



The Innominate Bone Sample from Krapina

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Abstract

The Croatian site of Krapina has yielded a large collection of human fossils attributed to the archaic Neandertals. The sample includes fourteen innominate bone specimens, minimum number of seven individuals (MNI=7). Among them, it is possible to distinguish two fully adults (one female, one male), two late adolescent or young adults (both males) and three children of unknown sex. Metric analysis reveals the Krapina hip bones to be characterized by relatively small vertical acetabular diameter compared to the classic Neandertals, and a long and remarkably slender pubis relative to living humans. Morphologically, the Krapina specimens are included within the Neandertal variation, showing a narrow, rounded and/or tilted bone surface between the coronal portion of the greater sciatic notch, and a distinctive morphology of the superior pubic ramus, the latter agreeing with the metric data. On the other hand, they can be distinguished from the modern human innominate bone in aspect related with the anterior inferior iliac spine, the topography of the posterior wall of the acetabulum, the supraacetabular sulcus and some traits of the superior pubic ramus.

INTRODUCTION

Excavations carried out by Prof. Dragutin Gorjanović-Kramberger, between 1899–1906 in the Hušnjakovo rock-shelter close to the village of Krapina (Croatia), yielded a large collection of faunal remains, stone tools and human fossils (1–5). The human fossil sample from Krapina is the largest Neandertal collection from a single site, with some 874 human remains present (6). The human fossils derive from seven of the nine stratigraphic levels (7) identified by Gorjanović-Kramberger in 1899, and are associated with a Middle Palaeolithic stone tool technology (8, 9). The human fossil sample has been dated to 130 ± 10 kyr (10) by combined ESR and U-series techniques on tooth enamel from associated faunal remains, and they have been widely considered as displaying a fully Neandertal suite of anatomical characteristics (11, 12). Importantly, the collection includes a large number of postcranial remains (6, 13–18), including a large sample of innominate bones (6, 13), one of the least represented portions of the human skeleton in the fossil record. Therefore, the Krapina sample can provide important insights into the evolution of the pelvis in Pleistocene *Homo*.

Prior studies have catalogued the innominate bone collection from Krapina (6, 13), and this sample has frequently been included as part of the comparative sample in studies of the evolution of this region of the body (19–22). However, to date, no detailed study has focused exclusively on this collection. The present study provides an in-depth inventory of

the hip bone collection, estimates the minimum number of individuals represented within the sample, and attempts to determine their corresponding ages at death, sex and body mass. In addition, anthropological measurements as well as the expression of morphological features in the Krapina specimens are compared with both Neandertals and modern humans to establish the morphological affinities of the Krapina specimens.

MATERIAL AND METHODS

The innominate bone sample from Krapina is composed of fourteen elements, ranging from almost complete specimens to more fragmentary remains. The first inventory of the Krapina remains was made at some point after 1924 (6) by the director of the excavations, Dragutin Gorjanović-Kramberger, who distinguished and numbered six innominate bones as *Coxal* 1 to 6. These labels, still visible today, were written on the bone in black ink. Based on this first inventory, the curator and subsequent director of the Croatian Natural History Museum, Josip Poljak, carried out an inventory of the human and faunal remains which included most of the currently-known sample. Radovčić *et al.* (6) have noted that this must have happened in the early 1930s. Poljak's inventory was based on a fractional numbering system, in which the most complete elements received individual numbers whereas fragmentary remains were provided with fractional ones, both labeled in red ink to distinguish them from the original black label assigned by Gorjanović. Several workers subsequently reviewed parts of the sample (13–18), and a complete catalogue was finally published in 1988 (6), updating that of Poljak by including the most fragmentary remains and those identified within the faunal sample that were not previously catalogued, together with the original Gorjanović notation. According to Radovčić *et al.* (6), the entire innominate collection was already labelled by Poljak and any

modification in the numbering system was done later. Therefore, in the present study we have adopted the catalogue number figured in Trinkaus (13) and Radovčić *et al.* (6), referring to both the catalogue number and the coxal number, when appropriate.

Data for the Krapina sample was collected on the original fossil collection housed at the Croatian Natural History Museum (CNHM) of Zagreb, where measurements, photographs and observations were undertaken on the 14 innominate bones. For comparative purposes, a sample of hominin fossils has been used, relying on data collected on original specimens and from high quality casts of the originals or from the literature. In addition, a large sample of recent humans has been used from the Beira litoral region of Portugal, housed at the Instituto de Antropologia of the Universidade de Coimbra (N=448, 209 females and 241 males) (Table 1).

To summarize and compare the fossil collection, a comprehensive inventory has been carried out, including a brief description of the element, which side it comes from and the approximate age at death. The age categories used in the present study are based on the ossification pattern of the different pelvic elements in modern humans, and include: child (no evidence of ossification of the triradiate cartilage), juvenile (close to or complete ossification of the triradiate cartilage, rest of epiphyses unfused), late adolescent (complete ossification of the triradiate cartilage and nearly complete ossification of the rest of the epiphyses) and adult (no evidence of unfused sutures, some degenerative processes may be evident). Based on the recent review of the developmental pattern of the pelvis in living humans (23), we have proposed a tentative age at death for some specimens. In the case of adult individuals, the age at death estimations were based on the degenerative modifications of the auricular surface of the sacroiliac joint (24, 25) and on the appearance of the articular surface of the acetabulum

TABLE 1

Comparative sample consulted in the present study.

| Taxon | Sample size | Specimens (source) |
|--------------------------------|---|---|
| <i>Australopithecus</i> | 4 | AL 288-1 (cast), Sts 14 (cast), Stw 431 (cast), MLD 25 (cast) |
| <i>Paranthropus</i> | 3 | SK 50 (cast), SK 3155 (cast), TM 1605 (cast) |
| <i>Homo ergaster</i> | 4 | KNM WT 15000 (cast), KNM ER 1808 (cast), KNM ER 3228 (cast), OH 28 (cast) |
| Middle Pleistocene <i>Homo</i> | 14 | Arago 44 (cast), Sima de los Huesos sample (fossil), Broken Hill E 719 (cast) |
| Neandertals | 10 | Villafamés 2 (cast, 83), Le Prince 1 (79), LHortus 45 (20), La Chapelle-aux-Saints 1 (79,80), La Ferrassie 1 (79), La Ferrassie 6 (66), La Ferrassie 8 (66), Neandertal 1 (cast), Amud 1 (fossil), Kebara 2 (fossil), Shanidar 1 (21, 70), Shanidar 3 (70), Tabun C1 (69) |
| Fossil <i>Homo sapiens</i> | 7 | Qafzeh 8 (fossil), Qafzeh 9 (fossil), Qafzeh 10 (fossil), Qafzeh 13 (fossil), Qafzeh 21 (fossil), Skhul 4 (cast), Skhul 5 (69) |
| Recent Humans | 451 Pooled sample (242 Males 209 Females) | Instituto de Antropologia de la Universidade de Coimbra |

Numbers in parentheses indicate source of comparative data (see reference list)

TABLE 2

Inventory of the Krapina sample.

| Specimen | Side | Age category | Age at death | Sex Attribution | Body Mass [†] (1) | Body Mass [†] (2) | Mean Body Mass |
|---------------------|------|---------------------------------|--------------|-----------------|----------------------------|----------------------------|----------------|
| Cx.1. 207* | R | Late Adolescent | c. 20 yrs | M | 62.5 kg | 67.3 kg | 64.9 kg |
| Cx.2. 208* | L | Middle-Aged Adult | 30–40 yrs | M | 65.1 kg | 69.8 kg | 67.5 kg |
| Cx.3+Cx.6. 209+212* | L | Old Adult | c. 50 yrs | F | 63.8 kg | 68.5 kg | 66.2 kg |
| Cx.4. 210 | L | Adult | – | ? | – | – | – |
| Cx.5. 211 | R | Late Adolescent/ Young Adult | c. 25 yrs | M? | – | – | – |
| 255.1 | L | Adult | – | ? | – | – | – |
| 255.3* | L | Child | 6–14 yrs | ? | – | – | – |
| 255.4* | L | Child | 6–14 yrs | ? | – | – | – |
| 255.5* | L | Child | 6–14 yrs | ? | – | – | – |
| 255.6 | L | Juvenile/Late Adolescent | – | ? | – | – | – |
| 255.7 | R | Adult | – | ? | – | – | – |
| 255.8* | L | Late Adolescent | – | M? | – | – | – |
| 255.9 | L | Adult | – | ? | – | – | – |
| 255.10 | R | Adult | – | F? | – | – | – |

* Elements representing minimum number of individuals (MNI)

[†] Estimate of femoral head diameter (FHD) from vertical acetabular diameter (ACET) derived by us from raw data used in reference (33):

$$\text{FHD} = 0.9465\text{ACET} - 5.6467; r = 0.949 \text{ (n = 143, pooled-sex)}$$

(1) Estimated according to the regression formula; $\text{BM} = 2.239\text{FHD} - 39.9$ $r = 0.98$ (pooled-sex) (29)

(2) Estimated according to the regression formula; $\text{BM} = 2.268\text{FHD} - 36.5$ $r = 0.92$ (pooled-sex) (30)

(26). However, a recently published test (27) of one of the auricular surface aging methods (25) revealed this technique to provide poor estimates of the ages at death. Therefore, estimates based on this technique must be considered with caution. Further, it is possible that the postcranial skeleton in Neandertals followed a somewhat different developmental pattern from that of modern humans, as has been shown to characterize the dentition (28). Finally, the minimum number of individuals (MNI) has been estimated based on developmental criteria, sex determination and repetition of anatomical parts.

At the same time, the hip joint is a weight-bearing articulation, and is closely correlated with the body weight. Several correlations (29–31) have been established between the femoral head diameter (FHD) and the body mass (BM). Since the hip joint is a ball and socket articulation, the head of the femur (the ball) and the diameter of the acetabulum (the socket) are highly correlated as shown by several studies (30, 32, 33), making it possible to estimate the body mass from the vertical acetabular diameter.

The hip bone is the most reliable skeletal element for sexual determination (34–40), and the anthropological and forensic literature since the late 19th century has provided an extensive list of sexually dimorphic features of the hip bone. There are two main approaches, morphological and metric, in sex determination. The morphological traits have been traditionally grouped in two different complexes, the pubic (39, 41–44) and the sacroiliac (45–54), each of them composed of different characters considered diagnostic in assigning sex. In addition, different techniques have tried to evaluate the sex based on both complexes (34–36, 54–56). Further, there are some features related to body size (i.e. robusticity and muscles attachments) that are useful in sexual determination in extant human populations. At the same time, the metric approach is based on quantifying both the above-mentioned traits and the dimensions related with body size. In extant populations, indices and discriminant functions have been developed to attempt to classify individuals according to sex based on this metric information (36, 37, 39, 57–65).

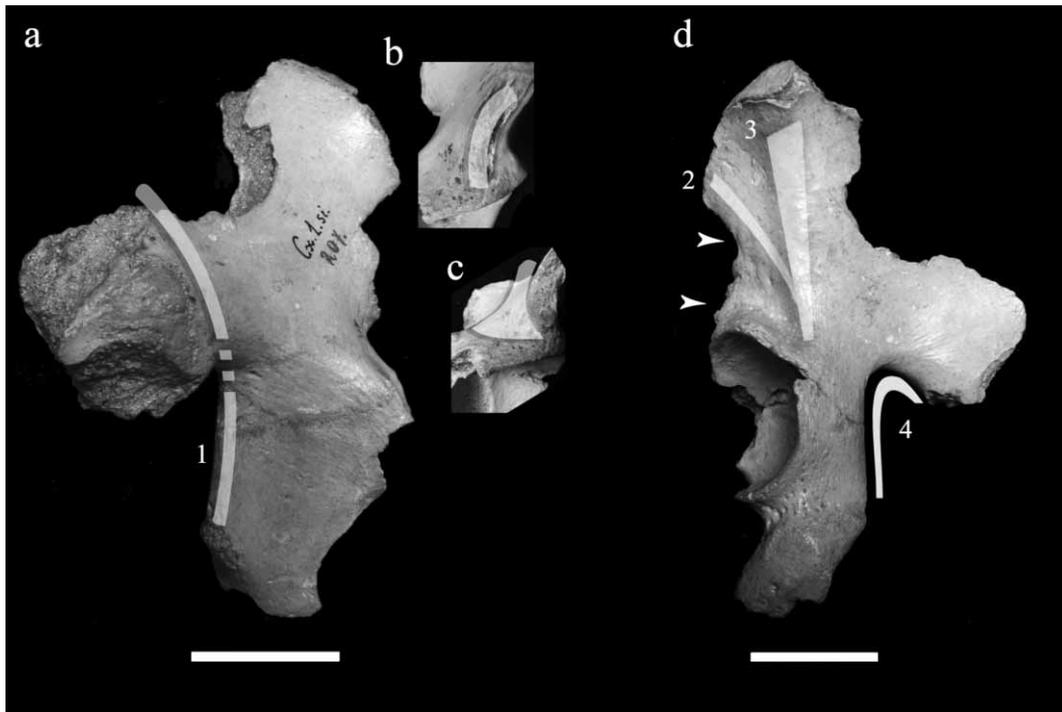


Figure 1. *Krapina 207 (Cx. 1).* Medial view (a) showing the distinguishable AIIS morphology in ventral (b) and medioventral (c) orientations. The ventral margin of the sacropelvic region and the anterior margin of the sciatic notch form a single arc (1). In lateral view (d) it is possible to observe the acetabulospinal buttress (2), the acetabulocrystal buttress (3), the aperture of the greater sciatic notch (4), the interspinous notch (upper arrow) and the supra-acetabular sulcus (lower arrow). Scale bar = 5 cm.

