Chapter 19
Brother or Other: The Place of Neanderthals in Human Evolution

Rachel Caspari, Karen R. Rosenberg, and Milford H. Wolpoff

Abstract Few have provided insights and thoughtful explanations for Neanderthals that equal what have been a central theme in Yoel Rak's publications. One of his deep understandings is that Neanderthals are another way of being human: not inferior, not superior, but different. Looking at what we now understand, Rak has been fundamentally correct in this insight, and where new discoveries have been unexpected, they serve to expand its scope and meaning. Unexpected new information about Neanderthal body form, demography, and even breeding behavior support and flesh out Rak's essential insight about the place of Neanderthals in human evolution. In this paper some of the new discoveries and interpretations of Neanderthals and their evolution are discussed in this context. We examine three aspects of how Neanderthals are another way of being human: body shape (as revealed in the pelvis), population structure (as revealed in their paleodemography), and breeding behavior (as revealed by paleogenetics, in the pattern of ancient gene flow). In these ways Neanderthals are like their ancestors, or more broadly are the plesiomorphic condition.

Keywords Interbreeding • Neanderthal body shape • Neanderthal breeding behavior • Neanderthal pelvic form • Neanderthal population structure

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Introduction

Few scholars have provided insights and thoughtful explanations for Neanderthals that equal those of our good friend, Yoel Rak (Fig. 19.1). Our conversations with Rak over many years often centered on his insistence that Neanderthals represent another way of being human: not inferior, not superior, but definitely different. Although we often find ourselves on opposite sides of paleoanthropological debates from Rak, it may surprise him to know that we agree with him on this central tenet. Neanderthals are different, yet human, and in this paper we review some of our work on Neanderthal morphology and culture that reflects the nature of that difference.

Over the last few years, unexpected new information about Neanderthal body form, demography, and breeding behavior support and flesh out Rak's essential insight about the place of Neanderthals in human evolution. In this paper we examine three aspects of Neanderthal biology: body shape (as reflected in the pelvis), population structure (as suggested by paleodemography), and breeding behavior (as suggested by paleogenetics in the pattern of ancient gene flow). We argue, and are sure Rak would agree, that in body form, demography, and population structure, Neanderthals reflect the plesiomorphic condition, and are unlike modern humans (people alive today and their immediate ancestors) in many ways. However, these differences exist within an open genetic system, with ancient contacts between archaic and modern humans that attest to Neanderthal humanity.

Neanderthal Body Form

One area of Neanderthal morphology that has received a great deal of attention is the pelvis. Early discoveries of Neanderthals from the Middle East (Shanidar in Iraq and Tabun in Israel) showed what was thought to be a distinctive morphology in the form of an elongated, thinned superior

Fig. 19.1 Exhibit "A"

pubic ramus. Scholars like Stewart (1960) described the trait, which he saw in specimens from Tabun and Shanidar (but not in the specimens from Skhul), as "peculiar" and interpreted it as a derived trait in Neanderthals that indicated contemporaneity of Neanderthals and modern humans in the Levant. The functional significance of the trait was not addressed and it was widely assumed that Neanderthals had a derived condition.

In the 1980s, several scholars considered the functional significance of this trait. A number of hypotheses (Trinkaus 1984; Dean et al. 1986; Rosenberg 1988) were based on the assumption that because in humans, females have a longer pubis than males, the elongated pubis in Neanderthals was indicative of an expanded birth canal, with a range of explanations for why Neanderthals might have had an expanded birth canal relative to modern humans. These hypotheses never satisfactorily explained the genuinely peculiar trait, namely an unusual pattern of sexual dimorphism in (the admittedly small sample of) Neanderthals. Neanderthal males had long pubic bones which were in some cases longer than those of females, in sharp contrast to the pattern we see in all human populations.

With the discovery of the Kebara pelvis (Kebara 2) in 1983, it was possible for the first time to examine a Neanderthal pubic bone in the context of the entire pelvic girdle. In his meticulous description of that specimen, Rak (1990, 1991b; Rak and Arensburg 1987) pointed to some interesting differences between it and the pelvis of more recent humans. This specimen is the only Neanderthal pelvis for which both pelvic inlet breadth and pubis length are known and Rak showed, in contrast to the expectations of earlier scholars, that even though the Kebara specimen has an elongated pubis compared to modern humans, it has an inlet size not much different from that expected based on body size in humans (but a wide overall pelvic girdle). Rak argued then that the long pubic bones were not related to obstetrical constraints, but were a reflection of the anterior position of the Neanderthal pelvic aperture relative to the acetabulum when compared with modern humans. He compared the position of the pelvic inlet within the frame of the pelvic girdle in Kebara 2 with a series of modern humans. Rak noted that as seen from above, the Kebara 2 pelvic inlet was more anteriorly positioned within the frame of the pelvis than the inlet of modern humans. This is associated with a corresponding anterior shift in the position of the sacrum (the inlet's rear), rendering this weight-bearing portion closer to the bi-acetabular line (compared to modern humans). In life the pelvis is tilted forward in most postures (so that the anterior-superior iliac spine and anterior-inferior iliac spine are on a vertical line), positioning the weight bearing surface at the top of the sacrum (this supports the trunk) directly above the acetabulum where weight is transmitted to the lower limbs. In the Kebara 2 specimen, less tilt is required. According to Rak, the front of the inlet is also more anterior because of the forward shift, which explains why the pubic bones are longer in this and certain other archaic specimens (see Fig. 19.2).

Additional features characterizing this pelvis (and some others including some of those attributed to European Neanderthals) are a consequence of the changed orientations required by this differing inlet position. The iliac blades are broader and the acetabula face more laterally, unchanged from the ancestral condition. But these unusual features are not unique to the Western Asian and European specimens. Important remains from this time period in East Asia such as the Jinniushan pelvis (also with an elongated pubis, Rosenberg et al. 2006) have not yet been described in detail. Later East Asians such as the 18 kyr Minatogawa (Okinawa) male also has pubic length elongation compared to acetabulum size, like the Neanderthal pattern. Rak's hypothesized shift in the position of the pelvic aperture relative to the hips has postural implications and this has been reflected in more recent reconstructions of Neanderthals (Sawyer and Maley 2005; Lloyd 2012) (Fig. 19.3). Rak (1991a) also studied pelvic shape in the australopithecine specimen, AL 288-1
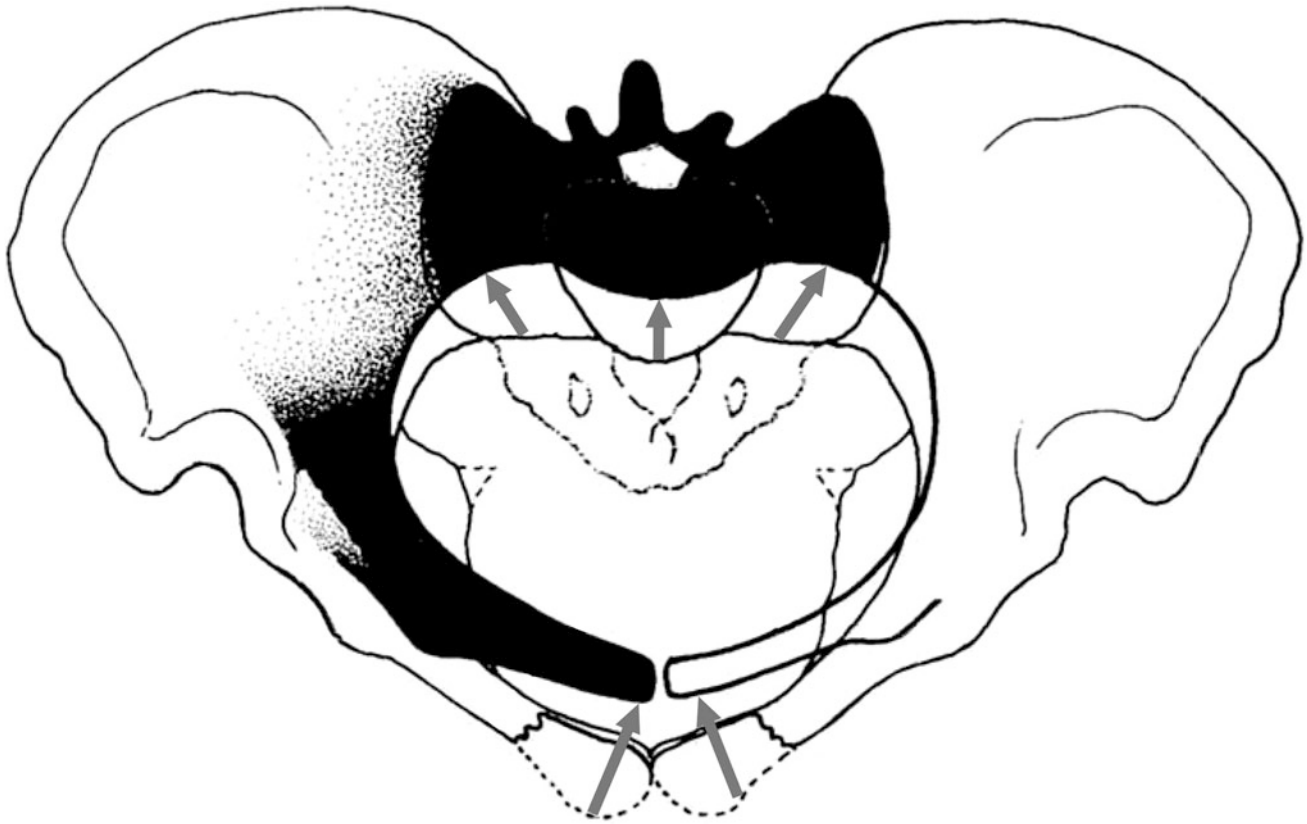
Fig. 19.2 This figure shows the hypothesized changes (*indicated by the arrows*) that would be necessary to go from a Neanderthal pelvis (*shown in white*) to a modern human pelvis (*shown in black or with black stippling*), according to Rak's model. The breadth of the inlet would remain the same in this modeling, but the length of the pubic bone would become shorter as the inlet moves posteriorly within the pelvic girdle. (modified from Rak and Arensburg 1987)

arguing that it, too, was extremely wide relative to body size. He argued "this width, when combined with the horizontal rotation of the pelvis, minimizes the vertical displacement of the center of mass during bipedal walking" (Rak 1991a: 283).

Rak's model of the position of the relationship of the length of the pubis with the position of the pelvic aperture within the pelvic girdle has not been rigorously tested, but his work has led to two robust observations: 1. The elongated pubis in Neanderthals is not a derived trait in that group but a retention of the primitive condition (Rak 1993) and 2. A wide pelvis overall is typical of all hominids.

We are interested here in why Neanderthals (and other hominids) had such a broad pelvis.

"It could be argued that the early *Homo* pelvis from Gona, Ethiopia refutes the climate hypothesis, because it may demonstrate that a wide pelvis was the primitive condition for the genus *Homo*. However, showing that a morphological feature is primitive for a taxonomic group does not explain why this feature persists in some descendant taxa and not others. Even if a wide pelvis was unrelated to climate in early *Homo*, climate adaptation is still the best explanation for why Neanderthals maintained a wide pelvis, early modern humans living closer to

the equator evolved a narrow pelvis, and recent humans who migrated to cold climates regained a wide pelvis." (Weaver 2009: 16032)

"Neanderthals tended to live in cold climates, where wide trunks are advantageous for thermoregulation, so maintaining the primitive pattern of transversely wide outlets would not have interfered with their climatic adaptations" (Weaver and Hublin 2009: 8154).

In his recent book, Churchill (2014) discusses Neanderthal body form in the context of cold adaptation that was important at least some of the time, but also suggests, as others have proposed, that the large Neanderthal thorax might be a retention of the plesiomorphic condition (Gómez–Olivencia et al. 2009). "The Neanderthals, despite their short and stocky build, suffered the legacy of a tropical ancestry, just as do modern Inuit and Eskimo" (Churchill 2014: 129). Yet, there is no question that he considers Neanderthals to be cold adapted (title of Sect. 5.7 is "Neanderthals *were* cold-adapted"). Thorax shape, of course, is reflected in dimensions of the pelvis.

