Musculoskeletal Stress and Adult Age Markers in the Krapina Hominid Collection: the Study of Femora 213 *Fe.1* and 214 *Fe.2*.

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Abstract

The purpose of this study was to examine morphological markers of activity and age on femora 213 Fe.1 *and 214* Fe.2 *of the Krapina hominid collection. This study is part of a large research on the Krapina collection aimed at studying morphological markers of activity (entheses, enthesopathies, articular modifications) and age, as well as dento-alveolar alterations and pathologies. For this purpose, we apply scoring methods that we have devised and standardized on modern Italian skeletal collections with known age, sex, activity during life, cause of death, etc.. This approach has been used to study other human skeletal series and it allows us to obtain homogeneous data that can be more easily compared and interpreted. On the basis of our recent investigations of Upper Palaeolithic skeletal remains of Taforalt (Morocco, 12000–11000), we also intend to re-examine the cut-marks on bones of the Krapina hominid collection to provide further knowledge about possible funerary practices of these Neandertalians.*

The study of markers of activity and age on femora 213 Fe.1 *and 214* Fe.2 *revealed strong robusticity and a postero-lateral position of the m.* gluteus maximus *enthesis, indicating morphological and size differences with respect to modern humans. The strong mechanical stress on the lateral parts of the proximal end of the femur seems to be confirmed by the partial dislocation of the hip joint suggested by the articular features observed on two coxal bones. Finally, we used our results to re-assess the attribution of age to the individuals represented by these two specimens.*

INTRODUCTION

Excavations in the Hušnjakovo rock shelter in the town of Krapina (Croatia) conducted by Prof. Dragutin Gorjanović-Kramberger between 1899 and 1905 brought to light hominid remains associated with middle Palaeolithic tools and faunal samples. The hominid sample dates to a long time period extending from the late last interglacial to early last glacial *(1, 2)*. The Krapina hominid collection has been investigated mainly since the 1970s starting with the reviews edited by Malez, including that of 1978 *(1)*. Based on the contributions by Gorjanović, Malez revised the stratigraphy and chronology of the site in relation to the faunal remains, tool industries and hominid bones. Complete inventories of the human bones are available *(3–8)*, and phylogenetic, biological and behavioural aspects of the Neandertalians

of Krapina have been studied in relation to functional and/or genetic causes with respect to both the geographical position of the specimens (south-central Europe vs. western Europe) and their chronological position (Early Neandertals of the Riss-Wurm interglacial vs. »classic« Neandertals) *(2–4, 6, 9–16)*. Despite the fragmentary state of the specimens, the Krapina hominid collection (approximately 900 human bones) is one of the richest samples of Pleistocene hominids from Europe and represents the largest sample of Neandertal specimens from a single locality *(15–17)*. Although it is not possible to determine the exact number of individuals represented, several hypotheses have been proposed *(3, 6, 7)*. For example, Trinkaus *(17)* suggested that the Krapina adolescent and adult samples contain 43 individuals, while Wolpoff *(6)* counted as many as 75 to 82 individuals on the basis of the dental remains.

The aim of our research project on the Krapina collection is to study skeletal morphological markers of activity (entheses, enthesopathies, articular modifications) and age, as well as dento-alveolar alterations and pathologies attributable to masticatory and non-masticatory activities (caries, tartar, periapical lesions, *ante mortem* tooth loss, chipping, occlusal wear and alterations related to anomalous use of the dentition). For this purpose, we apply scoring methods that we have devised and standardized on modern Italian skeletal collections (individuals who died between 1891 and 1944; »Frassetto« collections of the Museum of Anthropology of the University of Bologna) with known age, sex, activity during life, cause of death and other demographic parameters *(18–28)*. The collections consist of around 1000 skeletons deriving from exhumations of the cemeteries of Sassari (Sardinia) and Bologna (Emilia Romagna). The advantage of these methods is that the characters are scored in a homogeneous manner, which allows us to obtain good comparative data for more reliable interpretations. In fact, the proposed scoring method has proved useful for the study of past populations, from the Upper Palaeolithic (Taforalt, 12000–11000, Morocco) *(29–30)* and the protohistoric and historical periods *(31–40)*. We are aware of the limits of using data obtained from the application of modern human-based standards to prehistoric samples, especially in view of the possible differences due to genetic, ontogenetic and environmental factors *(41, 42)*. Nevertheless, the application of our methods to the Krapina collection could provide further information about the range of variation in archaic *Homo* with respect to modern humans.

