear distance from the mental foramen to the lingually located genial tubercles (LMF-GET) increased at a much faster rate and shorter duration, as did the distance between the mental foramen and the labial

Table 3  
Estimated growth coefficients from piecewise regression\*

Linear distance	Modern humans				Neandertals			
	$\beta_0$	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_0$	$\beta_1$	$\beta_2$	$\beta_3$
LMF-IDI	1.51	0.24	-0.01	12.01	1.62	0.28	-0.01	13.99
LMF-POG	1.36	0.23	-0.01	11.55	1.39	0.25	-0.01	12.66
LMF-GNA	1.40	0.24	-0.01	11.86	1.24	0.28	-0.01	14.21
LMF-GET	1.76	0.049	-0.001	24.32	1.11	0.30	-0.01	9.2
LMF-LI <sub>2</sub> C	1.365	0.06	-0.001	25.00	0.74	0.28	-0.01	14.05
LMF-LRAM	1.62	0.29	-0.01	14.63	1.37	0.34	-0.01	16.93
LMF-LGON	3.631	0.208	-0.004	24.731	2.106	0.511	-0.01	18.608
LMF-RMF	3.21	0.13	-0.003	21.02	3.44	0.17	-0.003	25

\* See text for description of  $\beta$  values, and Table 2 for descriptions of landmarks.

junction of I<sub>2</sub> and the canine (LMF-LI<sub>2</sub>C). Bimetal foramen breadth, LMF-RMF, grew at a faster rate but for a shorter duration in Neandertals (Figure 4). Other than Neandertals showing a higher initial growth rate ( $\beta_1$ ), there are no consistent differences between Neandertal and modern human coefficients of mandibular growth (Table 3).

#### Alveolar growth

Figure 6a depicts Neandertal and modern human modeled growth curves for mental foramen to alveolar landmarks. The two taxa exhibit similarities in growth between the mental foramen and the anterior ramus root (LMF-LRAM) and the mental foramen and infradentale (LMF-IDI); these contrast with differences in growth observed between the mental foramen and the junction of the second incisor and the canine (LMF-LI<sub>2</sub>C). The distance between the mental foramen and the I<sub>2</sub>/C junction is already large in young modern humans and increases only gradually during post-natal ontogeny. However, in young Neandertals, the distance between the mental foramen and the I<sub>2</sub>/C junction is small; this distance increased rapidly between infancy and the eruption of the second molar.

#### Corpus growth

Modeled growth curves for corpus dimensions are shown in Figure 6b. Neandertals and modern humans exhibit similar patterns of growth between the mental foramen and gnathion (LMF-GNA), and between the mental foramen and pogonion

(LMF-POG). Although LMF-GNA and LMF-POG exhibit similar patterns of monotonic increase, we expected to observe differences in growth between these two distances because of the development of the mental trigone in modern humans but not in Neandertals. Neandertals and modern humans exhibit dissimilar patterns of growth for the linear distance between the mental foramen and gonion (LMF-LGON). The growth of the posterior corpus region is influenced by the expansion of the ascending ramus (Ponce de León and Zollikofer, 2001). Modern human growth in this region is gradual compared to the stronger rate and magnitude of growth that characterized Neandertals. From juvenile ages to young adulthood, Neandertals developed a broad ramus for the attachment of the masseter muscles, thus displacing gonion farther posteriorly from the mental foramen.

#### PCA of modeled growth curves standardized for size

Figure 7 depicts a PCA of shape indices using all eight interlandmark distances standardized by MMS (Figure 5 represents one of these shape trajectories, LMF-RMF / MMS). Principal component axis 1, explaining 53.8% of the variance, separates Neandertal infants and adults, whereas PC axis 2, explaining 21.3% of the variance, separates modern human infants and adults. Neandertal subadults and adults fall along the negative segment of PC axis 1, reflecting changes in shape accompanying the extension of the gonial