A related question is why do Neanderthals have wide trunks? Ruff (1991, 1994) observed that Neanderthals had relatively wide bodies for their stature compared to modern
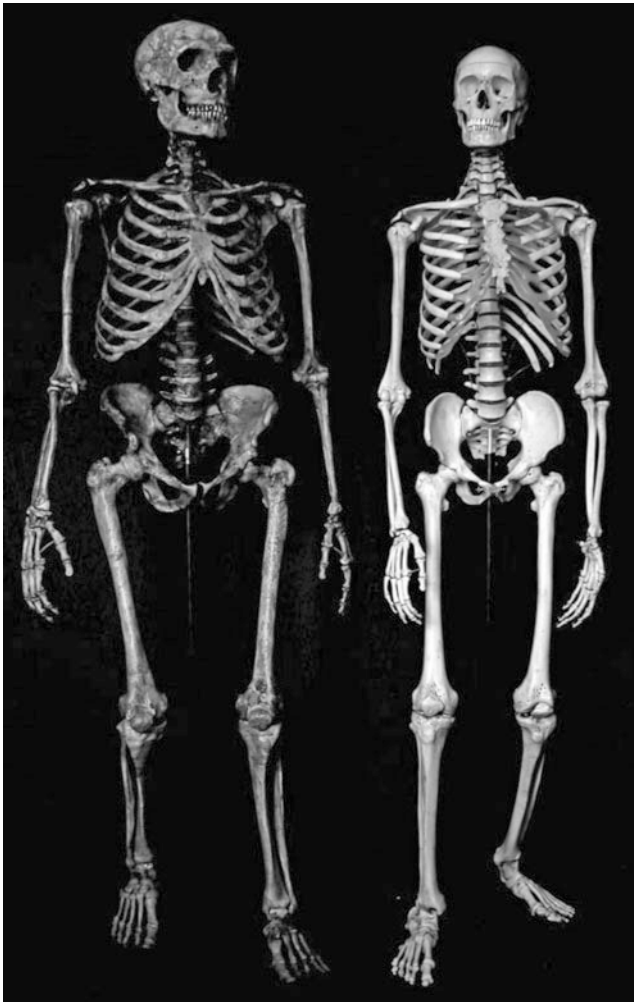
Fig. 19.3 Reconstructed Neanderthal and modern human skeleton. Note the difference in the anterior tilt of the pelvis: less in the Neanderthal, more tilted in the human skeleton shown. (Sawyer and Maley 2005)

humans. Arsuaga et al. (1999) noted that broad trunks were also found at Sima de los Huesos in a sample thought to be one of the ancestors of Neanderthals.

> "Our interpretation is that the pattern of a broad pelvis, a long femoral neck and marked iliac flaring is a shared primitive character already present in *Australopithecus afarensis* (as seen in the A.L. 288-1 specimen), in which case it should be also found in the early *Homo* fossils. However, based on the juvenile and very fragmentary WT 15000 pelvis (West Turkana, Early Pleistocene), the 'adult' bicrestal breadth of *Homo ergaster* has been estimated as narrow. In our opinion, the East African ER 3228 and OH 28 coxal bones are so similar in all the preserved regions to the SH coxal bones, also showing a marked lateral iliac flare, that the inferred narrow bicrestal breadth for WT 15000 might be an error. A narrow pelvis could be a unique modern human condition." (Arsuaga et al. 1999: 257)

Churchill (2014) developed and elaborated the details of Neanderthal body form, not just reconstructing Neanderthal

anatomy but also estimating its physiological needs in a glacial environment. But there is an important comparative context for understanding Neanderthal body form, throughout human evolution and in a wide range of environments. Today, we know much more about the evolution of hominid pelvic shape than we did in 1983 when Kebara 2 was found, because of an expanded fossil record from earlier time periods that includes the Gona specimen (Simpson et al. 2008), the Malapa material attributed to *Australopithecus sediba* (Kibii et al. 2011), the Jinniushan specimen (Rosenberg et al. 2006), and the material from Atapuerca (Arsuaga et al. 1999). In addition, even earlier specimens such as the australopithecines AL 288-1 and Sts 14 have pelvic girdles that are broad relative to stature. This is visually accentuated by the common reconstruction of australopithecine trunks as conically shaped. However, the cone-shaped reconstruction is likely incorrect. The Woranso-Mille skeleton from ca. 3.8 Ma is the earliest hominid skeleton to have sufficient information about trunk shape (preserving both a clavicle and a first rib) to demonstrate a broad, barrel-shaped trunk (Haile-Selassie et al. 2010). Australopithecines reconstructed to have a conical trunk invariably lack the anatomical information provided by the clavicle and first rib, and it now seems clear that a barrel-shaped trunk is the normal trunk shape for later hominids.

It seems to us that Rak was correct in his assertion that a broad pelvis is the primitive condition for hominids, just as Churchill was correct in describing a Neanderthal legacy from a tropical ancestry. In addition to knowing more, we have also unlearned something that we thought was true – namely that the Nariokotome *Homo erectus* specimen which was reconstructed based on very fragmentary pieces of the pelvis of a juvenile male, may not have been as narrow as had been thought (Ruff and Walker 1993; Walker and Ruff 1993). That specimen represented the only narrow-hipped individual in the human fossil record and its narrowness now appears to have been exaggerated in the reconstruction (Ruff 1995; Arsuaga et al. 1999; Simpson et al. 2008).

To further examine the Neanderthal condition in an evolutionary context, we examined pelvic dimensions relative to stature in all human fossils for which these dimensions could be measured or reliably estimated (Table 19.1). It should be noted that these data come from a range of sources and some include estimates (shown in parentheses). An explanation for the source of the data is provided with the table. Taking a broad comparative perspective, we examined relative pelvic breadth in fossil hominids over the last 3.5 million years. We plotted our best estimate of stature (based on whichever long bones were preserved for each specimen) for each fossil against bi-iliac breadth and transverse, anterior-posterior and estimated circumferential dimensions of the pelvic inlet (Fig. 19.4). We compared the

Table 19.1 Fossil pelvic remains and stature estimates. All measurements in mm

Specimen	Max bi-iliac breadth (M2)	Max inlet breadth	Max inlet A-P	Calculated circum. of inlet	Femur length (M1)	Arm bone length (M1) when femur length is unknown	Estimated stature
AL 288-1	247 (Wolpoff, measured on cast of Lovejoy reconstruction)	132 (Tague and Lovejoy 1986)	76	338	281 (max. length) (Wolpoff 1980, measured on cast of Lovejoy reconstruction)		1052
Sts 14	230 Wolpoff reconstruction	104	94	311	(276) (Lovejoy and Heiple 1970)		1034
Sediba (MH 2)	250 (Kiibi et al. 2011)	118	82	319	316 (De Silva pc)		1183
Gona	288 (Simpson et al. 2008)	125	98	353			1350
SH Pelvis 1	335 (Bonmati et al. 2010)	138	121	408	475 (Arsuaga et al. 1999)		1779
Jinniushan	344 (Rosenberg et al. 2006)	149 Rosenberg reconstruction	124	430		260 (ulna) (Rosenberg et al. 2006)	1689 (Rosenberg et al. 2006)
Kebara 2	313 (Rak 1990)	142 (Tague 1992)	118	410		324 (humerus) (Vandermeersch 1991)	1707 (Vandermeersch 1991)
Tabun C1	260 (McCown and Keith 1939); or 270 (Churchill 2014 citing Weaver and Hublin 2009)	144 (Ponce de León et al. 2008)	115	408	416 (McCown and Keith 1939)		1558
Skhul 4	280 (McCown and Keith 1939)				492.5 (McCown and Keith 1939)		1844
La Chapelle-aux-Saints	(295) (measured by Ruff 1994 from Boule's (1911) drawing): or 292 (Churchill 2014)				(433) (Ruff 1994)		1621

Bi-iliac breadth: Bi-iliac breadth of AL 288-1 was measured by Wolpoff on cast reconstruction by Lovejoy. Sts 14 was measured by Wolpoff on the original specimen; the three pieces were propped up into anatomical position with missing part of the pubis on the right side represented in clay. Simpson et al. (2008) reported the same number for Sts 14 and cited Robinson (1972). Arsuaga et al. (1999) initially published a value for SH Pelvis 1 of 340 but this was corrected to 335 in a later paper by Bonmati and colleagues (2010) (Table S2). The value for Tabun C1 is from McCown and Keith (1939). We do not have a great deal of confidence in this measurement and await estimates from Weaver (2009) and/or Ponce de Leon et al. (2008). The Skhul 4 measurement was taken from McCown and Keith (1939) and looks reasonable based on the completion of the specimen shown in drawings in the monograph. Although Qafzeh 9, Skhul 5 and 9 also include fragmentary pelvic elements, we were not confident enough in the estimates provided to include them

We have used Ruff's (1994) estimate of the La Chapelle-aux-Saints bi-iliac breadth, a measurement that was based on Boule's reconstruction of the skeleton which included a sacrum but lacked the pubic portions. Boule reconstructed these from plaster, but the reconstruction was done before elongated pubic bones had been observed in Neanderthals. For this reason we suspect that the pubic bones were longer and therefore the true breadth of the La Chapelle-aux-Saints pelvis was most probably greater than the 295 mm estimated by Ruff from Boule's drawing and given in Churchill (2014), or Trinkaus' (2011) estimate of 292 mm

Femoral Length and Stature Estimation

Whenever possible, when femora were preserved, we used femoral length to estimate stature (Table 2) using the Feldesman et al. regression formula given in Simpson et al. (2008) Supplementary Material because it gives estimates for AL 288-1 and WT 15000, at different ends of the size range, that were close to estimates of other workers. Femur length for Sts 14 was estimated geometrically from the STS 14 proximal femur and unassociated distal remains from Sterkfontein (Lovejoy and Heiple 1970)

The femur length for MH2 was estimated by DeSilva. He estimated tibia length for MH2 based on the tibia of MH4; in comparable parts MH2 is on average 97.9% as big as MH4, DeSilva used 97.9% of the MH4 tibial length as the estimate for MH2. He then examined the ratio between the lengths of the tibia and femur in the Turkana Boy and the Dmanisi skeleton (the only two Plio-Pleistocene skeletons with both tibia & femur preserved). The Dmanisi tibia is 80% length of femur; Nariokotome's is 88%. Applied to MH2 this suggests the femur was between 301 and 331 mm, an average of 316 mm – the value we have used for the MH2 stature estimate

For Atapuerca SH Pelvis 1, we accepted Arsuaga and colleagues' (1999) argument that two partial femora probably belong to the same individual: Femur X, a proximal left fragment that fits in the acetabulum and has "an atypical remodeling" on its head that marches a corresponding "atypical remodeling" on the surface of the acetabulum; and AT 432, a right diaphysis. These were reconstructed to a femur length between 47 and 48 cm

We used the length of forearm bones to reconstruct height in two other specimens. For Jinniusham, we use the estimate of Rosenberg et al. (2006) from the length of the complete ulna. Kebara 2 lacks a femur and we estimate its stature from its virtually complete humerus (Vandermeersch 1991)