Aspects of the above-mentioned topics have been discussed by numerous authors. Many studies on the relationships between long bone morphology and biomechanical stress, posture and locomotion have shown that Pleistocene humans had greater postcranial robusticity than modern populations. This was probably related to genetic adaptation and/or environmental factors during growth and development, with implications for the behaviour and cultural system of archaic and modern *Homo* *(9, 16, 43–54)*. Studies of the Krapina dental remains

have used various approaches, including morphological and metric traits, degrees and models of wear, and enamel and dentine lesions presumably related to non-masticatory activities *(6, 14, 55–59)*.

Finally, on the basis of our recent investigations of skeletal remains from the Upper Palaeolithic necropolis of Taforalt (Morocco, 12000–11000) in which the presence of ochre and cutmarks on many skeletons indicated complex funerary rites and practices *(40)*, we also intend to review the Krapina collection concerning the significance of bone breakage and cutmarks that many Authors put in relation to funerary practices, treatment of the body/skeleton in secondary burials, and/or cannibalism *(4, 17, 60–64)*.

Therefore, the Krapina collection represents an excellent opportunity to apply our methods to Pleistocene hominids, because of the large sample size and good preservation of the bones and teeth. The external surfaces of the bones are usually well preserved and largely intact *(3, 62, 63)*, even though the 80-year-old shellac used to preserve the bones makes it difficult in some cases to observe the traits on the bone surface.

In our first examination of the Krapina hominid collection in November 2005, we recorded skeletal indicators of activity on the shoulder girdle, upper limb, pelvic bones and lower limb. We also recorded dento-alveolar alterations and pathologies on all the teeth to provide a further contribution to the published data *(6, 14, 55–59)*, and we began to observe cutmarks. To identify the specimens, we referred to the published inventories cited above.

In this paper, we present the data on indicators of activity and age on the two most complete femora in the collection, specimens 213 *Fe.1* and 214 *Fe.2*.

MATERIALS AND METHODS

Specimens 213 *Fe.1* and 214 *Fe.2* refer to proximal third of the left femora bone, extending to the distal part of the gluteal tuberosity. Both femora are lacking fragments on the superior and antero-superior surface of the head and on the superior and posterior part of the greater trochanter. 214 *Fe.2* is also missing fragments on the posterior surface of the head and on the lesser trochanter. The femora are probably of a male and a female respectively *(7)*. However, since information about the stratigraphic position of most Krapina bones are not available, especially for the postcranial remains, the difficulty in associating leg and pelvic bones makes the sex attribution uncertain. Nevertheless, the difference in size and robusticity is quite evident (Figure 1). As Trinkaus reported *(12)*, femur 214 *Fe.2* was referred by Gorjanovic-Kramberger to an immature individual. However, since the epiphyses of the head and greater trochanter are completely fused, the bone is considered to be from an individual at least 20 years old *(12)*.

We applied our standards for the recording of the degree of development of the entheses of mm. *gluteus maximus*, *vastus medialis* and *iliopsoas*: the robusticity is classified in
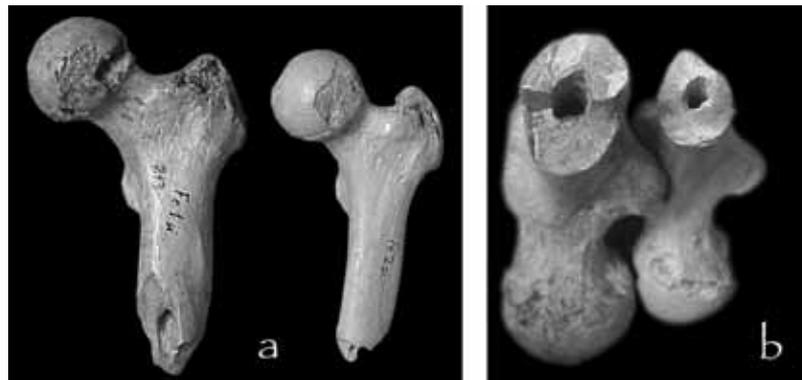
Figure 1. *Anterior (a) and inferior (b) views of the left proximal femora 213* Fe.1 *(at left side) and 214* Fe.2 *(at the right side) of the Krapina hominid collection: note the narrow medullary cavity and thick diaphyseal cortical bone.*

three degrees (1 [g1]: presence of a barely appreciable impression, 2 [g2]: medium to high development, 3 [g3]: very high development) while the enthesopathies (enthesophytic [OF] or osteolytic [OL] forms) can be absent or present, and in this case are also scored on a three-degree scale *(25)*. We also recorded other entheses (mm. *gluteus minimus*, *piriformis*, *vastus intermedius* and *lateralis*) and ligamentous attachments of the hip joint capsule, whose developmental degrees have not been defined in the reference standard.

