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Sex estimation of the adult Neandertal Regourdou 1 (Montignac, France):

Implications for sexing human fossil remains

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Abstract

Sex is a biological trait fundamental to the study of hominin fossils. Among the many questions that can be addressed are those related to taxonomy, biological variability, sexual dimorphism, paleoobstetrics, funerary selection, and paleodemography. While

new methodologies such as paleogenomics or paleoproteomics can be used to determine sex, they have not been systematically applied to Pleistocene human remains due to their destructive nature. Therefore, we estimated sex from the coxal bone of the newly discovered pelvic remains of the Regourdou 1 Neandertal (Southwest France, MIS 5) based on morphological and metric data employing two methods that have been recently revised and shown to be reliable in multiple studies. Both methods calculate posterior probabilities of the estimate. The right coxal bone of Regourdou 1 was partially reconstructed providing additional traits for sex estimation. These methods were cross validated on 14 sufficiently preserved coxal bones of specimens from the Neandertal lineage. Our results show that the Regourdou 1 individual, whose postcranial skeleton is not robust, is a male, and that previous sex attributions of comparative Neandertal specimens are largely in agreement with those obtained here. Our results encourage additional morphological research of fossil hominins in order to develop a set of methods that are applicable, reliable, and reproducible.

Keywords: Regourdou; Neandertal; Hip bone; Sex attribution; Sexual dimorphism; Probabilistic Sex Diagnosis

1. Introduction

Sexual dimorphism of the human pelvis is traditionally viewed in relation to the tight fit of the fetal head in the pelvic aperture, which is the consequence of competing selective pressures related to either bipedal locomotion or childbirth. Anteroposterior shortening of the bipedal pelvis limits pelvic canal space, which results in a much larger cephalo-pelvic proportion between the fetal head size and maternal pelvic canal size (Washburn, 1960; Rosenberg, 1992; Haeusler et al., 2021). However, the pelvis also

relates to overall body size and body shape, playing a role in thermoregulation and adaptation to climate (Ruff, 1994; Holliday, 2012; Kurki, 2013; Betti, 2017; Auerbach et al., 2018), locomotor economy and efficiency (Warrener et al., 2015), load-carrying (Wall-Scheffler, 2022), posture (Been et al., 2017), and pelvic floor stability (Uy et al., 2020; Stansfield et al., 2021). These factors vary across populations living in different geographical environments and following different lifestyles, correspondingly influencing pelvic morphology.

Despite the above-mentioned factors, sexual dimorphism of the obstetrically relevant parts of the pelvis follows a similar pattern in modern humans and is shared among primates and likely even among mammals (Tague, 1991; Fischer et al., 2021). The coxal bone is thus the most reliable skeletal region for sex estimation as has been empirically demonstrated by numerous studies on various human populations (Gonzalez et al., 2009; Klales et al., 2012; Novak et al., 2012; Brůžek et al., 2017; Rmoutilová et al., 2017; Santos et al., 2019; Galeta and Brůžek, 2020; Klales, 2020a). The magnitude of pelvic sexual dimorphism varies greatly among species, which can be attributed to the degree of cephalo-pelvic proportion between the fetal head size and maternal pelvic canal size (Leutenegger, 1974; Ridley, 1995) and to a lesser extent, to sexual dimorphism in body size and steroid hormone levels that trigger both dimorphic growth and remodeling of the pelvis (Tague, 2005). Therefore, sex estimation of archaic hominins is complicated as has been previously noted (Genovés, 1954) and extensively discussed (Smith, 1980; Trinkaus, 1980; Novotný, 1983; Hager, 2005; Bonmatí and Arsuaga, 2007; Trinkaus, 2016a; Hammond et al., 2017, 2018; Alonso-Llamazares and Pablos, 2019; Bethard and VanSickle, 2020). Despite this complexity, except for ancient DNA (Skoglund et al., 2013) or tooth enamel peptides (Lalueza-Fox et al., 2011; Stewart et al., 2017; Parker et al., 2019), the pelvis remains

the most reliable means of skeletal sex estimation. The main difficulty encountered in attempting morphological assessment of archaic human pelvis is the use of anatomically modern criteria on nonmodern hominins who differ in their patterns of pelvic morphology and/or degree of sexual dimorphism (Marchal, 1997). For this reason, modern methods are not guaranteed to be applicable to all hominin fossil taxa (Genovés, 1954; Hager, 1996; Bethard and VanSickle, 2020).

While sex attribution is fundamental to discussing hominin biological evolution (Fruyer, 1980; Weaver and Hublin, 2009; Hora and Sladek, 2014; Estalrich and Rosas, 2015), sex attributions of Neandertal coxal bones consist primarily of visual descriptions of morphological traits (see Supplementary Online Material [SOM] Table S1 and references therein), most of which were published before the establishment of sex estimation methods now known to be highly reliable for modern humans (Klaes et al., 2012; Brůžek et al., 2017; Santos et al., 2019). Neandertal body form shows strong adaptations to cold climate (Holliday, 1997; Weaver, 2003, 2009) with markedly wide pelvic breadth (Ruff, 1994). As highly encephalized hominins with encephalization quotients falling within the modern human range (Stanyon et al., 1993; Rosenberg and Trevathan, 2002; Ponce de León et al., 2008; Holliday, 2023), Neandertals would be expected to show comparable cephalo-pelvic proportions to modern humans and thus to have comparably difficult births. However, given the fragmentary nature of fossil pelvic remains, the attribution of sex for any individual specimen remains difficult. It is therefore critical to use multiple objective methods of sex estimation for fossil specimens, and to distinguish between sex assessment, which does not provide estimable error rates, and sex estimation with associated classification accuracy (Klaes, 2020b).

The aim of this study is to estimate the sex of the Regourdou 1 (R1) Neandertal, whose right coxal bone was reconstructed to provide new information on the individual's sex. Many large fragments of the R1 coxal bones have been recently identified among faunal remains from the site (Madelaine et al., 2008; Maureille et al., 2015), so it currently represents the only Western Eurasian Neandertal pelvis (Marine Isotope Stage [MIS] 5 to 3) with no taphonomic distortion and no prior physical restoration, as well as the only non-deformed sacroiliac articulation. To sex R1, we used morphological and metrical sex estimation methods previously standardized on modern human populations. Applied sex estimation methods were then cross validated with other Neandertal specimens to evaluate the reliability of methods developed on modern humans for sex estimation of these fossil hominins.

1.1. Comprehensive overview of the site and history of the Regourdou fossils

The site of Regourdou is located at the top of the Lascaux hill near Montignac in southwestern France. It is a partially collapsed karstic cave discovered by R. Constant, the Regourdou landowner, in 1954. The R1 fossil was accidentally discovered in 1957 during amateur underground excavations by friends of R. Constant and a Swiss citizen (Piveteau, 1959, 1963). Despite being authorized to excavate the site, Constant had no background in paleontology or prehistory and thus did not record provenience of his discoveries. Between 1961 and 1964, part of the site was scientifically excavated by E. Bonifay (Bonifay, 1964; Bonifay et al., 2007). A project to re-excavate the site and to study the collections was subsequently directed by one of us (B.M.) between 2013 and 2018 (Maureille, 2013; Discamps et al., 2016).

According to Bonifay's interpretation of the sedimentological filling of the cave (SOM Fig. S1), the R1 skeleton was discovered in layer 4 (Bonifay, 1964), which yielded a

few Discoid Mousterian lithics (Turq and Royer, 2016), and was associated with a temperate faunal assemblage dominated by *Ursus arctos* (Bonifay, 1964; Delpech, 1996; Cavanhié, 2009). During the formation of layer 4, the site functioned as a brown bear den as shown by a natural mortality profile of young and adult bears (Cavanhié, 2009). Based on the sedimentological and paleontological evidence, layer 4 was attributed to MIS 5 by Bonifay (1964) and Bonifay et al. (2007). This chronological attribution was confirmed during fieldwork at the Regourdou site between 2014–2016 (Maureille 2016, unpublished data). Moreover, red sandy sediments washed from the plateau above the Regourdou karstic cave roof were then water-deposited within the cave below resulting in a 50-cm-thick brown to red sandy laminated layer that is very easily identified. This sedimentological formation corresponds to Bonifay's layer 3 (Maureille, 2014). Layer 3 overlies Bonifay's layer 4 and has yielded preliminary optically stimulated luminescence dates of ca. 80 ka (Lebrun and Lahaye, 2014). Given its antiquity, R1 is now the earliest, best-preserved Western European Neandertal skeleton (Peyrégne et al., 2019). We have also demonstrated the existence of specific post-depositional taphonomic processes related to MIS 3 European rabbits (*Oryctolagus cuniculus*) digging burrows within Regourdou's sedimentological filling—burrows that had an impact on the integrity of the site's archaeological assemblages (Pelletier et al., 2017).

From 1957 to 2008, the R1 skeleton was limited to 100 bones or bony fragments with especially well-preserved, fully complete, upper limbs. From 2009 to 2018 several new pieces of the skeleton were recovered. Some were recovered from the faunal collections associated with the 1961 to 1964 excavations that have been curated at the Musée national de Préhistoire at Les Eyzies-de-Tayac since 2002. These collections were checked piece by piece in 2008 due to a French law mandating the

taking of inventories of national museum collections (Madelaine et al., 2008). These, plus investigations of the collection of Musée d'art et d'archéologie du Périgord and the Regourdou private site museum, led to the rediscovery and identification of 72 new pieces belonging to the R1 skeleton (Madelaine et al., 2008; Maureille et al., 2015), most of which are elements of the trunk, pelvis, and lower limbs. This has resulted in new studies of the skeletal anatomy of R1 (Gómez-Olivencia et al., 2013a, 2019; Pablos et al., 2019), including the sternum (Gómez-Olivencia et al., 2012) and sacrum (Rmoutilová et al., 2020) as well as the calcium isotope signatures of the hominin and the faunal taxa, which allowed the first evaluation of the diet and principal ungulate prey of R1 (Dodat et al., 2021). Moreover, it has also been confirmed that there was a second individual (Regourdou 2) discovered during Bonifay's fieldwork. Regourdou 2 is only represented by an isolated right calcaneus with Neandertal morphological affinities and it is larger and longer than those of R1 (Coutinho Nogueira et al., 2017). In contrast to most of the skeletal remains of R1, the Regourdou 2 calcaneus was not recorded by Bonifay, and thus its exact provenience within the site remains uncertain.

1.2. Previous sex attribution of Regourdou 1

Based on the available skeletal material, Regourdou 1 has been regarded as either a male (Vallois, 1965; Gómez-Olivencia et al., 2007; Volpato et al., 2012) or as sex-indeterminate (Trinkaus, 1980; Vandermeersch and Trinkaus, 1995; Meyer et al., 2011; Plavcan et al., 2014). Until 2008, only the sacrum, right ischium, and superior pubic ramus were recognized from the pelvis, but they lacked reliable features for sex attribution. For this reason, the sex of R1 was historically assessed based on the size and robusticity of its different skeletal regions (see below).

Male sex was initially proposed without any specific justification by Vallois (1965), who referred to previous papers by Piveteau (1959, 1963, 1964, 1966) in which no sex attribution was given. This initial attribution was later contradicted (Trinkaus, 1980; Vandermeersch and Trinkaus, 1995) on the basis of upper limb articulations and pubic ramus thickness that were reported to be closer to Neandertals considered females or to lie between the European Neandertals considered males and females. On the other hand, male sex was supported by Volpato et al. (2012) based on male proportions of the sacral body and alae.

With regard to the overall body size, several studies estimated the sex of R1 based on extra-pelvic measurements. In contrast to the above-mentioned gracile upper limb articulations, humeral, radial, and talar lengths were reported to be in the male Neandertal range of variation but lie within its lower portion (Trinkaus, 1980; Vandermeersch and Trinkaus, 1995), while canine breadth was reported to be within the upper range of European Neandertal variability (Volpato et al., 2012). Concordantly, R1 was classified as male using clavicular dimensions (maximum length and mid-shaft vertical and anteroposterior diameters; Carretero, 1994) or based on modern human formulae (Wescott, 2000) using second cervical vertebra (Gómez-Olivencia et al., 2007). Subsequent analyses led to small body mass estimates for R1 (64.4–65.6 kg; Table 1) compared to presumed male Neandertals (males: 65–85 kg, females: 60–75 kg; Plavcan et al., 2014) based on femoral head diameter and talar trochlea breadth (Plavcan et al., 2014; Pablos et al., 2019). Stature estimates of R1 based on various skeletal regions and equations yielded more variable results (Table 1). Estimates based on the humerus and the radius (162.2–167.5 cm) were lower than or close to the mean for Neandertals considered males (males: 167 cm, females: 155 cm; Carretero et al., 2012), while stature was higher when predicted from the lengths

of the talus, calcaneus, and third and fourth metatarsals, or from vertebral body heights (170.3–173.3 cm). These differences in stature estimates likely reflect different body proportions between Neandertals and extant reference samples (Holliday, 1997; Pablos et al., 2019).

Since 2008, new pelvic remains belonging to R1 have been identified in the faunal collections from the Regourdou site. Given the recorded location of skeletal remains, their articulation with the sacrum, estimated age, and taphonomic state, their assignment to R1 is the most parsimonious interpretation (Madelaine et al., 2008; Meyer et al., 2011; Maureille et al., 2015). Although both ilia show a rather deep and asymmetric morphology of the greater sciatic notch corresponding to male sex, both notches are incompletely preserved, resulting in uncertainty about their exact shape (Meyer et al., 2011; Plavcan et al., 2014). Here, we undertake a new sex attribution of R1 based on the original left and reconstructed right coxal bones using modern sex estimation methods.

2. Materials and methods

2.1. *Material*

Although the R1 pelvis is not completely preserved (SOM Fig. S2), it is one of the best preserved Neandertal pelves lacking taphonomic distortion or intrusive restoration. The right coxal bone preserves a partial ilium, nearly complete ischium, and a portion of the superior pubic ramus. The left coxal bone consists of the iliac ala preserving the posterior part of the iliac crest and two ischial fragments (portions of the acetabulum and ischial tuberosity). The sacrum preserves the first sacral segment and portions of the second and third segments. The right auricular surface is complete, but the lower portion of its inferior demiface is missing on the left side.

Micro-computed tomographic (μ CT) scans of Regourdou 1 were acquired on the AST-RX platform of the Musée de l'Homme in Paris and the PLACAMAT platform at the University of Bordeaux (μ CT scanners V|tome|x L 240 and V|tome|x S, GE Sensing & Inspection Technologies Phoenix X|ray). Based on object size, voxel size of the μ CT scans varied between 0.065 and 0.096 mm. To facilitate manipulation, μ CT scans were reduced before segmentation in ImageJ v. 1.53c (Rueden et al., 2017) to a resolution still sufficient for macroscopic analyses using a macro created by Renaud Lebrun (www.morphomuseum.com). Surface models were semi-automatically segmented in Avizo v. 9.1 Lite (Thermo Fisher Scientific, Waltham, Massachusetts).

The pelvic remains of 14 individuals considered to belong to the Neandertal lineage (two are considered pre-Neandertals) were used for comparison and cross-validation of the applied sexing methods (SOM Table S1). Nine individuals were widely considered to be males and five were considered females (Tables 2 and 3). Metric data for extant humans are from Brůžek et al. (2017).