Finally, Gona lacks a femur, or any other limb bone. We have taken the average of the maximum and minimum of Simpson et al.'s (2008) estimates for the Gona stature
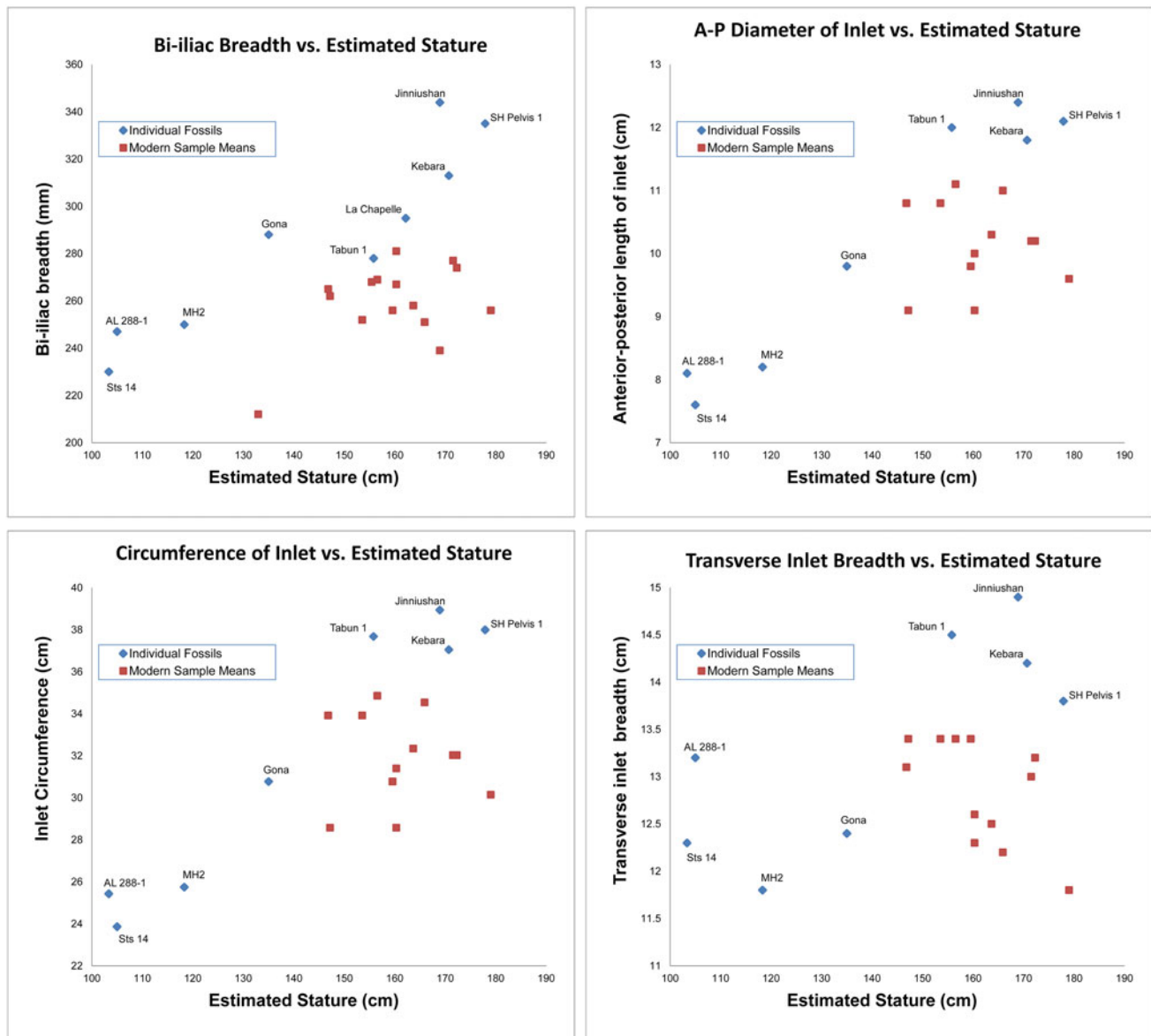
Fig. 19.4 Each graph shows fossil specimens (diamonds) and sex-specific sample means from modern human populations (squares). Stature for each fossil specimen represents our best estimate of stature depending on what skeletal elements were preserved. All fossil data are given in Table 19.1 with explanations about sources of measurements. (from Tague 1989)

fossil data to published mean sex-specific values for recent human populations from a wide geographic and climatic range (Tague 1989).

Across fossil specimens, there is a positive significant correlation between our estimate of stature and each of these dimensions of the pelvic aperture. For example, in Fig. 19.4, each graph shows a dimension of the pelvic girdle plotted against estimated stature. The blue dots represent the individual fossil specimens and the red dots the sex-specific means (or in one case a mixed-sex mean) of modern human populations. The fossil specimens all appear to have a greater bi-iliac breadth relative to stature than the modern

means. The modern human range (given that the red dots represent sample means) is at or below (but certainly never above) the fossils for bi-iliac breadth for a given stature. There is a systematic pattern of difference between the fossil and modern data; the fossil data lie around a line that falls above the modern human means. That is, modern humans are narrower in bi-iliac breadth relative to stature than the fossils.

We also examined direct measurements of the pelvic aperture at the level of the first pelvic plane (in females this dimension would be the inlet of the birth canal). Dimensions of the midplane and outlet are difficult given the poor

preservation of many of the fossils. Keep in mind that these are measurements of the pelvic aperture, which in females, but not in males, functions as the birth canal. Here, we examined the relationship between stature and transverse diameter of the inlet, AP diameter of the inlet and circumference of the inlet. Circumference of the inlet was calculated from the transverse and AP dimensions using the formula for the circumference of an ellipse given the lengths of the two axes. Because the neonatal head is malleable and is molded (the shape is changed) during labor, the circumference may in fact be the most important dimension for obstetrical purposes). These comparisons are based on data published by Tague (1989). The pattern of inlet dimensions relative to stature is similar to that of bi-iliac breadth discussed above, although in this case, some of the modern human samples fall between the early and later hominids, i.e., for their stature, they seem to have a transverse inlet dimensions similar to that of earlier humans. For most

dimensions of the pelvic inlet relative to stature, like bi-iliac breadth, modern human sex-specific sample means are the same size or smaller than the fossil humans.

Finally, we examined the relationship between bi-iliac breadth and pelvic inlet circumference to see if the difference between modern humans and earlier humans in bi-iliac breadth could be accounted for by a wider overall pelvis which would be reflected in greater inlet dimensions (Fig. 19.5). There is no clear difference between the fossil specimens and modern samples in this relationship suggesting that we cannot exclude obstetric differences as the source of the difference between modern humans and fossil specimens in dimensions of pelvic breadth.

Table 19.2 gives the correlation coefficients between stature and each dimension of the pelvis for fossil human individuals and modern human sex-specific means. The correlation coefficients which are statistically significant at the 0.05 level are shown in boldface.
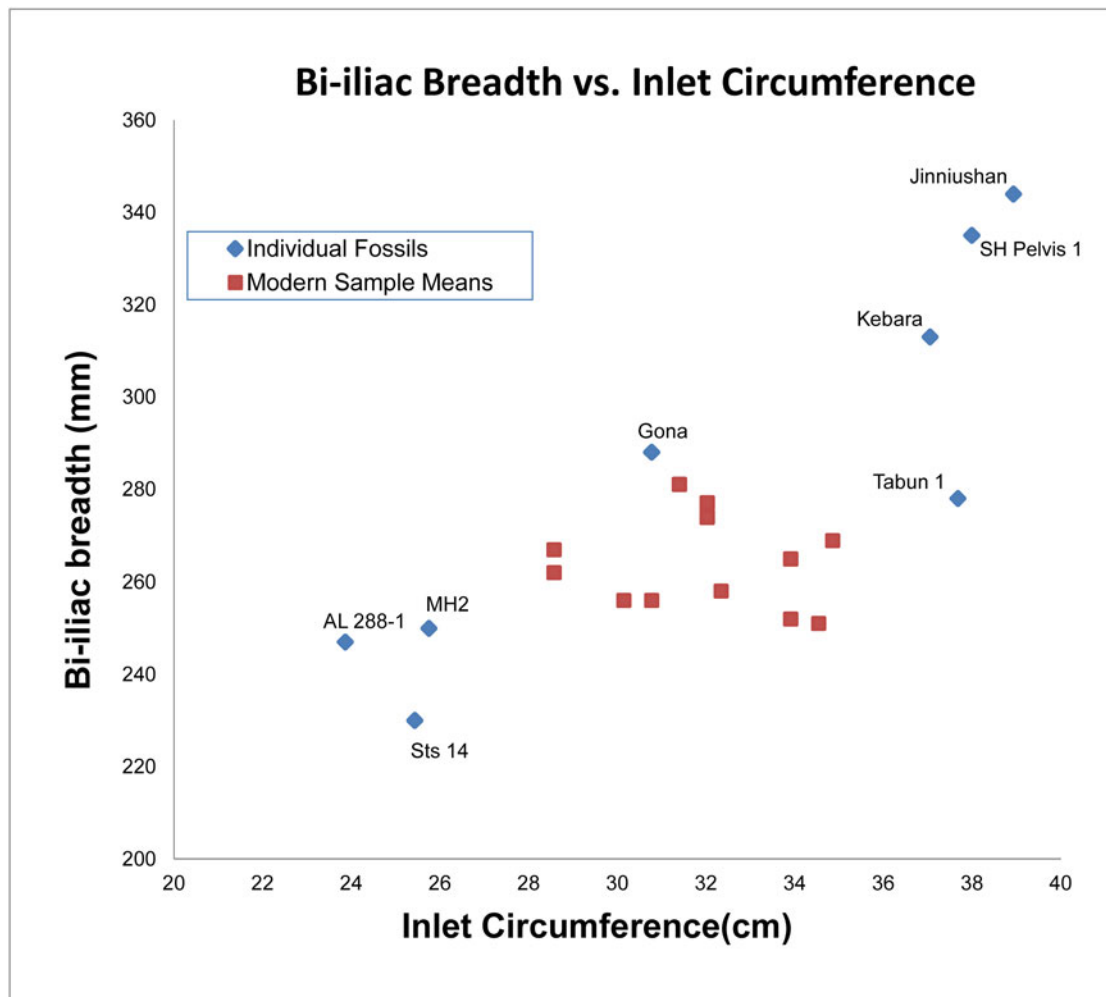
Fig. 19.5 Bi-iliac breadth vs. Inlet circumference. Each graph shows fossil specimens (diamonds) and sex-specific sample means from modern human populations (squares). All fossil data are given in Table 19.1 with explanations about sources of measurements. (from Tague 1989)

Table 19.2 Correlation coefficients across fossil individuals and modern sex-specific sample means. Values that are statistically significant at 0.05 level are shown with yellow highlights

	Stature vs bi-iliac breadth	Stature vs. inlet transverse	Stature vs. inlet ap	Stature vs. circumference
Fossil	**0.935**	**0.733**	**0.971**	**0.922**
Modern	0.086	**−0.588**	−0.129	−0.463

The fossil specimens span a much greater range of stature than the modern humans and it is hence not surprising that the correlation coefficients for stature vs. each of the pelvic dimensions are significant and positive. The correlation across modern population sex-specific means span a small range of stature and in those, only one correlation coefficient is statistically significant (for stature against pelvic inlet transverse diameter) but in a negative direction. That is, across the smaller range of modern populations, those populations that are on average taller, have relatively narrower transverse inlets.

What could account for the differences that we see between fossil specimens and modern samples? One possibility is thermoregulation which has long been regarded as an important determinant of body proportions and shape (Ruff 1991, 1994). However, both the fossil and the modern samples cover a wide and similar range of climates. Another possible explanation might be body size, but the pattern of differences between the two groups persists in specimens of similar body size.

It is possible that there could be locomotor differences between the groups. This hypothesis can be tested by looking for other evidence of locomotor differences between these groups. Finally, there could be obstetric-related differences between the groups – we can test this by looking at dimensions of the birth canal directly. If the differences between the fossil sample and modern humans are obstetrically related, we would expect to find differences in the birth canal as well as bi-iliac breadth.

In summary, although the samples are small and in some ways not comparable (note that the fossils are individuals, while the moderns are mean values for sex-specific population samples), the pattern is consistent. Relative to stature, modern humans have similar to or smaller bi-iliac pelvic breadths and all dimensions of the pelvic inlet than fossil humans. Most interesting, in Neanderthals, which are most similar to modern humans in body size (and brain size), this difference is still apparent. Although as a male, Kebara does not have a birth canal, Tague (1992) observed that the inlet (the top part of the pelvic aperture at the level of the arcuate lines) in Kebara 2 was relatively spacious compared to modern humans, although the lower planes of the pelvic aperture (the midplane and outlet) were more constrained. Because there seems to be a similar relationship between bi-iliac breadth and pelvic inlet dimensions in modern humans and Neanderthals, we suggest that the differences we discuss here may be related to differences in obstetric constraints, such that modern humans have smaller pelvic inlet dimensions relative to stature than Neanderthals. Two hypotheses that could account for this are:

- modern humans give birth to babies which are smaller than Neanderthals (Rosenberg 1988)
- modern humans have some unique obstetrically-related behavior that allows them to give birth to the same sized babies through a slightly smaller passage.