The attribution of specimens to possible age-classes was based on persistence of the epiphyseal lines of the long bones, with a scale of five stages: absence of fusion (g0) (epiphysis and diaphysis separate), fusion less than 50% (epiphysis and diaphysis fused but the metaphyseal perimeter is either not fused or less than half fused) (g1), fusion greater than 50% (epiphysis and diaphysis fused for more than half the metaphyseal perimeter) (g2), complete fusion with persistence of the epiphyseal line (epiphysis and diaphysis completely fused but a trace of the fusion line is still visible) (g3), complete fusion (g4) *(28)*.

RESULTS AND DISCUSSION

Skeletal markers of activity

Here we describe the muscles defined in modern humans as dorsal muscles of the hip, as well as other morphological features of the joint. These muscles are involved in controlling and stabilizing the hip joint during erect posture and locomotion.

The m. *gluteus maximus* is divided according to its area of origin on the coxal bone into a superficial and deep part, which is inserted on the gluteal tuberosity extending posteriorly on the femur. This muscle, the main extensor and lateral rotator of the hip joint, represents a »muscular safeguard« against collapse of the pelvis and is thus the muscle of erect posture. In modern humans, the complete extent of the enthesis of m. *gluteus maximus* can be observed in posterior view; it may also be accompanied by a hypotrochanteric fossa, which can be more or less developed and whose surface can be more or less

rugose, depending on the degree of development of the enthesis.

In femora 213 *Fe.1* and 214 *Fe.2*, the muscle is highly developed (g3) (Figure 2), although it does not seem to correspond to the modern human morphology. In our standard, grade 3 corresponds to very high development – »well-defined and very raised ridge; there may be a deep and rugose fossa, with its medial border forming a crest«. Both specimens lack a very raised ridge, but there is a large well-defined surface with a vaguely lanceolate shape, roughened in 213 *Fe.1* and relatively smooth in 214 *Fe.2*, developed mainly on the postero-lateral part of the femur and not completely on the posterior part as in modern humans. There is also a clear discontinuity of the enthesis with the rest of the surface of the femur, both medially where it is delimited by a border-ridge (less definite in 213 *Fe.1* and more evident with a raised and bulging smooth margin in 214 *Fe.2*) that separates its surface from the postero-medial one, and laterally where there is a clear discontinuity between the more rugose surface of

Figure 2. *Latero-posterior views of the left proximal femora 213* Fe.1 *(a) and 214* Fe.2 *(b) of the Krapina hominid collection: the development (g3) of the enthesis of the m.* gluteus maximus.

Figure 3. *Lateral views of the left proximal femora 213* Fe.1 *(at the left side) and 214* Fe.2 *(at the right side) of the Krapina hominid collection: the development (g3) of the enthesis of the m.* gluteus minimus.

the enthesis and the smooth surface of the lateral part of the femur.

The m. *gluteus minimus* originates from the ilium between the anterior and inferior gluteal lines and it is in-

serted on the greater trochanter of the femur. Together with m. *gluteus medius* and m. *piriformis*, it abducts the thigh. The m. *gluteus minimus* is well developed in both 213 *Fe.1* and 214 *Fe.2* (Figure 3).

The m. *piriformis*, which originates by several heads from the pelvic surface of the sacrum and the border of the greater sciatic notch and is inserted on the apex of the greater trochanter, presents a true horizontal plane in both 213 *Fe.1* and 214 *Fe.2*, forming a ridge on the lateral surface of the greater trochanter (Figure 4). In the erect position, it functions as a lateral rotator and abductor, assisting the function of the gluteal muscles.

In the two Krapina femora, the morphology of the entheses of mm. *gluteus minimus* and *piriformis* fall within the variability observed in modern populations.

The mm. *psoas major* and *iliacus*, the anterior muscles of the hip, join to form the m. *iliopsoas* which is inserted on the lesser trochanter. The m. *iliopsoas* is the most important flexor of the thigh, thus allowing locomotion; it also serves to flex the trunk anteriorly and to raise the trunk from a supine position. This muscle also acts as a lateral rotator at the hip joint. The enthesis of m. *iliopsoas* of femur 213 *Fe.1* (Figure 5) is grade 3 (»the medial margin is lipped and the muscle markings can present an in-
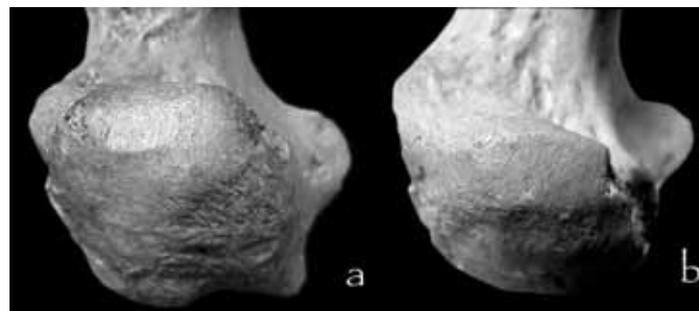
Figure 4. *Superior views of the left proximal femora 213* Fe.1 *(a) and 214* Fe.2 *(b) of the Krapina hominid collection: the development (g3) of the enthesis of the m.* piriformis.