For most of the comparative fossil specimens, the original specimens or virtual three-dimensional (3D) models were used in this study (see SOM Table S1). Previously published metric dimensions were used only for Las Palomas 96, Shanidar 1, and La Sima de los Huesos Pelvis 1; published morphological descriptions and photographs allowed for the evaluation of morphological sex traits. Not all specimens are included in every comparative analysis due to differential preservation and availability of data. With regard to linear measurements, if one of the delimiting points was missing but very close to the preserved morphology, the dimension was measured to the most probable location of the missing point assessed by visual inspection.

2.2. *Right coxal bone reconstruction of Regourdou 1*

The pelvic remains of R1 are curated in two different institutions—Musée national de Préhistoire and Musée d'Art et d'Archéologie du Périgord—complicating their analysis. Thus, the right ilium and ischium were 3D printed to reconstruct the R1 right coxal bone. The 3D printing was performed with ProJet 460Plus using VisiJet PXL powder glued by PXL Binder Clear. The printed models were solidified with Color Bond. All chemicals were fabricated by 3D Systems (Rock Hill, South Carolina). The right coxal bone was subsequently reconstructed by reassembling the ilium and ischium and attaching them with wax. The reassembly relied on small areas of direct contact along the anterior segment of the greater sciatic notch and lunate surface of the acetabulum and was further guided by continuity of the medial and posterior surfaces of the iliac and ischial bodies (Fig. 1). However, as areas of direct connections are limited, we reassembled the coxal bone twice to evaluate the impact of reconstruction on the analyzed variables. The reassembled coxal bone was 3D scanned by a HandySCAN 3D Silver portable scanner (Creaform Inc., Levis, Canada). The ilium and ischium segmented from the μ CT scans were superimposed on virtual models of the reconstructed coxal bone and both reconstructions were compared. MeshLab v. 2020.07 (Cignoni et al., 2008) was used for the superimposition using an iterative closest point algorithm that minimizes the distance between meshes via a least squares method (Besl and McKay, 1992).

The two right coxal bone reconstructions provided direct measurements of vertical acetabular diameter (54.2 and 53.1 mm, respectively) which can be used to estimate femoral head diameter using Ruff's (2010) equation $Y = 0.945X - 6.1$. Taking into account the 95% confidence intervals, the equation provides intervals of 42.7–47.5 mm and 41.7–46.5 mm, respectively, for both reconstructions. These largely overlap with

Plavcan et al.'s (2014) estimates of femoral head diameter (43.5 to 48.5 mm) based on the ischial portion of the lunate surface. However, as the reconstructions differ in the anteroposterior inclination of the ilium relative to the ischium (Fig. 1), this may have an impact on other aspects analyzed in this study. For this reason, we used both reconstructions in subsequent analyses.

2.3. *Sex estimation methods*

The new reconstruction of the R1 right coxal bone allowed us to analyze newly available sex traits and metric dimensions that are not well preserved on the left side. Two methods were chosen for sex estimation: the morphological method proposed by Brůžek (2002) and the Probabilistic Sex Diagnosis (DSP) morphometric method by Murail et al. (2005). Both methods were recently revised and validated (Brůžek et al., 2017; Santos et al., 2019) to provide posterior probabilities of the estimate, which express the probability of a given sex attribution based on a specific combination of values provided for a specimen. These two methods are commonly used in forensic (Chapman et al., 2014; Mestekova et al., 2015; Quatrehomme et al., 2017), bioarcheological (Jerković et al., 2018), and/or paleoanthropological studies (Henry-Gambier et al., 2002; Gambier et al., 2006; Villotte et al., 2007, 2015; Samsel et al., 2016; Guyomarc'h et al., 2017). In the current study, the posterior probability threshold of 95% was used to determine sex.

The revised morphological method of Brůžek (2002) was developed on a sample of 592 adult individuals of known sex from five modern human skeletal populations (SOM Table S2) freely available as the R package 'PELVIS' (Santos et al., 2019; <https://cran.r-project.org/web/packages/PELVIS/index.html>). Using this method, sex was estimated via logistic regression based on any combination of morphological traits

evaluated as male (m), female (f) or indeterminate (i; does not mean absent). To minimize subjectivity, the 'indeterminate' category was used to classify traits that did not show distinct male or female morphology or were ambiguous due to cortical bone erosion. Descriptions of morphological traits used in this study are presented in SOM Table S3. The preauricular morphology features are also well illustrated in Perréard Lopreno et al. (2022), which was used as a guide in the evaluation of negative relief in the preauricular region.

The second version of DSP (Brůžek et al., 2017) was developed using a pooled worldwide sample of 2040 coxal bones (SOM Table S4) and is freely downloadable (<http://projets.pacea.u-bordeaux.fr/logiciel/DSP2/dsp2.html>). Using this method, sex was estimated via linear discriminant analysis based on any combination of at least four out of 10 coxal measurements (SOM Table S5; Fig. 2). Following Brůžek et al. (2017), all combinations produced a low error rate (around 1% only) when the 95% posterior probability threshold was used.

All metric dimensions were first compared to extant humans and Neandertals using univariate analysis. Sexual dimorphism in the modern human sample was tested via the nonparametric, two-tailed Wilcoxon rank-sum test (alpha level 0.05). In addition, principal components analysis (PCA) was used to analyze the preserved variables for R1 (PCA-1) in multidimensional space. A similar combination of variables was preserved in three other Neandertals (La Chapelle-aux-Saint 1, Feldhofer 1, Kebara 2), all males according to previous studies. To control for the influence of size, the raw variables were divided by their geometric mean calculated for each specimen and then processed with natural log-transformation (Mosimann, 1970; Claude, 2013). Another PCA was carried out (PCA-2) with these size-adjusted variables. Both PCAs were performed on the extant human sample including values for R1 and comparative

Neandertal specimens as supplementary individuals using the R FactoMineR package (Lê et al., 2008). All analyses were performed in RStudio v. 2023.03.1 (RStudio Team, 2016).

As neither of these sex estimation methods have been previously used to sex Neandertal pelvic remains, the methods were cross validated on other Neandertal specimens and results were compared to the available literature. As Neandertals show exceptionally long pubic rami compared to modern humans (Trinkaus, 1976, 1984; Rosenberg, 1988), it has been suggested that the sacroiliac region is more suitable for sex estimation in archaic *Homo* (Marchal, 1999). Furthermore, the inferior pubic ramus is generally not well preserved in Neandertal specimens limiting the use of ischiopubic morphological traits in sex estimation methods. As a result, we excluded the pubic region from the morphological sex estimations using Brůžek's (2002) method but for DSP analyses we calculated results both with and without pubic length. For completeness, in several cases we provide descriptions of pubic morphology following Phenice (1969) and scoring of traits following Klales et al.'s (2012) morphological sex estimation method. However, the poor preservation of the pubic region did not allow us to estimate sex using these methods.

Finally, to analyze how sex estimation changes with differential preservation in Neandertals, all possible combinations of at least four metric variables were generated for each specimen. All combinations were subsequently used to compute sex estimates with DSP.

3. Results

3.1. *Morphological traits and sex estimation*

Morphological traits for R1 are illustrated in Figure 3 and scoring of R1 and other Neandertals is summarized in Table 2. The R1 right coxal bone has a smooth preauricular region (PrSu1 = m) and shows no signs of a depression in this area (PrSu2 = m). The area of positive relief is eroded, so although it appears there was no tubercle we remain cautious in our evaluation (PrSu3 = i). The greater sciatic notch has an asymmetrical contour (GrSN2 = m) with the posterior chord is shorter than the anterior (GrSN1 = m). There is no retroversion of the posterior notch chord, but the posterior contour is in part tangential to the perpendicular line (GrSN3 = i). Lastly, the anterior segment of the notch makes a single arc with the superior border of the auricular surface (cArc = m).

The left coxal bone has a shallow depression along its preauricular region (PrSu1 = m) which has indistinct margins and is weakly developed (PrSu2 = m). The area of the potential tubercle is not preserved. The greater sciatic notch is more symmetrical than on the right side, but the segments of the notch are incomplete so it is difficult to make a proper evaluation of this region (GrSN2 = i). Meyer (2013) previously described the anterior segment of the greater sciatic notch as forming double curves with the auricular outline. However, this feature is dependent upon accurate orientation of the bone, and while we lean towards it being a single arc we remain cautious in this evaluation (cArc = i; Fig. 3), especially since it is not as clearly developed as on the right coxal bone. This may relate to a marked asymmetry previously observed in the sacrum (Rmoutilová et al., 2020), which certainly impacted the coxal bones as well.

Amud 1, assessed to be male (Endo and Kimura, 1970; Trinkaus, 1980), has a preserved greater sciatic notch, but a large portion of its posterior segment is missing

as is its ischial spine, so it is not possible to evaluate greater sciatic notch morphology. Although the preserved contour has previously been described as asymmetrical in lateral view (Endo and Kimura, 1970), a missing portion of the posterior segment creates ambiguity in the evaluation of greater sciatic notch symmetry in medial view (the appropriate view for scoring this trait following Brůžek [2002]). A sufficient portion of the anterior segment is preserved to evaluate the composite arc, which tends to form a double curve with the outline of the auricular surface, but the auricular outline is not well preserved and therefore we remain cautious in the evaluation (cArc = i; Table 2).

Arago 44, assessed to be female (de Lumley, 2015), preserves all features analyzed in this study. There is a small depression in the preauricular surface approximately in the middle along the inferior auricular demiface (PrSu1 = f) which is clearly demarcated (PrSu2 = f; Table 2). There is also a marked protuberance in the lower portion of the preauricular region (PrSu3 = m). The greater sciatic notch has a shorter posterior than anterior chord (GrSN1 = m), but its general shape is rather symmetrical (GrSN2 = f) and there is no retroversion of the posterior notch chord (GrSN3 = f). The anterior segment of the notch is unusually straight, but it forms double arcs with the outline of the auricular surface (cArc = f).

La Chapelle-aux-Saints 1, assessed to be male (Boule, 1911–13; Trinkaus, 2011), preserves all features analyzed in this study. As the original was lost, we used a cast of the right coxal bone that was reconstructed based on the left counterpart soon after its discovery, and original illustrations and descriptions (Boule, 1911–13). There is a small, shallow groove in the preauricular region approximately in the middle along its inferior auricular demiface (PrSu1 = i). It is not well delimited (PrSu2 = m; Table 2) and represents a paraglenoid sulcus (Perréard Lopreno et al., 2022) rather than a preauricular sulcus. There is no clear protuberance (PrSu3 = f). The greater sciatic

notch is quite asymmetrical (GrSN2 = m) with its posterior chord shorter than the anterior (GrSN1 = m). There is no retroversion of the posterior notch chord (GrSN3 = f). The anterior segment of the notch makes a single arc with the outline of the auricular surface (CArc = m).

Feldhofer 1, assessed and genetically confirmed to be male (Schaaffhausen, 1888; Trinkaus, 1980; Skoglund et al., 2013), has a shallow depression along its preauricular region (PrSu1 = m) which is not well delimited (PrSu2 = m; Table 2). There is evidence of positive relief, but its surface is eroded, so we remain cautious in our evaluation (PrSu3 = i). Its greater sciatic notch is clearly asymmetrical (GrSN2 = m) with its posterior chord shorter than the anterior (GrSN1 = m). There is retroversion of the posterior notch chord (GrSN3 = m). The anterior segment of the notch makes a single arc with the outline of the auricular surface (cArc = m).

La Ferrassie 1, assessed to be male (Heim, 1982), has a well preserved greater sciatic notch on the left side with a missing portion of its posterior segment. There is no negative relief in the preauricular region (PrSu1 = m, PrSu2 = m) with a trace of a developed tubercle near the posterior inferior iliac spine. The rest of this region is missing so we remain cautious in our evaluation (PrSu3 = i; Table 2). The greater sciatic notch is quite asymmetrical (GrSN2 = m) with its posterior chord shorter than the anterior chord (GrSN1 = m). There is retroversion of the posterior notch chord (GrSN3 = m). The anterior segment of the notch makes a single arc with the outline of the auricular surface (cArc = m).

Grotte du Prince (de Lumley-Woodyear, 1973) preserves only a basal portion of the greater sciatic notch. The preauricular area is not well preserved, so it was not possible to evaluate traits in this region. The greater sciatic notch is symmetrical (GrSN2 = f; Table 2), but we could not evaluate its chords. That said, it is unlikely the perpendicular

line would cross the posterior contour of the notch (GrSN3 = f). The composite arc forms double arcs (cArc = f).

Kebara 2, assessed to be male (Rak and Arensburg, 1987), has a well preserved right coxal bone and a taphonomically deformed left counterpart. Both show sexually dimorphic features. The right coxal bone shows a small but distinct groove near the posterior inferior iliac spine with a vascular foramen, so it does not show a 'typical' female morphology (PrSu1 = i). The groove is shallow (PrSu2 = m; Table 2) and is consistent in position and morphology with a paraglenoid sulcus (Perréard Lopreno et al., 2022). There is also a tubercle in the preauricular region (PrSu3 = m). The greater sciatic notch is highly asymmetrical (GrSN2 = m) with its posterior chord shorter than the anterior (GrSN1 = m). There is retroversion of the posterior notch chord (GrSN3 = m). The anterior segment of the notch forms a single arc with the auricular outline (cArc = m). The left coxal bone shows slight negative relief with closed circumference near the auricular apex (PrSu1 = f); the groove is formed by two weakly-developed pits (PrSu2 = f). There is a trace of a developed tubercle in the lower part, but the rest of the region is missing, which limits unambiguous evaluation (PrSu3 = i). The greater sciatic notch is very similar to the right coxal bone: it is highly asymmetrical (GrSN2 = m) with the posterior chord shorter than the anterior chord (GrSN1 = m) and there is retroversion of its posterior notch chord (GrSN3 = m). The anterior segment of the notch forms a single arc with the auricular outline (cArc = m).

Krapina 207, assessed to be male (Smith, 1976; Bonmatí and Arsuaga, 2007; Trinkaus, 2016b), has an almost indistinctly depressed preauricular region (PrSu1 = m, PrSu2 = m; Table 2). The greater sciatic notch is asymmetrical (GrSN2 = m) with the posterior chord shorter than the anterior (GrSN1 = m) and there is likely retroversion of the posterior chord (GrSN3 = i). The auricular surface lies in a more

posterior position relative to the greater sciatic notch, so the anterior segment and the auricular outline form two separate curves (cArc = f).

Krapina 209, assessed to be female (Smith, 1976; Bonmatí and Arsuaga, 2007; Trinkaus, 2016b), has an intact posterior portion of the greater sciatic notch, but its anterior segment is almost completely missing. However, a portion of the anterior segment at the base of the ischial spine allowed us to infer the overall morphology of the notch. The preauricular surface is almost smooth (PrSu1 = i) with an indistinct depression (PrSu2 = m; Table 2). Posteriorly, there is a well-developed tubercle (PrSu3 = m). The greater sciatic notch is symmetrical (GrSN2 = f) with both chords of approximately equal length (GrSN1 = f). The perpendicular chord does not cross the notch outline but is superimposed on part of the posterior segment (GrSN3 = i). The anterior segment and auricular outline form two separate curves (cArc = f).

Las Palomas 96, assessed to be female (Walker et al., 2011), was evaluated based on photographs and morphological descriptions (Walker et al., 2011). The greater sciatic notch looks to be symmetrical (GrSN1 = f, GrSN2 = f; Table 2). The anterior segment and auricular outline form two separate curves (cArc = f).