Sex determination in a fossil population is complicated by a number of factors. In some cases, it is not clear that the sex-specific patterns of anatomical variation seen in extant populations are expressed similarly in the fossil specimens. In addition, the often fragmentary nature of fossil specimens severely limits the amount of morphological and metric information preserved, and particular

diagnostic regions may not be represented. This is the case with many of the specimens from the Krapina sample. Fortunately, some specimens do preserve diagnostic sex-related features. Nevertheless, these sexual determinations should be considered with caution, since the probability for a correct assessment decreases when just one shape or metric character is considered. In addition,

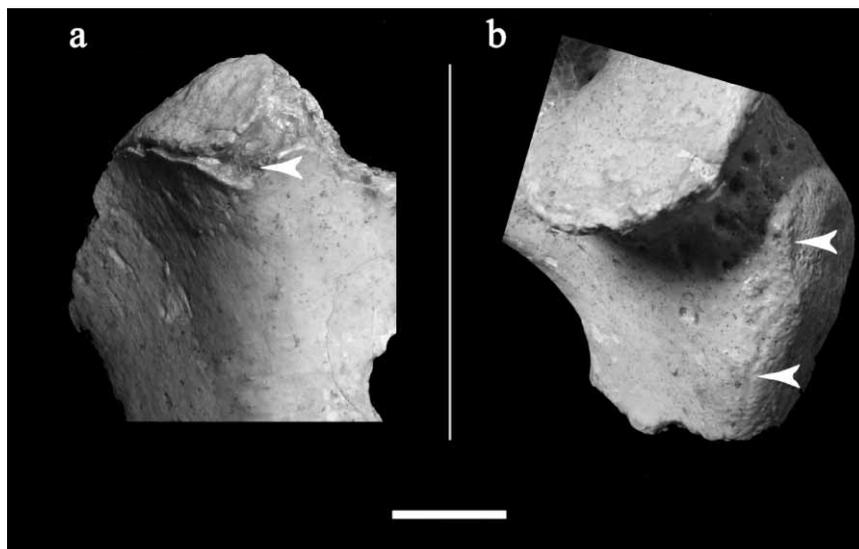


Figure 2. *Krapina 207 (Cx. 1).* Details of the ilium (a) and ischium (b), showing unfused sutures on the iliac crest (arrow, a) and ischial tuberosity epiphysis (arrows, b). Scale bar = 2 cm.

sexual attribution becomes much more complicated in immature individuals. Furthermore, although there is an extensive amount of literature addressing this problem, it is widely held that sexual dimorphism is not clearly expressed until puberty (23). Hence, no attempt has been



Figure 3. *Krapina 208 (Cx. 2).* Lateral view, showing the supra-acetabular sulcus (arrow). Scale bar = 5 cm.

made to sex the specimens in the youngest (child) age category.

Finally, the relevant anthropological measurements and morphological traits preserved in the adult Krapina specimens have been described and compared with Neandertals and modern humans in order to assess the population affinities of the Krapina fossils, and therefore, to place them in the context of the evolution of the innominate bone within Pleistocene *Homo*.

INVENTORY

As discussed above, the Krapina innominate bones were numbered from 1 to 6 by Gorjanović-Kramberger in 1924. The present inventory is based on these labels, together with the numbering system subsequently applied by Poljak. More detailed descriptions of the preservation of the individual Krapina specimens can be found elsewhere (6, 13). Table 2 summarizes the information related to the inventory.

Krapina Cx 1. 207. (Figures 1, 2, 20). This is a right innominate bone with a mostly complete ilium and ischium. Ossification has begun in the anterior portion of the iliac crest epiphysis, with its pelvic aspect in advance of the gluteal aspect (Figure 2a). In addition, all borders of the ischial tuberosity have almost completed fusion (Figure 2b). Based on modern human standards, we estimate an age at death of around 20 years (23). Further, the billowing of the auricular surface supports a late adolescent age at death for this individual.

Krapina Cx 2. 208. (Figures 3, 15–17). This is a left innominate bone with large portions preserved of the pubis, the ischium and the iliac body. The complete

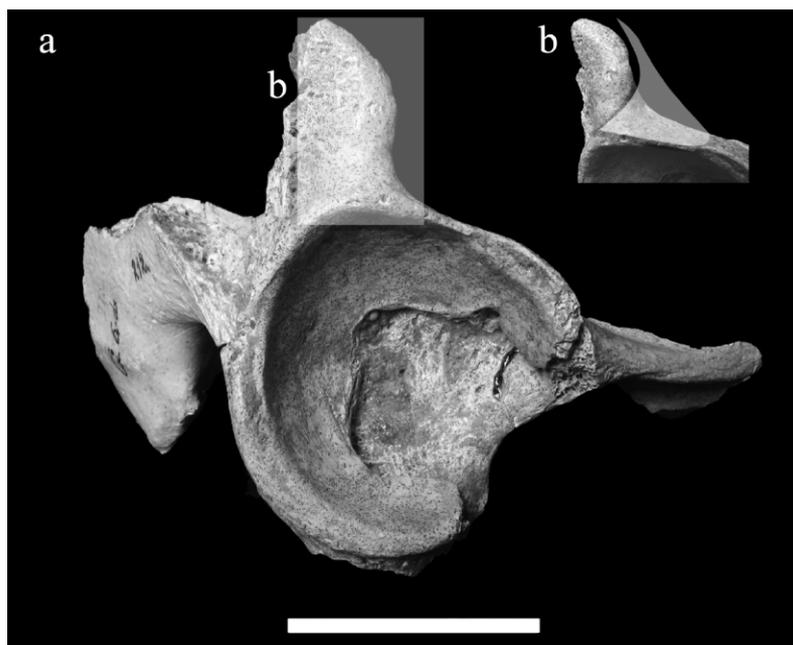


Figure 4. *Krapina 209+ 212 (Cx. 3+Cx. 6).* Lateral view (a) with details of the anterior inferior iliac spine and the morphology of the iliopsoas sulcus (b). Scale bar = 5 cm.

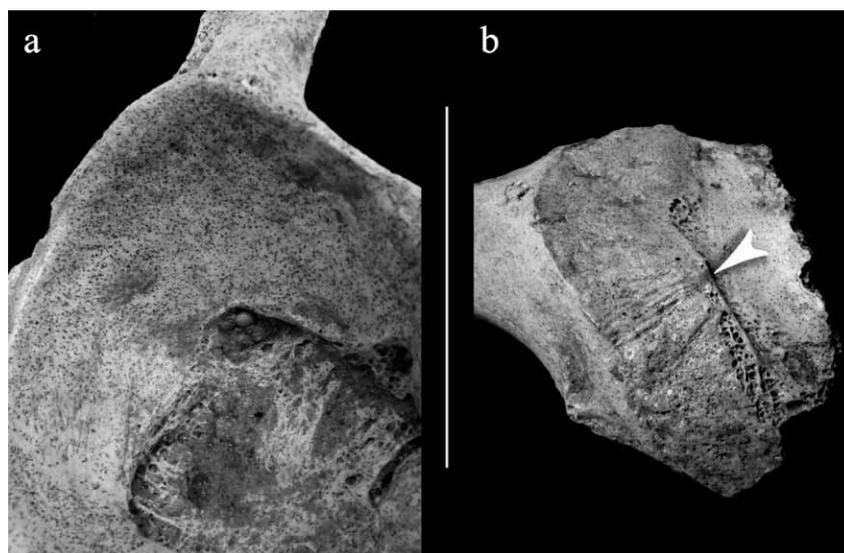


Figure 5. *Krapina 209+212 (Cx 3+Cx 6).* Appearance of the acetabulum (a) and striations of the auricular surface (arrow, b) suggest an adult age for this individual. Not to scale.

fusion of all the secondary ossification centres indicates an age at death of greater than 23 years in living humans (23). In addition, the acetabular margin is rounded with a smooth depression on its internal border, no osteophyte is present on either the anterior or posterior horns of the lunate surface, the acetabular fossa is slightly deeper than the lunate surface and some portions of its perimeter are transforming into trabecular bone. All these features indicate that this individual was probably between 30–40 years old (26).

Krapina Cx 3+Cx 6. 209+212. (Figures 4, 5, 17, 20). This is a left innominate bone with the complete acetabulum, most of the superior pubic ramus and the complete auricular surface. The secondary growth centres have completed ossification, indicating an age older than 23 years in modern populations. The modifications of the auricular surface yield a mean age of 51 years old,

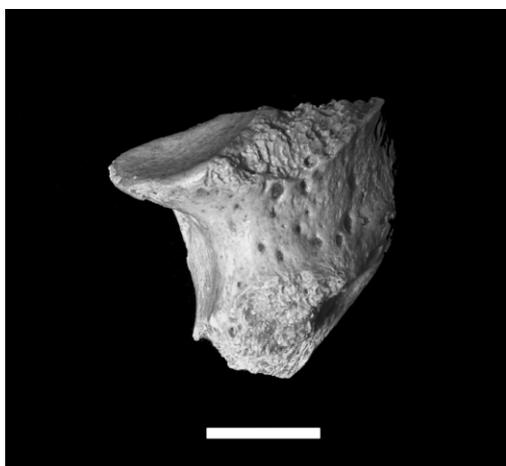


Figure 6. *Krapina 210 (Cx. 4).* Lateral view of the ischial body and preserved portion of the acetabulum. Scale bar = 2 cm.

according to the aging method of Buckberry *et al.* (25). However, the loss of the billowed pattern characteristic of immature individuals, together with some granular and transverse striations (Figure 5b), are conditions which are more commonly found in the fourth decade (24). Changes in the morphology of the acetabulum (Figure 5a), including a pronounced groove on the external margin of the lunate surface, the porosity on the posterior wall of the acetabulum and the micro- and macroporosity accompanied with bony activity on more than three quarters of the acetabular fossa, all suggest an age close to 50 years (26).

Krapina Cx 4. 210. (Figures 6, 15). This is a fragment of the right ischial body with part of the acetabulum. Based on the appearance of the lunate surface, this individual is most consistent with an adult morphology.

Krapina Cx 5. 211. (Figure 7). This is a left dorsal fragment of the ilium. The compact, very dense and smooth sacroiliac joint, together with the presence of an easily recognized transversal organization (billowing) in the inferior caudal ramus of the auricular surface (Figure 7b), suggest a maximum age of around 25 years (24).

Krapina 255.1. (Figure 8). This is a fragment of the left iliac body, with only the lateral cortical bone preserved. The anterior inferior iliac spine (AIIS) is fused, and there are no signs of immaturity in the articular surface of the acetabulum, suggesting an adult age for this individual.

Krapina 255.3. (Figure 9a). This is a fairly complete left ilium. None of the secondary epiphyseal centres show any signs of ossification, indicating an age at death younger than 11–14 years (23). Their values for the »anterior inferior iliac spine (AIIS)-ilioauricular point diameter« (Va 9 = 44.5 mm, Table 7) and the »AIIS greater sciatic notch diameter (Va 10 = 45.3 mm, Table 7) are higher than in La Ferrassie 8 [Va 9 = 22.1 mm; Va 10 = 21.2 mm (66)], La Ferrassie 6 [Va 9 = 28.6 mm; Va 10 =

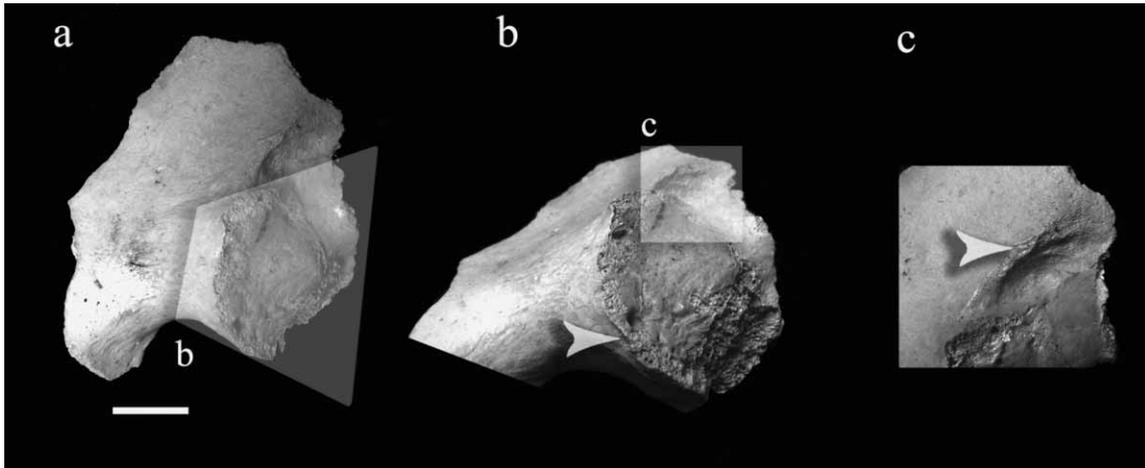


Figure 7. *Krapina 211 (Cx.5).* Medial view (a), showing the dense and smooth auricular surface (b) with transverse undulations pattern (billowing) at the sciatic notch margin (arrow, b) and the detail of the anterior fossa of the postauricular sulcus at the sacropelvic region (arrow, c). Not to same scale. Scale bar = 2 cm.