Figure 5. *Medio-posterior views of the left proximal femora 213* Fe.1 *(a) and 214* Fe.2 *(b) of the Krapina hominid collection: the development of the entheses of the mm.* iliopsoas *(g3 on femur 213* Fe.1 *and not detectable on 214* Fe.2) and vastus medialis *(g3 on femur 213* Fe.1 *and g1a on 214* Fe.2).

Figure 6. *Anterior view of the left proximal femora 214* Fe.2 *of the Krapina hominid collection: the development of the enthesis of the iliofemoral ligament and Allen's fossa. A trace of the line of epiphyseal fusion is still visible.*

ferior extension onto the side of the trochanter towards the femoral shaft. At times, the lesser trochanter may be flattened or have a very flattened and rugose superior facet«) and it falls within the variability of modern human populations. On 214 *Fe.2*, this feature cannot be scored due to the poor preservation of the lesser trochanter (Figure 5).

Enthesophytic and osteolytic formations were not observed for any of the above-mentioned entheses.

The enthesis of the lateral part of the *iliofemoral* ligament, which originates in an extracapsular position on the anterior inferior iliac spine and is inserted on the superior part of the intertrochanteric line, is well developed in 214 *Fe.2* (not recordable in 213 *Fe.1*) and presents OL of grade 2 (»diffuse porosity, with holes ca. 1 mm in diameter or presence of a small area of erosion [ca. 4 mm in length or diameter]«) (Figure 6). This is the strongest ligament in the body and not only reinforces the capsule but also prevents extensive movements. By means of torsion and tension (of its lateral and medial parts), this ligament allows maintenance of the erect position when the pelvis tilts posteriorly. When the thigh

is flexed, the two iliofemoral ligaments (lateral and medial parts) are distended, allowing the sitting position.

Finally, we examined the three most complete coxal bones of the collection: 207 *Cx.1* (male left immature specimen), 208 *Cx.2* (adult right) and 209/212 *Cx.3/6* (right adult female) composed of two fragments glued together. No indication about the possible association between coxae and femora has been reported *(7)*. A rugosity on the supero-lateral part of the coxal insertion of the capsule is observed on the left –207 *Cx.1*– and right –208 *Cx.2*– male specimens (not detectable on the right 209/212 *Cx.3/6* female specimen), indicating a strong mechanical stress, is observed (Figure 7). Partial dislocation of the hip joint is suggested by the features of the medial part of the acetabular rim of 208 *Cx.2* and 209/212 *Cx.3/6* (not detectable on 207 *Cx.1*) and on the latero-inferior part in 207 *Cx.1* and 209/212 *Cx.3/6* (not detectable on 208 *Cx.2*) (Figure 8).

There is an Allen's fossa on 214 *Fe.2* (Figure 6) and an iliac imprint in the same position on 213 *Fe.1* (Figure 9). These traits form in an intracapsular position. Allen's fossa is a osteolytic formation *(65, 66)*, here quite developed, while the iliac imprint is an exostosis or a plaque next to the femoral head which looks like an overgrowth or bony scar *(65)*.