It appears that in overall body shape and specifically in pelvic breadth (transverse dimensions), Neanderthals reflect the primitive condition for hominids. This is in spite of the fact that there were significant changes in the mechanism of birth over this time period (from australopithecines up until Neanderthals) that accompanied increasing body size and encephalization and that probably required accommodations of the pelvis in the anterior-posterior dimension.

Population Structure

Cultural behavior has been frequently cited as an area in which Neanderthals and modern humans differ significantly, with archaeological evidence often interpreted as evidence of Neanderthal cognitive inferiority compared to modern humans (reviewed by Shea 2011, and Henshilwood and Marean 2003; see also Tattersall 2002; Mellars 2005, 2006; Teyssandier 2008). But even the most entrenched precepts in paleoanthropology can change. More recently, there has been widespread recognition that Neanderthals were capable of complex behaviors reflecting symbolic thought (Soressi and d'Errico 2007), including the use of pigments (Roebroeks et al. 2012), jewelry (Zilhão et al. 2010), and feathers and raptor claws as ornaments (Peresani et al. 2011; Morin et al. 2012; Radovčić et al. 2015). All of this is probably evidence of symbolic social signaling, complementing the evidence of complexity of thought demonstrated by the multi-stage production of Levallois tools. Neanderthals were human. Yet, as Rak has suggested, Neanderthals may have been human in a different way. Symbolic associations are less frequent and arguably less sophisticated in Mousterian contexts than in Upper Paleolithic assemblages, perhaps reflecting another way of being human.

Behavioral evolution is exceptionally complex because "both genetic and non-genetic inheritance, and the interactions between them, have important effects on evolutionary outcomes" (Danchin et al. 2011: 475). Demography, as an interface between the biological and the cultural, reflects this complexity, and many authors have considered it to be the cause of the behavioral differences underlying the Middle and Upper Paleolithic (e.g., Shennan 2001; Caspari and Lee 2004, 2006; Hovers and Belfer-Cohen 2006; Zilhão 2007; Powell et al. 2009; Richerson et al. 2009). In this section we review Neanderthal and Upper Paleolithic modern human demography, and suggest ways that demography may account for these different ways of being behaviorally human (Hovers and Belfer-Cohen 2006; Caspari and Wolpoff 2013).

There are a number of difficulties that affect the demographic reconstruction of fossil groups; in particular, small sample sizes, dependence on the age structure of juvenile data, and difficulties determining ages in fragmentary adult skeletal material have long been problematic. There are a few Pleistocene sites such as Atapuerca (Sima de los Huesos) and Krapina whose large samples and presence of juveniles make them amenable to demographic reconstruction. These sites are unusual, however, and most Neanderthal material is fragmentary and isolated and therefore cannot be used in traditional analyses. Methods that employ coarser, categorical age estimates and pooled samples must be used to circumvent many problems of preservation and sampling (Caspari and Lee 2004, 2006). As we show below, demographic profiles of both Krapina and Sima de los Huesos have been individually characterized by high levels of young adult mortality, so high that they have sometimes been interpreted as anomalies. However, when compared to each other, and to the pooled Neanderthal sample, the demographic characteristics of these sites appear to reflect their life history (and can be broadly interpreted as the life history of Neanderthals) and not a consequence of environmental or taphonomic factors unique to these two sites. We believe it is therefore valid to interpret these data as reflecting part of a larger scale archaic demographic pattern, created and maintained by social strategies that appear to have been different from those of modern humans.

Archaic Human Survivorship: The Krapina Death Distribution

Over a century ago the Croatian paleontologist Dragutin Gorjanović-Kramberger excavated and described Neanderthal fossils from a rock shelter near Krapina, 40 km northwest of Zagreb. Although the fossils from the site are fragmentary, they represent the remains of perhaps more than 70 individuals, most found within two stratigraphic layers, with U-series and ESR dates of about 130,000 years BP (Rink et al. 1995). Because of the number and proximity of the fossils, because the sediments at the site accumulated rapidly over a short period of time, and because a number of the bones share unique non-metric features, many workers have treated the remains from Krapina as a single population. As such, Krapina is one of the few archaic European sites amenable to demographic analysis. Its large sample size and preservation of juveniles have made it possible to successfully age adult dentitions using wear-based seriation and reconstruct the demography of the population (Wolpoff 1979).

The dental remains at Krapina are extensive; there are over 190 isolated teeth, some associated as "dental individuals" (Wolpoff 1979), and many teeth are associated with the maxillae and mandibles in the collection. While demographic data have been assessed for other skeletal elements, none are as comprehensive as those based on the dentition and the demography discussed here is based solely on dental remains. Age at death was estimated using several methods: juveniles were aged based on dental eruption, and adult age estimates were based on Miles (1963) method ages (wear-based seriation) that depend on the juvenile estimations. The wear-based dental age estimates were further validated with assessments determined from relative pulp volume using μCT (Wolpoff 1979; Wolpoff and Caspari 2006; Caspari et al. 2009). All the age estimations used in this research are founded on conservative assumptions about eruption times in Neanderthals and other ancient samples; these have been independently validated, holding up well in comparisons with other recent age assessments for the same juvenile specimens (Smith et al. 2010, 2013).

The Krapina Survivorship Distribution

Figure 19.6 depicts the death distribution at Krapina transformed to a survivorship curve compared to the survivorship curve from Libben, a prehistoric Native American sample, and assuming the same survivorship in the earliest interval because infant survivorship cannot be obtained from the fossil sample. Sex determination was not possible for most of the isolated Krapina teeth, and sex differences in survivorship could not be addressed. Krapina is recognized as a sample with high mortality rates. Atapuerca S-H (not shown in Fig. 6) closely resembles the Krapina sample in this and other ways (Bermúdez de Castro 1995; Bocquet-Appel and Arsuaga 1999). To standardize the distributions (to compensate for the missing children in the fossil samples), we assumed 69% survivorship at 5 years of age, the number observed for the
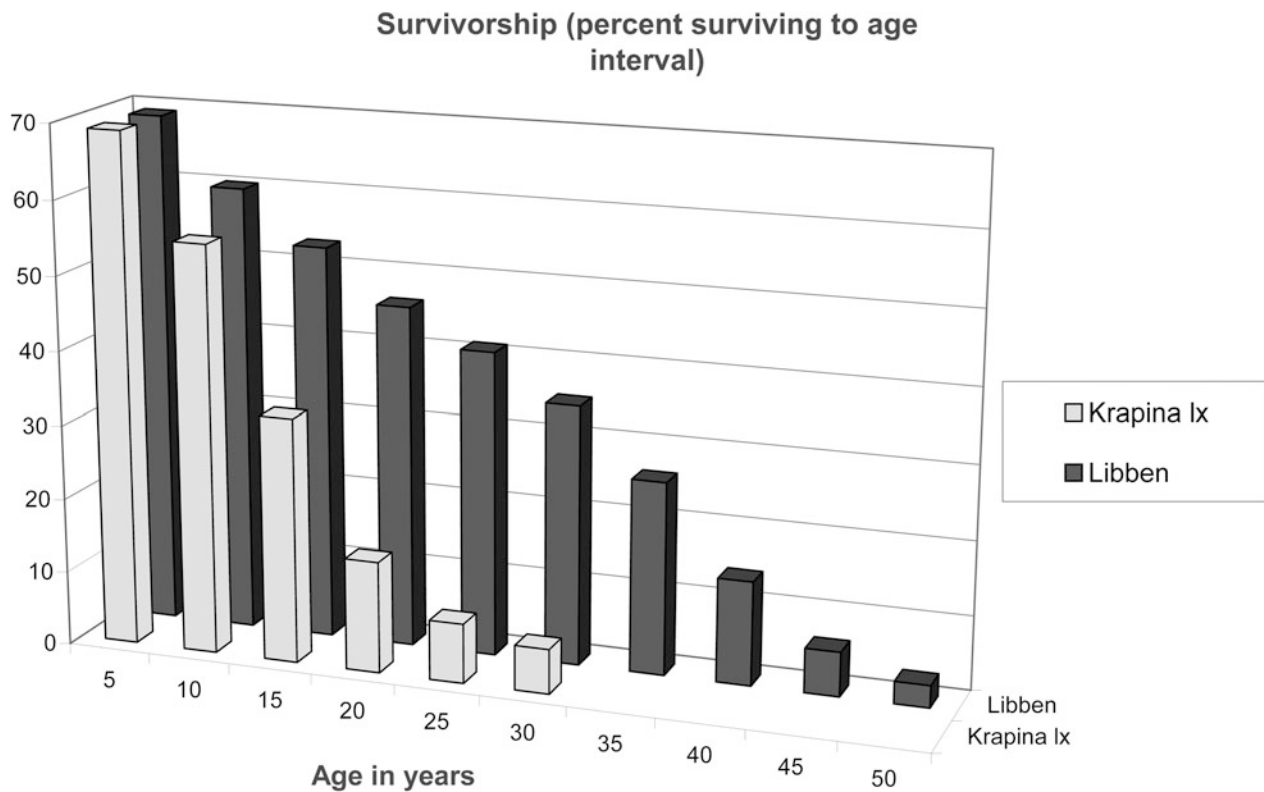
Fig. 19.6 The Krapina and Libben Survivorship Curves, adapted from Wolpoff and Caspari (2006)

Libben sample (Lovejoy et al. 1977; Lovejoy 1985). We also assumed a stationary population with a stable age distribution (Hoppa and Vaupel 2002), a reasonable assumption for comparisons, although it is unlikely to consistently describe individual populations at specific times, which probably fluctuated (Harpending 1997; Meindl et al. 2001). As shown, the Krapina survivorship pattern is unlike Libben or any recent or living human survivorship curve, with very high young adult mortality. Although Krapina is remarkable in having virtually no older adults (above age 30), the general pattern of high young adult mortality is not unusual. At Atapuerca, like Krapina, there are very high levels of juvenile and young adult mortality, with few individuals surviving to age 35. It is possible that these distributions reflect the peculiarities of specific sites – taphonomic or catastrophic occurrences that somehow selected against the preservation of older individuals (Bocquet-Appel and Arsuaga 1999). This, however, is unlikely since the death distribution does not resemble the age structure of living high-mortality hunter-gathers (e.g., the Ache), nor are the very young or old overly represented, two expectations of catastrophes (Wolpoff and Caspari 2006). Moreover, research focusing on the human fossil record more broadly suggests these curves were not exceptional; rather, they reflect an archaic life history pattern characterized by high young adult mortality (Caspari and Lee 2004).

OY Ratios and the Emergence of Modern Survivorship Patterns

High young adult mortality in archaic hominid groups was demonstrated by Caspari and Lee (2004) using Miles Method age estimations that were subsequently verified by assessments based on relative pulp volume using μCT (as cited above). OY ratios, the ratio of older to younger adults were calculated for large aggregates of fossil samples, as a simple approach to deal with longevity independent of understandings of juvenile mortality patterns, precise age estimates, and the problems of small samples of different sizes. It is important that the components of the OY ratio are of relative categories, independent of actual age; third molar eruption indicates adulthood, and we accept the implication that different times of eruption reflect different times that adulthood was attained. For our purposes double that age marks the beginning of older adulthood, the age one could first become a grandparent. Therefore groups with different maturation rates can be compared and variation in the OY ratio provides insights into longevity without assessing variation in actual lifespan, or treating the samples as populations. This approach circumvents some of the problems associated with paleodemography, yet allows the evaluation of evolutionary hypotheses.

