



Neandertal Pelvic Remains from Krapina: Peculiar or Primitive?

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Abstract

Although fragmentary, the rich collection of fossil pelvic remains from the Neandertal site of Krapina in Croatia shows much of the morphology long considered to be characteristic of Neandertals from elsewhere in Europe and the Levant. This includes a long superior pubic ramus that is vertically thin in cross-section and an anteriorly positioned iliac pillar. The condition of the fossil material precludes evaluation of a further Neandertal characteristic, namely a broad pelvis. Comparison of the Krapina and other Neandertal fossils with earlier material from Europe, Asia and Africa demonstrates that the long pubis and broad pelvis are primitive for hominids and probably not part of a single adaptive or functional morphological complex with the vertically thin ramus or the anteriorly positioned iliac pillar. Rather than considering Neandertals to be »peculiar« or derived in their elongated pubic morphology, we see that Neandertals exhibit the long-standing primitive condition for hominids. It is modern human males who deviate from this longstanding pattern in their short pubis and it is this unusual, derived condition that requires explanation.

Discussion of the place of Neandertals in human evolution has usually focused on cranial and dental morphology, but several aspects of the postcranial skeleton have also figured prominently in the debate. One that has been central to discussions about Neandertal phylogeny and behavior from the very beginning of our knowledge of Neandertal morphology (at a time when much of that knowledge came from the Croatian Krapina remains) is the form of the pelvis, specifically in the region of the superior pubic ramus.

Neandertal pelvic morphology is represented at Krapina by fifteen separate fossil specimens, inventoried and illustrated in Smith (1) and Radovčić, Smith, Trinkaus and Wolpoff (2) and listed here in Table 1. This sample constitutes the richest collection of pelvic remains of Neandertals (or any other non-modern hominid) from a single site and is also significant given its chronological status early in the Neandertal sequence. Many of the pelvic fossils from Krapina are quite fragmentary but several (Krapina 207, 208/210, 209/212 and 255.1) possess sufficiently preserved morphology that they have been central to discussions of Neandertal pelvic anatomy over the last fifty years. Gorjanović-Kramberger (3) observed that the Krapina specimens showed evidence of a wide obturator foramen, morphology that was later noted in the Tabun Neandertal by McCown and Keith (4) who described that

female specimen as presenting »an altogether peculiar pelvic picture« (page 71). They saw similarities between the pubis in Tabun and in the gorilla, in contrast to Skhul, and regarded this as evidence for a significant difference between the Neandertal material from Tabun and the (presumably modern human) specimens from the neighboring site of Skhul. In his analysis of the Shanidar Neandertal specimens from Iraq, Stewart (5, 6) followed McCown and Keith's lead with observations of the »same peculiar form of the pubis« in the three Shanidar specimens that included an intact pubis, and argued that, along with the morphology seen in Tabun, this was evidence that these individuals were representatives of a separate Neandertal species that coexisted in the Near East with anatomically modern humans (like Skhul) that were not characterized by that morphology. More recently, Trinkaus (7) argued that like the more complete La Ferrassie 1 specimen, and other fragmentary Neandertal fossils, the Krapina 208 innominate was characterized by an elongated superior pubic ramus that was also flattened superior-inferiorly.

Until the 1980s, no functional hypotheses had been proposed to explain the significance of this characteristic (and apparently unique) Neandertal morphology, but it had generally been regarded as evidence of their distinctiveness from early anatomically modern humans at the species level with implications for the evolutionary relationship between these two groups. Several scholars (8, 9, 10, 11, 12, 13) took a more functional approach and proposed a number of hypotheses to account for the observed differences between pubic morphology in Neandertals and early modern or recent humans. Based on the pattern of sexual dimorphism observed in humans and other primates, all of these hypotheses depended on the assumption that an elongated pubis reflected an enlarged birth canal (or at least an enlarged pelvic aperture in the case of the male specimens). They related the elongated pubis to newborn size and therefore focused on various differences in life history pattern, reproductive patterns or body proportions (such as longer gestation length, accelerated fetal growth or large maternal size) as potential causes of the hypothesized large newborns in Neandertals. Because the hypotheses related to constraints on the pelvic aperture in its role as the passage through which the newborn passed during the birth process, these hypotheses naturally focused attention on the anatomy of females more than males.