In both femora, the strong entheseal development and the articular traits of the hip joint suggest strong mechanical effort of the joint in extension and lateral stabilization and control of the thigh. The strong development of the gluteal muscles (postero-lateral position and massive development of m. *gluteus maximus*, even though with some differences between the specimens) and abductor muscles (mm. *gluteus minimus* and *piriformis*) indicate medio-lateral reinforcement to resist high mechanical stress on the proximal femoral shaft of the Krapina hominids. The partial dislocation of the hip joint could be related to the medio-lateral mechanical effort needed to stabilize the trunk during erect posture and locomotion.
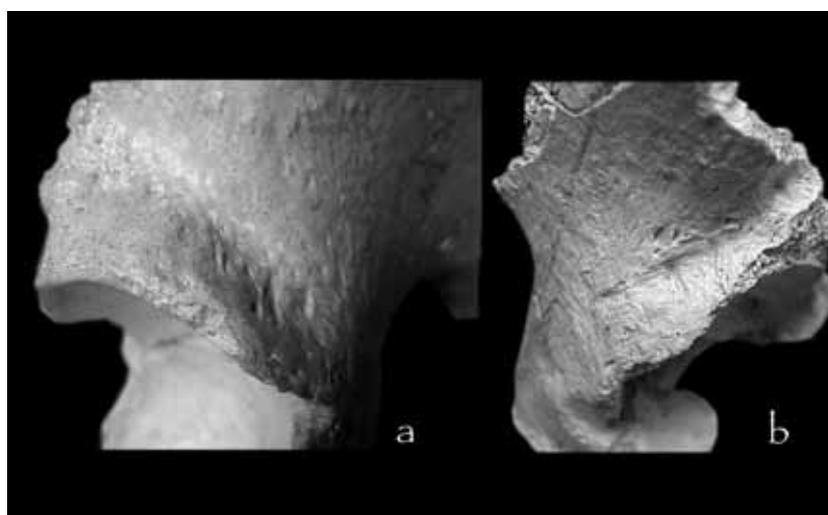
Figure 7. *Supero-lateral part of the acetabula of the left (207* Cx.1*) (a) and right (208 Cx.2) (b) coxae of the Krapina hominid collection.*
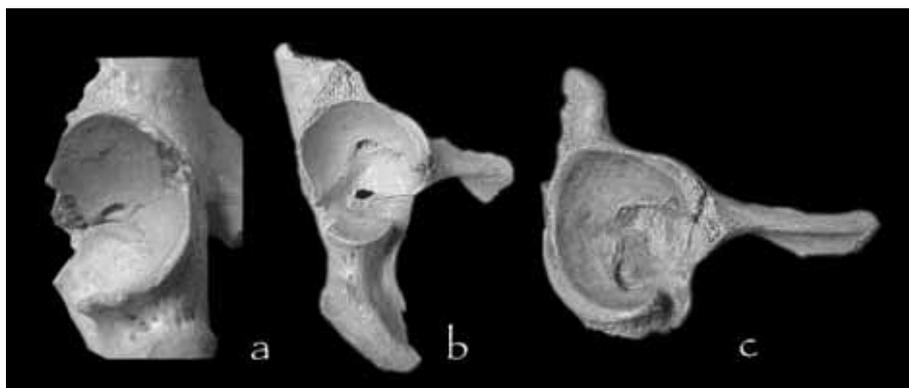
Figure 8. *Acetabular rims of the left (207* Cx.1*) (a), right (208* Cx.2*) (b) and right 209/212* Cx.3/6 *(c) coxae of the Krapina hominid collection.*

Trinkaus *(9, 12, 16)* observed some of these features in the Krapina specimens and in Upper Pleistocene hominids of Europe and the Near East. He hypothesized an integrated complex that served to absorb high levels of biomechanical stress. In particular, he concluded that the Neandertal femoral shaft was subjected to high medio-lateral bending stress: the iliotibial tract and its associated gluteal muscles would have been strongly developed. He described lateral-proximal swelling of the shaft and a »hypotrochanteric fossa« for the m. *gluteus maximus* enthesis that was very different from the situation in modern humans *(9)*. That trait may correspond to the above-mentioned morphology of the enthesis in the two Krapina femora. He also indicated that the medio-lateral robustness is associated with an absence of the pilaster that reinforces the shaft against antero-posterior bending stress but contributes little reinforcement against the predominant medio-lateral stress. Biomechanically the relatively low femoral neck-shaft angle and the long pubic rami, with a consequent increase of the interacetabular distance, may have been important factors contributing to the characteristic morphology of the femoral shaft *(9, 12)*. Although only the proximal third of the shaft is present in the two Krapina femora, the pilaster does not seem to be appreciable in either specimen and linea aspera is roughened only in 213 *Fe.1*. Finally, Trinkaus *(9,16)* ob-

served that the massive muscle *gluteus maximus* insertion was also present in some immature Neandertal bones (Roc de Marsal 1, La Ferrassie 6, Shanidar 7).