Caspari and Lee (2004) reported a large and significant increase in the OY ratio between Neanderthals (and other archaic hominids) and the modern humans of the Upper Paleolithic: the ratio for Upper Paleolithic Europeans is approximately 2.0 (as is the OY ratio of Libben); that for European Neanderthals is 0.4. Thus, for every 10 young Neanderthal adults in the death distribution (between ages 15–30), there are only 4 older adults (over 30). Re-analysis limited to non-burials yielded similar results, and the systematic nature of the changes and the many different site histories sampled made a purely taphonomic explanation unlikely (Caspari and Lee 2004). The major conclusion to emerge from this study was that adult survivorship increased dramatically in the European Upper Paleolithic. A subsequent study comparing Middle Paleolithic modern humans from western Asia with Neanderthal and Upper Paleolithic European samples indicated that the increase in survivorship was an attribute of the Upper Paleolithic rather than an attribute of modern humans as a whole (Caspari and Lee 2006). Despite living in much harsher conditions approaching the glacial maximum, the OY ratio of the Upper Paleolithic Europeans was more than double that of the Middle Paleolithic modern humans. Phylogeny and ecology dismissed as causes of Upper Paleolithic longevity, we concluded that the changes in mortality patterns were likely caused by cultural changes. It can be argued that this shift represents a change from an archaic to a modern life history pattern that had implications for the success of modern humans.

Model Mortality Curves

Model mortality curves based on OY ratios further suggest that the Krapina and Atapuerca distributions may not be anomalies, but reflect the archaic life history pattern. Adult mortality curves were calculated based on OY ratios assuming a constant number of mortalities per generation (Van Arsdale 2009). This is not a constant rate, but rather a uniform decline in the standing population. Thus, for example if OY is 0.4, a cohort of 100 individuals entering young adulthood at age 15 should lose 71.4 of their members by age 30 and the remaining 28.6 as old adults (over 30), or 4.76 individuals a year, assuming a constant number of deaths/year. Therefore, in this archaic scenario, the mortality risk of a 16 year old is very high (4.76%), increasing to 14.27% in a 30 year old and by 37, there are no survivors. This is consistent with the pattern seen in the Krapina and Atapuerca samples. Models based on higher OY ratios yield mortality curves with increases in mortality rate occurring at a later age, and again assuming a constant number of deaths/year the maximum age in the population will increase. With an OY value of 2 (the value of both the Upper Paleolithic sample and Libben) the deaths/year with an incoming cohort of 100 young adults is 2.22; the mortality risk of a 30 year old is only 3.3% and the maximum age of members of the population is 61. Figure 19.7 compares the mortality curves across three scenarios. The significantly higher mortality rates of Neanderthals would have important
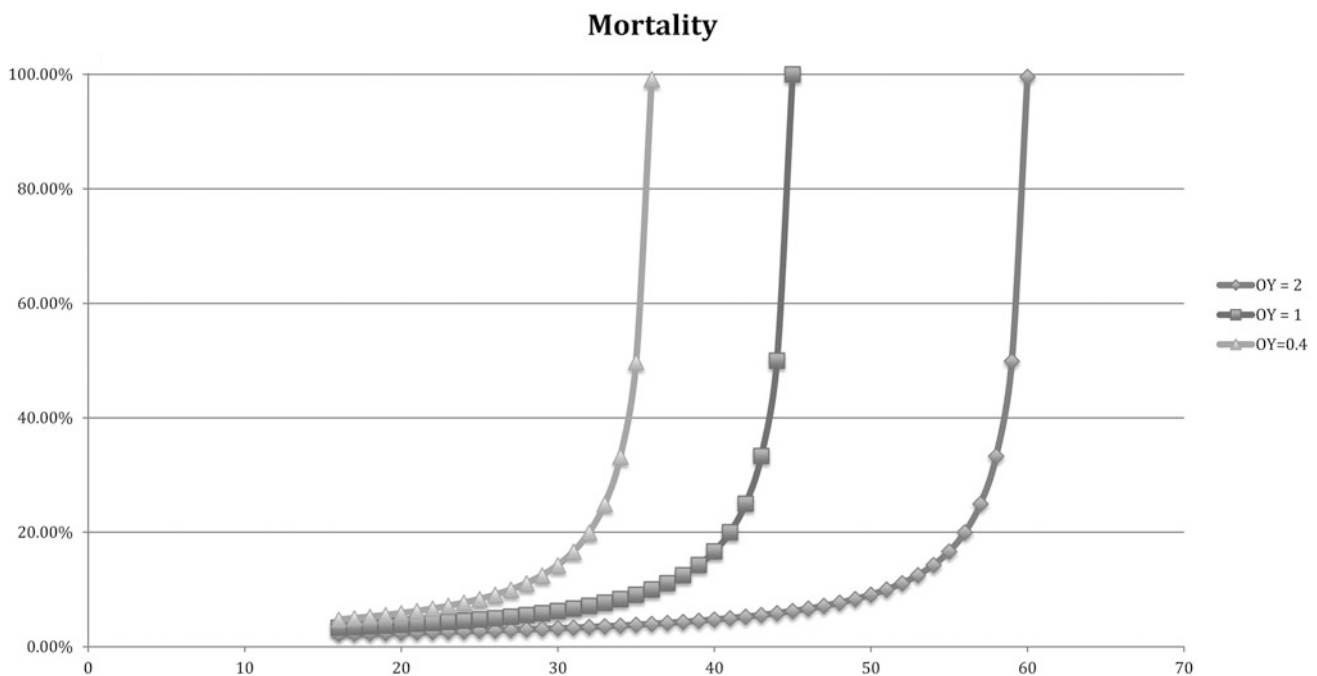
Fig. 19.7 Mortality curves for populations with different OY ratios. Figure courtesy of Adam Van Arsdale

implications for other demographic factors: with OY ratios of 0.4, fertility rates would need to be high, and populations would be less resilient to stochastic fluctuations in population size.

Fertility and Population Stability

Using the Brass Polynomial, a model of declining fertility with age (Gage 1998) Van Arsdale (2009; Caspari et al. 2010) calculated the total fertility rates necessary to replace birth cohorts in populations with different OY ratios. A 50% child mortality rate was assumed. Neanderthals, with OY ratios of 0.4 would need a total fertility rate of over 6.3 births, Upper Paleolithic populations, with OY ratios of 2.0, would require only 5.3 births. This also would affect population stability. Van Arsdale's stochastic models testing the outcomes of variation in fertility rates suggest that Upper Paleolithic populations would avoid population collapse much more easily than Neanderthals (Van Arsdale 2009; Caspari et al. 2010).

Behavioral Implications

By many estimates, Neanderthal population numbers and overall densities were very low (Castellano et al. 2014; Churchill 2014), with relatively few contacts with other groups and little opportunity for specialization. In contrast, the increased survivorship and longevity in the Upper Paleolithic would allow for increases in population growth and expansion that could foster behavioral modernity. It has been argued that with population growth, resources become scarcer (Stiner et al. 1999) and modern behaviors and technologies are the human response. It has also been suggested that modern behaviors appear more often, are more persistent (for reasons discussed below) and disperse more effectively because of population growth and an increased number of interpopulational contacts (Shennan 2001), and the rate of cultural change accelerates. Therefore, the cultural changes associated with the Upper Paleolithic may reflect a ratcheting, positive feedback process.

The same may be the case for increased longevity in the Upper Paleolithic. Longevity itself, in addition to its effects on population growth, may have contributed to the emergence and persistence of modern behaviors, and increased longevity may have persisted through a positive feedback process with these behavioral outcomes. Initially the result of cultural adaptations and/or perhaps climatic factors (d'Errico and Stringer 2011), longevity may have become a prerequisite for the unique and complex behaviors that mark modernity, innovations that in turn promoted both the

importance and the survivorship of older adults. Caspari and Lee (2004, 2006) suggested that adult survivorship increased in response to cultural factors promoting the importance of older adults whose experience benefited their kin groups in the harsh conditions of Upper Pleistocene Europe. The experience of older members could also underlie the material expressions associated with the Upper Paleolithic. There are a number of ways in which the demographic changes and intergenerational transfer effects associated with increased adult survivorship could result in the complex behaviors thought to be reflected in Upper Paleolithic archaeology (Lee 2003; Rosenberg 2004).

In the emerging complex adaptations of the Upper Paleolithic, older adult survivorship was likely beneficial to social groups as a whole, promoting intergenerational transfer of a variety of economic and cultural resources (Lee 2003). In humans, as in other social species, there is transfer of resources among individuals, which contributes to the inclusive fitness of a kin group. Intergenerational transfer is particularly important for humans, where it extends over several generations. Grandparents routinely contribute economic and social resources to their descendants, increasing the fertility of their children and the survivorship of their grandchildren. The importance of the economic contributions of older adults to their social groups has been well documented (Kaplan and Robson 2002; Hawkes 2003). In fact, studies of living hunter/gatherers indicate that because of the skill-intensive techniques of resource acquisition, peak production rates occur in individuals over age 30 (Robson and Kaplan 2003). Cultural information is effectively transmitted by older members of society, reinforcing complex social connections. Multiple aspects of cultural knowledge are transmitted, from social identity, to experiences dealing with unusual environmental conditions to technological innovations that promote the survival of social groups. Such knowledge is often embedded in oral traditions in which cross-generational transmission plays an important role.

Survival of periodic subsistence crises is largely dependent on a group memory of past crisis situations and of the strategies appropriate for dealing with the altered environmental conditions. One mechanism utilized by non-literate societies for the preservation of survival knowledge is its incorporation in oral tradition. As a body of reference knowledge, oral traditions potentially operate over two time scales. Secular oral traditions (folktales, songs, and histories) depend on repetition for perpetuation with inherent potential for distortion. In contrast, sanctified oral traditions, such as ritual performances, rely on a correct reproduction of the ritual order to achieve supernatural efficacy. Rituals accordingly assume an invariant character appropriate for the transmission of survival information over extended periods of time (Minc 1986: 39).

Moreover, as has been recently modeled by Strimling and colleagues ([2009]), repetition – the repeated learning of cultural traits – is a critical factor in cultural learning more generally, and it has the potential to drive cultural evolution:

> Here we show that repeated learning and multiple characteristics of cultural traits make cultural evolution unique … We find that the possibility to predict long-term cultural evolution by some success index, analogous to biological fitness, depends on whether individuals have few or many opportunities to learn. If learning opportunities are few, we find that the existence of a success index may be logically impossible, rendering notions of' 'cultural fitness' meaningless. On the other hand, if individuals can learn many times, we find a success index that works, regardless of whether the transmission pattern is vertical, oblique, or horizontal (Strimling et al. [2009]: 13870).

Multigenerational families have more (and more knowledgeable) members to teach and re-teach important lessons. We suggest longevity promoted the intergenerational accumulation and transfer of information that allowed for complex kinship systems and other social networks that are uniquely human.

However, the population growth discussed above is perhaps the most important consequence of increased adult survivorship, the basis of the Upper Paleolithic population expansions reflected in archeological and genetic evidence (Shennan [2001]; Templeton [2002]; Powell et al. [2009]). Not only does increased survivorship create the potential for greater lifetime fertility for individuals who are living longer, but the investment of older individuals in their children's families influences their inclusive fitness both by increasing the fertility of their children and the survivorship of their grandchildren. These selective advantages promote continued population increase. Therefore the increase in survivorship we observe is a significant factor in the evolution of modernity not only through its importance for intergenerational information transfer, but because of its relationship to population expansion.

These demographic changes provide social pressures that we believe led to extensive trade networks, increased mobility, and more complex systems of cooperation and competition between groups, resulting in increased personal ornamentation, material expressions of individual and group identity, and other forms of material information exchange between groups (Wobst [1977]). Modern human behavior, then, is a response to demographic pressures.

So where does this leave Neanderthals? While possessing the capacity for symbolic behavior evidenced by recent archaeological discoveries, their symbolic associations are less frequent and less sophisticated than in Upper Paleolithic assemblages. This is likely a reflection of their archaic life history pattern, and a different way of being human.