La Sima de los Huesos Pelvis 1, assessed to be male (Arsuaga et al., 1999; Bonmatí et al., 2010), was evaluated based on photographs and morphological descriptions (Arsuaga et al., 1999; Bonmatí et al., 2010). From this documentation we could not evaluate the morphology of the preauricular area. The greater sciatic notch is asymmetrical (GrSN2 = m) with the posterior chord shorter than the anterior chord (GrSN1 = m; Table 2). The course of the perpendicular line could not be evaluated. The anterior segment of the notch forms a single arc with the auricular outline (cArc = m).

Tabun C1, assessed to be female (McCown and Keith, 1939), has a very taphonomically distorted pelvis that has been reconstructed using mirror-imaging (Weaver and Hublin, 2009) and the reconstruction allowed us to evaluate the morphology of the greater sciatic notch. The notch is symmetrical ($GrSN2 = f$; Table 2). Although the auricular outline cannot be easily identified, it can be inferred that the anterior segment of the notch and the auricular outline form two separate curves ($cArc = f$).

Although not included in the final sex estimation analysis, ischiopubic proportion was visually evaluated following Brůžek (2002) in five specimens, four presumed males and one female. In all specimens the pubis was longer than the ischium leading to female morphology (Table 2). Pubic morphology was partially observed in five specimens allowing us to evaluate ventral arc and medial aspect following Kiales et al. (2012). Kebara 2 has weakly developed ventral arc (score 4) as well as La Ferrassie 1 (4), whose medial aspect of the inferior pubic ramus is moderately robust (3 or 4). Shanidar 1 has a weakly developed ventral arc (4) and the inferior ramus is rather robust, but a moderately sharp ridge is present below the pubic symphysis (3). Sima de los Huesos Pelvis 1 shows no ventral arc (5). Tabun C1 shows mildly developed ventral arc (3 to 4).

Using the classification method of Santos et al. (2019) based on the above-described morphological traits, R1 was assessed to be a male. The reconstructed right coxal bone provided more traits for the evaluation and a higher posterior probability, exceeding the 0.95 threshold, while the left coxal bone provided slightly lower posterior probability but still indicating male sex (0.721; Table 2). Using all preserved traits from both sides, R1 is classified as a male with 0.955 posterior probability.

Application of the morphological method was possible for all Neandertal coxal bones except Krapina 208 and Shanidar 1 (Table 2). Excluding ischiopubic proportion, this method provided a sex estimate (posterior probability ≥ 0.95 for males or females) for nine bones, and all were congruent with the previously published sex attributions. Four bones were indeterminate; three of them reached considerably high posterior probabilities between 0.8 to 0.9. The more probable sex was congruent with the literature except for the left coxal bone of Kebara 2, which provided a different result than its right coxal bone. However, classifying both coxal bones together, Kebara 2 was classified as a male. Posterior probabilities for Amud 1 were around 0.5 leading to a low certainty of the estimated sex. As all Neandertals had female-like ischiopubic proportions, this trait decreased the posterior probability of being male, but only in Krapina 207 was the difference important enough to favor female sex. Considering differential preservation of fossil specimens, all combinations of traits led to overall accuracy between 93 and 99% using 10-fold cross-validation based on individuals with posterior probability ≥ 0.95 (Santos et al., 2019).

3.2. *Metric dimensions and sex estimation*

Univariate analysis Six metric dimensions were available following the reconstruction of the R1 right coxal bone: greater sciatic notch height, ischial postacetabular length, spino-sciatic length, spino-auricular length, cotylo-sciatic breadth, and vertical acetabular diameter (Table 3). Dimensions affected by the reconstruction process (greater sciatic notch height, ischium postacetabular length, and vertical acetabular diameter) were measured on both reconstructions and both values are provided. As the posterior inferior iliac spine is slightly eroded, greater sciatic notch height was measured several times, minimum and maximum values were rounded to the

respective lower or upper limits, and both values were considered in subsequent analyses separately. Univariate comparisons of both R1 reconstructions with extant humans and other Neandertals are provided in Figure 4 and Table 3.

The modern human sample shows marked sexual dimorphism for all linear dimensions except spino-auricular length and Neandertals show similar patterns of sexual dimorphism for individual variables (Table 3; SOM Table S5). Greater sciatic notch height is the only measurement that shows sexual dimorphism with modern females having significantly greater values than males (Fig. 4). Neandertal values tend to fall in the lower portion of the modern human range of variation for both males and females. Both minimum and maximum values of greater sciatic notch height for R1 fall within the range of Neandertal male variation. Ischial postacetabular length shows strong sexual dimorphism with moderate overlap between males and females. Sex differences in Neandertals are accentuated, with males in the upper portion of extant male variation while the sole Neandertal female, represented by the small Tabun C1 specimen, falls at the lowest end of extant female variation. Regourdou 1 falls well within the range of variation for extant males but at the lower end of the Neandertal male range. Spino-sciatic length shows greater overlap between modern males and females as well as in Neandertals. Similarly, greater overlap is also apparent in Neandertal males and females while both tend to have slightly shorter spino-sciatic length than modern humans. Regourdou 1 lies well within Neandertal variation. The spino-auricular length does not show any sexual dimorphism in modern humans or Neandertals. Neandertal values are distributed around the modern human median with a slight tendency toward the upper portion of variation. Regourdou 1 is at the median of modern humans. Cotylo-sciatic breadth shows moderate sexual dimorphism in modern humans as well as in Neandertals. Neandertals tend to have a shorter cotylo-

sciatic breadth than modern humans. Regourdou 1 is close to the modern female median and lies well within the Neandertal male range of variation. Vertical acetabular diameter shows strong sexual dimorphism in modern humans with Neandertals again falling towards the upper range of modern human variation. Regourdou 1 falls below the modern male median and at lower end of the Neandertal male range of variation.

Multivariate analysis For PCA-1 (performed on the raw variables) we first chose two principal components (PCs) having eigenvalues greater than 1 based on Kaiser-Guttman rule (Peres-Neto et al., 2005). Together they comprise 80.6% of the total variance (Table 4). Principal component 1 (57.2% of the variance) represents the overall size of the coxal bone and except for greater sciatic notch height, all variables are positively correlated with PC1 (Table 4). Principal component 2 (23.4% of the variance) is strongly positively correlated with greater sciatic notch height and mildly correlated with spino-auricular length. Both PCs reflect differences between extant males and females (Table 4; Fig. 5a); males have more positive values along PC1, while females have more positive values along PC2. This indicates differences in general body size and shape related to the shape of the greater sciatic notch and position of the auricular surface. Except for La Chapelle-aux-Saints 1, all other Neandertal males including both reconstructions of R1 and minimum and maximum measurements of greater sciatic notch height fall within the range of variation of extant modern males and outside the extant female range. Neandertal males tend to have positive values for PC1 indicating larger general size, while all of them have negative values for PC2 showing narrower greater sciatic notches and rather short spino-auricular lengths.

In PCA-2 (natural log-transformed shape variables), three PCs have eigenvalues greater than 1, together comprising 88.6% of the total variance (Table 4). Principal

component 1 (52.4% of the variance) correlates positively with size-adjusted variables except for greater sciatic notch and spino-auricular length, which show strong to moderate negative correlations with PC1. This means that with positive values, coxal bones have large acetabula (vertical acetabular diameter) and ischia (ischium postacetabular length; cotylo-sciatic breadth), and broad iliac bodies (spino-sciatic length), but narrow greater sciatic notches and more anteriorly positioned auricular surfaces (short spino-auricular length). Principal component 2 (19.0% of the variance) shows moderate positive correlations with spino-sciatic length and cotylo-sciatic breadth and a negative correlation with vertical acetabular diameter. Principal component 3 (17.2% of the variance) shows a strong positive correlation with spino-auricular length and is negatively correlated with cotylo-sciatic breadth.

In PCA-2, sexual dimorphism between extant males and females is captured by PC1, with no sexual dimorphism apparent along PC2 or PC3 (Fig. 5b; SOM Fig. S3). Regourdou 1 clusters with other Neandertal males who tend to have positive values along PC1 and PC3 (SOM Fig. S3) and negative values along PC2 (Fig. 5). Neandertal males tend to have extreme male morphology along PC1 having relatively large acetabula, ischia, and lower ilia, but narrow greater sciatic notches with anteriorly positioned sacra (Table 4). Based on PC2 and PC3 they have narrow iliac bodies relative to acetabula and a longer distance to the sacrum relative to ischial body breadth (Fig. 5; SOM Fig. S3; Table 4).

Sex estimation with probabilistic sex diagnosis Using all preserved dimensions, R1 was estimated to be a male with a posterior probability of 0.96–0.99 based on the minimum and maximum values of the greater sciatic notch (Table 3).

The metric method was applied to 12 comparative Neandertal specimens (Table 3). Excluding acetabulo-symphyseal length, sex was provided (posterior probability \geq

0.95) for eight individuals. Of those individuals, only one was classified differently from the literature (Amud 1). All four indeterminate individuals reached relatively high posterior probabilities (between 0.7 and 0.95) and all except Arago 44 were assigned in accordance with previously published studies. Due to the inconsistency in the classification of Amud 1 and Arago 44, we consider them indeterminate.

Inclusion of acetabulo-symphyseal length in Kebara 2, Krapina 208 and 209, La Ferrassie 1, La Sima de los Huesos 1, and Tabun C1 decreased the posterior probability of male sex, weakening and reinforcing classification of males and females, respectively. Except for Kebara 2, inclusion of pubic length generally did not change final sex attribution (Table 3).

Probabilistic sex diagnosis with different variable combinations In total, 22 combinations of at least four variables were possible for all preserved dimensions of R1 (Table 5; Fig. 6). A distribution of posterior probabilities was clearly skewed and shifted towards the male range. Most of the combinations indicated male sex with posterior probability ≥ 0.95 , while no combination indicated female sex with high probability (Table 5; Fig. 6). Both R1 reconstructions yielded similar results.

Sex estimation results were comparably distributed for all other Neandertal specimens, i.e., they tended to accumulate in the male or female portion of the spectrum based on the result of all preserved variables (Fig. 6). Most specimens had a median posterior probability still higher than 0.95 for the respective sex (Table 5); the exceptions are Arago 44, Grotte du Prince, Krapina 207, and Krapina 209.

We further analyzed the potential effect of number of variables on sex estimation (SOM Fig. S4). Generally, combinations with fewer variables led to greater variance of results and an increased number of results in the indeterminate zone, which corresponds to the use of DSP in modern human populations (Brůžek et al., 2017). By

increasing the number of variables, the certainty of sex estimation increased. This was most evident in Feldhofer 1 and Kebara 2 which produced a combination of four variables that yielded the opposite (female) sex, in contrast to results using a larger number of variables. Nevertheless, for Arago 44, Krapina 207, and Krapina 209, this trend was not observed, as the results with the highest posterior probabilities were achieved using fewer variables (SOM Fig. S4).

Finally, to analyze the possible effect of certain variables or combinations of variables, we plotted sex estimation results against specific variables appearing in a given combination (SOM Fig. S5). No strong tendency across specimens was observed, but Arago 44, Feldhofer 1, and Kebara 2 shared a combination of variables that led to their assignment as female, the opposite of the majority of the results. This combination consisted of four variables: coxal breadth, spino-sciatic length, spino-auricular length, and cotylo-sciatic breadth. Especially in Kebara 2, it is apparent that combinations containing these variables more frequently led to female sex attribution (SOM Fig. S5). By contrast, combinations containing the two variables cotylo-pubic width and greater sciatic notch height show far fewer results in the female spectrum.

4. Discussion

4.1. Sex estimation of Regourdou 1

To sex the R1 skeleton, we took advantage of a number of preserved Neandertal pelvic remains to compare two methods of sex estimation and cross-validate them on the Neandertal sample. The R1 right coxal bone indicates male sex with high probability (0.956–0.995) using both the morphological (Brůžek, 2002; Santos et al.,

2019) and morphometric methods (Murail et al., 2005; Brůžek et al., 2017). While the left counterpart is not as well preserved (thus only morphological traits could be evaluated), it also indicated male sex, but with a smaller (albeit still relatively high) probability (0.721). This slight difference could be related to the previously observed asymmetry of the sacrum having an abnormally short right lateral ala (Rmoutilová et al., 2020).

Morphometrically, R1 lies well within the modern male pelvic range of variation (Figs. 4 and 5) despite its spino-sciatic length and cotylo-sciatic breadth, which are more within the female range. However, other Neandertal males are also shifted toward modern females in these dimensions, which may indicate systematic differences in Neandertal pelvic morphology. Based on our results, R1 was a male of an intermediate stature (162–172 cm) among Neandertals considered males (see references in Table 1) and smaller body mass (64–66 kg) based on its relatively small lower limb articulations (Table 1).

4.2. *Cross-validation in the Neandertal sample*

With respect to poor preservation and unusual morphology in the pubic region, the greater sciatic notch has been used preferentially to assess sex in Neandertals (Boule, 1911–13; McCown and Keith, 1939; Trinkaus, 1980; Heim, 1982; Walker et al., 2011). However, validated sex estimation methods providing posterior probability of the result have been used in only few Neandertal specimens. Kebara 2 was analyzed via DSP (Chapman, 2017) with and without its acetabulo-symphyseal pubic length, which showed how pubic length biases sex estimation in Neandertals. Comparison of morphological and metric approaches was performed on the coxal bones from Krapina (Bonmatí and Arsuaga, 2007). General shape of the greater sciatic notch and the

composite arc were evaluated with the morphological approach while three iliac dimensions were used for morphometric classification. The latter was based on a modern human sample in which the overall accuracy reached an intermediate discriminatory power of 82% (Bonmatí and Arsuaga, 2007). This method applied to the Krapina sample and other fossil specimens yields female sex in most individuals (including Amud 1, Feldhofer 1, Kebara 2) which contradicted previous morphological assessments, indicating either the overall inefficacy of the discriminant model or differences in sexual dimorphism. Morphological features in the Krapina coxal bones were also evaluated by Smith (1976) and Trinkaus (2016b). While there is agreement in the general morphology of the greater sciatic notch, other traits show disparities in their evaluation between observers (see SOM Table S1); in particular the composite arc was susceptible to low interobserver agreement as a subtle difference in inclination of the coxal bone may greatly influence the viewing angle.

In most cases our cross-validation on other Neandertal coxal bones resulted in similar sex assignments, which also corresponded to the most frequent sex in the literature (Table 6), but there were some exceptions (discussed below). Including the pubic region in Neandertals reduced the posterior probability of male sex but in most Neandertals considered males were still indicated as male. Both methods that we used are very successful, reaching almost 100% accuracy with every combination of traits/variables and with respect to results having posterior probability ≥ 0.95 . Both methods were developed on a geographically diverse modern human populations and they were successfully used in Upper Paleolithic modern humans (Brůžek et al., 2006; Gambier et al., 2006; Villotte, 2009) as has been confirmed by analysis of ancient DNA multiple times (Fu et al., 2016; Mittnik et al., 2016). Although ancient genetic and proteomic methods (Stewart et al., 2017; Buonasera et al., 2020) are important in sex

estimation of fragmentary remains, they are destructive and thus have not been used to determine sex of most of the well preserved Neandertal skeletons; the exception from our sample is Feldhofer 1 (Skoglund et al., 2013).