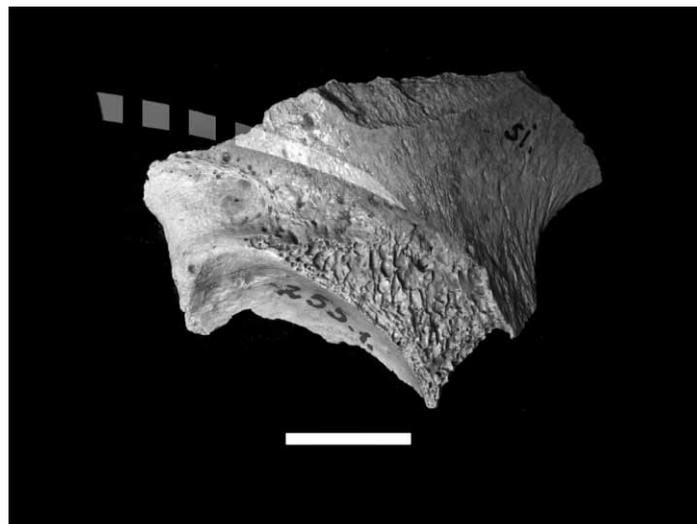


Figure 8. *Krapina 255.1.* Lateral view of the iliac body and lunate surface, with the path of the supra-acetabular sulcus drawn over the specimen. Scale bar = 2 cm.

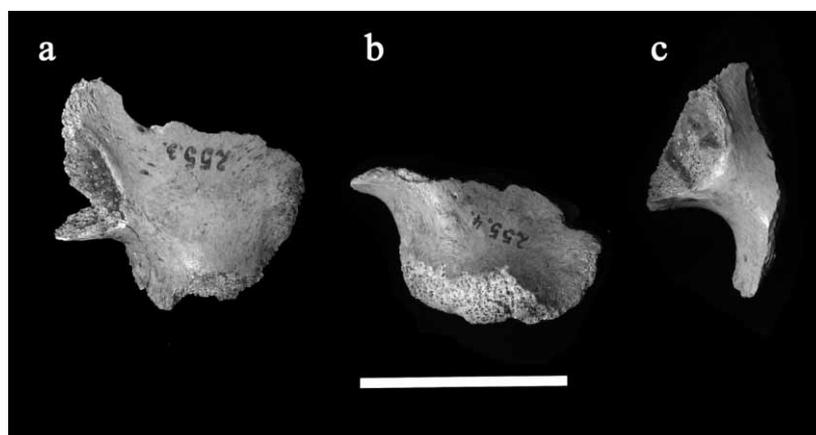


Figure 9. *Krapina 255.3 (a), 255.4 (b) and 255.5 (c).* Lateral views. Scale bar = 5 cm.

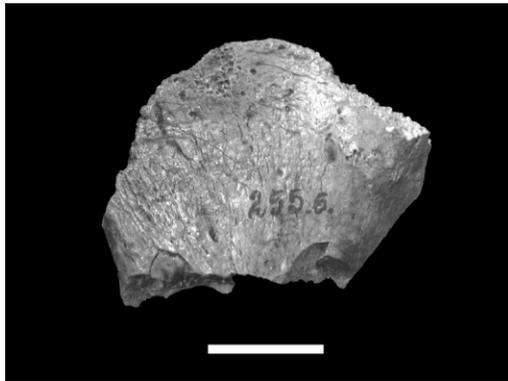


Figure 10. *Krapina 255.6. Lateral view, showing the region running from the anterior superior corner of the ilium to the iliac tubercle. Scale bar = 2 cm.*

30.5 mm (66)], Qafzeh 21 (Va 9 = 29.3 mm; Va 10 = 30.0 mm), Qafzeh 10 (Va 9 = 35.3 mm; Va 10 = 38.9 mm), Lagar Velho I [Va 9 = 31.2 mm; Va 10 = 29.2 mm (66)] (among whom the oldest is 6 years old) and a modern human sample between 3–6 years of age [Va 9 = 33.1 ± 4.0 mm; Va 10 = 30.8 ± 2.8 (67)]. Therefore, we can estimate an age for Krapina 255.3 between 6 years and 14 years old, based on the dimensions achieved by this individual at the moment of death.

Krapina 255.4. (Figure 9b). This is the left iliac body of an immature individual. The portion preserved suggests an age at death close to the Krapina 255.3, considering its similar epiphyseal developmental stage and dimensions (Va 10 = 47.8 mm, Table 7). The value for the «AIIS-greater sciatic notch diameter» is slightly higher than Krapina 255.3 and any of the fossil and modern immature comparative specimens cited above. Hence, we have also estimated an age between 6 and 14 years old for this specimen, but perhaps slightly older than Krapina 255.3.

Krapina 255.5. (Figure 9c). This is a left sciatic notch and anterior auricular surface of a child probably of similar age as Krapina 255.4 and 255.5 (6 and 14 years old), according to the size of the portions preserved and the developmental evidence. However, no osteometric standard measurement could be taken to compare with the comparative sample.

Krapina 255.6. (Figure 10). This is the anterior superior portion of the left iliac blade. Its cranial margin is probably coincident with the iliac suture between the crest and the blade; therefore, we suggest that the iliac crest was either unfused or only weakly fused with the blade, indicating a juvenile but most probably a late adolescent age at death for this individual.

Krapina 255.7. (Figure 11). This is a fragment of a right ischial body, with part of the lunate and the posterior wall of the acetabulum. The preserved region shows a fully adult morphology with no trace of immaturity.

Krapina 255.8. (Figure 12). This is a left ilium, with preserved portions of the iliac body and anterior margin, together with the cranial portion of the acetabulum. The

epiphysis for the AIIS is complete, although bone formation is still present at the articular surface of the acetabulum (Figure 12c). This corresponds to a late adolescent individual.

Krapina 255.9. (Figures 13, 16). This is a fragment of a fairly complete left ischium. The lunate surface and the ischial tuberosity show a mature appearance without any traces of periostitic processes, suggesting an adult aged individual.

Krapina 255.10. (Figures 14, 17). This is a fragment of a right superior pubic ramus with part of the acetabulum attached. It does not preserve any evidence of immaturity, and therefore, we estimate an adult age for this individual.

Minimum number of individuals

A minimum number of 7 individuals (MNI = 7) was established for the sample based on the ilium (greater sciatic notch) and relying on the number of repeated elements, the developmental ages of the specimens, antimeric symmetry and size compatibility. These 7 individuals are represented by: Cx.1 (207), Cx.2 (208), Cx.3+Cx.6 (209+212), 255.3, 255.4, 255.5 and 255.8 (Table 3). We have discarded an association based on antimeric symmetry between 255.8 (R) and Cx.2 (L), Cx.3+Cx.6 (L) and Cx.5 (L), according to the thickness of the sciatic notch at its deepest point [Cx.3+Cx.6 = 19.1 mm; Cx.5 = 18.6 mm; 255.8 = 21.5 mm], the cross-sectional shape of the arcuate line on both 255.8 (sharper) and Cx.3+Cx.6 (rounded) and the width of the lunate surface from the acetabular point of Genoves (35) to the AIIS (Cx.2 = 22.9 mm; 255.8 = 31.2 mm).

Possible associations

Among the remainder of the elements it is possible to establish some potential associations, as well as, incompatibilities (Table 3).

§Krapina Cx.4 is a close morphological antimeric of Cx.2 at the level of both the lunate surface and the tuberoacetabular sulcus (Figure 15). Thus, values of the minimum width of this sulcus (68) are virtually identical: Cx.2 = 17.1 mm; Cx.4 = 17.7 mm. Therefore, we agree with Trinkaus (13) in associating these two elements.

§Although Krapina Cx.5 is incompatible with 6 of the 7 individuals used to calculate the MNI, we can not discard association between this element and Krapina Cx.1, based on the similarity in developmental age, morphology and dimensions (Thickness of sciatic notch at its deepest point: Cx.1 = 18.3 mm; Cx.5 = 18.6 mm. Maximum thickness of the iliac blade at the level of the sacroiliac joint: Cx.1 = 25.7 mm; Cx.5 = 25.8 mm). Accordingly, these two specimens could be associated to the same individual.

§Krapina 255.1 is symmetrically incompatible with Krapina Cx.1 and Krapina 255.8, and its age at death is significantly older than that of Krapina 255.3, Krapina 255.4 and Krapina 255.5. In contrast, Krapina Cx.3+Cx.6 and Krapina 255.1 show a morphological affinity in

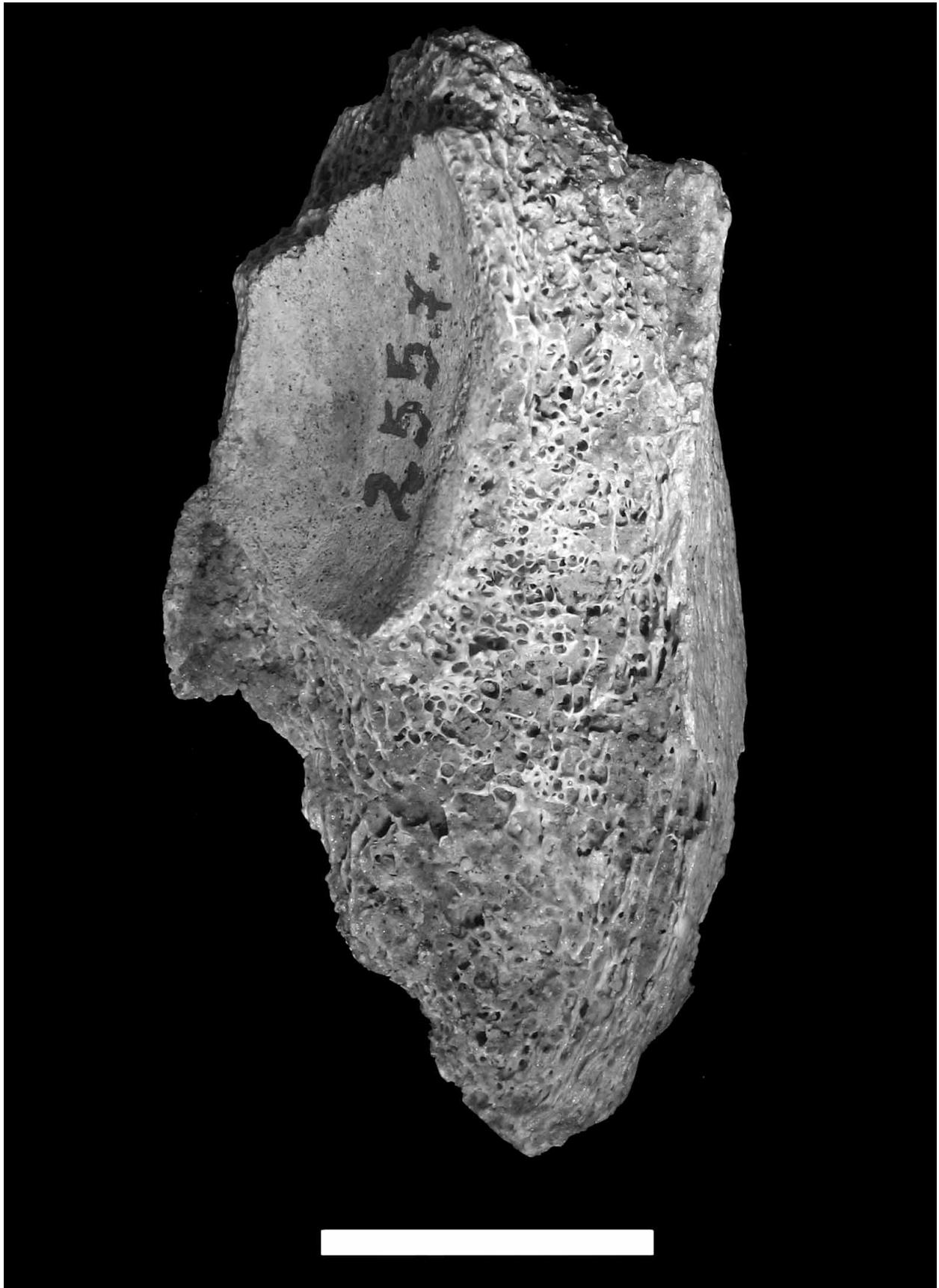


Figure 11. *Krapina 255.7. The articular surface can be seen in medial view. Scale bar = 2 cm.*

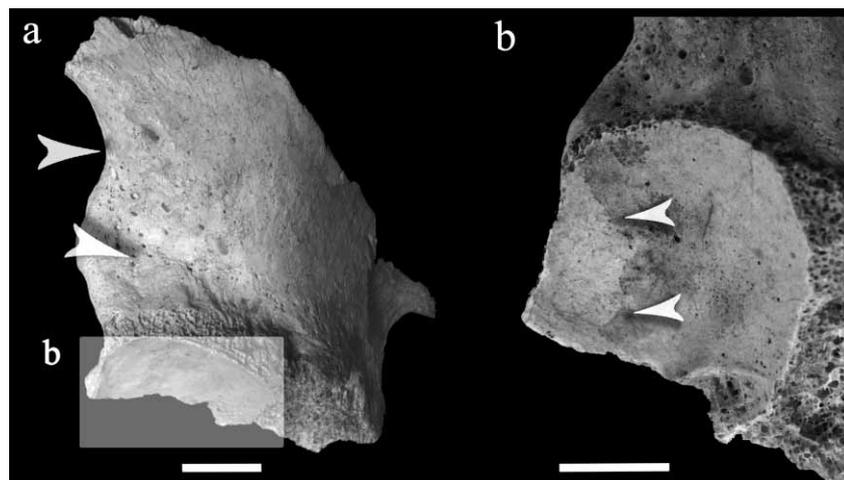


Figure 12. *Krapina 255.8.* Lateral aspect (a) with the interspinal notch (upper arrow) and the supra-acetabular sulcus above the acetabular margin (lower arrow). The lunate surface (b) shows the margins of the ossifying sheet of bone covering the joint socket of the acetabulum (arrows). Scale bar = 2 cm.