Neanderthals as a Human Subspecies

We agree with Rak about most things, but phylogenetics is an area where long ago we agreed to disagree! However, recent genetic data have caused us to revisit our ideas about Neanderthal taxonomy. These data have done much to elucidate phylogenetic issues concerning Neanderthals, but introduce a paradox. While demonstrating what we consider widespread gene flow between archaic and modern humans, paleogenetics also indicates Neanderthal differences; there is much greater population structure in the late Pleistocene than we see today. We review these findings in the context of the history of the taxonomic placement of Neanderthals. Modern human population structure is a poor model for the population structure of Neanderthals. Modern humans have no races, but it is very likely that Neanderthals were a human subspecies.

In the second part of the 20th century, the interpretation of Neanderthals as a separate species gained ground and eventually became the majority opinion. This was more a consequence of changes in how species were defined and identified, than a reflection of new Neanderthal discoveries. The species interpretation of Neanderthal variation began with the first Neanderthal to be recognized. The Feldhofer Neanderthal was first described as a species by William King ([1864]) because of how different from living humans it appeared to be. King wrote "so closely does the fossil cranium resemble that of the chimpanzee, as to lead one to doubt the propriety of generically placing it with Man." In the half century following the Feldhofer discovery, evolution of humans was rejected by many scientists. A number of them found the Neanderthal to be somewhat less different than King described, actually no different in type from other human races, although more primitive. But in those times, recognized races were often named as species because they were interpreted in a polygenic framework (Wolpoff and Caspari [1997], [2013]) where races were thought to have had separate origins, sometimes in different primate species. The practice persisted well into the 20th century, largely without comment, until it resulted in absurdity. Thus, in describing the human remains from the Lower Cave at Zhoukoudian, the "Peking Man" sample that many paleoanthropologists formally place in the species *Homo erectus*, Weidenreich named the remains "*Sinanthropus pekinensis*" out of respect for Davidson Black who named the first Zhoukoudian specimens in a scientific paper (Black [1929]). In reality, however, Weidenreich believed they were *Homo sapiens*, and wrote that his use of "*Sinanthropus pekinensis*" was a convenience

. . . without any "generic" or "specific" meaning or, in other words, as a "latinization" of Peking Man.. . . it would not be correct to call our fossil "*Homo pekinensis*" or "*Homo erectus pekinensis*"; it would be best to call it "*Homo sapiens erectus pekinensis*." Otherwise it would appear as a proper "species," different from "*Homo sapiens*," which remains doubtful, to say the least (Weidenreich 1943: 246).

But this was not the end. A subsequent series of publications addressed the issue of how fossil species can be recognized and whether or not there should be an attempt to reconcile the definition of fossil species with the biological species concept as defined by Mayr (1942) and others: a group of populations that can actually or potentially interbreed and produce fertile offspring, and which are reproductively isolated from populations in other species. For most of those who did not think such reconciliation was possible, Neanderthals became a distinct species (e.g., Eldredge and Cracraft 1980; Tattersall 1986, 1992).

The final twist in this story came with the discovery of nuclear DNA in human fossils (Green et al. 2010), because this demonstrated the possibility that the interbreeding criterion for biological species could actually be applied to some human fossils (Hawks 2013); in particular, to Neanderthal fossils. Continued discoveries of Neanderthal introgressions into other human populations demonstrate (see below) without question that Neanderthals are a variety of *Homo sapiens*. The demonstration that effective biological barriers to interbreeding can be expected to take a million years or more to become established (Curnoe et al. 2006; Holliday 2006) is compatible with these new data.

The question of some Neanderthal ancestry is informed by the establishment of significant gene flow from Neanderthals (Lohse and Frantz 2014), in many cases bringing adaptive features enhancing climatic selection into other populations (including pigmentation features such as the melanocyte-stimulating hormone receptor gene MC1R (Ding et al. 2014a), red hair and freckles, as well as increased skin thickness with more hair and fewer pores (Vernot and Akey 2014), Neanderthal alleles that affect skin and hair such as keratin filaments (Sankararaman et al. 2014), and specific to certain populations, European lipid catabolism (Khrameeva et al. 2014), the cellular response to ultraviolet-B irradiation in Asians (Ding et al. 2014b). Other cases of gene flow from Neanderthals involve disease adaptation, including HLA class 1 alleles (Abi-Rached et al. 2011), but some genes inherited from Neanderthals may also heighten the risk of diseases such as Type-2 diabetes, liver cirrhosis, lupus and Crohn's disease (Sankararaman et al. 2014).

Several other adaptive genes are shared with Neanderthals (this work is in its infancy), although the direction of gene flow is uncertain and may well be bidirectional. These are cases where the presence of the gene in a common ancestor is unlikely. Human FOXP2 is well-studied, including in Neanderthals (Krause et al. 2007), because its homologues are widespread and because of its importance in speech production (Enard et al. 2002). The initial suggestion was that "[d]ata [may be] consistent with low rates of gene flow between modern humans and Neanderthals" (Coop et al. 2008: 1257). Later, Maricic and colleagues (Maricic et al. 2013) reported on a regulatory variant in a transcription factor affecting the expression of the FOXP2 gene that is found in two Iberian Neanderthals (Sidron cave) and a Croatian Neanderthal (Vindija cave), and is fairly common in some human populations. Theirs is a complex reconstruction in which the Neanderthal FOXP2 and its regulators fall within the human range of variation, while at the same time "this is the only nucleotide variant in that region where the majority of present-day people carry a derived variant that is not present in Neanderthals and Denisovans. Thus, it is possible that this change was positively selected recently during the evolution of fully modern humans (Maricic et al. 2013: 849)".

When gene flow is paired with positive selection, the minimum magnitude of gene flow allowing the genes to be established in other populations is difficult to determine. However, the direct evidence of gene flow negates all arguments that the number of mating events between Neanderthals and other populations were too small to have been important. They could not validly be described as rare, or occasional given that there are many different Neanderthal genes in different human populations, and their effects were anything but too small to be important (Hawks and Throckmorton 2013). With a significant role for selection guiding the dynamics of genetic exchanges, increasing evidence that Neanderthal behavioral capacities fall well within the human range (Villa and Roebroeks 2014) should not be surprising.

This pattern of introgression from Neanderthals demonstrates that past human evolution, like the present, occurs within a network of on-and-off interconnected populations within a single evolving lineage. It has been observed over a time period long enough for the complete replacements of human populations by one or more successive new African species to be evident if they had happened. Our working hypothesis is that Pleistocene human evolution is an example of evolution within a species lineage (Wolpoff et al. 1994; Wildman et al. 2003) described by a geographically diverse widely dispersed network of (intermittently) interconnected populations. If past human variation is within that lineage, it is possible that such variation could be described as subspecies (Wolpoff 2009), even though human subspecies do not exist today (Marks 1995; Templeton 1998, 2013; Caspari 2003, 2010; Wolpoff and Caspari 2013).

The dismissal of human races as an organizing structure for living human biology occurred for many reasons, including political reasons, but there is a firm biological

basis for it in the distribution of genetic variation (Templeton 1998), that to some extent is reflected in the distribution of anatomical variation.

- Extant human anatomical variation does not attain the subspecies level; populations are neither different enough, nor separated enough, for a subspecies interpretation of their variation to be valid.
- The ratio of within group to between group variance is very high in humans.
- There is no treeness for human groups (Templeton 1998, 2013).

Thus, the idea that there were once pure human races is dead and buried, and if race cannot reflect unique common descent, and if there is no validity to the precept that human races are constellations of biological characters that show greater differences between each other than variation within one of them, race can only have a social definition (Marks 1995; Caspari 2003; and many others). There simply are no clearly distinct types of humanity (Graves 2001), and there is no racial taxonomy for the living.

Were Neanderthals a Past Human Race?

Outside of anthropology, race is most often used as a synonym for subspecies (Mayr 1969, p. 44; Futuyma 1986: 107–109; Templeton 1998), and for most of its history this has also been true within paleoanthropology (Boule 1923; Dobzhansky 1944; Weidenreich 1946, 1947). Subspecies, however, are not a favored topic in modern biology; they don't exist in the indexes of many recent textbooks, and when they do appear there are some times when subspecies refer to a taxonomically distinct variety of a species, but others when they are used to describe "a species in the making". Subspecies are traditionally defined as geographically circumscribed, genetically differentiated populations. Subspecies are also described as distinct evolutionary lineages within a species. A good example would be the three different subspecies of gorilla, three groups that are physically and geographically distinct (Relethford 2008: 379).

Has this always been the case? Given that there are no human races today – accepting that human geographic variation is not taxonomic – does this mean that there were no races in the human past? Or, is it possible that Neanderthals fit the description of a subspecies as we understand it today? The modern understanding of subspecies comes from the New Synthesis, especially from the works of Mayr (1942) and Dobzhansky (1944). For them, subspecies combined groups of local populations by anatomical similarity and geographic distinctness, in a taxonomic grouping (by descent). Although criticized by Wilson and Brown

(1953), subspecies continue to describe intraspecies variation when it is distinctly geographic; but admittedly, for the most part modern usage is not common because intraspecies variation is not often studied. However, this happens to be a significant problem in human studies where, as discussed above, this variation is almost never regarded as taxonomic.

Dobzhansky (1944) directly addressed the question of whether past hominid samples such as Neanderthals might be subspecies. For him the compelling support for identifying a Neanderthal subspecies came from the newly published Mount Carmel remains (Skhul and Tabun; McCown and Keith 1939), which he interpreted as the result of mixture between two subspecies that were obviously not reproductively isolated, and not as a single population "in the throes of evolutionary change", as McCown and Keith had interpreted the sample. Dobzhansky (1944: 259) noted that "The Mount Carmel population also shows that . . . a morphological gap as great as that between the Neanderthal and the modern types may occur between races, rather than between species."

Jolly (2001) also noted that Neanderthals fit the description of subspecies as allotaxa ("morphologically diagnosable yet not reproductively isolated" populations). Jolly (2001: 1767) proposed "Neanderthals and AfroArabian 'pre-modern' populations may have been analogous to extant baboon (and macaque) allotaxa".

But in our view the most important new evidence for regarding Neanderthals as a past subspecies of *Homo sapiens* is discussed above. Neanderthal genes dispersed under selection into populations with descendants wherein they persist today. Many of these genes led to significant adaptive changes. The fact that so many Neanderthal genes persist as different genes making up different combinations in different individuals is the strongest argument that Neanderthals are *Homo sapiens*. The percentage contribution of Neanderthal genes to gene pools of non-Africans today approximates estimates of the number of Neanderthals that lived at any time as a fraction of the human population at that time.

A good number of the Neanderthal genes that dispersed into other populations were under selection, as we noted above. The fact that many of these gene dispersals are described as introgressions is also important. Introgressions are the transfers of genes that evolved at a much earlier time. Introgressions in Neanderthals suggest that Neanderthal populations were significantly (but not completely) isolated from other human populations, as they may well have been from each other (helping account for significant Neanderthal population structure). The evidence of restricted gene flow with Neanderthals, combined with older observations of a distinct geographic range, and the magnitude of anatomical differences between Neanderthals and their penecontemporaries, suggest that unlike any population today, it is reasonable to interpret Neanderthals as a human subspecies.

Because the human species does not have subspecies today, this supports the notion that Neanderthals are another way of being human. Neanderthals, it would appear, are the best-established demonstration that humans in the past, like many other mammals (Mayr 1963), formed distinct races.

Conclusion

Even as paleogenetics has affirmed Neanderthal humanity, it also brings focus on their difference. As Rak has long recognized, Neanderthals represent another way to be human. The observations on Neanderthal body form, demography, and breeding behavior that we reviewed here reinforce ideas of Neanderthal difference and hopefully provide insight into the nature of that difference. We conclude that in body form, demography and population structure, Neanderthals are unlike modern humans, in some cases reflecting the ancestral condition. We view them therefore as both "brother" and "other," simultaneously expressing some archaic hominid characteristics as well as aspects of the modern condition to which they contributed genetically, anatomically and behaviorally.