Despite having a relatively large body size and the tallest stature of all Neandertals (Trinkaus, 1980; Carretero et al., 2012), Amud 1 was classified as a female by the metrical method. However, some of the metric dimensions preserved in Amud 1 show a general tendency toward modern female values in all Neandertals. Another exception was Arago 44, whose morphological features indicate female sex while metrically it is classified as a male. This specimen has a well-preserved greater sciatic notch which is more female-like than other Neandertals considered males, while other dimensions indicate larger body size. As there is evidence of exceptionally robust females in the Middle and Late Pleistocene fossil record (Rosenberg et al., 2006; de Lumley, 2016), it may be prudent to reconsider the sex of these two individuals.

The final exception was Kebara 2 which preserves both coxal bones. This individual is considered male, which is supported by the right coxal bone (both methods), but its left counterpart clearly shows traits considered female (Table 2), including a previously described depression in the preauricular area (Rak, 1991). Its sacroiliac region as well as the auricular surface are clearly asymmetrical especially in the shape of the inferior demiface (Duday and Arensburg, 1991). Importantly, this specimen shows multiple developmental anomalies in the pelvic region (Duday and Arensburg, 1991; Trinkaus, 2018) including vascular abnormalities in the preauricular region, and so the depressions in this area cannot be interpreted as a classical female trait (Duday and Arensburg, 1991).

The analysis of all possible combinations (Fig. 6; Table 5) confirmed a tendency toward the more probable sex in all specimens. In general, a large number of

combinations produced indeterminate results, but results pointing to the opposite sex were rare. The opposite sex was predicted only for Arago 44, Kebara 2, and Feldhofer 1, all based on the identical combination of variables (coxal breadth, spino-sciatic length, spino-auricular length, cotylo-sciatic breadth) which are generally less effective in the DSP method (Brůžek et al., 2017). However, this result may also reflect a systematic bias in Neandertal morphology.

Neandertals differed from modern humans in body size and shape (Holliday, 1997; Gómez-Olivencia et al., 2018) and it has been suggested that the Neandertal pelvis showed different postural and biomechanical adaptations (Rak, 1993; Marchal, 2000). Specifically, Neandertals had extremely long pubic bones (Trinkaus, 1984; Rosenberg, 1988), posteriorly positioned acetabula within the pelvic ring (Rak and Arensburg, 1987; Rak, 1990; Adegboyega et al., 2021), and a more posteriorly tilted sacrum (Been et al., 2017). In addition, it has been suggested that Neandertals did not necessarily follow the modern human pattern of sexual dimorphism in two aspects. First, pubic length is extremely long in Neandertal males, suggesting a lower degree of sexual dimorphism. This could potentially be the result of large body size (Rosenberg, 1988), adaptation to cold (Weaver, 2003, 2009), and/or different locomotor and postural adaptations (Rak, 1991; Weaver et al., 2016). Simultaneously, it has been suggested that Neandertals could have had more pronounced sexual dimorphism in pubic orientation in contrast to length dimorphism (Weaver and Hublin, 2009) to accommodate the Neandertal fetus during birth that may not have involved rotation of the fetal head (Weaver and Hublin, 2009; Franciscus, 2009; but see Ponce de León et al., 2008). Second, structural differences in the posterior pelvis may have had consequences for the greater sciatic notch showing a rather closed morphology (Brůžek and Tillier, 1996), and thus a lower degree of sexual dimorphism (Bonmatí et

al., 2010; VanSickle, 2014). However, a posteriorly tilted sacrum (Been et al., 2017) may lead to a more posterior position of the auricular apex relative to greater sciatic notch, potentially changing spatial relationships between these two structures and shifting Neandertals toward modern female variation as seen in SOM Figure S6. Although it has been suggested that the sacroiliac region is more suitable for sexing hominin fossil remains (Marchal, 1999), these aspects of Neandertal pelvic morphology may hinder sex estimation on the basis of modern human metric standards.

Despite the general pattern of sexual dimorphism in the pelvis shared by primates (Fischer et al., 2021), the pelvis consists of relatively independent morphological units (Grabowski et al., 2011; Lewton, 2012) which may differ in relative contributions to sexual dimorphism among different species or populations. As sex estimation is usually performed on aspects of pelvic morphology determined by preservation in fossil specimens, we need to analyze morphological variation of these traits in fossil hominins and to better understand functional aspects of their morphological differences.

5. Conclusions

Based on our results the Regourdou 1 individual was classified as male via both morphological and metric methods based on the coxal bones. Sex estimation methods used in this study provided consistent results for most comparative Neandertal specimens with few exceptions. Our results imply that both methods can be used on this fossil sample. However, morphological variation in individual aspects of the Neandertal pelvis needs to be analyzed in more detail to better understand the underlying sexual dimorphism.

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Figure captions

Figure 1. Two possible alignments (grey and transparent green) of the right ilium to the ischium on the left with detailed view of areas that guided the alignment on the right.

Figure 2. Metric variables used in DSP (Brůžek et al., 2017). The variable indicated in red (PUM) was excluded in the final sex estimation due to systematic differences between Neandertals and modern humans. DCOX = coxal length, IIMT = greater sciatic notch height, ISMM = postacetabular length, PUM = acetabulo-symphyseal pubic length, SA = spino-auricular length, SCOX = coxal breadth, SIS = cotylo-sciatic breadth, SPU = cotylo-pubic width, SS = spino-sciatic length, VEAC = vertical acetabular diameter. See SOM Table S5 for variable definitions.

Figure 3. Morphological traits in Regourdou 1 following Brůžek (2002) and Santos et al. (2019): a) evaluation of the greater sciatic notch, b) single arc in the right coxal bone, and c) indeterminate arc in the left coxal bone (the auricular outline is not in direct continuation with the greater sciatic notch, but it does not constitute two regular arcs either).

Figure 4. Six coxal dimensions preserved in Regourdou 1 (R1) compared with modern humans (boxplots) and other Neandertal and Middle Pleistocene individuals (points). Boxplots: central bar = median, box = interquartile range, whiskers = minimum and maximum, black dots = outliers beyond 1.5 of the interquartile range from either end of the box. Fossil specimens are marked by their acronyms and plotted separately by sex as suggested in the literature. Sex assignment for the fossil specimens based on our analysis is indicated by point colors (grey = indeterminate). A1 = Amud 1, A44 =

Arago 44, C1 = La Chapelle-aux-Saints 1, FH1 = Feldhofer 1, F1 = La Ferrassie 1, GP = Grotte du Prince, K2 = Kebara 2, K207 = Krapina 207, K208 = Krapina 208, K209 = Krapina 209, S1 = Shanidar 1, SH1 = La Sima de los Huesos Pelvis 1, T1 = Tabun C1.

Figure 5. Principal components analysis of six metric dimensions preserved in Regourdou 1 (R1). a) principal components analysis on raw variables (PCA-1), b) principal components analysis on log-shape variables (PCA-2). Ellipses indicate 95% confidence intervals for modern males and females. Regourdou 1 is represented by two different reconstructions of the right coxal bone and minimum and maximum values of greater sciatic notch height. C1 = La Chapelle-aux-Saints 1, FH1 = Feldhofer 1, K2 = Kebara 2. Regourdou 1 falls close to other Neandertal males who tend to be near the extreme edge of modern male variation.

Figure 6. Posterior probability of male for every combination of each specimen's preserved variables. To avoid excessive overplotting, points are randomly scattered in vertical dimension. La Chapelle 1 = La Chapelle-aux-Saints 1. The majority of combinations classifies Regourdou 1 as male. For most of other specimens results are distributed toward the previously estimated sex (see Table 3).

Table 1

Stature and body mass estimates of Regourdou 1.

Skeletal element	Estimate	Error	Method	Reference sample	Reference
Body mass [kg]					
Femoral head	65.6	–	Ruff (2010)	Mean from pooled sex samples ^a	Plavcan et al. (2014)
Talar trochlea	64.4	–	McHenry (1992)	Khoisan and African Pygmies	Pablos et al. (2019)
Stature [cm]					
Humerus, radius	166.1–167.5	–	Trotter and Gleser (1952)	Terry Collection Euro-American males	Vandermeersch and Trinkaus (1995)
	162.2–162.4	4.9–5.0	Sjøvold (1988)	Mean from pooled sex samples	Carretero et al. (2012)
Foot	172.3	4.3	Pablos et al. (2013)	Hamann-Todd Collection males	Pablos et al. (2019)
Sacral vertebrae ^b	170.3	6.8	Pelin et al. (2005)	Turkish males	This study
Thoracic and lumbar vertebrae ^c	171.0	5.5	Tibbetts (1981)	Terry Collection Afro-American males	This study

^a Living US sample (Ruff et al., 1991), Khoisan and African Pygmies (McHenry, 1992), African, European and Native Americans (Grine et al., 1995)

^b Heights of S1 and S2 were measured.

^c Data from Gómez-Olivencia et al. (2013a; b). Heights of missing vertebrae were estimated following Vilas-Boas et al. (2019).

Table 2

Scoring of Neandertal sexual traits based on the method of Santos et al. (2019).

Specimen ^a	Side	PrSu1	PrSu2	PrSu3	GrSN1	GrSN2	GrSN3	CArc	IsPu ^b	P(M)	P(F)	Sex	Lit. ^c
Regourdou 1	right	m	m	i	m	m	i	m	–	0.995	0.005	M	M/I
	left	m	m	–	–	i	–	i	–	0.721	0.279	I (M)	
	both									0.955	0.045	M	
Amud 1	left	–	–	–	–	–	–	i	–	0.586	0.414	I (M)	M
Arago 44	left	f	f	m	m	f	f	f	–	0.003	0.997	F	F
Feldhofer 1	left	m	m	i	m	m	m	m	–	0.993	0.007	M	M
Grotte du Prince	right	–	–	–	–	f	f	f	–	0.035	0.965	F	F
Kebara 2	right	i	m	m	m	m	m	m	f	0.995 (0.904) ^b	0.005 (0.096) ^b	M	M
	left	f	f	i	m	m	m	m	–	0.189	0.811	I (F)	
	both									0.813	0.187	I (M)	
Krapina 207	left	m	m	–	m	m	i	f	f	0.920 (0.172) ^b	0.080 (0.828) ^b	I (M)	M
Krapina 209	right	i	m	m	f	f	i	f	–	0.064	0.936	I (F)	F
La Chapelle 1	both	i	m	f	m	m	f	m	–	0.987	0.013	M	M
La Ferrassie 1	left	m	m	i	m	m	m	i	f	0.963 (0.877) ^b	0.037 (0.123) ^b	M	M
Las Palomas 96	right	–	–	–	f	f	–	f	–	0.014	0.986	F	F
SH Pelvis 1	left	–	–	–	m	m	–	m	f	0.964 (0.505) ^b	0.036 (0.495) ^b	M	M
Tabun C1	both	–	–	–	–	f	–	f	f	0.038 (0.006) ^b	0.962 (0.994) ^b	F	F

Abbreviations: GrSN, greater sciatic notch; CArc, composite arc; PrSu, preauricular sulcus; IsPu, ischiopubic proportion; P(M), posterior probability of

belonging to a male; P(F), posterior probability of belonging to a female; Lit., literature; m or M, male; f or F, female; i or I, indeterminate.

The en dash is used when a trait is not preserved or available (e.g., the case of Palomas 96).

^a Krapina 208 was not sufficiently complete to evaluate morphological traits.

^b IsPu was systematically excluded from sex estimation analyses, but posterior probabilities including this feature are provided in parentheses.

^c Sex suggested in previous studies (see references in Table 6).

Table 3

Linear dimensions (in mm) of Regourdou 1 (different reconstructions indicated by a and b) and other Neandertal specimens for sex diagnosis using the metrical (DSP) method (Murail et al., 2005; Brůžek et al., 2017).^a

Specimen ^b	Side	PUM ^c	SPU	DCOX	IIMT	ISMM	SCOX	SS	SA	SIS	VEAC	P(M)	P(F)	Sex	Lit. ^g
Regourdou 1a	right	–	–	–	<u>29.8</u> <u>33.0^d</u>	<u>110.5^d</u>	–	66.8	75.2	34.5	54.2	0.966–0.986	0.014–0.034	M	M/I
Regourdou 1b	right	–	–	–	<u>28.0</u> <u>32.0^d</u>	<u>109.5^d</u>	–	66.8	75.2	34.5	53.1	0.956–0.985	0.015–0.044	M	
Amud 1	left	–	<u>24</u>	–	–	–	–	74.2	90.6	38.7	57.1	0.017	0.983	F	M
Arago 44	left	–	–	–	43	–	<u>177</u>	<u>72</u>	<u>88</u>	37	61.5	0.732	0.268	I(M)	F
Feldhofer 1	left	–	–	<u>228</u>	34.4	<u>123</u>	<u>160</u>	68.9	83.3	39.2	61.8	1.000	0	M	M
Grotte du Prince	right	–	–	–	–	–	–	67.2	85	32	58.1	0.081	0.919	F	F
Kebara 2	right	<u>87.5</u>	31	227.5	31.8	111.9	<u>157.9</u>	63.9	76	31.9	58.9	1.000 (0.344) ^c	0 (0.656) ^c	M	M
Krapina 207	left	–	–	<u>205</u>	<u>32</u>	–	–	<u>68</u>	<u>78</u>	31.3	53.2	0.719	0.281	I(M)	M
Krapina 208	right	<u>81</u>	30.7	–	–	<u>120</u>	–	–	–	<u>36</u>	56.1	0.992 (0.955)^c	0.008 (0.045) ^c	M	M
Krapina 209	right	<u>83</u>	25.3	–	36.3	–	–	63.9	78.8	<u>31</u>	54.8	0.291 (0.001) ^c	0.709 (0.999) ^c	I (F)	F
La Chapelle 1	both	–	–	–	<u>30.4</u>	<u>123</u>	–	64	68.4	40	61	1.000	0	M	M
La Ferrassie 1	left	<u>89.7</u>	30.7	–	28.4	<u>119</u>	–	–	–	36.2	59.9	1.000 (0.856) ^c	0 (0.144) ^c	M	M
Shanidar 1	right	93	–	–	–	–	–	–	–	33	–	–	–	–	M
SH Pelvis 1 ^e	left	83.9	–	240	–	–	180.8	–	–	–	58.8	0.970 (0.904) ^c	0.030 (0.096) ^c	M	M
Tabun C1	both	80.5	26	<u>200</u>	–	<u>90.2</u>	–	60.5	73.1	29.9	<u>48^f</u>	0.002 (0) ^c	0.998 (1.000) ^c	F	F
Modern males	right	69.9 ± 5.2	29.6 ± 2.9	214.9 ± 13.4	40.0 ± 5.7	113.1 ± 6.8	157.0 ± 10.9	74.3 ± 5.8	75.3 ± 6.3	39.5 ± 4.0	57.0 ± 3.4	–	–	–	–
Modern females	right	72.4 ± 5.2	24.5 ± 2.6	197.7 ± 11.2	45.6 ± 5.6	101.3 ± 5.4	152.8 ± 10.5	68.1 ± 4.9	75.4 ± 6.9	35.7 ± 3.5	51.1 ± 2.9	–	–	–	–

Abbreviations: PUM, acetabulo-symphyseal pubic length; SPU, cotylo-pubic width; DCOX, coxal length; IIMT, greater sciatic notch height; ISMM, postacetabular length; SCOX, coxal breadth; SS, spino-sciatic length; SA, spino-auricular length; SIS, cotylo-sciatic breadth; VEAC, vertical acetabular diameter; P(M), posterior probability of belonging to a male; P(F), posterior probability of belonging to a female; Lit., literature; I, indeterminate.