TABLE 3

Minimum number of individuals (MNI) and associations between elements from the Krapina site

| MNI | Left Side | Right Side |
|-----|-----------------------|------------|
| 1 | Cx.5.211 | Cx.1.207 |
| 2 | Cx.2.208 | Cx.4.210 |
| 3 | Cx.3+Cx.6. 206+212 | 255.10 |
| 4 | 255.3 | – |
| 5 | 255.4 | – |
| 6 | 255.5 | – |
| 7 | 255.8 | – |

those common portions preserved, as well as a similar value of the minimum width of the ilium (35) (255.1 = 54.6 mm; Cx.3 = 55.6 mm approx.). Therefore, we agree with Trinkaus (13) in associating these two fragments to the same individual.

§The area of the left ilium preserved in Krapina 255.6 makes it anatomically incompatible with Krapina Cx.1, which also preserves this region. Although it was not possible to directly articulate this specimen with Krapina 255.8, we cannot discard their association.

The similarity in appearance of the articular surface of the acetabulum in both Krapina 255.7 and 255.8 makes them ontogenetically compatible. The morphology and developmental similarity between Krapina Cx.1 and Krapina 255.7 also makes its association possible. However, due to the fragmentary nature of Krapina 255.7, it was not possible to obtain standard osteometric measurements to support these associations. On the other hand, this specimen is clearly incompatible based on symmetry and developmental age with Cx.2, Cx.3+Cx.6, 255.3, 255.4, 255.5 and 255.6.

§Krapina 255.9 could be developmentally compatible with Krapina Cx.3+Cx.6. However, it is clearly incompatible, due to lack of symmetry, with Krapina Cx.2 (Figure 16) and due to repetition of anatomical parts with Krapina Cx.1 and Krapina Cx.4. At the same time, it is developmentally incompatible with Krapina 255.3, Krapina 255.4 and Krapina 255.5, which represent immature individuals.

§Krapina 255.10 could theoretically be associated with either Krapina Cx.2 or Krapina Cx.3+Cx.6. However, morphologically it is clearly more similar to Krapina Cx.3+Cx.6 (Figure 17). In addition, measurement over the depth (69) and thickness of the superior pubic ramus (70) agrees with this a priori visual inspection (Cranio-Caudal Depth: Cx.2 = 8.9 mm; Cx.3+Cx.6 = 8.2 mm; 255.10 = 8.2 mm. Dorso-Medial to Vento-Lateral Width: Cx.2 = 21.9 mm; Cx.3+Cx.6 = 17.3 mm; 255.10 = 16.9 mm). Therefore, we consider an association between 255.10 and Cx.3+Cx.6 possible (*contra* 13).

Body Mass

Table 2 summarize body mass estimations for Krapina Cx.1, Krapina Cx.2 and Krapina Cx.3+Cx.6 specimens. Regressions formulae from three different studies (29, 30, 33) have been used to calculate the body mass from the acetabular vertical diameter (see Material and Method). These equations are based on diverse and combined sex modern human samples. Mean values of the two estimates show a range of body mass from 64.9 kg to 67.5 kg. Although slightly different values in body mass estimates of the Krapina specimens were obtained by Ruff *et al.* (29 – *supplementary information*), our results fall within 2 standards deviation from the mean body mass obtained by these authors for early Late Pleistocene populations (67.7 ± 2.4 kg) (29 – Table 1).

SEXUAL ASSESSMENT

Only the elements preserving portions that are relevant for sex assessment have been considered (Cx.1, Cx. 2,



Figure 13. *Krapina 255.9. Fragment of a nearly complete left ischium. Scale bar = 2 cm.*

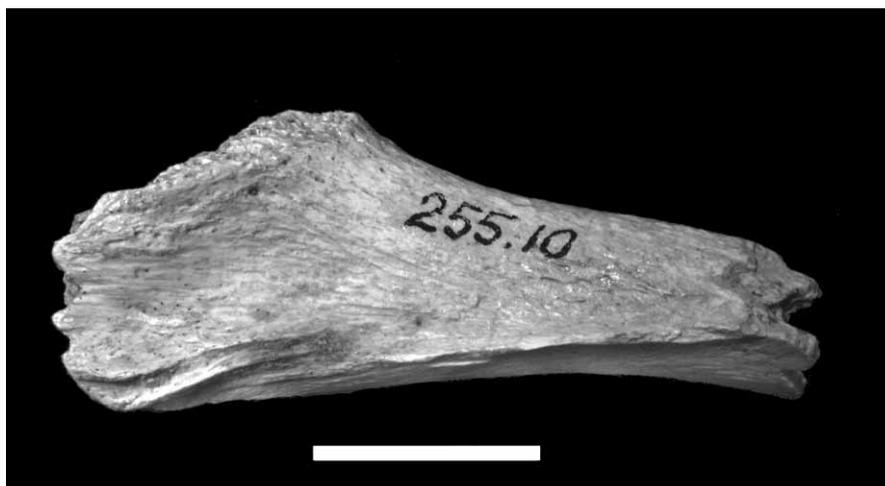


Figure 14. *Krapina 255.10. A superior pubis ramus in cranial view, showing the wide pectineal surface and the eroded but sharp pectineal crest. Scale bar = 2 cm.*

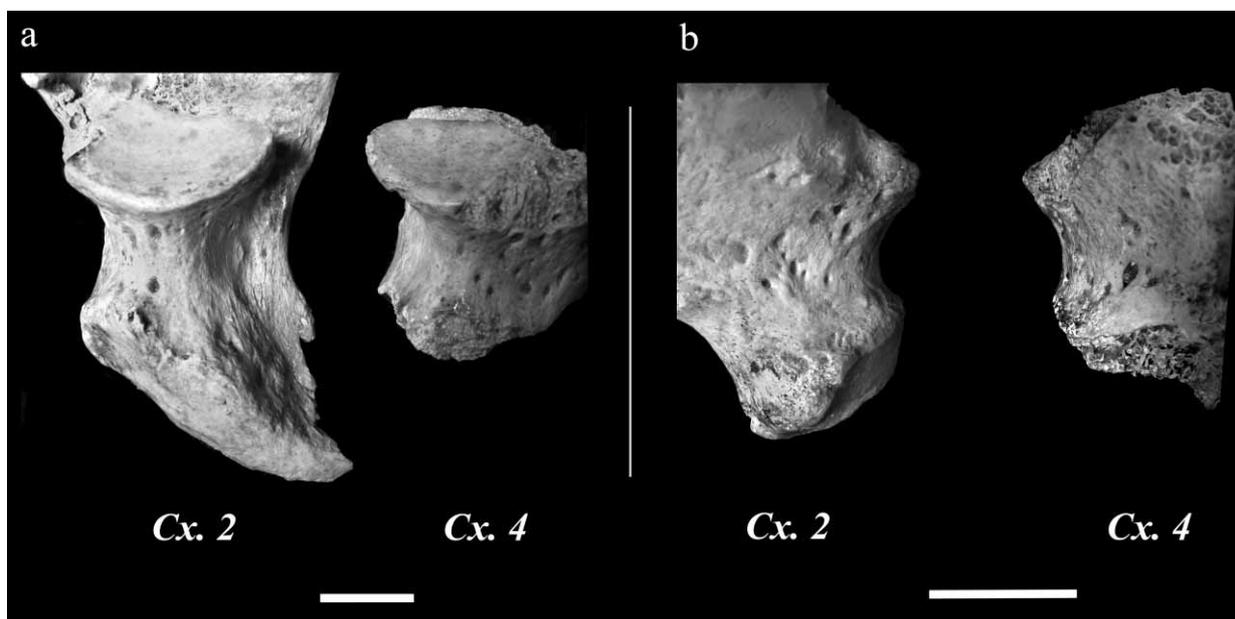


Figure 15. *Krapina Cx.2 (208) and Cx.4 (210). Lateral (a) and dorsal (b) views showing morphological similarity in those regions preserved in both specimens. Scale bar = 2 cm.*

Cx.3+Cx.6, 255.8, 255.10 and 255.11). We have approached the sexual assessment from the morphological traits as well as from osteometric data. A summary of the sex attribution of the Krapina specimens is shown in Table 2.

Morphological features for sex determination

Krapina Cx.1. 207. The morphology of the greater sciatic notch (Figure 1d₄), closely resembles closely to the stage 5 proposed by Walker (53 – Figure 1) a category which encompasses, 90% of males. In addition, when the hip bone is oriented with the internal side facing the observer, the anterior margin of the sciatic notch and the anterior margin of the sacroiliac joint describe a single

imaginary arc [i.e. absence of the composite arc, according to Genoves (35)], and therefore, there is no space between these two margins. This trait is more commonly found in males individuals (1 – Figure 1). Hence, morphological data suggests a male sex for this individual (*in agreement with 13*)

Krapina Cx.2. 208. Neither the sacroiliac nor the pubic diagnostic regions are preserved in this individual. Nevertheless, dimensions related with body size (acetabular diameter) and robusticity (pubic width and depth, size of the ischial tuberosity) (Table 7) are at the top of the range of variation within the Krapina sample. Thus, we propose a probable male sex for this individual.

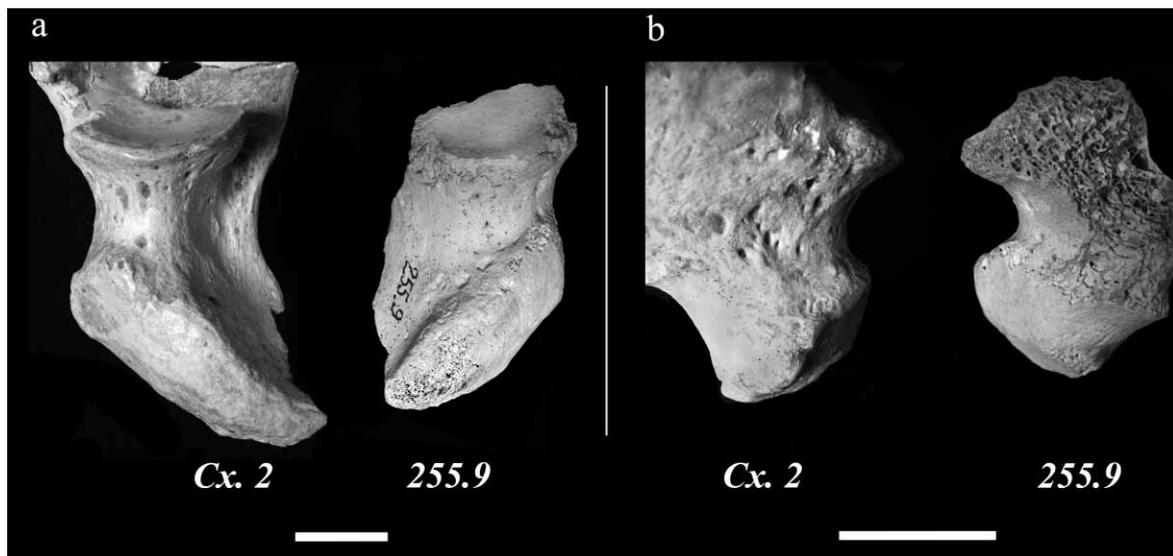


Figure 16. Krapina Cx.2 (208) and 255.9. Lateral (a) and dorsal (b) views showing the asymmetrical anatomy of the ischial body in these two specimens. Scale bar = 2 cm.