Allen's fossa and the iliac imprint are believed to have a mechanical aetiology, related to an adaptive response of the articular and para-articular areas to flexion/extension of the hip joint *(65, 67, 68)*. As regard to the Allen's fossa in modern human samples (males N=96), its incidence decreases from young adults to old adults (young adults: 30%, middle adults: 11%, old adults: 0%) *(20)* and it is present only in the males in an Italian Early Middle Age sample *(36)*. As regard to the iliac imprint, Trinkaus *(69)* refers to the feature observed on the specimen 213 *Fe.1* as »Poirier's facet«, defined as »an extension of the articular surface of the femoral head onto the anterior-superior surface of the neck«. He related this characteristic to the degree of habitual flexion and abduction during normal locomotion and to the pressure exerted by the m. *iliopsoas (65, 70)* or *rectus femoris* tendons *(71)*. We would underline that a general agreement on the terminology of the facets and imprints of the proximal femoral end is lacking. We utilized the iliac imprint term taking into account two reasons. First, we referred to Angel *(65)* that identified the »empreinte iliaque« of Poirier as an exostosis or a plaque next to the femoral head which looks like an overgrowth or bony scar. Secondly, we observed a discontinuity between the femoral head and the imprint (Figure 9) that seems to indicate that the articular cartilage did not extend onto the imprint; in fact, Kostick *(67)* and Angel *(65)* indicated that the presence of the cartilage is often taken as prerequisite for a Poirier's facet and then a continuity of the articular lamella onto the neck is taken as acceptable evidence of a Poirier's facet. As regard to the etiology of the iliac imprint of the specimen 213 *Fe.1*, taking into account also the high development of the enthesis of the m. *iliopsoas*, we could think that the pressure exerted by this flexor muscle to check the tight extension during locomotion, as suggested by Angel *(65)*, could be considered an etiological factor. In an Italian Early Middle Age sample we observed that the iliac imprint was only present in males, constituting around 49% of the adult sample (98 adults), and was more frequent on the left femur (around 40% on the right and 60% on

Figure 9. *Iliac imprint on the left proximal femur 213* Fe.1 *of the Krapina hominid collection.*

the left) *(36)*. Therefore, the Allen's fossa and iliac imprint could indicate a common aetiology (postural mechanical stress related to flexion/extension of the hip joint) that is influenced by age, causing different effects; age-related changes in hormonal and metabolic levels of a bone subjected to biomechanical stress may cause differential adaptive effects. Therefore, the presence of Allen's fossa can be interpreted as an indicator of the young age of the individual represented by femur 214 *Fe.2*.

In the group of anterior thigh muscles, the m. *quadriceps femoris*, extensor of the knee joint, flexor of the hip joint and propulsor during locomotion, consists of four parts (mm. *rectus femoris*, *vastus intermedius*, *medialis*, *lateralis*) inserted by a single tendon on the patella and continuing as the patellar ligament to be inserted on the tibial tuberosity.

The m. *vastus medialis* originates from the medial lip of linea aspera. The development of this muscle in both 213 *Fe.1* and 214 *Fe.2* is similar to that observed in modern humans. In the former femur, the entheseal development is of grade 3 (Figure 5) – »very raised and/or rugose crest«. The development of the enthesis in 214 *Fe.2* (Figure 5) is of grade 1a, i.e. an »impression barely appreciable: the surface is practically smooth, even though an oblique line is perceptible to the touch«. The enthesis is characterized by fine porosity. The development of this muscle in both the specimens is comparable to that in modern humans.

The m. *vastus intermedius* originates from the proximal three-quarters of the antero-lateral surface of the femur, set beneath the mm. *vastus lateralis* and *medialis*. This muscle is particularly well developed in 213 *Fe.1*: on the antero-lateral surface, at least two adjoining imprints are appreciable, a smaller proximal and a larger distal one, both vaguely ogival and rhomboidal in shape with the long axis oriented medio-laterally with respect to the femoral axis (Figure 10).

The heads of m. *quadriceps femoris* have a very different appearance in the two specimens. In 214 *Fe.2*, the enthesis of m. *vastus medialis* presents a slight fossa barely perceptible to touch. Many authors have reported an enthesis »sous forme de fosse« *(72)* in juvenile subjects (especially adolescents) at the attachment sites of the costo-clavicular ligament (clavicle), m. *pectoralis major* and m. *latissimus dorsi/teres major* (humerus), m. *gluteus maximus* (femur), m. *soleus* (tibia) and, more rarely, in other entheses *(26, 73–75)*. Therefore, this particular entheseal morphology seems to be due to the strong modelling/remodelling processes accompanying growth, during which there is a continuous »migration« of the enthesis in the growing bone *(76)*. We can also hypothesize an interaction between biomechanical factors and the manner of development in the formation of these traits. There may be a different bone response (periosteal/endosteal apposition and/or resorption) to mechanical loading during growth, and the periosteal surface appears to be more sensitive to increased or decreased mechanical loading during childhood and adolescence *(49)*.
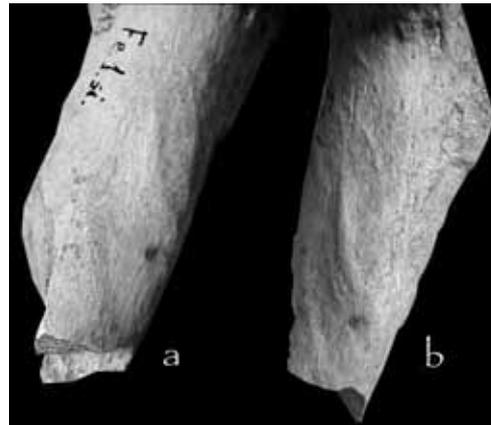
Figure 10. *Anterior (a) and lateral (b) views of the left proximal femur 213* Fe.1 *of the Krapina hominid collection: the development of the enthesis of the m.* vastus intermedius.