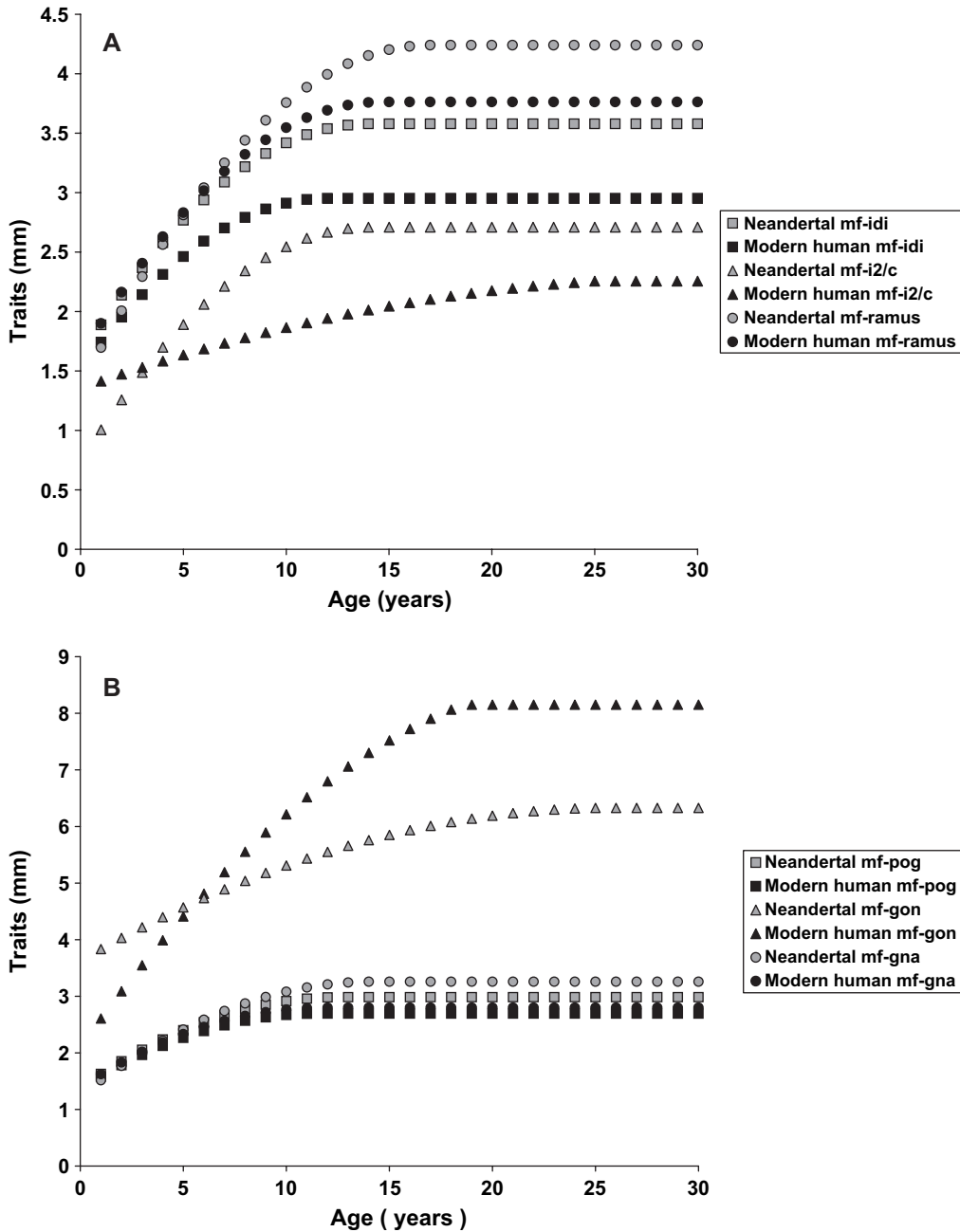


Figure 6. A) Modeled alveolar growth, with respect to the mental foramen, in Neandertals and modern humans. B) Modeled corpus growth, with respect to the mental foramen, in Neandertals and modern humans.

angle with respect to the mental region. The squared mental region of Neandertal infants (Minugh-Purvis, 1988; Stringer et al., 1990; Williams et al., 2002), bordered by the mental

foramina, explains the high positive loadings of most shape indices (Table 4) and accounts for the projection of Neandertal infants on the positive end of PC axis 1; Neandertal infant