References

Abi-Rached, L., Jobin, M. J., Kulkarni, S., McWhinnie, A., Dalva, K., Gragert, F., et al. (2011). The shaping of modern human immune systems by multiregional admixture with archaic humans. *Science, 334*, 89–94.

Arsuaga, J. L., Lorenzo, C., Carretero, J. M., Gracia, A., Martínez, I., García, N., et al. (1999). A complete human pelvis from the Middle Pleistocene of Spain. *Nature, 399*, 255–258.

Bermúdez de Castro, J.-M. (1995). The hominids from the Sima de los Huesos of the Sierra de Atapuerca karst: Minimum number of individuals, age at death, and sex. In J-M. Bermúdez, J.-L. Arsuaga, & E. Carbonell (Eds.), *Human evolution in Europe and the Atapuerca evidence. Volume 1.* (pp. 263–281). Valladolid: Sever-Cuesta.

Black, D. (1929). Sinanthropus pekinensis: The recovery of further fossil remains of this early hominid from the Chou Kou Tien deposits. *Science, 6*, 674–676.

Bocquet-Appel, J. P., & Arsuaga, J.-L. (1999). Age distributions of hominid samples at Atapuerca (SH) and Krapina could indicate accumulation by catastrophe. *Journal of Archaeological Science, 26*, 327–338.

Bonmatí, A., Gómez-Olivencia, A., Arsuaga, J. L., Carretero, J. M., Gracia, A., Martínez, I., et al. (2010). Middle Pleistocene lower back and pelvis from an aged human individual from the Sima de

los Huesos site, Spain. *Proceedings of the National Academy of Sciences USA, 107*, 18386–18391.

Boule, M. (1911). *L'Homme fossile de La Chapelle-aux-Saints.* Annales de Paléontologie VI.

Boule, M. (1923). *Les Hommes fossiles. Eléments de paléontologie humaine.* Paris: Masson.

Caspari, R. (2003). From types to populations: A century of race, physical anthropology and the American Anthropological Association. *American Anthropologist, 105*, 63–74.

Caspari, R. (2010). Deconstructing race: Racial thinking, geographic variation, and implications for biological anthropology. In C. S. Larsen (Ed.), *A companion to biological anthropology* (pp. 104–123). Chichester, West Sussex: Wiley-Blackwell.

Caspari, R. (2011). The evolution of grandparents. *Scientific American, 305*, 44–49.

Caspari, R., & Lee, S.-H. (2004). Older age becomes common late in human evolution. *Proceedings of the National Academy of Sciences USA, 101*, 10895–10900.

Caspari, R., & Lee, S.-H. (2006). Is human longevity a consequence of cultural change or modern human biology? *American Journal of Physical Anthropology, 129*, 512–517.

Caspari, R., Lee, S.-H., & Van Arsdale, A. (2010). Implications of reduced mortality risk for late Pleistocene humans. *American Journal of Physical Anthropology, 141*, 79.

Caspari, R., Meganck, J. A., Radovčić, J., Begun, D., Kroll, T., & Goldstein, S. A. (2009). Assessing age at death in adult dentitions: A new approach using three-dimensional microcomputed tomography and its application to fossil samples. *American Journal of Physical Anthropology, 138*, 104.

Caspari, R., & Wolpoff, M. H. (2013). The process of modern human origins: The evolutionary and demographic changes giving rise to modern humans. Chapter 11. In F. H. Smith & J. C. M. Ahern (Eds.), *The origins of modern humans: Biology reconsidered* (pp. 355–390). New York: Wiley.

Castellano, S., Parra, G., Sánchez-Quinto, F. A., Racimo, F., Kuhlwilm, M., Kircher, M., et al. (2014). Patterns of coding variation in the complete exomes of three Neandertals. *Proceedings of the National Academy of Sciences USA, 111*, 6666–6671.

Churchill, S. E. (2014). *Thin on the ground: Neandertal biology, archeology and ecology.* Oxford: Wiley-Blackwell.

Coop, G., Bullaughey, K., Luca, F., & Przeworski, M. (2008). The timing of selection at the human FOXP2 gene. *Molecular Biology and Evolution, 25*, 1257–1259.

Curnoe, D., Thorne, A., & Coate, J. A. (2006). Timing and tempo of primate speciation. *Journal of Evolutionary Biology, 19*, 59–65.

Danchin, É., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., & Blanchet, S. (2011). Beyond DNA: Integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics, 12*, 475–486.

Dean, M. C., Stringer, C. B., & Bromage, T. G. (1986). Age at death of the Neanderthal child from Devil's Tower, Gibraltar and the implications for studies of general growth and development in Neanderthals. *American Journal of Physical Anthropology, 70*, 301–309.

d'Errico, F., & Stringer, C. B. (2011). Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philosophical Transactions of the Royal Society B, 366*, 1060–1069.

Ding, Q., Hu, Y., Xu, S., Wang, C. C., Li, H., Zhang, R., et al. (2014a). Neanderthal origin of the haplotypes carrying the functional variant Val92Met in the MC1R in modern humans. *Molecular Biology and Evolution, 31*, 1994–2003.

Ding, Q., Hu, Y., Xu, S., Wang, J., & Jin, L. (2014b). Neanderthal introgression at chromosome 3p21. 31 was under positive natural selection in East Asians. *Molecular Biology and Evolution, 31*, 683–695.

Dobzhansky, T. H. (1944). On species and races of living and fossil man. *American Journal of Physical Anthropology, 2*, 251–265.

Eldredge, N., & Cracraft, J. (1980). *Phylogenetic patterns and the evolutionary process: Method and theory in comparative biology.* New York: Columbia University Press.

Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S., Wiebe, V., Kitano, T., et al. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature, 418*, 869–872.

Futuyma, D. J. (1986). *Evolutionary biology.* Sunderland: Sinauer.

Gage, T. B. (1998). The comparative demography of primates: With some comments on the evolution of life histories. *Annual Review of Anthropology, 27*, 197–221.

Gómez-Olivencia, A., Eaves-Johnson, K. L., Franciscus, R. G., Carretero, J. M., & Arsuaga, J.-L. (2009). Kebara 2: New insights regarding the most complete Neandertal thorax. *Journal of Human Evolution, 57*, 75–90.

Graves, L. L. (2001). *The emperor's new clothes: Biological theories of race at the millennium.* New Brunswick: Rutgers University Press.

Green, R. E., Krause, J., Briggs, A. W., Maricic, T., Stenzel, U., Kircher, M., et al. (2010). A draft sequence of the Neandertal genome. *Science, 328*, 710–722.

Haile-Selassie, Y., Latimer, B. M., Alene, M., Deino, A. L., Gibert, L., Melillo, S. M., et al. (2010). An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proceedings of the National Academy of Sciences USA, 107*, 12121–12126.

Harpending, H. (1997). Living record of past population change. In R. R. Paine (Ed.), *Integrating archaeological demography: Multidisciplinary approaches to prehistoric population* (pp. 89–100). Carbondale: Southern Illinois University.

Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology, 15*, 380–400.

Hawks, J. (2013). Significance of Neandertal and Denisovan genomes in human evolution. *Annual Review of Anthropology, 42*, 433–449.

Hawks, J., & Throckmorton, Z. (2013). The relevance of archaic genomes to modern human origins. In F. H. Smith & J. C. M. Ahern (Eds.), *The origins of modern humans: Biology reconsidered* (pp. 339–354). New York: Wiley.

Henshilwood, C. S., & Marean, C. W. (2003). The origin of modern human behaviour: Critique of the models and their test implications. *Current Anthropology, 44*, 627–665.

Holliday, T. W. (2006). Neanderthals and modern humans: An example of a mammalian syngameon? In K. Harvati & T. Harrison (Eds.), *Neanderthals revisited: New approaches and perspectives* (pp. 281–298). Dordrecht: Springer.

Hoppa, R. D., & Vaupel, J. W. (2002). *Paleodemography: Age distribution from skeletal samples* (Vol. 31). Cambridge: Cambridge University Press.

Hovers, E., & Belfer-Cohen, A. (2006). "Now you see it, now you don't" – modern human behavior in the Middle Paleolithic. In E. Hovers & S. L. Kuhn (Eds.), *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age* (pp. 295–304). New York: Springer.

Jolly, C. (2001). A proper study of mankind: Analogies from the papionin monkeys and their implications for human evolution. *Yearbook of Physical Anthropology, 44*, 177–204.

Kaplan, H. S., & Robson, A. (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences USA, 99*, 10221–10226.

Khrameeva, E. E., Bozek, K., He, L., Yan, Z., Jiang, X., Wei, Y., et al. (2014). Neanderthal ancestry drives evolution of lipid catabolism in contemporary Europeans. *Nature Communications, 5*, 1–8.

Kibii, J. M., Churchill, S. E., Schmid, P., Carlson, K. J., Reed, N. D., De Ruiter, D. J., et al. (2011). A partial pelvis of *Australopithecus sediba. Science, 333*, 1407–1411.

King, W. (1864). On the Neanderthal skull, or reasons for believing it to belong to the Clydian Period and to a species different from that represented by man. *British Association for the Advancement of Science, Notices and Abstracts for, 1863*, 81–82.

Krause, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R. E., Burbano, H. A., et al. (2007). The derived FOXP2 variant of modern humans was shared with Neandertals. *Current Biology, 17*, 1908–1912.

Lee, R. D. (2003). Rethinking the evolutionary theory of aging: Transfers, not births, shape senescence in social species. *Proceedings of the National Academy of Sciences USA, 100*, 9637–9642.

Lloyd, J. (2012). Prehistoric autopsy: Our ancient past. *Focus (BBC) Science and Technology*, Issue 246.

Lohse, K., & Frantz, L. A. (2014). Neandertal admixture in Eurasia confirmed by maximum-likelihood analysis of three genomes. *Genetics, 196*, 1241–1251.

Lovejoy, C. O. (1985). Dental wear in the Libben population: Its functional pattern and role in the determination of adult skeletal age at death. *American Journal of Physical Anthropology, 68*, 47–56.

Lovejoy, C. O., & Heiple, K. G. (1970). A reconstruction of the femur of *Australopithecus africanus. American Journal of Physical Anthropology, 32*, 33–40.

Lovejoy, C. O., Meindl, R. S., Pryzbeck, T. R., Barton, T. S., Heiple, K. G., & Kotting, D. (1977). Paleodemography of the Libben site, Ottawa County, Ohio. *Science, 198*, 291–293.

Maricic, T., Günther, V., Georgiev, O., Gehre, S., Ćurlin, M., Schreiweis, C., et al. (2013). A recent evolutionary change affects a regulatory element in the human FOXP2 gene. *Molecular Biology and Evolution, 30*, 844–852.

Marks, J. (1995). *Human biodiversity: Genes, race, and history.* New York: Aldine de Gruyter.

Mayr, E. (1942). *Systematics and the origin of species from the viewpoint of a zoologist.* New York: Columbia University Press.

Mayr, E. (1963). *Animal species and evolution.* Cambridge: Belknap Press of Harvard University Press.

Mayr, E. (1969). *Principles of systematic zoology.* New York: McGraw-Hill.

McCown, T. D., & Keith, A. (1939). *The Stone Age of Mount Carmel: The fossil human remains from the Levalloiso-Mousterian* (Vol. 2). Oxford: Clarendon Press.

Meindl, R. S., Mensforth, R. P., & York, H. P. (2001). Mortality, fertility, and growth in the Kentucky Late Archaic: The paleodemography of the Ward site. In O. H. Prufer, S. E. Pedde, & R. S. Meindl (Eds.), *Archaic transitions in Ohio and Kentucky prehistory* (pp. 87–109). Kent, OH: Kent State University Press.

Mellars, P. A. (2005). The impossible coincidence: A single species model for the origins of modern human behaviour in Europe. *Evolutionary Anthropology, 14*, 12–27.

Mellars, P. A. (2006). Archeology and the dispersal of modern humans in Europe: Deconstructing the "Aurignacian". *Evolutionary Anthropology, 15*, 167–182.