Therefore, age appears to play an important role in the »fossa« formation of this enthesis. Thus, the differences between the two femora could be attributed to an age difference, with 214 *Fe.2* being from a younger individual than 213 *Fe.1* (even though a sex difference cannot be excluded).

The morphology of m. *vastus intermedius* in femur 213 *Fe.1* does not appear to fall within the variability of modern human populations, whose anterior femoral surface is smooth. Moreover, the morphology is not present in the other Krapina femur 214 *Fe.2* (Figure 1) nor has it been described in other Neandertalian specimens. Condemi *(77)* described the development of some entheses of the Neandertalian femur BD5 from La Chaise and, referring to the development of m. *vastus intermedius*, she reported that the anterior diaphyseal surface was regular and smooth.

For the Krapina specimens, age and/or sex might be invoked as aetiological factors that determined the differences in m. *vastus intermedius*. Since this muscle is part of the m. *quadriceps femoris* (extremely important for knee extension during the taligrade phase of locomotion), we can hypothesize a different physical expenditure. However, the massive imprint on femur 213 *Fe.1* could represent an individual variation related to intrinsic and/or external factors (particular postural habits, repetitive stressful activities involving hyperextension of the knee, traumatic events, *etc.*). Further specific observations on other samples of archaic *Homo* may provide more information about the possible range of variation of this trait.

Skeletal markers of adult age

Although the epiphysis of the femoral head is completely fused in both 213 *Fe.1* and 214 *Fe.2*, a trace of the line of epiphyseal fusion is still visible (Figures 6, 11) and corresponds to stage 3 of our standard. Although not clearly appreciable in photographs, the femoral head of 214 *Fe.2* is more »open« than that of 213 *Fe.1*.
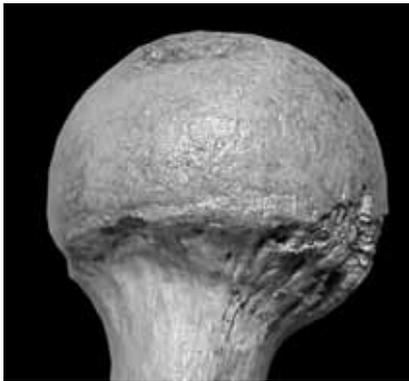
Figure 11. *Medial view of the left proximal femur 213 Fe.1 of the Krapina hominid collection: a trace of the line of epiphyseal fusion is still visible.*

In a study of modern skeletal series, stage 3 was observed between 22–23 years and 30–33 years in males and between 18–20 years and 37–38 years in females in both the sample from Sassari (Italy) and in the Portuguese osteological collection (Colecção de esqueletos identificados, Coimbra) used for comparison *(28)*. This probably indicates precocious development in females but a delay in completion of the ossification processes, perhaps due to sex differences in the energy input necessary to complete the fusion (unpublished data). These results would exclude the attribution of advanced age to an individual presenting this stage of the trait, at least for modern populations. Although application of these data to archaic human populations may be problematical because of possibly different times and modes of development and aging, stage 3 of this trait seems to exclude the attribution of advanced age to both Neandertalian individuals represented by the Krapina femora. Indeed, Gorjanovic-Kramberger attributed 213 *Fe.1* to an immature individual and Trinkaus *(12)* suggested an age of at least 20 years.

Several studies *(78–81)* have suggested that maturation in Neandertals was faster than in modern humans. In particular, dental maturation, an important indicator of somatic development, indicates that Neandertals had a short period of development and faster somatic growth than Upper Palaeolithic-Mesolithic modern humans, probably fuelled by a high metabolic rate and a high-caloric diet. If the developmental rate was faster than in modern humans, complete epiphyseal closure probably occurred earlier than in modern humans. Therefore, although the stage of epiphyseal closure observed in the Krapina femoral heads corresponds in modern humans to relatively young adults, it may indicate even younger individuals in Neandertals.