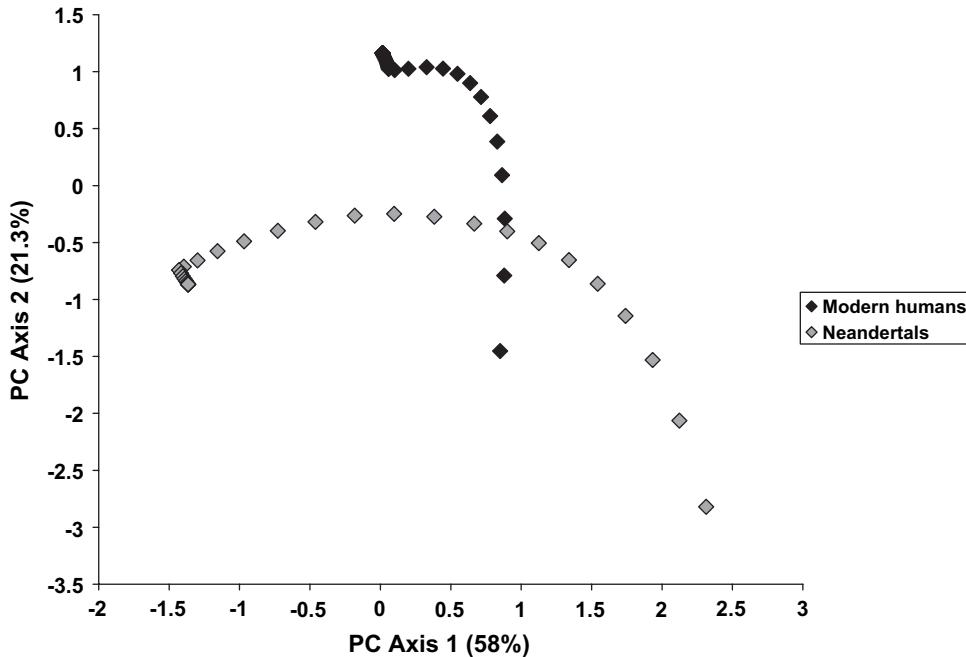


Figure 7. PCA of eight modeled shape trajectories.

mandibles exhibit relatively deep mental regions and thick corpora relative to modern humans of all ages, and relative to other Neandertal postnatal ages. Principal component axis 2 may be considered a contrast vector, separating individuals with relatively elongated tooth rows (modern human adults), from individuals with relatively wide anterior mandibles (Neandertal infants, and to some extent, modern human infants). Principal component axis 3, accounting for 17.2% of the variance, is not shown here as it largely duplicates the pattern of shape change difference contained in the first two axes (i.e., Neandertals and modern humans exhibit dissimilar shape paths).

It is clear from Figure 7 that Neandertal and modern human mandibles follow different ontogenetic shape paths. If pedomorphosis adequately described the differences in mandibular shape between Neandertals and modern humans, we would expect to see substantial overlap of their shape trajectories. Although modern human adults are similar in shape to six to nine year old Neandertals along PC axis 1, and Neandertal adults are similar in shape to one to three year old modern humans along PC axis 2, heterochrony

does a poor job of describing the differences between these two taxa because modern human adults are not broadly similar to any pre-adult Neandertal stage and, more importantly, the two taxa follow dissimilar shape paths.

Table 4

Component loadings for PCA of eight modeled shape trajectories\*

Interlandmark distances	PC axis 1	PC axis 2
LMF-IDI/MMS	0.975	-0.102
LMF-POG/MMS	0.947	0.297
LMF-GNA/MMS	0.858	0.492
LMF-GET/MMS	0.814	-0.258
LMF-LI <sub>2</sub> C/MMS	0.096	0.056
LMF-LRAM/MMS	0.187	0.966
LMF-LGON/MMS	-0.736	0.295
LMF-RMF/MMS	0.689	-0.527

\* See Table 2 for landmark descriptions. MMS = Modeled Mandibular Size (see methods).

#### *PCA of life cycle stages*

We cross-checked our modeled shape analysis by examining mean shape indices to the PCA for Neandertal and modern human life cycle stages

(Figure 8). Principal component axis 1, describing 58.6% of the variance, carries an ontogenetic signal, as it separates infants from adults of both taxa. Neandertals are projected over a greater distance along PC axis 1 than are modern humans, indicating that Neandertal mandibles undergo more shape change during postnatal ontogeny. Neandertal and modern human infants, with relatively small alveolar processes with respect to mandibular size (LMF-I<sub>2</sub>C), are polarized from Neandertal adults on PC axis 1. Neandertal and modern human adults, characterized by relatively slender mental regions (LMF-GEN), fall on the positive segment of PC axis 1. Neandertal adults are further distinguished on PC axis 1 by a poorly developed anterior extension of the mental region (LMF-POG). Infants of both taxa exhibit wide bimental foramen breadths (LMF-RMF), with respect to size, that reflect the puffy and broad mental regions holding the developing germs of the permanent dentition; these characteristics separate infants from both adults on PC axis 1 (Figure 8; Table 5).