^a Underlined values were slightly estimated; usually one of the delimiting points was not preserved but was very close to the preserved morphology. Missing values (–) were not preserved or available in the literature. Values in bold are above the 0.95 posterior probability threshold. Modern males and females are indicated by mean ± standard deviation. All variables except for SA were significant ($p < 0.05$) for sexual dimorphism in the modern sample based on the nonparametric two-tailed Wilcoxon rank-sum test.

^b Kebara 2 left coxal bone and Las Palomas 96 were not measured due to poor preservation or inaccessibility.

^c PUM was systematically excluded from sex estimation analyses but posterior probabilities including this measurement are provided in parentheses.

^d For IIMT, the delimiting point close to the auricular surface was not clear in R1. Therefore, minimum and maximum values were used. For ISMM, the anterior tip of the ischial tuberosity is not preserved but borders of the tuberosity appear to be converging. Therefore, the ISMM was measured to the most anterior preserved point on the ischial tuberosity, which has minimal impact on the final value.

^e For La Sima de los Huesos 1, only three measurements were available after excluding PUM from sex estimation which is below the minimum number of variables used for DSP. Therefore, to estimate the sex of this specimen, we performed our own linear discriminant analysis based on the sample used in DSP provided by Brůžek et al. (2017).

^f This value was estimated by McCown and Keith (1939) as the acetabulum is crushed.

^g Sex suggested in previous studies (see references in Table 6).

Table 4

Results of the raw (PCA-1) and log-transformed shape (PCA-2) principal components (PC) analyses including eigenvalues, percentage of variance explained, and correlations between the original variables and the principal components.^a

	PCA-1 (raw variables)		PCA-2 (log-shape variables)		
	PC1	PC2	PC1	PC2	PC3
Eigenvalue	3.43	1.4	3.15	1.14	1.03
% variance	57.2	23.4	52.4	19.0	17.2
IIMT	0.01	0.92	-0.91	-0.32	-0.17
ISMM	0.91	-0.20	0.85	-0.35	0.10
SS	0.92	0.04	0.62	0.50	0.42
SA	0.61	0.67	-0.59	0.38	0.61
SIS	0.80	-0.06	0.49	0.56	-0.64
VEAC	0.86	-0.26	0.78	-0.46	0.23

Abbreviations: IIMT, greater sciatic notch height; ISMM, postacetabular length; SS, spino-sciatic length; SA, spino-auricular length; SIS, cotylo-sciatic breadth; VEAC, vertical acetabular diameter.

^a Only PCs with eigenvalues > 1 are represented. Strong correlations (absolute value above 0.6) are represented in bold.

Table 5Results of probabilistic sex diagnosis for all possible combinations of variables.^a

Specimen	Side	<i>n</i> of combinations				Male posterior probability		
		Total	Male	Indeterminate	Female	Median	25%	75%
Regourdou 1a	right	22	12	10	0	0.977	0.679	0.994
Regourdou 1b	right	22	12	10	0	0.976	0.634	0.994
Amud 1	left	6	0	2	4	0.032	0.017	0.110
Arago 44	left	22	5	16	1	0.870	0.342	0.942
Feldhofer 1	left	163	143	19	1	0.999	0.994	1.000
Grotte du Prince	right	1	0	1	0	0.065	0.065	0.065
Kebara 2	right	382	290	91	1	0.993	0.954	0.999
Krapina 207	left	22	1	21	0	0.724	0.329	0.860
Krapina 208	right	1	1	0	0	0.992	0.992	0.992
Krapina 209	right	22	0	17	5	0.329	0.068	0.603
La Chapelle 1	both	22	21	1	0	1.000	0.998	1.000
La Ferrassie 1	left	6	6	0	0	1.000	1.000	1.000
Tabun C1	both	64	0	9	55	0.004	0.001	0.025

^a Both reconstructions of Regourdou 1 coxal bone were analyzed.

Table 6

Comparison of sex estimation methods.

Specimen	Side	Visual method (Santos et al., 2019)		Metrical method (Brůžek et al., 2017)		Lit. ^b	Reference
		P(M) ^a	Sex	P(M) ^a	Sex		
Regourdou 1	right	0.995	M	0.956–0.986	M	I/M	Vandermeersch and Trinkaus (1995); Meyer et al. (2011)
	left	0.721	I (M)		-		
	both	0.955	M		-		
Amud 1	left	0.586	I (M)	0.017	F	M	Endo and Kimura (1970); Trinkaus (1980)
Arago 44	left	0.003	F	0.899	I(M)	F	de Lumley (2015)
Feldhofer 1	left	0.993	M	1.000	M	M	Schaaffhausen (1888); Trinkaus (1980)
Grotte du Prince	right	0.035	F	0.081	I(F)	F	de Lumley-Woodyear (1973)
Kebara 2	right	0.984	M	1.000	M	M	Rak and Arensburg (1987)
	left	0.189	I (F)	-	-		
	both	0.813	I (M)	-	-		
Krapina 207	left	0.920	I (M)	0.719	I (M)	M	Smith (1976); Trinkaus (1980); Bonmatí and Arsuaga (2007)
Krapina 208	right	-	-	0.992	M	M	Smith (1976); Bonmatí and Arsuaga (2007)
Krapina 209	right	0.064	I (F)	0.291	I (F)	F	Smith (1976); Trinkaus (1980); Bonmatí and Arsuaga (2007)
La Chapelle 1	both	0.987	M	1.000	M	M	Boule (1911–1913); Trinkaus (1980)
La Ferrassie 1	left	0.963	M	1.000	M	M	Trinkaus (1980); Heim (1982)
Las Palomas 96	right	0.014	F	-	-	F	Walker et al. (2011)
Shanidar 1	right	-	-	-	-	M	Trinkaus (1983)
SH Pelvis 1	left	0.964	M	0.970	M	M	Arsuaga et al. (1999); Bonmatí et al. (2010)
Tabun C1	both	0.038	F	0.002	F	F	McCown and Keith (1939); Trinkaus (1980)

^a P(M) is a posterior probability of male sex. Posterior probability of female sex, P(F), can be computed as 100 – P(M). Values in bold reach the 0.95 probability threshold, allowing a reliable sex diagnosis. Results not reaching this threshold should be considered indeterminate (I), but we also give the sex that is more probable in brackets.

^b Sex suggested in previous studies (see Reference column).

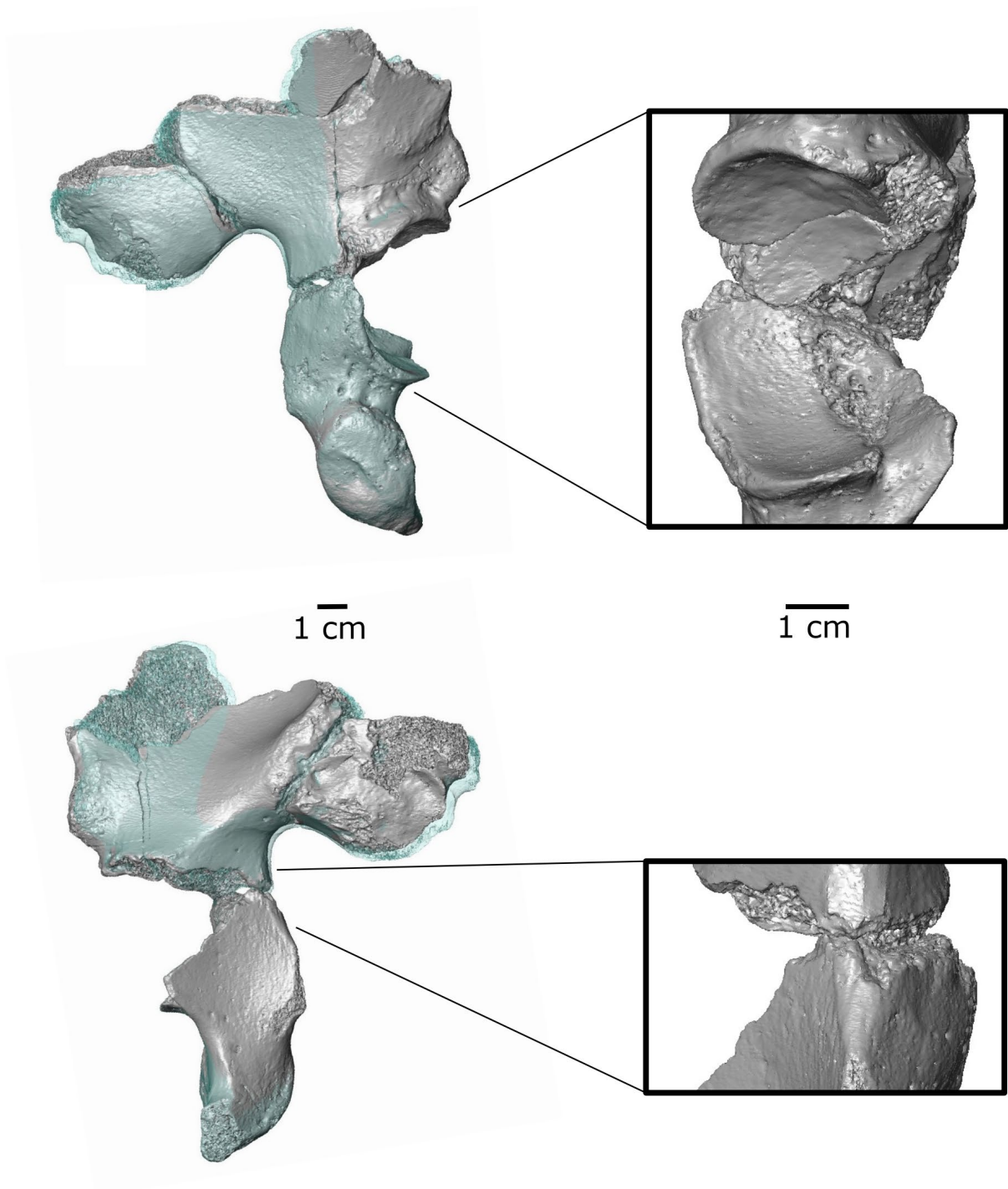


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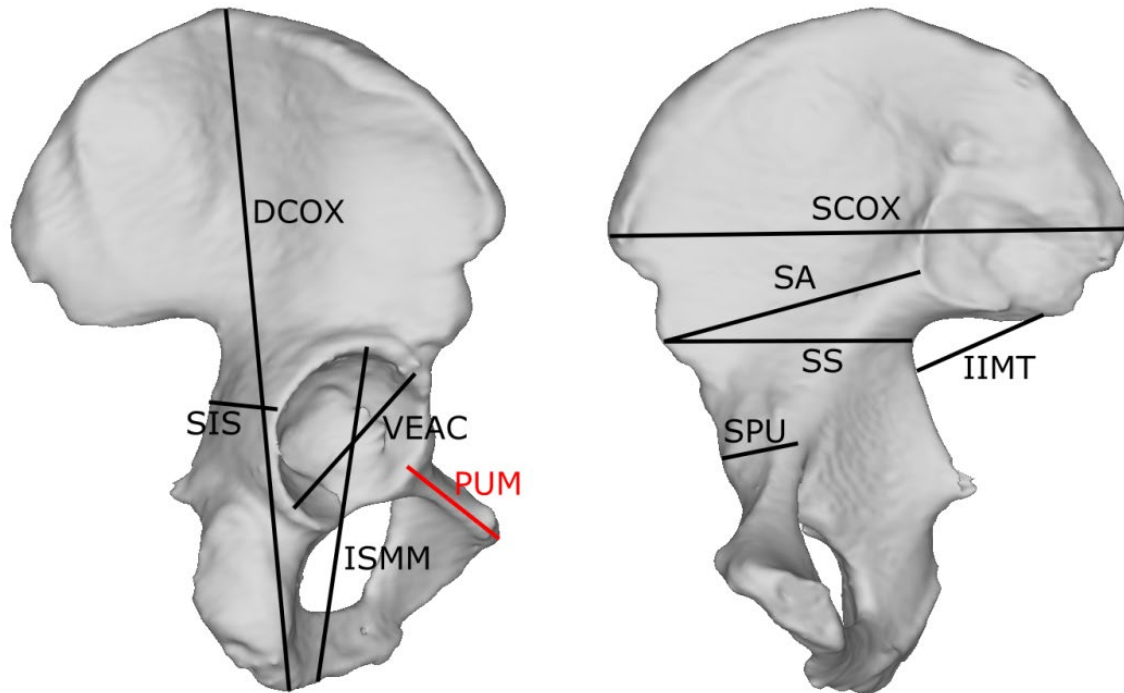


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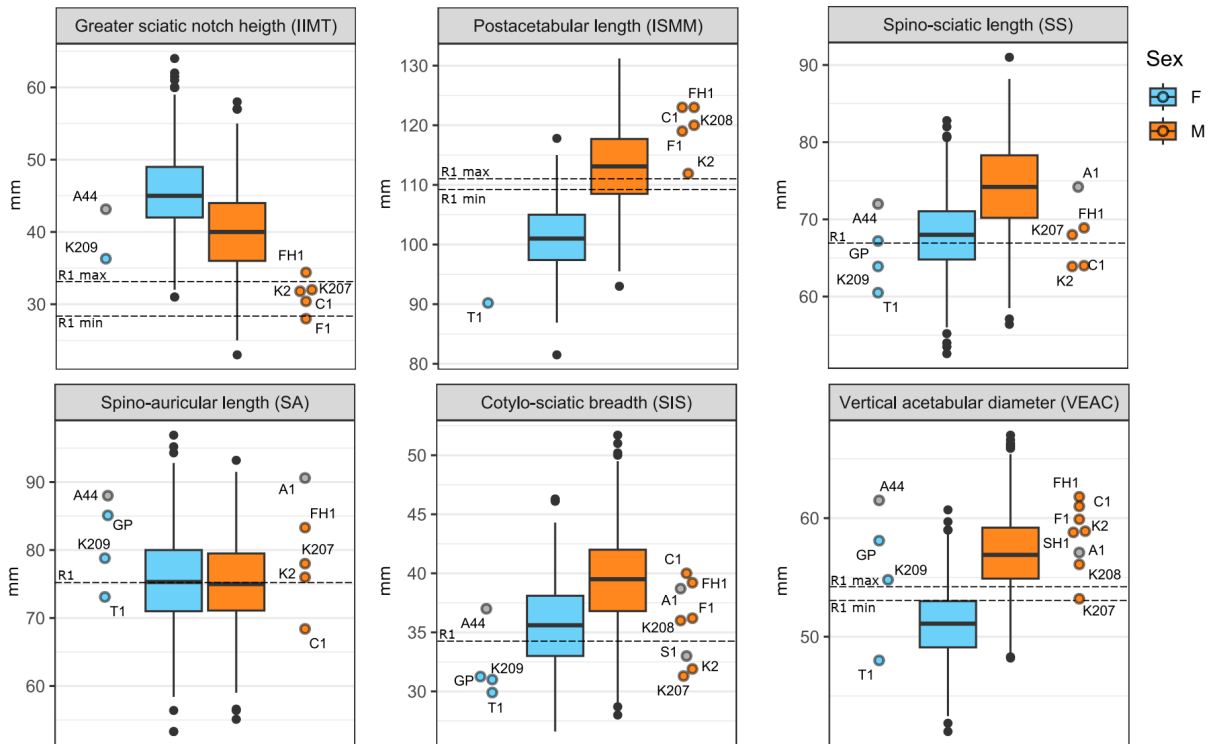


Figure 3. Morphological traits in Regourdou 1 following Brůžek (2002) and Santos et al. (2019): a) evaluation of the greater sciatic notch, b) single arc in the right coxal bone, and c) indeterminate arc in the left coxal bone (the auricular outline is not in direct continuation with the greater sciatic notch, but it does not constitute two regular arcs either).