CONCLUDING REMARKS

The following conclusions emerged from our examination of femora 213 *Fe.1* and 214 *Fe.2* of the Krapina hominid collection:

1. The particular morphology of the m. *gluteus maximus* enthesis, i.e. a massive imprint in a postero-lateral position compared to the posterior one in modern humans, confirms the observations by Trinkaus *(9, 12, 16)* in the Krapina collection and in most samples of European and Near Eastern Early Neandertals. The presence of these features in subadult Neandertals *(9, 16)* and the relatively small differences that we observed in the entheseal development of the gluteal and abductor muscles suggest that these traits are relatively unrelated to sex and age. In fact, femora 213 *Fe.1* and 214 *Fe.2* have been attributed to a male and female respectively *(7)*, and femur 214 *Fe.2* to a young individual. According our observations, both femora can be attributed to young adults, albeit of different ages (214 *Fe.2* younger than 213 *Fe.1*).

2. The massive imprint of m. *vastus intermedius* on the antero-lateral surface of femur 213 *Fe.1* does not agree with the morphology in modern human populations and seems to be absent in other Neandertals *(77)*. Sex and/or age, as well as particular individual activities or traumatic events, could be invoked to explain this feature. More observations on other Neandertal specimens may provide more details about this trait, also considering that this muscle is part of m. *quadriceps femoris,* which is mainly involved in knee extension and thus in propulsion during locomotion.

3. The development and position of the other muscles do not seem to differ from the situation in modern human populations.

4. When compared with our results for modern human skeletal series, some of the observed traits help attribute an age at death to the Krapina specimens. Based on the persistence of the epiphyseal lines, both femora can be attributed to young adults, as suggested previously. The morphology of the m. *vastus medialis* enthesis and the presence of the osteolytic formation of Allen's fossa in 214 *Fe.2* suggest its attribution to a younger individual than 213 *Fe.1*.

The differences between Neandertalians and modern human populations might be explained by genetic and/or environmental factors during ontogeny and growth (frequent high levels of biomechanical stress and/or persistent and repetitive stressful activities, posture and locomotion, *etc.*). According to Trinkaus *(51)*, in human foraging, the loads on the lower limb depend on the distances travelled, the intensity of activity and the load transported. The robusticity of the lower limb of Neandertals suggests biological compensation for less effective cultural systems than those of anatomically modern humans. Indeed, the reduction of femoral robusticity may have been related to the increased cultural and technological complexity in modern human societies in the transition between the Middle and Upper Palaeolithic *(9, 16, 48)*.

With regard to some Epipalaeolithic populations, the observations of Ferembach *(82)* and our results on the sample of Taforalt (Morocco, 12000–11000) revealed strong

robusticity in both gross morphology and the generalized and specific development of entheses. Moreover, we found sexual dimorphism in muscle development in the upper and lower limbs *(30)*. Although the term »robusticity« can have different meanings, as underlined by Ruff and co-workers *(48)*, the Taforalt sample appears to be robust and dimorphic in terms of the muscle insertions and sizes. Therefore, we can hypothesize that these populations were subjected to high physical stress (absence of sedentariness, long foraging movements, etc.); genetic-geographical components may also have had an important role in the morphogenesis of the bones. The Epipaleolithic population of Taforalt still exhibits high robusticity compared with recent humans and a different kind of robusticity compared to the pre-recent samples, intending by this term, used by Ruff and co-workers *(48)*, humans up to early modern *Homo sapiens*. Therefore, in view of the probable local origin of the Taforalt populations in North Africa and the new information about the origin and evolution of Ibero-Maurusian populations *(83)*, different geographical patterns of the transition to the Upper Palaeolithic must be taken into account.

Finally, the Krapina hominids exhibit many typical features in the shoulder girdle *(4, 15, 84, 85)*, hands *(5)*, scapula (dorsal axillary groove) *(11)* and superior pubic ramus (long and thin) *(4, 12, 10)*, as well as in the average degree of robusticity. These features differ from those of modern humans and fit within the range of Neandertal morphological variation. Many morphological patterns have been proposed to recognize a Neandertal specimen. Therefore, although the traits that we examined may have to be reconsidered after we complete our observations on the entire Krapina collection and they must be tested on other samples of archaic *Homo*, some of them could help to define the variability of Neandertalian characters in relation to physical activity, age, sex, and ontogenetic and phylogenetic factors.

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