Principal component axis 2 explains 39% of the variance, and carries a strong taxonomic signal by completely separating the life cycle stages of

Neandertals from those of modern humans. Modern human infants and adults exhibit an anteriorly extended gnathion on the mental trigone, with respect to size, as indicated by the high positive loading of LMF-GNA. Modern humans, regardless of life cycle stage, also exhibit a relatively elongated tooth row with respect to mandibular size when compared to the dental arcade typical of Neandertals (LMF-LRAM). Neandertal adults are projected on the negative segment of PC axis 2 largely due to the posterior placement of their mental foramina (with respect to the dentition), as the high negative loadings of the shape indices LMF-IDI and LMF-LI<sub>2</sub>C reflect the more posterior position of the mental foramen relative to the central incisors and the I<sub>2</sub>/C junction, respectively (Table 5). In other words, adult Neandertals exhibit posteriorly placed mental foramina only with respect to the tooth row, and not with respect to overall mandibular size. Pedomorphosis cannot account for the posterior placement of the mental foramen in Neandertals because modern human adults fail to correspond to any preadult Neandertal stage. Instead, it is likely that differences in the size of the teeth (Franciscus and Trinkaus, 1995) and mandible

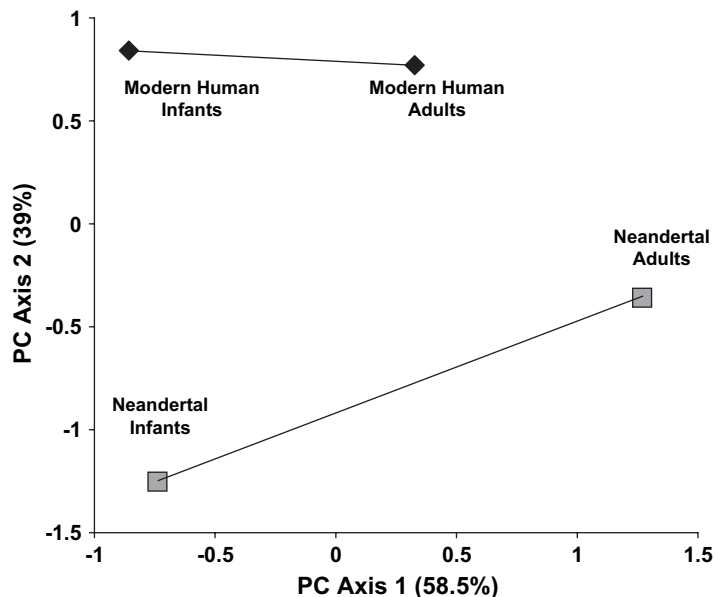


Figure 8. PCA of life cycle stages. The means of seven shape indices for each life cycle stage per taxon are shown in this multivariate shape space.

Table 5  
Component loadings for PCA of Neandertal and modern human life cycle stages\*

Interlandmark distances	PC axis 1	PC axis 2
LMF-IDI/MS	0.048	-0.999
LMF-POG/MS	0.981	0.245
LMF-GNA/MS	-0.481	0.866
LMF-GET/MS	0.931	0.318
LMF-LI <sub>2</sub> C/MS	-0.768	-0.640
LMF-LRAM/MS	-0.760	0.638
LMF-RMF/MS	0.994	-0.064

\* See Table 2 for landmark descriptions. MS = Mandibular Size (see methods).

(Rosas, 1997, 2001) are responsible for the appearance of a more posteriorly located mental foramen in Neandertals. Since bi-mental foramen breadth relative to mandibular size is similar in the two taxa (Figure 5), and a t-test reveals that adults of the two taxa do not differ significantly for this relationship ( $p = 0.227$ ), another kind of analysis is necessary to clarify the relationship between the mental foramen position, the tooth row, and total mandibular size.