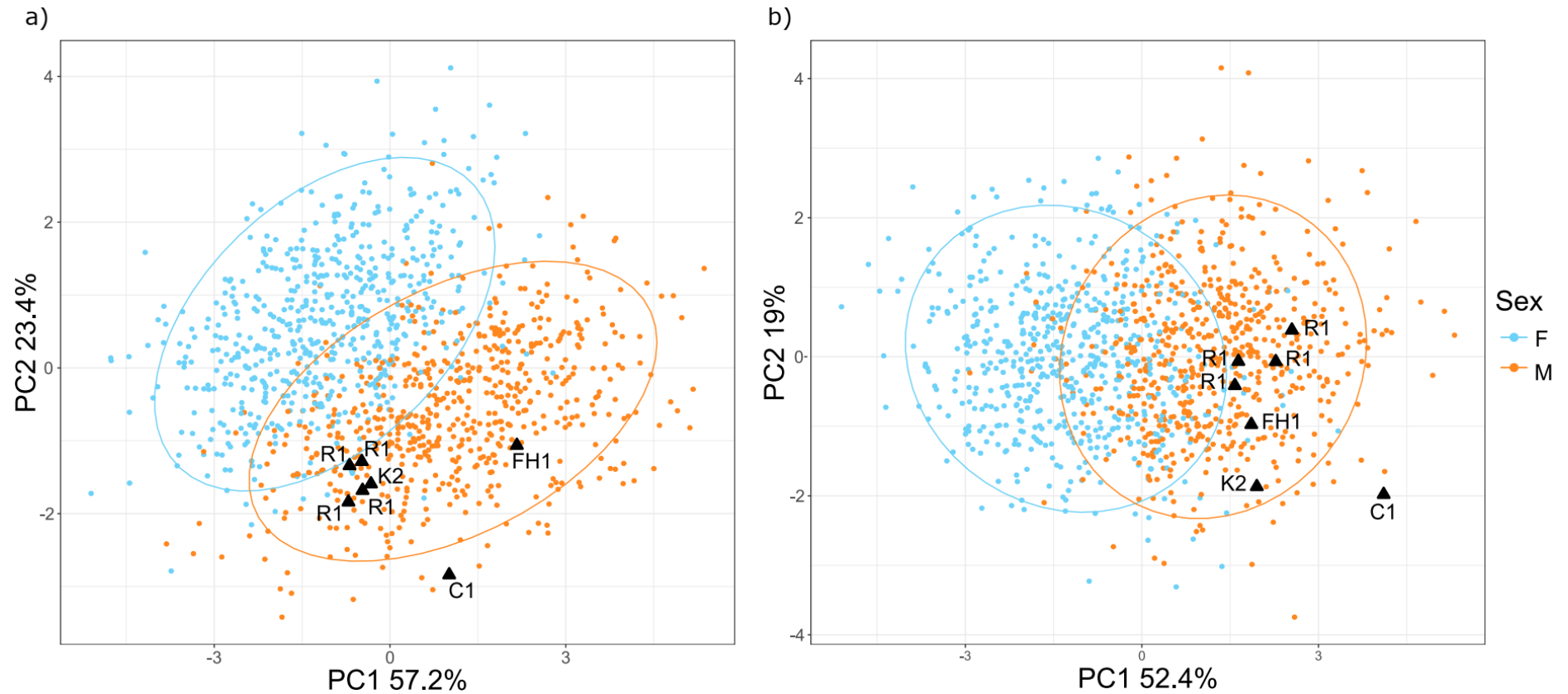


Figure 4. Six coxal dimensions preserved in Regourdou 1 (R1) compared with modern humans (boxplots) and other Neandertal and Middle Pleistocene individuals (points). Boxplots: central bar = median, box = interquartile range, whiskers = minimum and maximum, black dots = outliers beyond 1.5 of the interquartile range from either end of the box. Fossil specimens are marked by their acronyms and plotted separately by sex as suggested in the literature. Sex assignment for the fossil specimens based on our analysis is indicated by point colors (grey = indeterminate). A1 = Amud 1, A44 = Arago 44, C1 = La Chapelle-aux-Saints 1, FH1 = Feldhofer 1, F1 = La Ferrassie 1, GP = Grotte du Prince,

K2 = Kebara 2, K207 = Krapina 207, K208 = Krapina 208, K209 = Krapina 209, S1 = Shanidar 1, SH1 = La Sima de los Huesos Pelvis 1, T1 = Tabun C1.

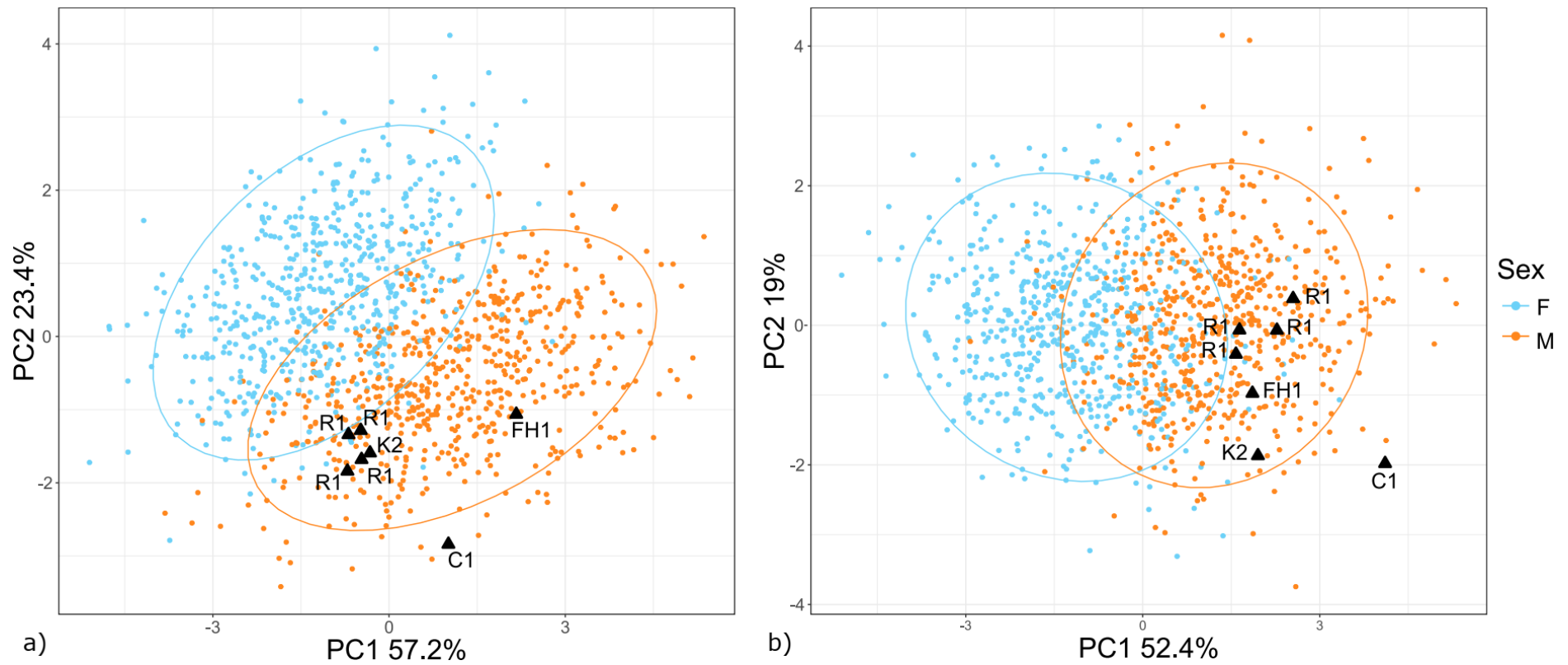


Figure 5. Principal components analysis of six metric dimensions preserved in Regourdou 1 (R1). a) principal components analysis on raw variables (PCA-1), b) principal components analysis on log-shape variables (PCA-2). Ellipses indicate 95% confidence intervals for modern males and females. Regourdou 1 is represented by two different reconstructions of the right coxal bone and minimum and maximum values of greater sciatic notch height. C1 = La Chapelle-aux-Saints 1, FH1 = Feldhofer 1, K2 = Kebara 2. Regourdou 1 falls close to other Neandertal males who tend to be near the extreme edge of modern male variation.

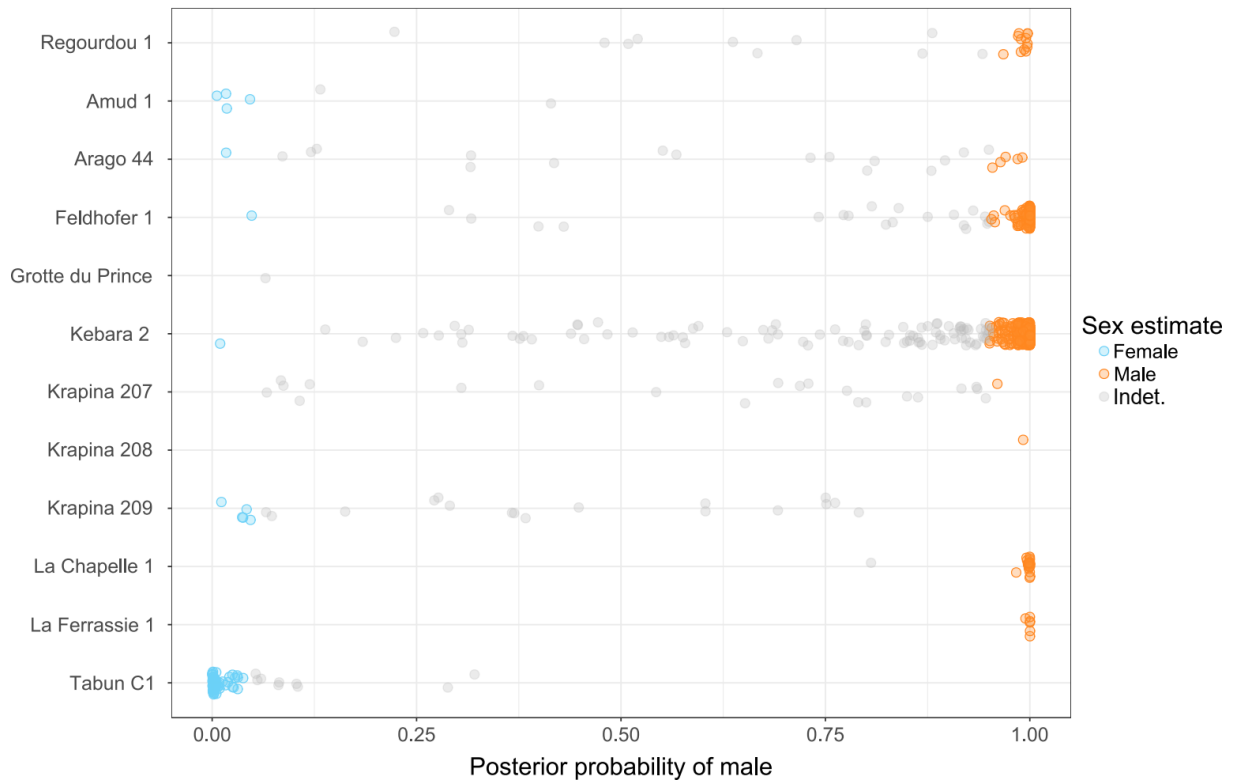


Figure 6. Posterior probability of male for every combination of each specimen’s preserved variables. To avoid excessive overplotting, points are randomly scattered in vertical dimension. La Chapelle 1 = La Chapelle-aux-Saints 1. The majority of combinations classifies Regourdou 1 as male. For most of other specimens results are distributed toward the previously estimated sex (see Table 3).

Supplementary Online Material (SOM):

Sex estimation of the adult Neandertal Regourdou 1 (Montignac, France):

Implications for sexing human fossil remains

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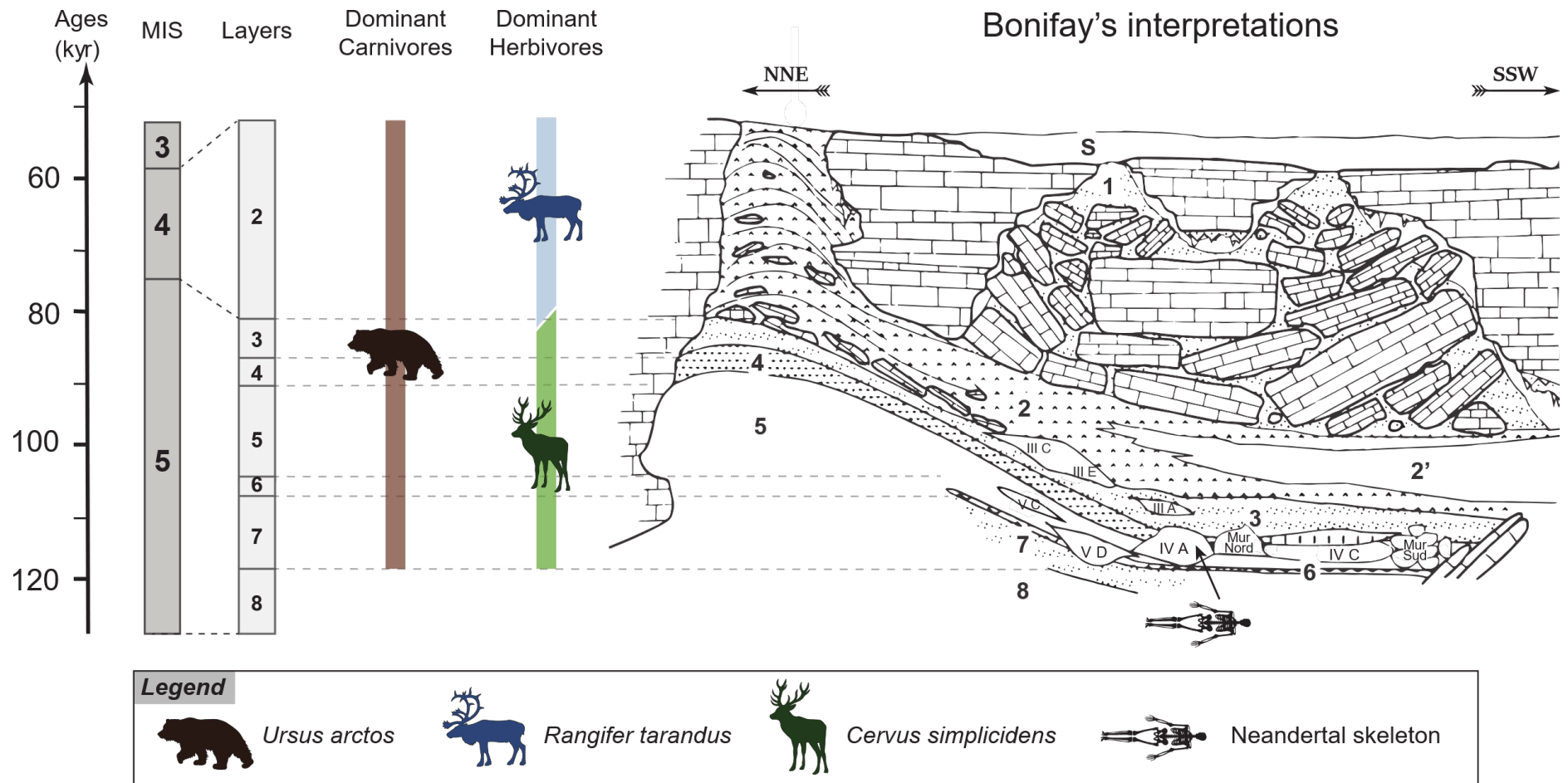
^g *Musée national de Préhistoire, 1 rue du Musée, 24620, Les Eyzies-de-Tayac Sireuil, France*