At about the time that these functional hypotheses were being proposed and tested, the Kebara Neandertal specimen was discovered in Israel and described by Rak and Arensburg (14, 15, 16) providing for the first time an opportunity to examine Neandertal pelvic morphology in a fairly complete individual. It is ironic that the first complete pelvic girdle of a Neandertal to be discovered belonged to a male and was found just at the time when competing hypotheses about Neandertal anatomy focused on female reproductive biology. Rak and Arensburg (14) showed that although the pubis was long in Kebara compared to modern humans, the transverse and anteropos-

terior diameters of the pelvic inlet were not as great as would be expected if a modern human individual were scaled to a pubis of that length. They (14) suggested that obstetric requirements could not explain the »uniqueness of the Neandertal pelvis« and suggested instead that they related to possible locomotor and posture related differences. In a comparison of the pelvises from Kebara and Qafzeh, Rak (16) concluded that the distinctions he observed reflected significant differences between Neandertals and modern humans in the form of the pelvis and provided support for »the concept of two distinct evolutionary lineages for these hominids« (16: 323). In all of this work, whether the proposed functional hypotheses related to obstetrics, locomotion or posture, attention was focused on what the morphology of the Neandertal pelvis, in particular the pubis, might mean for the relationship between Neandertals and modern humans. That is, the question being asked was »how and why were Neandertals different from modern humans?« At that time, very little was known about the morphology of the pelvis in middle Pleistocene hominids (one of the rare fossils known, the Arago specimen, did not include the anterior portion of the pelvis) so that it was difficult to evaluate the morphology of Neandertals relative to their recent ancestors or close Pleistocene relatives.

Workers on this material have pointed to four aspects of Neandertal pelvic morphology that differ from what is generally seen in modern humans: the length of the pubis, the vertical thinness of the pubis, a broad pelvic girdle and an anterior position of a strong iliac pillar. Because the features were observed together on many specimens they have often been treated as part of a single adaptive complex, however, they may well not be functionally related as discussed below.

FOSSILS FROM KRAPINA

The Krapina remains were among the earliest Neandertal fossil pelvic material discovered. As new Neandertal discoveries followed in the twentieth century, they were always compared to and described as similar to the pelvic morphology of the Krapina material. However the Krapina fossils have generally not been treated quantitatively because of their fragmentary nature, especially in the region of the pubis. Krapina 207 consists of a left acetabulum with partial ilium and ischium. Based on the sciatic notch it is probably male. The iliac crest is not completely fused indicating that the individual was not mature. Smith (1) argued that this specimen did not have an anteriorly placed iliac buttress as McCown and Keith suggested other Neandertals had. In fact, the Krapina 207 specimen looks remarkably similar to a modern human. Krapina 208/210 consists of a right acetabulum with much of the superior pubic ramus, the ischial tuberosity and a bit of iliac blade also present. The relatively small size of the acetabulum suggests that this individual was female. Because the pubis is broken laterally to the pubic symphysis, acetabulosphymphyseal length for the Krapina 208/210 specimen can only be estimated. Estimates have centered on 80–85 mm (75–90 mm (7),