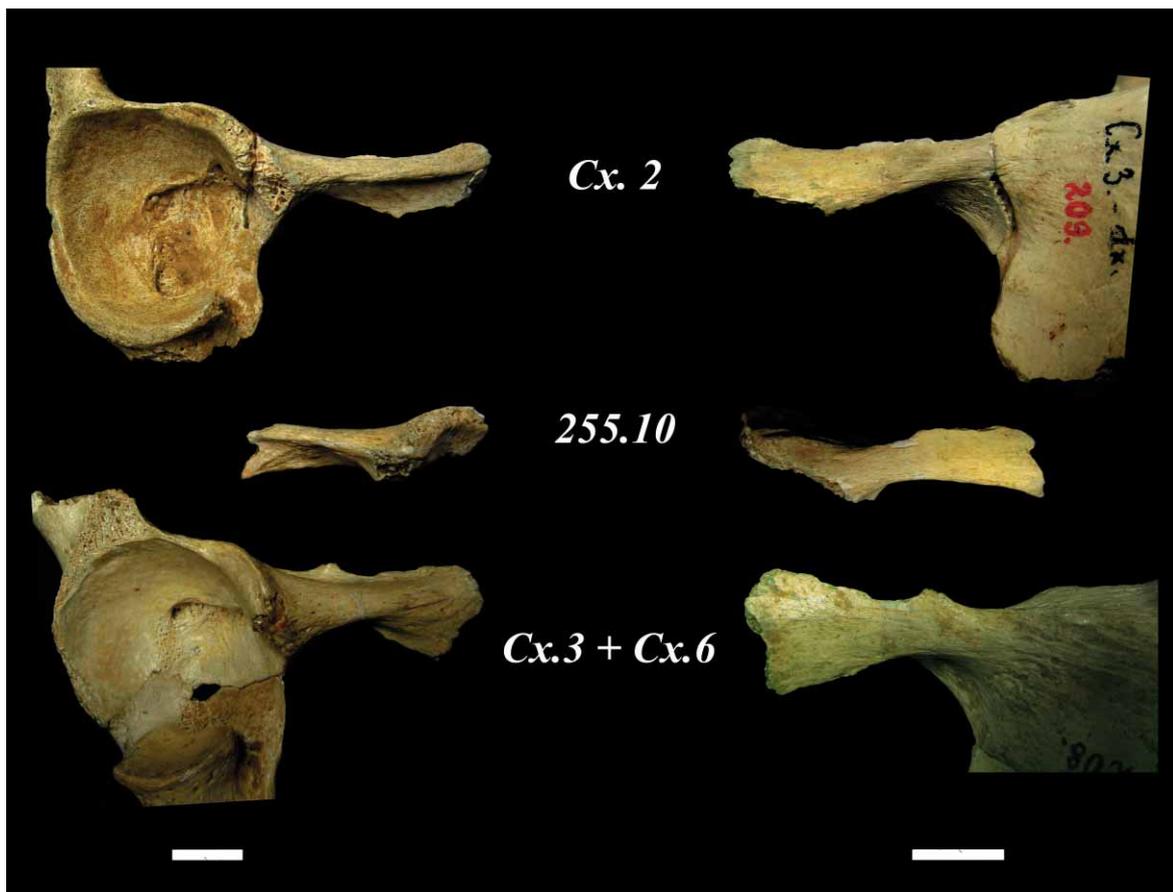


Figure 17. Krapina Cx.2 (208), Cx.3+Cx.6 (209+212) and 255.10. Lateral (a) and medial (b) views. According to the morphology and robusticity, 255.10 resembles the anatomy of Cx.3+Cx.6 more than it does Cx.2. Scale bars = 2 cm.

Krapina Cx.3+Cx.6, 209+212. Based on the definition proposed by Genoves (35), the composite arc is present when the outline of the anterior margin of the

sacroiliac joint and that of the anterior margin of the sciatic notch are not part of the same arc. This is the condition of Cx.3+Cx.6. In modern humans, this mor-

TABLE 4
Discriminant analysis summary.

| Variables | Males | | Females | | N | | Wilks' Partial | | F - remove (1,404) | | p-level | | Tolerance | | Classification functions | |
|---|----------------------------------|--|--------------------------------|--|-----|--|----------------|---------|--------------------|---------|---------|-------|-------------------|---------------------|--------------------------|----------|
| | Mean (± s.d.) (range) (n) | | Mean (± s.d.) (range) (n) | | | | Lambda | Lambda | | | | | Males (p=0.54187) | Females (p=0.45813) | | |
| "Minimum width of the ilium" / "Supraacetabular-Ilioauricular diameter" Index | 89.47 (±5.80) (104.5-70.9) (220) | | 78.8 (±5.94) (96.9-64.8) (186) | | 406 | | 1,00000 | 0,54843 | 332,65450 | 0,00000 | 1,00000 | 2,594 | 2,2844 | | | |
| Constant | | | | | | | | | | | | | | | | -90,7924 |

See Table 7 for variable definitions.

TABLE 5

Discriminate analysis classification matrix in the modern human sample.

| | M (p=0.54187) | F (p=0.45813) | % correct classification |
|---------|---------------|---------------|--------------------------|
| Males | 184 | 36 | 83,64 |
| Females | 36 | 150 | 80,65 |
| Total | 220 | 186 | 82,27 |

Rows indicate observed classifications, columns predicted classifications

phology is usually seen in female individuals. In addition, the preserved portion of the pubis in Cx.3+Cx.6 is very long and slender (Figure 17). These traits have been widely noted as classic Neandertal features (19, 21, 71). Modern humans are characterized by sturdier and shorter pubic bones; nevertheless, there is significant sexual dimorphism in the pubic length between extant males and females (35, 37 – among others). Although none of the Krapina remains preserve a complete superior pubic ramus, Krapina Cx.2 and Krapina Cx.3+Cx.6 are preserved approximately to the same point along the superior margin of the obturator foramen; the Cx.3+Cx.6 specimen seems to be longer than Cx.2 (Table 7). Further, the Cx.3+Cx.6 pubis is relatively (compared with the vertical acetabular diameter) longer than Cx.2 (Table 7). Regarding the pubic thickness, all the Krapina specimens have a notably flattened pubis compared with modern humans (21), although Krapina Cx.3+Cx.6 and Krapina 255.10 exhibit higher values for the flattening index (see above) than Cx.2. However, this index has not been proven to be a reliable indicator of sexual dimorphism in modern humans (16, 37). Thus, all the evidence seems to suggest female affinities for Cx.3+Cx.6 and we consider this individual to be most probably a female (in agreement with 13).

Cx.5. 211. We consider this element to belong to a male individual based on its anatomical similarity, and consequently its association (see above), with Krapina Cx.1.

255.8. The anterior margin of the auricular surface forms a single arc with the contour of the sciatic notch (i.e. absence of the composite arc). Further, the acute and prominent arcuate line and the large size of the preserved areas are indicative of robusticity. Consequently, we tentatively consider this individual as male.

255.10. We consider this element to belong to a female individual based on its anatomical similarity, and consequently its association (see above), with Krapina Cx.3+Cx.6 (Figure 17).

Quantitative approach to sex determination

As commented above, multiple methods based on indices and discriminant analysis have emerged and have

TABLE 6

Discriminant analysis posterior probabilities in the fossil human sample.

| Specimen | M (p=0.54187) | F (p=0.45813) | Most Probable Sex Determination |
|-------------------------|---------------|---------------|---------------------------------|
| AL 288-1 ("Lucy") | 0,007598 | 0,992402 | F |
| Sts 14 | 0,029990 | 0,970010 | F |
| SK 3155b | 0,012667 | 0,987333 | F |
| KNM ER 3228 | 0,499510 | 0,500490 | ? |
| AR 44 | 0,036187 | 0,963813 | F |
| OH 28 | 0,150541 | 0,849459 | F |
| Broken Hill E 719 | 0,716370 | 0,283630 | M |
| Krapina 207 Cx. 1 | 0,041441 | 0,958559 | F |
| Krapina 209+212 Cx. 3/6 | 0,014804 | 0,985196 | F |
| Krapina 255.3 | 0,877959 | 0,122041 | M |
| Neandertal 1 | 0,111759 | 0,888241 | F |
| Amud 1 | 0,060729 | 0,939271 | F |
| Kebara 2 (R) | 0,077733 | 0,922267 | F |
| Qafzeh 9 (L) | 0,974072 | 0,025928 | M |
| Skhul 4 | 0,988360 | 0,011640 | M |
| AT Pelvis 1 (L) | 0,489938 | 0,510062 | ? |
| AT Pelvis 1 (R) | 0,531139 | 0,468861 | ? |
| AT 800 | 0,259834 | 0,740166 | F |
| AT 1004 | 0,028178 | 0,971822 | F |
| AT 500+AT 501+AT 708 | 0,431229 | 0,568771 | ? |
| AT 3454+AT 3819+AT 3856 | 0,277668 | 0,722332 | F |
| AT 3809+AT 3807+AT 3808 | 0,301613 | 0,698387 | F |

See Table 7 for variable definitions.

been tested on extant humans. Although these quantitative approaches could theoretically be used on fossil populations, the state of preservation of the Krapina sample limits the collection of standard osteological measurements. Therefore, we have decided to use an index which we believe reflects sexual dimorphism in extant humans, and can be established in some specimens of the Krapina sample ($n=3$). We have calculated this index according with the following formula: (Minimum width of the ilium (35) / Supraacetabular – Ilioauricular chord (35) * 100) (Tables 7–9). This index is a measure of the relative distance between the anterior margin of the sciatic notch and the anterior margin of the sacropelvic region and is highly correlated with the size of the posterior space of the pelvic inlet which is significantly larger in modern females than in males. Thus, females tend to show lower values for this index than males (Table 4).

First, we performed a standard discriminant function analysis to assess the accuracy of this index in sex determination in our modern human sample (Table 4). The

value of the Partial Lambda (0.548425) indicates an intermediate discriminatory power for this index. The correct sex assignment for males is 83.64% (a priori classification probability (p) = 0.54187), whereas the accuracy for females is 80.65% (p = 0.45813) (Table 4). Next, we have investigated the probability that a modern human with the corresponding index value to that of the Krapina specimens ($n=3$) would be a male or female. We have also performed this analysis on the specimens of the fossil sample that preserve the corresponding anatomical landmarks ($n=19$). The probabilities for each of the specimens of the fossil sample, including Krapina, are presented in Table 6. Regarding the Krapina sample, two individuals (Krapina Cx.1 and Cx.3+Cx.6) show a higher probability of being assigned to the female sex, whereas the third one exhibits a higher probability of being a male individual (Krapina 255.3). As determined above, Krapina Cx.1 was morphologically attributed to a male individual, whereas for Krapina Cx.3+Cx.6 both visual determination and the metric data are in agreement.

TABLE 7
Linear measurements (mm) of the Krapina innominate bones.

| | Cx.1 | Cx.2 | Cx.3+Cx.6 | Cx.4 | Cx.5 | 255.1 | 255.3 | 255.4 | 255.7 | 255.8 | 255.9 | 255.10 |
|--|---------|-------|-----------|--------|------|-------|--------|--------|--------|--------|-------|--------|
| 1. Maximum height (35) | (178.4) | - | - | - | - | - | - | - | - | - | - | - |
| 2. Iliac height (35) | (111.3) | - | - | - | - | - | - | - | - | - | - | - |
| 3. Maximum iliac width (35) | +126.2 | - | - | - | - | - | - | - | - | - | - | - |
| 4. Projection of the ASIS (35) | 73.1 | - | - | - | - | - | - | - | - | - | - | - |
| 5. Supraacetabular-Ilioauricular diameter (35) | 73.8 | - | 79.4 | - | - | 41.9 | - | - | - | - | - | - |
| 6. Minimum width of the ilium (35) | 54.2 | 54.6 | (55.6) | - | - | 54.6 | 37.7 | (44.6) | - | 61.7 | - | - |
| 7. Supraacetabular point – PIIS diameter* | - | 114.2 | - | - | - | - | - | - | - | - | - | - |
| 8. Supraacetabular point – ASIS diameter (35) | 47.1 | - | - | - | - | - | - | - | - | - | - | - |
| 9. AIIS-Ilioauricular point diameter (35) | +75.1 | - | 80.7 | - | - | - | 44.5 | - | - | - | - | - |
| 10. AIIS-Greater sciatic notch diameter (81) | +60.6 | - | (63.8) | - | - | 60.1 | 45.3 | 47.8 | - | 69.4 | - | - |
| 11. AIIS – PIIS diameter (35) | - | - | 122.6 | - | - | - | - | - | - | - | - | - |
| 12. Iloauricular point – ASIS diameter(35) | 99.7 | - | - | - | - | - | - | - | - | - | - | - |
| 13. Ilioauricular point– Interspinal notch diameter (35) | (80.0) | - | - | - | - | - | (45.2) | - | - | - | - | - |
| 14. Ilioauricular point– Greater sciatic notch diameter* | 28.5 | - | 36.9 | - | - | - | 21.9 | - | - | - | - | - |
| 15. Height of the acetabulocrestal buttress (69) | 90.9 | - | - | - | - | - | - | - | - | - | - | - |
| 16. Thickness of the acetabulocrestal buttress (82) | 12.4 | - | - | - | - | - | - | - | - | - | - | - |
| 17. ASIS – Acetabulocrestal buttress diameter (35) | 54.7 | - | - | - | - | - | - | - | - | - | - | - |
| 18. Minimum width of the iliac fossa (35) | 95.3 | - | - | - | - | - | - | - | - | - | - | - |
| 19. Height of the sciatic notch (57) | 29.2 | - | (36.2) | - | - | - | +17.7 | - | - | - | - | - |
| 20. Length of the auricular surface (35) | +29.5 | - | 50.0 | - | - | - | - | - | - | - | - | - |
| 21. Height of the auricular surface (37) | +37.1 | - | 25.3 | - | 30.6 | - | - | - | - | - | - | - |
| 22. Cotilosciatic width (57) | 31.6 | +27.7 | 28.8 | - | - | - | - | - | (27.9) | (31.5) | - | - |
| 23. Puboacetabular width (81) | (21.9) | 29.3 | 26.3 | - | - | - | - | - | - | - | - | - |
| 24. Width of the tuberoacetabular sulcus (68) | 11.8 | 17.1 | - | (17.7) | - | - | - | - | - | - | 14.2 | - |
| 25. Ischial length (35) | 74.6 | 94.4 | - | - | - | - | - | - | - | - | - | - |