^h *Tulane University; Department of Anthropology, 101 Dinwiddie Hall, New Orleans, LA, 70118, USA*

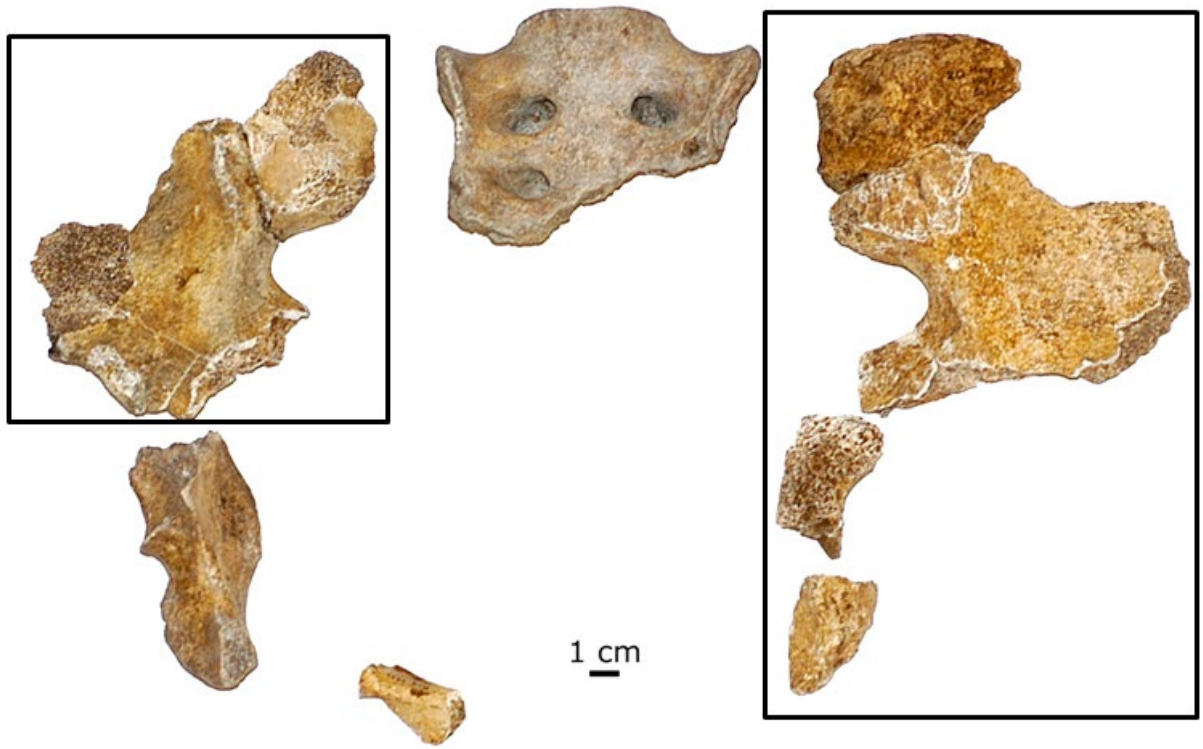
ⁱ *Centre for the Exploration of the Deep Human Journey, University of the Witwatersrand, Private Bag 3, Wits 2050, RSA*

***Corresponding author.**

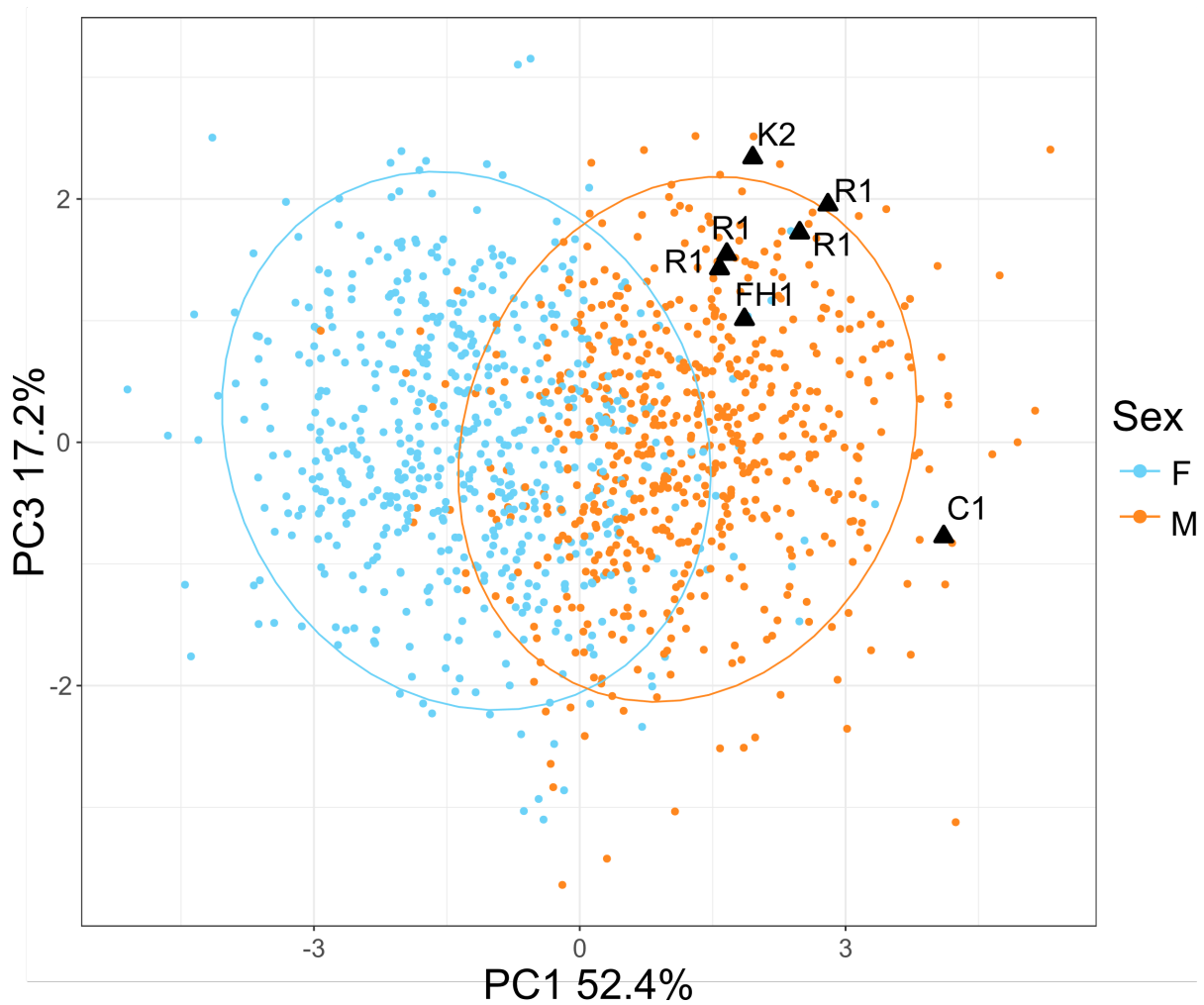
Email address: vejnaror@natur.cuni.cz (R. Rmoutilová)



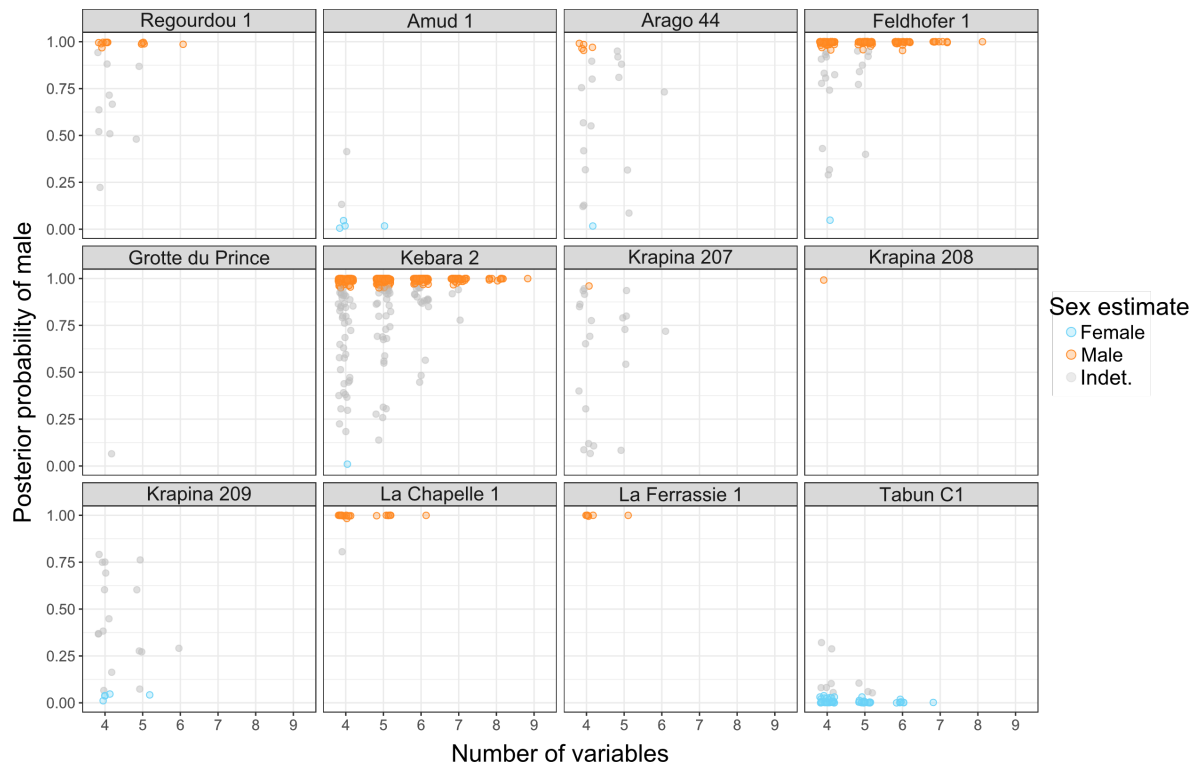
SOM Figure S1. Stratigraphy of Regourdou cave (Pelletier et al., 2017).



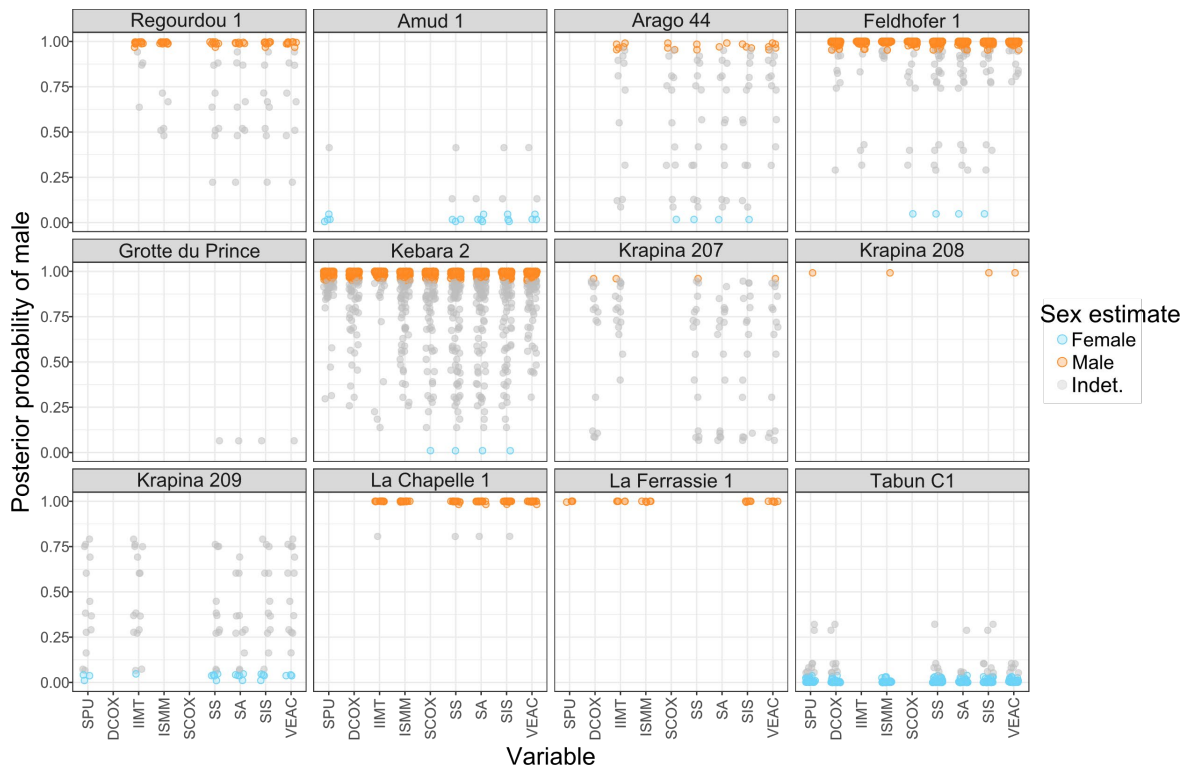
SOM Figure S2. Pelvic remains of Regourdou 1. Fragments in rectangles have been discovered since 2008.