80–90 mm (17) and 80–85 mm (12). These estimates put it in the range of Neandertal specimens (the other female specimen, Tabun C1, for example, has an acetabulosity length of 79.5 mm, while the male Neandertal specimens are even longer). Krapina 208/210 had a thin superior pubic ramus with a vertical height of 7.5 mm. Krapina 209/212 includes a complete acetabulum, a portion of the superior pubic ramus and a portion of iliac blade. The fairly wide sciatic notch suggests that this individual was female. The superior pubic ramus of this specimen is also very thin, 4.9 mm in thickness at its thinnest point (2). Finally, Krapina 255.10 is a left superior pubic ramus discovered in the Krapina faunal material by Tim White in 1985. This specimen shows the extreme thinning described as Neandertal-like with a superior pubic ramus that is 9.6 mm at what appears to be the thinnest point. Unfortunately, the length of this pubis cannot be measured since it is broken at both ends. Other specimens from Krapina that include portions of pelvic morphology are more fragmentary and do not show regions of anatomy in which claims of characteristic Neandertal morphology have been made. In general, cross-sectional dimensions of the superior pubic ramus group the Krapina specimens with other Neandertals in being very thin compared to anatomically modern or recent humans (see data in Table 1 (9), Table 2 (12, 15)). The iliac blades of some of the Krapina specimens like other Neandertals and earlier *Homo* also show a strong iliac pillar that is anteriorly positioned on the iliac blade. Wolpoff (18) has suggested that this last trait, also seen in earlier hominids, is related to the elongated pubic bones that rotate the ilia backwards. An iliac pillar that is more anteriorly situated with respect to the iliac blade is actually in a similar position relative to the hip joint compared to modern humans. Overall, those aspects of pelvic morphology in Krapina that seem to conform to the pattern described as characteristically Neandertal are the apparently elongated superior pubic ramus, the thinning of that ramus and the anteriorly positioned iliac pillar. Because of the fragmentary nature of the Krapina fossils, the breadth of the pelvis cannot be determined.

OTHER NEANDERTALS PELVIC FOSSILS

Unlike the Krapina material, the Kebara specimen does allow comparison of one Neandertal pelvic girdle with modern humans. Tague (19) showed that the Kebara specimen is broader at the inlet than almost all of the modern human males in his sample (95.8%) and that the false pelvis (comparable to bi-iliac breadth) is broader than even more (99.5%) although he did find that it was not as broad inferiorly at the outlet. Similarly, Ruff (20) showed that Kebara was broader in bi-iliac breadth relative to its reconstructed stature than most modern human males, even cold adapted populations of Inupiat/Aleuts who have the broadest trunks relative to stature.

Analysis of sexual dimorphism in the length of the pubis in Neandertals compared to more recent humans showed that while both male and female Neandertals had pubic bones that were absolutely longer than male

TABLE 1
Hominid Pelvic Specimens from Krapina.

Krapina Hominid Number	Gorjanović-Kramberger Number	Skeletal Element
207	Cx1	Left immature partial ilium
208	Cx2	Right adult partial acetabulum, ischium and pubis
209	Cx3/6	Adult ilium and pubis
210	Cx4	Portion of adult left acetabulum. Fits with 208
211	Cx5	Posterior portion of right adult ilium
212	Cx6	Part of Krapina 209
255.1		Fragment of adult ilium (including acetabulum)
255.3		Left immature inferior ilium
255.4		Left immature ilium (including acetabulum)
255.5		Left immature ilium (including greater sciatic notch)
255.6		Left anterosuperior portion of adult ilium
255.7		Right adult ischium
255.8		Left adult anterior ilium
255.9		Left adult ischium
255.10		Left adult superior pubic ramus

and female modern humans, females were within the range predicted by their large body size while males are outside that range (11, 12). That is, although they are at the upper end of the range of modern human females in both acetabulosity length and body size (estimated from femoral head diameter), female Neandertals follow the same pattern as modern humans with respect to the relationship between these variables, indicating that they were similar in shape to, but at the upper end of the size range of modern females. Their long pubic bones can be explained by their large body size. This is not the case for males however. Even taking their large body sizes into account, the pubic bones of the Neandertal males are extremely long (12). In fact, Neandertal males seem to follow a relationship between pubic length and body size (estimated from a skeletal measure like femoral head diameter) that is similar to female Neandertals rather than modern males. This is in contrast to modern humans in which the slope of the sex-specific regressions of pubic length on femoral head diameter (Figure 3 in (22)), are similar in males and females but the y-intercept is higher for females (that is, on average, females have a longer pubis for their femoral head diameter than males). This suggests that whatever accounts for the distinctive morphology in male Neandertals, it is not selection due

to birth (as many of the hypotheses from the 1980s proposed) since the females follow a modern human pattern in the relative breadth of the anterior portion of the birth canal. It seems that at least with respect to the length of the pubis, it is male Neandertal morphology that is distinctive from modern humans rather than both male and female morphology.