TABLE 8

Summary statistics of the metrical variables (mm) for modern humans.

| Variable | Coimbra Modern Human Sample | | |
|---|-----------------------------------|-----------------------------------|------------------------------------|
| | Males | Females | Pooled Sample |
| 1. Maximum height (35) | 211.9(±9.3) (238.0-189.0)(208) | 196.3(±9.4) (219.0-166.0)(182) | 204.5(±12.3) (239.0-166.0)(390) |
| 2. Iliac height (35) | 124.1(±6.2) (143.6-104.0)(208) | 118.7(±6.7) (141.0-97.8)(176) | 121.6(±7.0) (143.6-97.8)(384) |
| 3. Maximum iliac width (35) | 155.6(±7.9) (185.0-136.5)(192) | 152.9(±7.9) (174.0-130.0)(165) | 154.4(±8.00) (185.0-130.0)(357) |
| 4. Projection of the ASIS (35) | 83.9(±5.1) (97.4-72.0)(192) | 82.6(±5.9) (100.3-64.9)(165) | 83.3(±5.6) (100.3-64.9)(357) |
| 5. Supraacetabular-Ilioauricular diameter (35) | 68.1(±5.0) (82.9-57.4)(220) | 69.7(±6.0) (87.0-55.2)(186) | 68.9(±5.5) (87.0-55.2)(406) |
| 6. Minimum width of the ilium (35) | 60.8(±3.8) (69.7-51.6)(221) | 54.8(±3.4) (65.0-46.7)(187) | 58.0(±4.7) (69.7-46.7)(408) |
| 7. AIIS-Ilioauricular point diameter (35) | 71.8(±5.2) (85.0-60.2)(213) | 72.3(±5.9) (87.0-58.3)(185) | 72.0(±5.5) (87.0-58.3)(398) |
| 8. AIIS-Greater sciatic notch diameter (81) | 70.3(±4.5) (86.8-55.0)(214) | 63.8(±4.1) (74.0-52.7)(185) | 67.3(±5.4) (86.8-52.7)(399) |
| 9. Height of the sciatic notch (57) | 37.1(±4.8) (51.6-24.0)(212) | 41.2(±5.4) (55.9-29.0)(151) | 38.8(±5.4) (55.9-24.0)(363) |
| 10. Length of the auricular surface (35) | 51.7(±4.5) (66.0-40.8)(211) | 48.0(±4.7) (59.5-35.6)(178) | 50.0(±4.9) (66.0-35.6)(389) |
| 11. Cotilosciatic width (57) | 36.9(±3.1) (45.5-30.0)(218) | 33.4(±2.8) (41.0-26.9)(189) | 35.3(±3.5) (45.5-26.9)(407) |
| 12. Puboacetabular width (81) | 26.7(±2.7) (38.3-17.7)(206) | 21.3(±2.9) (31.3-15.0)(182) | 24.2(±3.8) (38.3-15.0)(388) |
| 13. Ischial length (35) | 94.5(±4.8) (112.0-79.6)(200) | 84.9(±4.2) (94.0-72.0)(155) | 90.2(±6.7) (112.0-72.0)(355) |
| 14. Non-articular ischial length (37) | 48.7(±3.1) (56.1-40.0)(213) | 43.1(±2.9) (54.6-34.2)(185) | 46.1(±4.1) (56.1-34.2)(398) |
| 15. Pubic length (35) | 86.5(±5.6) (99.6-68.1)(187) | 87.9(±5.8) (102.5-71.0)(167) | 87.1(±5.7) (102.5-68.1)(354) |
| 16. Non-articular pubic length (35) | 66.9(±4.2) (79.0-54.6)(188) | 69.5(±4.4) (81.0-56.9)(166) | 68.1(±4.5) (81.0-54.6)(354) |
| 17. Depth of the superior pubis ramus (69) | 15.3(±2.4) (22.9-9.3)(212) | 13.8(±2.1) (18.4-8.8)(184) | 14.6(±2.4) (22.0-8.8)(396) |
| 18. Maximum horizontal acetabular diameter (35) | 54.3(±3.0) (64.2-46.0)(207) | 49.1(±2.8) (59.2-41.8)(183) | 51.9(±3.91) (64.2-41.8)(390) |
| 19. Maximum vertical acetabular diameter (35) | 55.2(±2.8) (62.0-48.2)(213) | 49.9(±2.7) (60.5-41.7)(186) | 52.7(±3.8) (62.0-41.7)(399) |
| 20. Maximum depth of the acetabulum (35) | 25.1(±2.5) (34.5-18.5)(187) | 22.8(±2.2) (29.0-16.6)(173) | 24.01(±2.7) (34.5-16.6)(360) |

Source of the variable definitions in parentheses.

projection of ASIS» compared with other Neandertal specimens (Neandertal 1, Amud 1 and Kebara 2), and in a lesser degree, with the modern human sample. This could be partly due to the incomplete fusion of the iliac crest epiphysis which is important in determining the value of these variables. When Neandertals are compared with the pooled-sex modern human sample, only one individual (Amud 1) out of four (Neandertal 1, Kebara 2, Krapina Cx.3+Cx.6) shows a significantly different value in the »AIIS-Ilioauricular distance«. In addition, the Z-score for the »projection of the ASIS« in Amud 1(2, 76) indicates this individual differs significantly from living humans. The »supraacetabular-ilioauricular chord« is significantly greater than modern humans in Neandertal 1 and Amud 1, whereas it is within the modern human range of variation in Kebara 2, Tabun C1, Krapina Cx.1 and Krapina Cx.3+Cx.6.

§Ischium

From the Z-score analysis, Krapina Cx.2 shows a significantly higher value for the »non-articular ischial length« relative to modern humans and is also very long compared to other Neandertals (La Ferrassie 1, Neandertal 1 and Kebara 2). Furthermore, La Ferrassie 1 shows values for the »non-articular ischial length« which are more than 2 Z-scores below the modern human mean, whereas the two other individuals (Neandertal 1 and Kebara 2) show values that fall within the modern human variation.

The value for the »cotilosciatic width« in the Le Prince 1 specimen is 2.67 Z-scores below the modern human mean value, while all eight individuals in both the Krapina and Neandertal samples are within the modern human range.

§Pubis

All the Neandertal specimens in which the non-articular pubic length could be measured (La Ferrassie 1, Kebara 2, Shanidar 1, Shanidar 3, Tabun C1) show significantly greater values than the modern human sample. Regarding the »depth of the superior pubic ramus«, Shanidar 1, Tabun C1, Krapina Cx.2 and Krapina Cx.3+Cx.6 show significantly lower values than modern humans, whereas Amud 1 and Kebara 2 are within but close to the lower limits of the modern range of variation.

§Acetabulum

The value of the »vertical acetabular diameter« of the Krapina specimens (Krapina Cx.1, Cx.2 and Cx.3+Cx.6) is within the modern human range of variation but is small compared with some other Neandertals. Specifically, La Chapelle-aux-Saints 1, La Ferrassie 1 and Neandertal 1 are significantly larger than the modern human sample. Krapina Cx.3+Cx.6 also shows a small value in the »maximum depth of the acetabulum« within the Krapina and Neandertal samples but it is not significantly smaller than in modern humans. On the other hand, Neandertal 1, Kebara 2 and Krapina Cx.1 show significantly higher values for the »depth of the acetabulum« compared with living humans.

Morphological analysis within the fossil record

Apart from the metric analysis, some morphological differences, which are difficult to quantify metrically, emerge when the Krapina specimens are compared with both the modern and fossil human samples. These differences are found in 6 anatomical regions: the anterior margin of the ilium, the supraacetabular sulcus, the ilio-sciatic buttress, the sacropelvic region, the posterior wall of acetabulum and the lesser sciatic notch, and the superior pubis ramus (Table 11).

§Anterior Margin of the Ilium

Since Krapina 255.6 is an isolated fragment of the anterior iliac border, it is not possible to orient it properly relative to any other element of the hip bone. Therefore, Krapina Cx.1 and 255.8 are the only elements in which the morphology and orientation of the entire ventral margin of the ilium can be described (Figure 1). In the genus *Homo* (including Krapina specimens), when the anterior border of the ilium is oriented in medial view, with the ventral border of the sciatic notch in vertical position and the gluteal surface against the observer, a pronounced dorsally concave notch (interspinal groove) can be seen between the anterior inferior iliac spine (AIIS) and the anterior superior iliac spine (ASIS) (Figure 1b, 18b,c). The depth and width of the interspinal groove is a very variable trait within both the fossil specimens and extant humans. In contrast, specimens assigned to *Australopithecus* and *Paranthropus* (AL 288-1, Stw 431, SK 50, SK 3155, TM 1605) tend to have a wider and more asymmetrical interspinal groove (Figure 18a).

Regarding the anterior inferior iliac spine (AIIS) morphology, three specimens from Krapina (Cx.1, Cx.3+Cx.6 and 255.8) show a deeply excavated pelvic surface of the AIIS (sulcus iliacus) for the passage of the fibres of the iliopsoas muscle and its sinovial bursae (Figure 1c). When the spine is observed in ventral view, it seems to be »twisted« caudally and flattened mediolaterally, showing an apparently gracile morphology (Figure 1b). From this same perspective, the AIIS forms an obtuse angle with the ventral margin of the iliac blade (Figure 1c). This morphology is commonly found in the fossils from the Middle Pleistocene of Europe (Arago, Sima de los Huecos) and in their Neandertal descendents (Neandertal 1, Kebara 2, Amud 1, La Chapelle-aux-Saints 1). On the other hand, some specimens of *Australopithecus* (AL 288-1, Sts 14) and *Paranthropus* (SK 3155) show a flat pelvic surface of the AIIS (Figure 19a), while others (SK 50, Stw 431) show a concave morphology of this area. In addition, the *Australopithecus* AIIS is straight and aligned with the anterior margin of the iliac blade (Figure 19a), whereas in *Paranthropus* the AIIS forms an obtuse angle with the iliac blade. In *Homo ergaster* (KNM ER 3228, OH 28, Figure 19b) and fossil (Qafzeh 9, Skhul 4) and recent modern humans (Figure 19c), the pelvic surface of the AIIS also shows a concave shape, although it is not excavated, and therefore, the AIIS is not twisted caudally.

TABLE 9
Linear measurements (mm) for the Neandertal Sample.

| | Villafamés 2 | Le Prince 1 | La Chapelle (L) | La Ferrassie 1 | Neandertal 1 | Amud 1 | Kebara 2 (R) | Shanidar 1 | Shanidar 3 (R) | Tabun C1 |
|---|-----------------|----------------|--------------------|-------------------|-----------------|---------|-----------------|------------|-------------------|----------|
| 1. Maximum height (35) | - | - | - | - | (220.9) | - | 221,5 | - | - | (188) |
| 2. Iliac height (35) | - | - | - | - | (133.6) | (128.7) | 134,5 | - | - | - |
| 3. Maximum iliac width (35) | - | - | - | - | (163) | - | - | - | - | (143) |
| 4. Projection of the ASIS (35) | - | - | - | - | (90.6) | (98.6) | 89,7 | - | - | - |
| 5. Supraacetabular-Ilioauricular diameter (35) | - | - | - | - | 83,1 | 87,5 | 75 | - | - | (67) |
| 6. Minimum width of the ilium (35) | - | - | - | - | 63,9 | 65,4 | 56,7 | - | - | - |
| 7. AIIS-Ilioauricular point diameter (35) | - | - | - | - | 81,7 | 87,4 | 71,1 | - | - | - |
| 8. AIIS-Greater sciatic notch diameter (81) | - | 68.0 | 70 | - | -68.6 | 73,5 | 63,3 | - | - | - |
| 9. Height of the sciatic notch (57) | - | 36.0 | - | - | 36 | -30.3 | 28,8 | - | - | - |
| 10. Length of the auricular surface (35) | - | - | - | - | 47,1 | - | 50,3 | - | - | - |
| 11. Cotilosciatic width (57) | (34.0) | (26.0) | - | - | 40,3 | 37,8 | 30,2 | 33 | - | 30 |
| 12. Puboacetabular width (81) | - | (28.0) | - | - | - | (24.3) | 31 | - | - | - |
| 13. Ischial length (35) | - | - | - | - | 90,1 | - | 87,4 | - | - | - |
| 14. Non-articular ischial length (37) | - | - | - | 37 | 45,5 | - | 43,3 | - | - | - |
| 15. Pubic length (35) | - | - | - | - | - | - | (98.8) | - | - | - |
| 16. Non-articular pubic length (35) | - | - | - | 100 | - | - | (87.3) | (93) | (85) | (80.5) |
| 17. Depth of the superior pubis ramus (69) | - | - | - | - | - | 10 | 10,9 | 7 | - | (6.75) |
| 18. Maximum horizontal acetabular diameter (35) | - | - | - | - | - | - | 51,1 | - | - | - |
| 19. Maximum vertical acetabular diameter (35) | - | (59.0) | 65 | 60,5 | 61,9 | 57,1 | 59 | - | - | - |
| 20. Maximum depth of the acetabulum (35) | 29.0 | - | - | - | 32,5 | 28.2 | 30 | - | - | - |

Source of the variable definitions in parentheses.