Miles, A. E. W. (1963). The dentition in the assessment of individual age in skeletal material. In D. R. Brothwell (Ed.), *Dental anthropology* (pp. 191–209). Oxford: Pergamon Press.

Minc, L. D. (1986). Scarcity and survival: The role of oral tradition in mediating subsistence crises. *Journal of Anthropological Archaeology, 5*, 39–113.

Morin, E., & Laroulandie, V. (2012). Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS ONE, 7*, e32856.

Peresani, M., Fiore, I., Gala, M., Romandini, M., & Tagliacozzo, A. (2011). Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proceedings of the National Academy of Sciences USA, 108*, 3888–3893.

Ponce de León, M. S. P., Golovanova, L., Doronichev, V., Romanova, G., Akazawa, T., Kondo, O., et al. (2008). Neanderthal brain size at

birth provides insights into the evolution of human life history. *Proceedings of the National Academy of Sciences USA, 105,* 13764–13768.

Powell, A., Shennan, S., & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science, 324,* 1298–1301.

Radovčić, D., Sršen, A. O., Radovčić, J., & Frayer, D. W. (2015). Evidence for Neandertal jewelry: Modified white-tailed eagle claws at Krapina. *PLoS ONE, 10,* e0119802.

Rak, Y. (1990). On the differences between two pelvises of Mousterian context from the Qafzeh and Kebara caves, Israel. *American Journal of Physical Anthropology, 81,* 323–332.

Rak, Y. (1991a). Lucy's pelvic anatomy: Its role in bipedal gait. *Journal of Human Evolution, 20,* 283–290.

Rak, Y. (1991b). The pelvis. In O. Bar-Yosef & B. Vandermeersch (Eds.), *Le squelette Moustérien de Kébara 2 (Cahiers de Paléoanthropologie)* (pp. 147–156). Paris: Editions CNRS.

Rak, Y. (1993). Morphological variation in *Homo neanderthalensis* and *Homo sapiens* in the Levant: A biogeographic model. In W. H. Kimbel & L. B. Martin (Eds.), *Species, species concept and primate evolution* (pp. 523–536). New York: Plenum Press.

Rak, Y., & Arensburg, B. (1987). Kebara 2 Neanderthal pelvis: First look at a complete inlet. *American Journal of Physical Anthropology, 73,* 227–231.

Relethford, J. H. (2008). *The human species* (7th ed.). Boston: McGraw-Hill.

Richerson, P. J., Boyd, R., & Bettinger, R. L. (2009). Cultural innovations and demographic change. *Human Biology, 81,* 211–235.

Rink, W. J., Schwarcz, H. P., & Smith, F. H. (1995). ESR ages for Krapina hominids. *Nature, 378,* 24.

Robinson, J. R. (1972). *Early hominid posture and locomotion.* Chicago: University of Chicago Press.

Robson, A., & Kaplan, H. (2003). The evolution of human life expectancy and intelligence in hunter-gatherer economies. *American Economic Review, 93,* 150–169.

Roebroeks, W., Sier, M. J., Nielsen, T. K., De Loecker, D., Parés, J. M., Arps, C. E. S., et al. (2012). Use of red ochre by early Neandertals. *Proceedings of the National Academy of Sciences* USA, *109,* 1889–1894.

Rosenberg, K. R. (1988). The functional significance of Neandertal pubic length. *Current Anthropology, 29,* 595–617.

Rosenberg, K. R. (2004). Living longer: Information revolution, population expansion, and modern human origins. *Proceedings of the National Academy of Sciences USA, 101,* 10847–10848.

Rosenberg, K. R., Lü, Z., & Ruff, C. B. (2006). Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. *Proceedings of the National Academy of Sciences USA, 103,* 3552–3556.

Ruff, C. B. (1991). Climate, body size and body shape in hominid evolution. *Journal of Human Evolution, 21,* 81–105.

Ruff, C. B. (1994). Morphological adaptation to climate in modern and fossil hominids. *Yearbook of Physical Anthropology, 37,* 65–107.

Ruff, C. B. (1995). Biomechanics of the hip and birth in early *Homo. American Journal of Physical Anthropology, 98,* 527–574.

Ruff, C. B., & Walker, A. (1993). Body size and body shape. In A. Walker & R. E. Leakey (Eds.), *The Nariokotome Homo erectus skeleton* (pp. 234–265). Cambridge: Harvard University Press.

Sankararaman, S., Mallick, S., Dannemann, M., Prüfer, K., Kelso, J., Pääbo, S., et al. (2014). The genomic landscape of Neanderthal ancestry in present-day humans. *Nature, 507,* 354–357.

Sawyer, G. W., & Maley, B. (2005). Neanderthal reconstructed. *The Anatomical Record, 283B,* 23–31.

Shea, J. J. (2011). *Homo sapiens* is as *Homo sapiens* was: Behavioral variability versus "behavioral modernity" in Paleolithic archaeology. *Current Anthropology, 52,* 1–35.

Shennan, S. (2001). Demography and cultural innovation: A model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal, 11,* 5–16.

Simpson, S. W., Quade, J., Levin, N. E., Butler, R., Dupont-Nivet, G., Everett, M., et al. (2008). A female *Homo erectus* pelvis from Gona, Ethiopia. *Science, 322,* 1089–1092.

Smith, T. M., Machanda, Z., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Muller, M. N., et al. (2013). First molar eruption, weaning, and life history in living wild chimpanzees. *Proceedings of the National Academy of Sciences USA, 110,* 2787–2791.

Smith, T. M., Tafforeau, P., Reid, D. J., Pouech, J., Lazzari, V., Zermeno, J. P., et al. (2010). Dental evidence for ontogenetic differences between modern humans and Neandertals. *Proceedings of the National Academy of Sciences USA, 107,* 20923–20928.

Soressi, M., & d'Errico, F. (2007). Pigments, gravures, parures: les comportements symboliques controversés des néandertaliens. In B. Vandermeersch & B. Maureille (Eds), *Les néandertaliens. Biologie et cultures* (pp. 297–309). Paris: Éditions du CTHS.

Stewart, T. D. (1960). Form of the pubic bone in Neanderthal man. *Science, 131,* 1437–1438.

Stiner, M. C., Munro, N. D., Surovell, T. A., Tchernov, E., & Bar-Yosef, O. (1999). Paleolithic population growth pulses evidenced by small animal exploitation. *Science, 283,* 190–194.

Strimling, P., Enquist, M., & Eriksson, K. (2009). Repeated learning makes cultural evolution unique. *Proceedings of the National Academy of Sciences USA, 106,* 13870–13874.

Tague, R. G. (1989). Variation in pelvic size between males and females. *American Journal of Physical Anthropology, 80,* 59–71.

Tague, R. G. (1992). Sexual dimorphism in the human bony pelvis, with a consideration of the Neandertal pelvis from Kebara Cave, Israel. *American Journal of Physical Anthropology, 88,* 1–21.

Tague, R. G., & Lovejoy, C. O. (1986). The obstetric pelvis of AL 288-1 (Lucy). *Journal of Human Evolution, 15,* 237–255.

Tattersall, I. (1986). Species recognition in human paleontology. *Journal of Human Evolution, 15,* 165–175.

Tattersall, I. (1992). Species concepts and species identification in human evolution. *Journal of Human Evolution, 22,* 341–350.

Tattersall, I. (2002). *The monkey in the mirror. Essays on the science of what makes us human*. Oxford: Oxford University Press.

Templeton, A. R. (1998). Human races: A genetic and evolutionary perspective. *American Anthropologist, 100,* 632–650.

Templeton, A. (2002). Out of Africa again and again. *Nature, 416,* 45–51.

Templeton, A. R. (2013). Biological races in humans. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 44,* 262–271.

Teyssandier, N. (2008). Revolution or evolution: The emergence of the Upper Paleolithic in Europe. *World Archaeology, 40,* 493–519.

Trinkaus, E. (1984). Neandertal pubic morphology and gestation length. *Current Anthropology, 25,* 509–514.

Trinkaus, E. (2011). The postcranial dimensions of the La Chapelle aux Saints 1 Neandertal. *American Journal of Physical Anthropology, 14,* 461–468.

Van Arsdale, A. P. (2009). Reduced adult mortality and the expansion of the human bio-cultural niche in the Late Pleistocene. *American Journal of Physical Anthropology, 138,* 259.

Vandermeersch, B. (1991). La ceinture scapulaire et les member supérieurs. *Le squelette Moustérien de Kébara 2 (Cahiers de Paléoanthropologie)* (pp. 157–178). Paris: Editions du CNRS.

Vernot, B., & Akey, J. M. (2014). Resurrecting surviving Neandertal lineages from modern human genome. *Science, 343,* 1017–1021.

Villa, P., & Roebroeks, W. (2014). Neandertal demise: An archaeological analysis of the modern human superiority complex. *PLoS ONE, 9*, e96424.

Walker, A., & Ruff, C. B. (1993). Reconstruction of the pelvis. In A. Walker & R. E. Leakey (Eds.), *The Nariokotome Homo erectus skeleton* (pp. 221–233). Cambridge: Harvard University Press.

Weaver, T. D. (2009). The meaning of Neandertal skeletal morphology. *Proceedings of the National Academy of Sciences USA, 106*, 16028–16033.

Weaver, T. D., & Hublin, J.-J. (2009). Neandertal birth canal shape and the evolution of human childbirth. *Proceedings of the National Academy of Sciences USA, 106*, 8151–8156.

Weidenreich, F. (1943). The skull of *Sinanthropus pekinensis*: A comparative study of a primitive hominid skull. *Palaeontologia Sinica*, New Series D, Number 10.

Weidenreich, F. (1946). Generic, specific, and subspecific characters in human evolution. *American Journal of Physical Anthropology, 4*, 413–431.

Weidenreich, F. (1947). Are human races in the taxonomic sense "races" or "species"? *American Journal of Physical Anthropology, 5*, 369–371.

Wildman, D. E., Uddin, M., Liu, G., Grossman, L. I., & Goodman, M. (2003). Implications of natural selection in shaping 99.4% non-synonymous DNA identity between humans and chimpanzees: enlarging genus *Homo*. *Proceedings of the National Academy of Sciences USA, 100*, 7181–7188.

Wilson, E. O., & Brown, W. L. (1953). The subspecies concept and its taxonomic application. *Systematic Zoology, 2*, 97–111.

Wobst, H. M. (1977). Stylistic behavior and information exchange. In C. E. Cleland (Ed.), *For the Director: Research essays in honor of James B. Griffin* (pp. 317–342) (Anthropological Papers Number 61). Ann Arbor: Museum of Anthropology.

Wolpoff, M. H. (1979). The Krapina dental remains. *American Journal of Physical Anthropology, 50*, 67–113.

Wolpoff, M. H. (1980). *Paleoanthropology*. New York: Knopf.

Wolpoff, M. H. (2009). How Neandertals inform human variation. *American Journal of Physical Anthropology, 139*, 91–102.

Wolpoff, M. H., & Caspari, R. (1997). *Race and human evolution*. New York: Simon and Schuster.

Wolpoff, M. H., & Caspari, R. (2006). Does Krapina reflect early Neandertal paleodemography? *Periodicum Biologorum, 108*, 425–432.

Wolpoff, M. H., & Caspari, R. (2013). Paleoanthropology and race. In D. Begun (Ed.), *A companion to paleoanthropology* (pp. 321–338). London: Wiley-Blackwell.

Wolpoff, M. H., Thorne, A. G., Jelínek, J., & Zhang, Y.-Y. (1994). The case for sinking *Homo erectus*. 100 years of *Pithecanthropus* is enough! *Courier Forschungsinstitut Senckenberg, 171*, 341–361.

Zilhão, J. (2007). The emergence of ornaments and art: An archaeological perspective on the origins of "behavioral modernity". *Journal of Archaeological Research, 15*, 1–54.

Zilhão, J., Angelucci, D. E., Badal-García, E., d'Errico, F., Daniel, F., & Dayet, L. (2010). Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proceedings of the National Academy of Sciences USA, 107*, 1023–1028.