Furthermore, two points suggest that sexual dimorphism in Neandertals may have been different from the pattern that we see in modern humans. First, for those specimens for which a pubis is present, the males have a longer pubis than the females (12, 22). Admittedly, this conclusion is based on a small sample, but it is in striking contrast to the pattern known for any living human group. Second, based on his analysis of the male Kebara specimen Tague (19) argued that if Neandertal sexual dimorphism in the pelvis followed the modern human pattern, and if Neandertal newborns were larger in size than those of modern humans (as several of the hypotheses from the 1980s predicted and as we would expect from their body size alone) Neandertal females would have »had a less favorable fetal cephalo-maternal pelvic relationship in the lower pelvic planes« (19: p. 19) (i.e., the pelvic outlet). This would imply that Neandertal childbirth was more difficult (and hence more dangerous) than modern childbirth. Given the strong selection acting on childbirth in humans today and in the recent past, this seems extremely unlikely.

COMPARISON WITH EARLIER *HOMO* AND *AUSTRALOPITHECUS*

In recent years, two important middle Pleistocene sites from across the full geographic span of the Old World have yielded new pelvic remains that make appropriate comparisons with the Krapina pelvic material and other (chronologically later) Neandertal specimens. These fossils allow us to look backwards from the pelvic morphology that is seen as characteristic of Neandertals and ask questions about how it compares with pelvic morphology in ancestral middle Pleistocene hominids.

In China, the Jinniushan specimen was discovered in 1984 in a fissure in Pleistocene cave deposits in an isolated karst prominence in the province of Liaoning in northeastern China (23, 24). The specimen has been dated by uranium series, ESR and faunal comparisons to 260,000 years ago (25). The specimen includes many elements of the postcranial skeleton and a cranium and is almost certainly female (21) based on cranial morphology. The left innominate is well preserved and shows a typical Neandertal pattern in which the superior pubic ramus seems to be elongated mediolaterally (21) and as a result the obturator foramen appears to be large. The superior pubic ramus is somewhat thin in cross-section though not as thin as in many of the Neandertals. Although sexed as female, the Jinniushan individual was very large in body size (an estimated 78.6 kg according to Rosenberg, Lü and Ruff (26) and the great length of her pubic bone (87.4 mm according to Rosenberg (21) is the

result of this large body size (21). Her bi-iliac breadth relative to body height was also extremely broad. The Arago XLIV specimen (27) has not generally been considered in discussion of mid-late Pleistocene pelvic morphology since so much of that discussion has focused on the pubis and that region of anatomy is not preserved on Arago. Like Jinniushan, the Arago specimen was large in size and those aspects of pelvic morphology that are preserved on the Arago XLIV individual show that it was almost identical to the Jinniushan specimen, suggesting that as far as we can tell, there was a similarity of morphology in this anatomical region across the Old World.

In Spain, a complete human pelvis from the middle Pleistocene was discovered at Sima de los Huesos in Sierra de Atapuerca, in Spain, dating to more than 200,000 years ago (28, 29). Pelvis 1 is broad overall with a very long superior pubic ramus (82 mm), significant iliac flare and a long femoral neck. Although male, the pelvis is so broad that its describers suggest that its »birth canal« [sic] could have been »easily negotiated by a fetus of modern human dimensions« (28, p. 258).

Our knowledge of middle-Pleistocene pelvic morphology from the Jinniushan, Arago and Atapuerca specimens tells us something very important about the pelvic morphology of the Krapina and other (chronologically later) Neandertals. The morphology that we have thought of as unusual in male Neandertals (because we were comparing it to modern humans) in fact extends back into the past. It seems that a long pubis and broad pelvis (at least superiorly at the level of bi-iliac breadth or the pelvic inlet) was present in archaic *Homo* across the Old World.