#### Growth allometries

A comparison of Neandertal and modern human growth allometries that approximates the anterior-posterior placement of the mental foramen (LMF-IDI) and the length of the dental arcade (IDI-LRAM) with respect to total mandibular size further corroborates that the mental foramen is not more posteriorly located in Neandertals than in modern humans (Table 6). When LMF-IDI is compared to mandibular size, the null hypothesis of isometry cannot be rejected for either Neandertals or modern humans. This suggests that in both taxa, adults do not differ from infants in the anterior-posterior placement of the mental foramen. However, when IDI-LRAM

is compared to mandibular size, modern humans exhibit slight positive allometry whereas the pattern for Neandertals is isometry. In other words, modern human adults exhibit relatively longer dental arcades than do infants and the relative length of the dental arcade increases as mandibular size increases, whereas these proportions remain roughly constant in Neandertals throughout ontogeny. Coupled with the isometric growth of LMF-IDI, this suggests that modern human adults exhibit a mental foramen that is slightly more anterior with respect to the length of the tooth row (but not mandibular size) compared to its placement in Neandertals. The mesiodistally short premolars characterizing Neandertals (Williams, 2001) exaggerate the appearance of a posteriorly positioned mental foramen in Neandertal adults.

#### Discussion

Although Neandertals and modern humans follow similar shape trajectories when bi-mental foramen breadth is compared to mandibular size, in multivariate treatments of the data (with the exception of PC axis 1 in Figure 8), the two taxa follow dissimilar shape paths. While the bivariate comparison suggests that modern humans are not paedomorphic, the multivariate analyses suggest that Neandertals and modern humans are not on the same “Gouldian” clock. If the two taxa were on the same clock, we would expect modern humans to exhibit a mental foramen position similar to some nonadult Neandertal life cycle stage. We would also expect the surrounding structures to be similarly built. However, Neandertal and modern human infants differ substantially in the mental region (Minugh-Purvis, 1988; Tillier, 1989; Stringer et al., 1990; Williams, 2001;

Table 6  
Growth allometry coefficients (k)

	Neandertals (n = 9)			Modern humans (n = 266)		
	k	SE	Allometry	k	SE	Allometry
LMF-IDI	1.067	0.05	Isometry	1.020	0.018	Isometry
IDI-LRAM	1.032	0.062	Isometry	1.101	0.025	Positive

Coqueugniot and Minugh-Purvis, 2003). Although some of the linear distances (e.g., LMF-POG and LMF-GNA) exhibited similar growth patterns, the trajectories that capture shape change from the mental foramen to other mandibular structures differ considerably (see Figure 7). With respect to the mental foramen and the mental region generally, neomorphosis may better describe the ontogenetic differences between Neandertals and modern humans.

Neandertal growth of mandibular traits, with respect to the mental foramen, appears to proceed at a faster rate (provided Neandertals and modern humans matured at similar dental ages; cf. Ramirez Rozzi and Bermudez de Castro, 2004). Many researchers have suggested, following Bolk (1926), that Neandertals experienced accelerated rates of absolute growth (Smith, 1991). For example, Williams (2001) noted that Neandertal masticatory traits appear to have grown at an overall faster rate than typical of modern humans. Minugh-Purvis (1988) noted a faster rate of occipital growth in Neandertals, and Tillier (1989) suggested that neurocranial growth proceeded more rapidly in Neandertals with respect to modern humans. On the basis of the number of incisal perikymata exhibited by the Devil's Tower (Gibraltar 2) child, Stringer et al. (1990) argued that Neandertals experienced accelerated growth of the neurocranium vis-à-vis dental development. In a study of CT scans of Le Moustier 1, Thompson and Illerhaus (1998) found that the rate of growth in facial height was accelerated compared to modern human controls.

A faster rate of growth of some traits relative to others may help to explain many of the apomorphic features that characterize Neandertals. However, a faster rate of growth of bi-mental foramen breadth does not by itself account for the difference in mental foramen position between Neandertals and modern humans. Neandertals have relatively small teeth (with respect to jaw size) compared to modern humans (Franciscus and Trinkaus, 1995). This relative tooth size difference is what accounts for the "posterior" position of the mental foramen in Neandertals, rather than the position of the mental foramen itself.

Rosas (2001) observed that larger mandibles from the Atapuerca Sima de los Huesos site have more posteriorly located mental foramina, and suggested that a scaling relationship could account for differences in the position of this character with respect to mandibular size. If larger mandibles exhibit more posteriorly located mental foramina, we would expect to see differences between the placement of the mental foramen in Neandertals and modern humans. Although absolute bi-mental foramen breadth does increase at a faster rate in Neandertals (Table 3), so does mandibular growth generally. Bi-mental foramen breadth relative to size in Neandertals does not differ significantly from that observed in modern humans. The extent to which a scaling relationship exists between the placement of the mental foramen and mandibular size depends on whether tooth size is considered.