TABLE 10
Z-scores values for the Krapina and Neandertal samples compared with the modern human pooled-sex sample.

| | Krap. Cx.1 | Krap. Cx.2 | Krap. Cx.3 | Krap. 255.1 | Krap. 255.7 | Krap. 255.8 | Krap. 255.10 | Villaf amés 2 | Le Prince 1 | La Chap elle (L) | La Ferras sie 1 | Neandertal 1 | Amud 1 | Kebar a.2 (R) | Shani dar 1 | Shani dar 3 (R) | Tabun C1 | |
|---|-------------|--------------|--------------|-------------|-------------|-------------|--------------|---------------|--------------|------------------|-----------------|--------------|-------------|---------------|--------------|-----------------|-------------|--------------|
| 1. Maximum height (35) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 2. Iliac height (35) | -1,49 | - | - | - | - | - | - | - | - | - | - | 1,34 | - | 1,39 | - | - | - | -1,35 |
| 3. Maximum iliac width (35) | - | - | - | - | - | - | - | - | - | - | - | 1,08 | - | 1,85 | - | - | - | -1,42 |
| 4. Projection of the ASIS (35) | -1,84 | - | - | - | - | - | - | - | - | - | - | 1,31 | 2,76 | 1,15 | - | - | - | - |
| 5. Supraacetabular-Ilioauricular diameter (35) | 0,89 | - | 1,90 | - | - | - | - | - | - | - | - | 2,57 | 3,36 | 1,11 | - | - | - | -0,34 |
| 6. Minimum width of the ilium (35) | -0,81 | -0,72 | -0,51 | -0,72 | - | 0,78 | - | - | - | - | - | 1,24 | 1,56 | -0,28 | - | - | - | - |
| 7. AHS-Ilioauricular point diameter (35) | - | - | 1,56 | - | - | - | - | - | - | - | - | 1,74 | 2,77 | -0,17 | - | - | - | - |
| 8. AHS-Greater sciatic notch diameter (74) | - | - | -0,65 | -1,33 | - | 0,39 | - | - | 0,13 | 0,51 | - | - | 1,16 | -0,74 | - | - | - | - |
| 9. Height of the sciatic notch (57) | -1,77 | - | -0,48 | - | - | - | - | - | -0,52 | - | - | -0,52 | - | -1,84 | - | - | - | - |
| 10. Length of the auricular surface (35) | - | - | 0,00 | - | - | - | - | - | - | - | - | -0,59 | - | 0,06 | - | - | - | - |
| 11. Cotilosciatic width (57) | -1,06 | - | -1,86 | - | - | - | - | -0,36 | -2,67 | - | - | 1,46 | 0,73 | -1,46 | -0,65 | - | - | -1,52 |
| 12. Puboacetabular width (74) | - | 1,34 | 0,56 | - | - | - | - | - | 1,00 | - | - | - | 0,04 | 1,78 | - | - | - | - |
| 13. Ischial length (35) | - | 0,63 | - | - | - | - | - | - | - | - | - | -0,02 | - | -0,43 | - | - | - | - |
| 14. Non-articular Ischial length (30) | - | 2,07 | - | - | - | - | - | - | - | - | -2,24 | -0,15 | - | -0,69 | - | - | - | - |
| 15. Pubic length (35) | - | - | - | - | - | - | - | - | - | - | - | - | - | 2,04 | - | - | - | - |
| 16. Non-articular pubic length (35) | - | - | - | - | - | - | - | - | - | - | 7,13 | - | - | 4,29 | 5,57 | 3,78 | 2,77 | - |
| 17. Depth of the superior pubis ramus (62) | - | -2,39 | -2,69 | - | - | - | -2,69 | - | - | - | - | - | -1,93 | -1,55 | -3,19 | - | - | -3,29 |
| 18. Maximum horizontal acetabular diameter (35) | - | 1,26 | -0,30 | - | - | - | - | - | - | - | - | - | - | -0,19 | - | - | - | - |
| 19. Maximum vertical acetabular diameter (35) | 0,41 | 0,73 | 0,57 | - | - | - | - | - | 1,65 | 3,22 | 2,04 | 2,41 | 1,15 | 1,65 | - | - | - | - |
| 20. Maximum depth of the acetabulum (35) | 2,11 | 1,81 | -0,42 | - | - | - | - | - | - | - | - | 3,20 | 1,58 | 2,26 | - | - | - | - |

A value greater than or equal to ± 2 (bold) is taken to indicate a significant difference from the modern human mean value. Source of the variable definitions in parentheses.

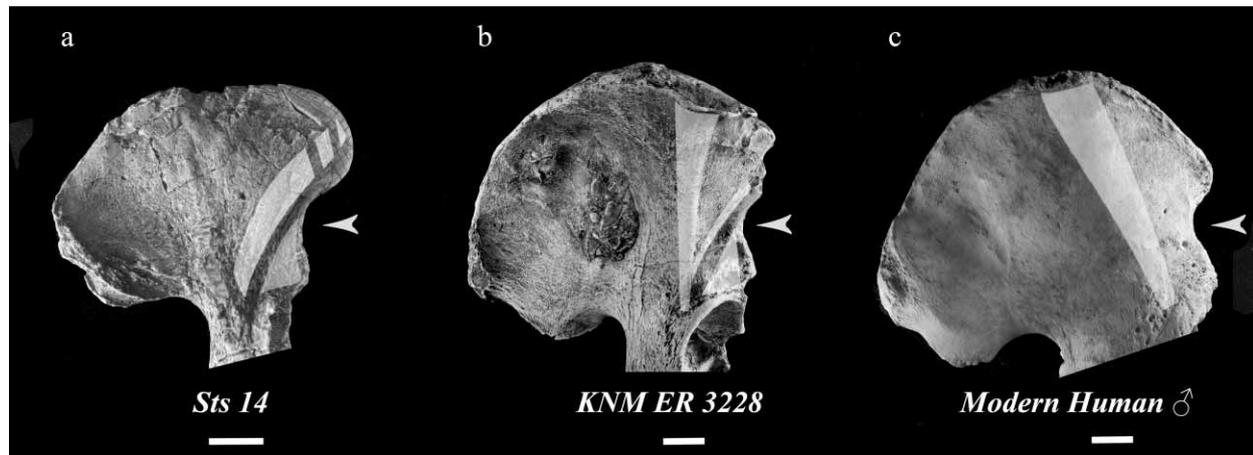


Figure 18. Lateral view of *A. africanus* (a, cast), *H. ergaster* (b, cast) and a modern human male (c, original), showing differences and similarities in the anterior portion of the iliac blade. The rectangular shaded regions represent the acetabulospinal (anterior) and acetabulocrystal (posterior) buttresses and the triangular shaped regions, the supra-acetabular sulcus. Arrows point to the interspinous notch. Scale bar = 2 cm.

However, the AIIS of *H. erectus* and *H. sapiens* forms an obtuse angle with the iliac blade (Figure 19c,d).

The vertical iliac buttress is split in two at the level of the AIIS in Krapina Cx.1 (Figure 1d), with one branch running anteriorly to the ASIS (acetabulospinal buttress) and the other superiorly to the iliac tubercle (acetabulocrystal buttress), with a smooth depression between both buttresses. Although clearly noticeable, these structures are topographically continuous with the adjacent margins of the external surface of the iliac blade. The hip bones attributed to *Australopithecus* show a single ventral iliac buttress (acetabulospinal buttress) close to the anterior margin (Figure 18). Regarding the genus *Homo*, two buttresses are found in specimens attributed to *Homo ergaster* (KNM ER 3228, OH 28, Figure 18b), *Homo heidelbergensis* [Arago 44, Sima de los Huesos sample (77)] and *Homo neanderthalensis* (Neandertal 1, Kebara 2, Amud 1, La Ferrassie 1, La Chapelle-aux-Saints 1) resembling those observed in the Krapina specimens. Among fossil modern humans, Qafzeh 9 is distorted but it is possible to distinguish a ventral buttress (acetabulospinal buttress) close to the anterior border, whereas Skhul 4 shows the acetabulocrystal buttress. Modern *Homo sapiens* commonly show a single acetabulocrystal buttress (Figure 18c), however, some individuals do possess an acetabulospinal buttress together with a depressed area between them.

§Supraacetabular sulcus

In fossils and extant modern humans, the region of the ilium just above the cranial portion of the acetabulum, where the reflected head of the rectus femoris muscle is attached, shows a diverse morphology from convex or flat shape (i.e. absent of supraacetabular sulcus) to slightly or more rarely well-depressed areas (Figure 18c). *Australopithecus* also shows a large degree of variation (AL 228-1 and Stw 431, slightly depressed; Sts 14, well depressed, Figure 18a), whereas *Paranthropus* (SK50, SK3155)

and early representatives of the genus *Homo* (KNM ER 3228 -Figure 18b-, KNM WT 15000) have a well-depressed triangular area that runs between the acetabulospinal buttress and the cranial portion of the acetabular margin. This configuration is also developed in the later Lower and Middle Pleistocene African specimens OH 28 and Broken Hill E719 as well as the European Neandertal lineage specimens. Krapina Cx.1, Cx.2, 255.1 and 255.8 resemble other Neandertals and archaic members of the genus *Homo* in showing a wide and deep sulcus (Figures 1b, 3, 8, 12).

Interestingly, in Krapina Cx. 1 and 255.8, the superior margin of the acetabulum protrudes greatly in lateral direction, whereas other remains (Krapina Cx.2 and 255.1) show however, in all the Krapina specimens, the supra-acetabular sulcus is clearly distinguishable, suggesting that this feature is not only the result of the protrusion of the acetabular margin, but, rather represents a clear depression on the subchondral bone of the ilium.

§Iliosciatic buttress

In Krapina Cx.1, Cx.3+Cx.6, Cx.5 and 255.8, the surface spreading from the arcuate line to the deepest portion of the greater sciatic notch (iliosciatic buttress) tends to show a narrow and pillar-shaped morphology (Figure 20a,b). Within the fossil record, the iliosciatic morphology is greatly variable, ranging from narrow and pillar-shaped morphologies (SK 3155, SK 50, Arago 44, AT-Pelvis 1, AT-800) to wider and flatter morphologies (AL 288-1), as well as intermediate shapes (Sts 14, KNM ER 3228, OH 28, AT-3807+AT-3808+AT-3809+AT-3300, AT-1004). However, when Neandertals, including the Krapina sample are compared with fossil and modern humans, the former tend to show a narrower and more robust morphology than do the latter, which commonly show a gracile, wider, flatter and in some cases slightly depressed morphology (Figure 20c).

TABLE 11
Summary of the morphological features of the innominate bone in fossil and living humans.

| | <i>Australopithecus</i> | <i>Paranthropus</i> | <i>Homo ergaster/ erectus</i> | European Middle Pleistocene <i>Homo</i> |
|---|-----------------------------------|--------------------------------------|--|---|
| 1. Interspinal groove | Wider and asymmetric groove | Wider and asymmetric groove | Variable depth and tendency to symmetry | Variable depth and tendency to symmetry |
| 2. Sulcus iliacus | Commonly flat shape | Variable | Depressed, non excavated AIIS pelvic surface | Depressed, excavated AIIS pelvic surface |
| 3. Orientation of the AIIS in ventral view | Oriented along the ventral margin | Obtuse angle with the ventral margin | Obtuse angle with the ventral margin | Obtuse angle with the ventral margin |
| 4. Morphology of the AIIS | Straight | Straight | Straight | Twisted |
| 4. Iliac Buttress | Single ventral buttress | Single ventral buttress | Double buttress (ventral and lateral) | Double buttress (ventral and lateral) |
| 5. Supraacetabular sulcus | Variable | Well-depressed | Well-depressed | Well-depressed |
| 7. Iliosciatic buttress shape | Variable | Narrow, pillar shape | Wide, robust shape | Variable |
| 8. Anterior fossa of the postauricular sulcus | Variable | Absent | Variable | Presented |
| 9. Posterior wall of the acetabulum | Flat surface | Flat surface | Flat surface | Flat surface (except Arago 44 -convex surface-) |
| 10. Obturator internus sulcus position | Cranial | - | Variable | Variable |
| 11. Pectineal surface morphology | Rounded | - | - | Flat to dorsally depressed |
| 12. Development of the obturator nerve sulcus | Poorly | - | - | Well-developed |
| 13. Section at the obturator nerve sulcus | Rounded morphology | - | - | S-I Flattering, plate-like morphology |

Table 11 (continuation)

| | Neandertals | Fossil <i>Homo sapiens</i> | Extant humans |
|---|--|--|---|
| 1. Interspinal groove | Variable depth and tendency to symmetry | Variable depth and tendency to symmetry | Variable depth and tendency to symmetry |
| 2. Sulcus iliacus | Depressed, excavated AIIS pelvic surface | Depressed, non excavated AIIS pelvic surface | Variable |
| 3. Orientation of the AIIS in ventral view | Obtuse angle with the ventral margin | Obtuse angle with the ventral margin | Obtuse angle with the ventral margin |
| 4. Morphology of the AIIS | Twisted | Straight | Straight |
| 4. Iliac Buttress | Double buttress (ventral and lateral) | Variable | Variable |
| 5. Supraacetabular sulcus | Well-depressed | Variable | Commonly flat or slightly depressed |
| 7. Iliosciatic buttress shape | Narrow, pillar shape | Wide, Flat shape | Variable, tendency to wider and flatter shape |
| 8. Anterior fossa of the postauricular sulcus | Absent or slight depression (Kebara 2) | Absent | |
| 9. Posterior wall of the acetabulum | Flat surface | Concave-convex margins, convex surface | Convex surface |
| 10. Obturator internus sulcus position | Variable | Caudal | Variable |
| 11. Pectineal surface morphology | Flat to dorsally depressed | Irregular to ventrally curved | Irregular to ventrally curved |
| 12. Development of the obturator nerve sulcus | Well-developed | Well-developed | Well-developed |
| 13. Section at the obturator nerve sulcus | Extreme S-I Flattering and plate-like morphology | Rectangular bar-like morphology | Rectangular bar-like morphology |

§Sacropelvic region

The sacropelvic region of the innominate bone shows three easily distinguishable areas, from ventral to dorsal direction, the auricular surface that directly articulates the ilium with the sacrum, the postauricular sulcus that runs parallel to the posterior margin of the auricular surface, and the iliac tuberosity, the very rough and prominent area for the attachment of the sacroiliac ligaments. In the Krapina sample, the sacropelvic region is only partially preserved in Cx.3+Cx.6 and Cx.5. Both specimens preserve the auricular surface and the postauricular sulcus. The latter shows a smooth and polished appearance of the subchondral bone, a regular width and well defined margins all along its extension. However, none of the remains in the Krapina collection preserve the iliac tuberosity.