We can also examine earlier members of the genus *Homo* and *Australopithecus*. The fragmentary and juvenile WT 15000 pelvis (Nariokotome) from West Turkana was reconstructed by Ruff and Walker (30, 31) as having a narrow pelvis and tropically adapted body breadth although this estimate was based on remains in which both the anterior portion of the pelvis including the pubis and the sacrum are either not present or are reconstructed from very small fragments (18, 23). Other specimens of early *Homo* (OH 28 and KNM-ER 3228) also fail to include the pubic bones, but Ruff has shown that they probably were quite flat (platypelloid) in their pelvic shape (32) resembling later *Homo*. Finally, the two fairly complete Australopithecine specimens from South Africa (Sts 14) and Ethiopia (AL 288-1) exhibited broad flat pelvic girdles (33, 34) and long pubic bones (35) so that this shape is almost certainly a primitive hominid condition shared by all earlier hominids. However, the flatness (platypelloidy) of australopithecine and early *Homo* pelvic morphology is different from later hominids, including Neandertals. Ruff (32) has argued that the expansion of the antero-posterior diameter of the pelvic aperture evolved to accommodate rotational birth which accompanied encephalization of newborns in the late Middle Pleistocene. In summary, although the details of australopithecine pubic morphology were different (for example, they did not have the same cross-sectional shape

as Neandertals), the significance of their long pubis and the presence of that morphology in middle-Pleistocene hominids from Atapuerca and Jinniushan suggests that the Neandertals were not »peculiar« in this morphology but rather retained the plesiomorphic or primitive condition for *Homo* and perhaps for hominids (22).

CONCLUSIONS

As mentioned above, the »suite« of features previously thought to be characteristic of Neandertals may not be part of a single functional or adaptive complex. In fact, as Trinkaus (22) points out, the strength of the iliac pillar in Neandertals may not be secondary to the elongation of the pubis since they do not vary together. Similarly, the extreme thinning seen in the vertical dimension of the superior pubic ramus (which does occur in Jinniushan, though less so in Atapuerca and not at all in the australopithecines) cannot be explained as part of an adaptive or morphological complex that includes the elongated pubis since australopithecines share the elongated pubis with later hominids but have a completely different cross-sectional shape of the ramus. Furthermore, in modern humans, pubic length is positively correlated with thickness of the superior pubic ramus rather than thinness as a model linking these traits would predict. Clearly questions about the cross-sectional shape of the superior pubic ramus continue to be unanswered.

In a recent review and analysis of the polarity of many morphological traits that differ between Neandertals and modern humans, Trinkaus (22) also argues that Neandertals shared absolutely and relatively elongated superior pubic rami with middle Pleistocene *Homo*, early *Homo* and *Australopithecus*. Similarly, Arsuaga and colleagues (28) see this morphology as primitive based on their analysis of pelvis 1 from Atapuerca and Rak (36) argues that while Neandertal facial morphology is derived relative to other hominids, its pubic morphology was a retention of the primitive condition. According to Trinkaus, Neandertals exhibit the primitive condition inherited from and shared by earlier hominids and modern humans show the unusual, derived condition for the length of the pubis, a pattern seen in many other traits that he examined. Trinkaus (22: 607) concludes that, based on the likely polarities of traits throughout the skeleton and dentition, »it is not the Neandertals who appear unusual, special, derived, autapomorphous. It is we.« Based just on the evidence presented here for the length of the pubis, we can say more specifically that it is not Neandertals who were »peculiar« in the form of their pubis, but modern human males who are distinctive among hominids in differing from a long-standing hominid pattern. The evidence that is available today from all over the Old World and throughout the Plio-Pleistocene suggests that a broad pelvis was almost certainly the primitive condition for hominids. The wide obturator foramen that Gorjanović-Kramberger observed in the Krapina Neandertal material over a hundred years ago was the first hint of this primitive condition in an archaic human.

An understanding of the differences between Neandertal and modern human form must take into account which morphology is »peculiar«, i.e. what is the primitive condition. The question to be answered is not »why did Neandertal males have such a long pubis« but »why do modern human males differ from what appears to have been a universal archaic human pattern extending back to the australopithecines. Future research should focus on the functional and evolutionary implications of the short pubis in modern human males.

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