Changes in tooth size and mandibular form during the late Pleistocene may signal an evolutionary and/or biomechanical response to various selection pressures. The fact that most Neandertal and middle Pleistocene *Homo* mandibles exhibit a suite of symplesiomorphic traits suggests that changes in the developmental program occurred during the evolution of modern human mandibular form. As noted by Ponce de León and Zollikofer (2001), perinatal shifts in the deposition and resorption of bone in the anterior mandible characterize modern humans, but not Neandertals. These changes may have been initiated by the emergence of a distinct mental trigone.

Incipient aspects of the mental trigone arise early in gestation (Schwartz and Tattersall, 2000), and the mental foramen is related to this developmental complex as the nerves and blood vessels it carries supply the mental region (Coqueugniot and Minugh-Purvis, 2003). It is possible that the embryonic positioning of the mental nerve and blood vessels (and thus also the foramen) may lead to the development of the anteriorly everted borders of the mental region during the second trimester of gestation, particularly since the mental foramen is the initial site of mandibular bone ossification (Kjaer, 1989, 1990; Rodriguez-Vazquez et al., 1997; Ishizeki et al., 1999).

After parturition, the mental trigone continues to develop as the mandibular symphysis ossifies (Scheuer and Black, 2000). However, during the first years of life, the mental trigone becomes largely obscured as the developing germs of the deciduous and permanent anterior dentition decrease the indentation of the *incurvatio mandibularis* (Minugh-Purvis, 1988; Schwartz and Tattersall, 2000). During much of this time period, the mental foramina migrate very little, if at all, in modern humans (i.e., prior to the eruption of  $M_1$ ). Upon the eruption of  $M_1$ , the mental foramen begins to migrate posteriorly until the eruption of  $M_2$ , or shortly thereafter (FLW, unpublished data).

Although it is difficult to reconstruct the prenatal ontogeny of Neandertals, the early mandibular shape changes characterizing this taxon most likely differed considerably from those typical of modern humans. The mental region of the youngest Neandertal mandibles (e.g., Amud 7) is thickened, and the mental foramina border a broad alveolar process that retreats inferiorly from infradentale to gnathion. In contrast to modern humans, Neandertals may have experienced less remodeling of the anterior mandibular arch during early postnatal ontogeny (Coqueugniot and Minugh-Purvis, 2003). The extensive roots of the buccolingually thickened permanent incisors and canines, that would have formed during early Neandertal infancy, might have prevented the formation of extensively excavated *incurvatio mandibularis*. These indentations form the lateral borders of the mental trigone during modern human development (Schwartz and Tattersall, 2000). The mental foramen is displaced at a faster rate in Neandertals compared to modern humans (Table 3); this may account for the significant difference in mental foramen position among Neandertal and modern human late infants and juveniles observed by Coqueugniot (2000). The inferior marginal tubercles, directly inferior to the mental foramina on the inferior border of Neandertal adult mandibles (Schwartz and Tattersall, 2000), probably formed after  $M_2$  eruption when the mental foramen was already located in the position characteristic of Neandertal adults.

## Conclusions

Although Neandertal mandibular ontogeny is only partially preserved and difficult to reconstruct, the results of this examination undoubtedly support the following conclusions. Neandertal mandibular traits increase in size at a faster rate than those of modern humans, although the duration is variable. These accelerated patterns may explain some of the derived features of Neandertal adult morphology, such as strong genial tubercles, squared mental regions, and more obtuse gonial angles; ultimately Neandertals exhibit a greater amount of postnatal mandibular shape change. Neandertals and modern humans follow distinct shape paths during mandibular ontogeny, particularly due to the development of a prominent (and neomorphic) mental trigone early in modern human development. When bimental foramen breadth is compared to mandibular size, the two taxa are broadly similar. The degree to which modern humans are paedomorphic in mental foramen position is only a reflection of its position with respect to the post-canine teeth. Ontogenetic changes in the relative size of the tooth row characterizing modern humans, but not Neandertals, coupled with the mesiodistally short premolars typical of Neandertals, leads to a mental foramen in Neandertals that appears more posterior than it actually is with respect to mandibular size. Therefore qualitative assessments of mental foramen position in Neandertals and modern humans may be misleading because they do not take into account differences in tooth size between taxa.

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