The size, shape and appearance of each of the three sacropelvic areas in both fossil and extant humans are highly variable. However, Lower and Middle Pleistocene members of the genus *Homo* which preserve the iliac tuberosity (KNM ER 3228, OH 28, Arago 44, AT-Pelvis 1, AT-800, AT-1004) show a very protruding and wide morphology of this area, remarkably elevated from the rest of the sacropelvic region. In addition, the outline of this tuberosity resembles a rhomboid shape in medial view. These features are not seen in the rest of the fossil sample studied and are rarely found in the same degree in *Homo sapiens*.

Interestingly, Krapina Cx.3+Cx.6 and Cx.5 show a remarkable groove (anterior fossa of the postauricular sulcus) in the superior ventral portion of the sulcus, just at the border with the iliac fossa (Figure 7c). This region is only preserved in a few fossil specimens. The innominate bones from Sterkfontein (Sts 14), and particularly, from Olduvai (OH 28), Sima de los Huesos (AT-1004, AT-800 and AT-3807+AT-3808+AT-3809+AT-3300), and Arago show this fossa well developed. Relying on associations between hip bones and sacra in the Sima de los Huesos collection, this fossa articulates with the la-

tero-dorsal portion of the sacrum alae. In contrast, the remaining fossil specimens show no development of this fossa and the living human sample possesses it in very low frequencies.

§Posterior wall of the acetabulum and lesser sciatic notch

The posterior wall of the acetabulum is preserved in four specimens of the Krapina sample; Cx.1, Cx.2, Cx.3+Cx.6 and 255.7. In lateral view, perpendicular to the acetabular plane, the surface remains flat and is not adapted to the convex posterior acetabular margin. This morphology appears to be the normal condition in both *Australopithecus* and archaic members of the genus *Homo*, including Neandertals (Kebara 2), and is also seen in Skhul 4. However, Arago 44, and especially modern humans, show a slightly bulky morphology, adapted to the convex posterior acetabular margin.

All of the innominate bones that preserve relevant portions of the ischial tuberosity and the adjacent lesser sciatic notch for the passage of the obturator internus muscle (Cx.1, Cx.2 and 255.9) show a continuous margin of the ischial tuberosity. Therefore, none exhibit a concave dorsal margin of the tuberosity, as other Neandertals do (Kebara 2 and Neandertal 1). To analyze the frequency and taxonomic utility of this trait, Trinkaus (78) proposed classifying its expression into three categories according to the position of the obturator internus sulcus relative to ischial tuberosity. Based on these categories, he reported an »intermediate« configuration for Krapina Cx.1, and a »cranial« configuration for Cx.2 and 255.9. However, in our opinion, all three specimens fall within the intermediate configuration of his classification. Within the fossil record, Sts 14, AL 288-1, OH 28 and AT-1004 show a cranial configuration, AT-Pelvis 1, AT-800, AT-3807+AT-3808+AT-3809+AT-3300, Broken Hill E719 and Neandertal 1 exhibit an intermediate one, whereas KNM ER 3228, Arago 44, Kebara 2 (right ischium), Skhul 4 (left ischium) and Skhul 5 show a caudal

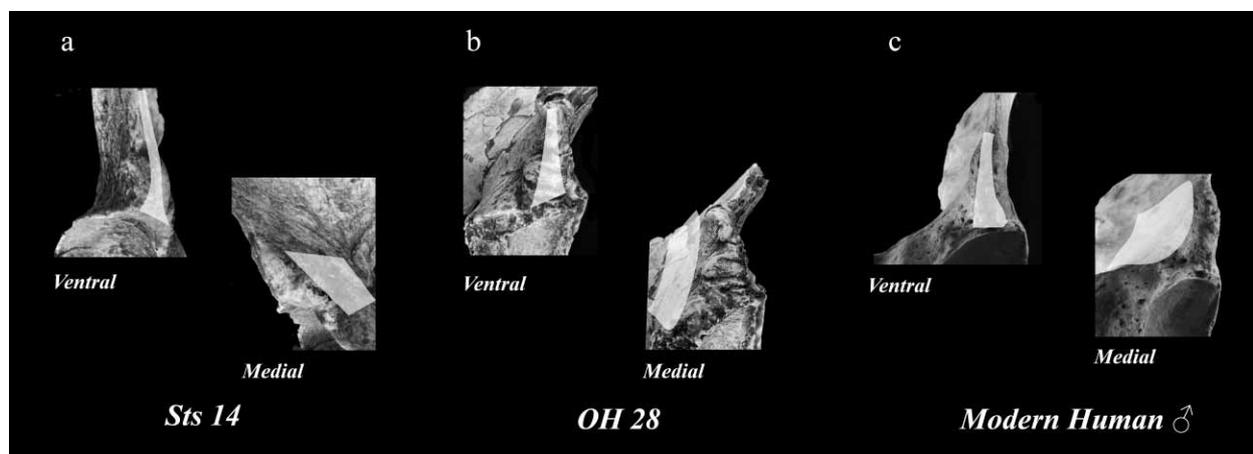


Figure 19. Ventral and medial views of the AIIS in three different specimens corresponding to *A. africanus* (a), *H. ergaster* (b) and modern humans (c). Shaded regions show distinctive morphological traits (see text). Not pictured to the same scale.

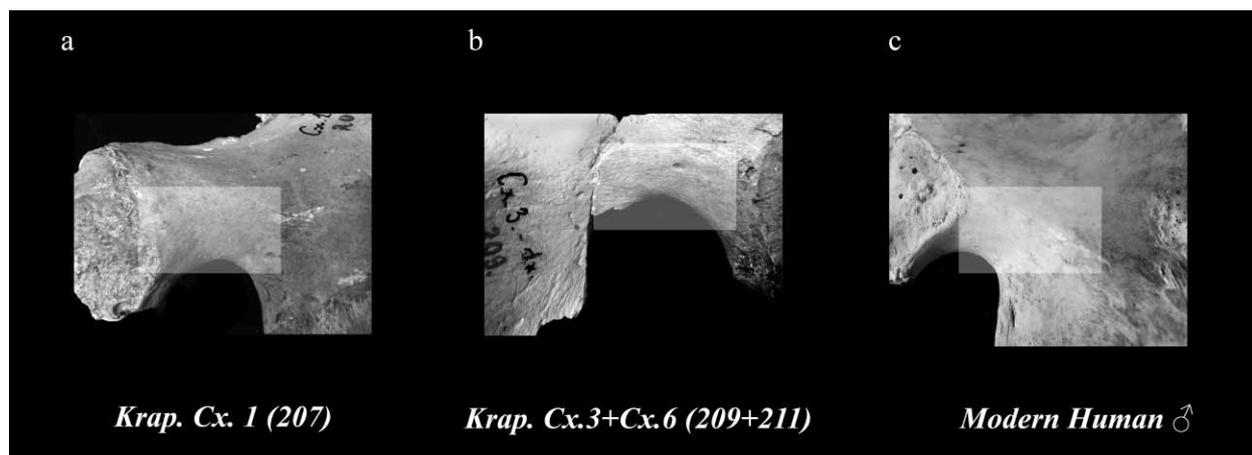


Figure 20. The iliosciatic buttress (shaded regions) in two specimens from Krapina (a, b) and a modern human male (c), showing morphological differences in extension and robusticity. Not to scale.

position of the obturator internus sulcus relative to the ischial tuberosity. The large degree of variation in the expression of this trait does not appear to closely follow taxonomic categories (78), making the significance of an intermediate configuration in the Krapina specimens difficult to interpret.

§The superior pubic ramus

As mentioned previously, the length and cranio-caudal thickness of the pubic bone is one of the most characteristic and well-known features of the Neandertal pelvis, including those of the Krapina sample, and it clearly separates them from *Homo sapiens*. In addition to the metric differences on the variables (Table 10), the pubic bone in Neandertals, including Krapina, also shows a distinctive morphology in the proximal half of the superior ramus. This area includes the pectineal surface cranially and the obturator nerve sulcus, limited by the obturator crests, caudally. Antero-posteriorly, it is limited by a rounded ventral border and a usually flatter dorsal border with the pectineal crest along its cranial margin of the latter.

In the great apes, the pubic ramus is mostly flattened in the A-P direction. Accordingly, the proximal half of its superior pubis shows cranially a thin and acute pectineal crest. The obturator nerve sulcus is formed by ventral and dorsal crests derived from the obturator crest that are poorly developed and run very close to each other. As a result, they exhibit a short and narrow obturator sulcus.

The innominate bones attributed to the genus *Australopithecus* (AL 288-1, Sts 14, Sts 65, Stw 431) show an intermediate morphology between apes and the genus *Homo*. Cranially, the proximal half of the superior pubis ramus is more developed in the A-P direction than apes, and therefore, it exhibits a rounded bar-like morphology, although no specimen shows a well-developed pectineal crest. However, the obturator nerve sulcus is similar in size and shape to that of the great apes. No superior pubis ramus is sufficiently preserved to observe this trait in

Homo ergaster / erectus. Several Middle Pleistocene *Homo* specimens from the European site of the Sima de los Huesos (AT-1006, AT-3497+AT-3813+AT-3814, AT-1693+AT-1709, AT-2502+AT-2508, among others) exhibit a marked S-I flattening of the superior ramus, showing a wide and mostly flat pectineal surface which is depressed parallel to a well-defined pectineal crest (77).

Neandertal specimens (Kebara 2, Tabun C1, Shanidar 1, Shanidar 3, La Ferrassie 1, Amud 1), including those from Krapina (Cx.2, Cx.3+Cx.6 and 255.10) have exaggerated this morphology, and the proximal half of the superior pubis takes on an extreme plate-like morphology. In contrast, modern *Homo sapiens* show a rounded bar-like shape of the superior ramus, with a curved pectineal surface. In addition, the pectineal crest shows a pitted and rugose appearance and is rarely projected as a bony sheet. However, both Neandertal lineage specimens and modern *Homo sapiens* show a long, deep and wide obturator sulcus, probably because of a larger space between the ventral and dorsal portions of the obturator crest.

CONCLUSIONS

The innominate bones from the Krapina site are one of the most important collections to study the evolution of the hip bone. This sample is composed of 14 elements representing a minimum of seven individuals: two adults (Krapina Cx. 2 and Cx.3+ Cx.6), two late adolescents (Krapina Cx. 1 and 255.8), and three children (Krapina 255.3, 255.4, 255.5). Among the adult individuals, one is probably a male (Krapina Cx.2), whereas the other is most probably a female (Krapina Cx.3+Cx.6). The two sub-adult individuals most likely represent males, whereas the younger immature individuals are of unknown sex. The body mass calculated for three individuals (Krapina Cx.1, Cx.2 and Cx.3+Cx.6) ranges from 64.9-66.2 kg.

The Krapina specimens show some metric differences compared with other Neandertals, particularly in their

small values for the »maximum vertical acetabular diameter«, and one specimen (Cx. 2) shows a remarkably high value for the »non-articular ischial length«. Interestingly, studies of the dentition (18) and the temporal bone (84) have also identified a few metric aspects which appear to be particular to the Krapina sample. Despite these slight differences, when the entire Neandertal sample (including Krapina) is considered, the »pubic length«, and probably also the »depth of the superior pubic ramus«, are significantly different from modern humans, and these two traits could be considered unique Neandertal characters.

Regarding the morphological features, none of the Krapina specimens show any derived trait that distinguishes them from the rest of the Neandertal sample. However, Neandertals can be distinguished from all other hominid taxa (Table 11), by the pillar-shaped and narrow space between the cranial border of the greater sciatic notch and the arcuate line and the extreme S-I flattening and plate-like morphology of the superior pubic ramus. This distinctive pelvic morphology can be seen in a less-developed state in their European Middle Pleistocene precursors.

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