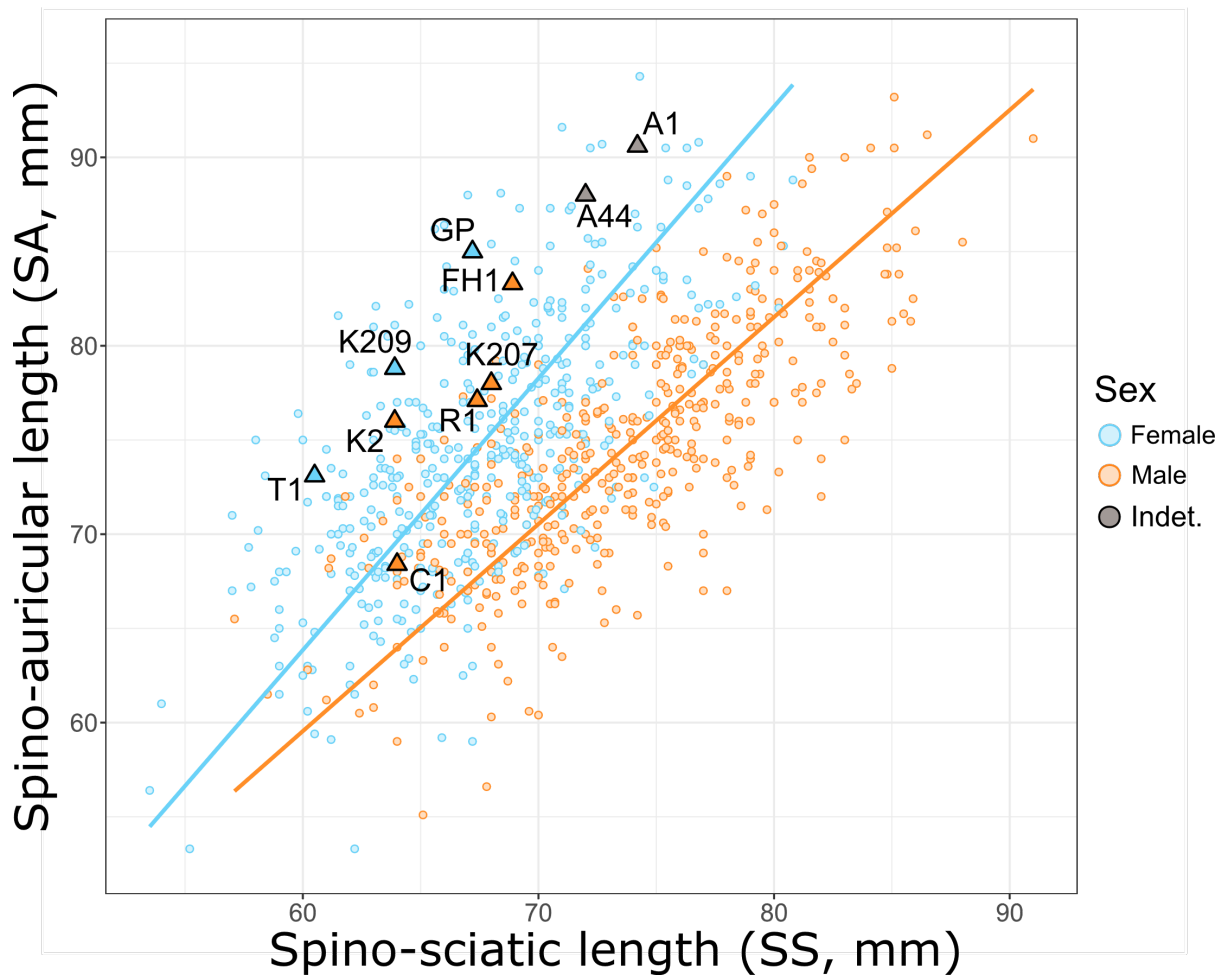
SOM Figure S3. Principal components analysis (PC1 vs. PC3) of six size-adjusted metric dimensions (PCA-2) preserved in Regourdou 1. Ellipses indicate 95% confidence intervals for modern males and females. Regourdou 1 is represented by two different reconstructions of the right coxal bone and minimum and maximum values of greater sciatic notch height. C1 = La Chapelle-aux-Saints, FH1 = Feldhofer 1, K2 = Kebara 2, R1 = Regourdou 1.



SOM Figure S4. The relationship between the number of variables and sex estimation. To avoid excessive overplotting, points are randomly scattered in horizontal dimension. La Chapelle 1 = La Chapelle-aux-Saints 1.



SOM Figure S5. The relationship between selected variables and sex estimation. Variables are defined in SOM Table S3. To avoid excessive overplotting, points are randomly scattered in horizontal dimension.



SOM Figure S6. A bivariate plot of selected metric dimensions. Modern humans are indicated by dots and regression lines, Neandertals are indicated by triangles. Regression lines computed using reduced major axis, reducing error in both axes. A1 = Amud 1, A44 = Arago 44, C1 = La Chapelle-aux-Saints, FH1 = Feldhofer 1, GP = Grotte du Prince, K2 = Kebara 2, K207 = Krapina 207, K209 = Krapina 209, R1 = Regourdou 1, T1 = Tabun C1.

SOM Table S1

Published descriptions of sexually dimorphic features in the Neandertal pelvic remains^{a-b}.

Specimen	GrSN	CArc	PrSu	General	Sex	Location	Date (ka BP)	Reference	Acronym	Use in this study
Altamura 1		-	-	"From the general robusticity of the bones and the rather high and narrow iliac fossa, the skeleton can be judged that of a male." (Pesce Delfino and Vacca, 1994)	M	Italy	150	(Pesce Delfino and Vacca, 1994)	-	-
Amud 1		-	(translation) "On the pelvic fragment from La Ferrassie 1, no trace of a sulcus preauricularis can be distinguished; neither does it exist in Neandertal, nor Amud, nor on the presumed male fragments of Krapina 207 and 211." (original) "Sur le fragment pelvien de La Ferrassie 1, on ne distingue aucune trace d'un sulcus preauricularis; il n'en existe	"The margins, crests and elevations in the various regions of the hip-bone are generally rather thin or sharp in Amud I. The thickness of this bone seems to belong to the smaller class." (Endo and Kimura, 1970) The fragment of the hip-bone of Amud I shows: 1. A large ilium, 2. A wide iliac wing, and 3. A thin and slim feature as a	M	Israel	60	(Endo and Kimura, 1970; Trinkaus, 1980)	A1	Original

	(Endo and Kimura, 1970)	pas non plus chez Néandertal, ni sur les fragments présumés masculins de Krapina 207 et 211." (Heim, 1982)							
Arago 44	"The curvature of the greater sciatic notch (trait #10) is close to the male or indeterminate condition in Jinniushan and Arago 44 according to modern standards while SH Pelvis 1 is hypermale." (Bonmatí et al., 2017)	-	-	F	France	450	(de Lumley, 2015; Bonmatí et al., 2017)	A44	3D (cast)
Feldhofer 1 ^c	(translation) "The posterior arm of the greater sciatic notch is longer than usual, the apex of the latter protrudes from the base of the ischial spine 63 mm, on the normal pelvis only 55" ... "The notch itself is	(translation) "On the pelvic fragment from La Ferrassie 1, no trace of a sulcus preauricularis can be distinguished; neither does it exist in Neandertal, nor Amud, nor on the presumed male fragments of Krapina 207 and 211." (original) "Sur le fragment pelvien de La Ferrassie 1,		M	Germany	40	(Schaaffhausen, 1888; Trinkaus, 1980)	FH1	3D (original)

narrower than usual...”

(original) “Der hintere Schenkel der Incisura ischiadica major ist länger als gewöhnlich, der Scheitel der letzteren steht von der Basis der Spina ossis ischii 63 mm ab, an dem normalen Becken nur 55 ... Die Incisur selbst ist schmaler als gewöhnlich...” (Schaaffhausen, 1888)

on ne distingue aucune trace d'un sulcus preauricularis; il n'en existe pas non plus chez Néandertal, ni Amud, ni sur les fragments présumés masculins de Krapina 207 et 211.” (Heim, 1982)

Grotte du Prince

(translation) “The large diameter of the greater sciatic notch confirms its attribution to the female sex.”

(original) “La grande diamètre de la grande échancrure

-

(translation) “The weak projection of the muscular reliefs, the tubercle of the gluteus medius, the upper and lower anterior iliac spines, a slightly sinuous iliac crest are in favor of the female sex.”

(original) “La faible saillie des reliefs musculaires, du

F France

130–300 (de Lumley-
(Riss Woodyear,
glacial) 1973)

GP

3D (cast)

sciatique confirme
cette attribution au
sexe féminin.“ ...
(de Lumley-
Woodyear, 1973)

tubercule du moyen fessier,
des épines iliaques
antérieures supérieure et
inférieure, une crête iliaque
peu sinueuse, sont en faveur
du sexe féminin.“ (de Lumley-
Woodyear, 1973)

Kebara 2

“The posterior and -
inferior flaring of
the posterior
portion of the ilium
yields a rather
constricted greater
sciatic notch, a
clear indication of
the specimen's
male gender”
(Rak, 1991)

“On the left innominate -
bone, a small pre-auricular
sulcus is present, and a
very deep post-auricular
sulcus separate the auricle
from the iliac tuberosity;
these structures are absent
on the right side.” (Rak,
1991)

M

Israel

60

(Rak and
Arensburg,
1987)

K2

3D (original)

Krapina 207

“In addition, the morphology of the greater sciatic notch appears male. The notch is narrow, a fairly reliable male characteristic” (Smith, 1976)
“The morphology of the greater sciatic notch

“... 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)”

“There appears to be no -
preauricular sulcus,
indicating that Krapina 207
is a male.” (Smith, 1976)

M

Croatia

130

(Smith, 1976;
Trinkaus, 1980;
Bonmatí and
Arsuaga, 2007)

K207

3D (original)

(Figure 1d) closely (Bonmatí and
resembles closely Arsuaga, 2007)
[sic] to the stage 5
proposed by “Given this, Krapina
Walker (53 – 207 (in contrast to
Figure 1) a its greater sciatic
category which notch shape) has a
encompasses, separation of the
90% of males.” two arches and
(Bonmatí and hence the ‘female’
Arsuaga, 2007) pattern.” (Trinkaus,
2016)

“Only the greater
sciatic notch of
Krapina 207
permits close
approximation of
standard
measurements (cf.
Brůžek, 2002). For
it, the
perpendicular from
the line between
the ischial spine
and the top of the
piriform tubercle to
the superior notch
is close to the
posterior notch, or
in the ‘male’
position”
(Trinkaus, 2016)

Krapina 208	-	-	-	<p>“Both the greater sciatic notch/I/M and sacroiliac articular areas are missing as is the subpubic area. Thus, sex is not determinable.” (Smith, 1976)</p> <p>“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.” (Bonmatí and Arsuaga, 2007)</p>	Croatia	130	(Smith, 1976; Bonmatí and Arsuaga, 2007)	K208	3D (original)	
Krapina 209	<p>“The greater sciatic notch is wide; thus the specimen appears to be female.” (Smith, 1976)</p> <p>A more general approximation of the position of the ischial spine for Krapina 209 would place the</p>	<p>“... 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.”</p>	<p>“The sacroiliac articular surface is preserved, and a nice preauricular sulcus is present.” (Smith, 1976)</p>	-	F	Croatia	130	(Smith, 1976; Trinkaus, 1980; Bonmatí and Arsuaga, 2007)	K209	3D (original)

perpendicular from (Bonmatí and
 this line to the Arsuaga, 2007)
 superior notch
 close to the middle “However, Krapina
 of the notch, and 209 with its
 hence in the distinctly ‘female’
 ‘female’ position. greater sciatic
 (Trinkaus, 2016) notch, has
 contiguous arches.”
 (Trinkaus, 2016)

La Chapelle-aux Saints 1

(translation) “This - -
 one (Pl. IX, fig. 1
 and 2, *g.éc.*) is
 deep, very narrow,
 with wide and
 steep edges,
 which proves that
 the skeleton of La
 Chapelle-aux-
 Saints belonged to
 a male individual.”

(original) “Celle-ci
 (Pl. IX, fig. 1 et 2,
g.éc.) est
 profonde, très
 étroite, à bords
 larges et
 escarpés, ce qui
 prouve bien que le
 squelette de La
 Chapelle-aux-

(translation) “The right ilium is M
 a robust, massive bone.”
 (original) “L’ilion droit est un
 os robuste, massif.” (Boule,
 1911–1913)

France 50

(Boule, 1911– C1
 1913; Trinkaus,
 1980)

3D (original,
 cast)

	Saints a appartenu à un individu mâle." (Boule, 1911–1913)						
La Ferrassie 1	(translation) "As in - the male Neandertals of La Chapelle, Neandertal and Amud, the greater sciatic notch of La Ferrassie 1 is deep, narrow and provided with a rectilinear and elongated anterior edge due to the low position of the sciatic spine." (original) "Comme chez les Néandertaliens masculins de La Chapelle; de Néandertal et d'Amud, la grande échancrure sciatique de La Ferrassie 1 est profonde, étroite et pourvue d'un bord	(translation) "On the pelvic - fragment from La Ferrassie 1, no trace of a sulcus preauricularis can be distinguished" (original) "Sur le fragment pelvien de La Ferrassie 1, on ne distingue aucune trace d'un sulcus preauricularis" (Heim, 1982)	M	France	45	(Trinkaus, 1980; F1 Heim, 1982)	3D (original)

	antérieur rectiligne et allongé du fait de la position basse de l'épine sciatique." (Heim, 1982)								
La Ferrassie 2	(translation) "In La - Ferrassie 2, the greater sciatic notch is much more flared, which is consistent with the female sex." (original) "Chez La Ferrassie 2, la grande échancrure sciatique est nettement plus évasée ce qui s'accorde avec le sexe féminin." (Heim, 1982)	-	-		F	France	45	(Trinkaus, 1980; - Heim, 1982)	-
Las Palomas 96	"The greater - sciatic notch, although incomplete, has the open form associated with females in recent humans. It is	-	-		F	Spain	50	(Walker et al., - 2011)	Published data

similar to the open ones of the probably female La Ferrassie 2 and Prince 1 Neandertals, and it contrast with the semi-circular ones of the probably male Amud 1, La Chapelle-aux-Saints 1, Feldhofer 1, La Ferrassie 1, Kebara 2 and Shanidar 4 Neandertals.” (Walker et al., 2011)

Regourdou 1

<p>(translation) “The greater sciatic notch is incomplete [right side]. It is therefore difficult to decide on its narrowness or its depth. Nevertheless, the posterior arm and the portion of the preserved anterior arm show that the</p>	<p>(translation) “The anterior border of the auricular surface and the anterior arm of the greater notch [left side] form a composite arc of Genovés”</p> <p>(original) “La bordure antérieure de la surface auriculaire et le</p>	<p>(translation) “A well-marked depression is present on the pre-auricular surface [left side]. It can be related to the insertion of the ventral sacroiliac ligament.”</p> <p>(original) “Une dépression bien marquée est présente sur la surface pré-auriculaire [left side]. On peut la rapporter à l’insertion du ligament</p>	<p>(translation) “Let’s just say that their examination showed that this was a presumably male, young adult specimen.”</p> <p>(original) “Disons seulement que leur examen a montré qu’il s’agissait là d’un sujet sans doute masculin et adulte jeune.” (Vallois, 1965)</p> <p>“Its sex is not possible to determine. The only preserved pieces of the</p>	<p>I/M France 80–130 (VandermeerschR1 and Trinkaus, 1995; Meyer et al., 2011)</p>	<p>3D (original)</p>
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notch is rather narrow.”

(original) “La grande incisure ischiatique est incomplète [right side]. Il est donc difficile de statuer sur son étroitesse ou sa profondeur. Néanmoins, le bras postérieur et la portion de bras antérieur présents permettent d’observer que l’incisure est plutôt étroite.” (Meyer et al., 2011)

(translation) The greater sciatic notch is clearly visible here [left side]. It is relatively closed and symmetrical.

(original) “La grande incisure ischiatique est ici bien observable

bras antérieur de la sacro-ilique ventral.” grande incisure [left side] forment un arc composé de Genovés” (Meyer et al., 2011)

pelvis, a segment of the right superior pubic ramus and a piece of the right ischium with the inferior acetabular margin, are not diagnostic as to sex. Overall size [...] place Régourdou [sic] 1 in the overlap range between the male and female European Neandertal remains” (Vandermeersch and Trinkaus, 1995)

[left side]. Elle est
relativement
fermée et
symétrique.”
(Meyer et al.,
2011)

Shanidar 1

“It appears from -
the portions -
preserved that the -
sciatic notch
curved strongly
inferiorly posterior
to the middle of
the sciatic notch.
Although no
reconstruction of
the preauricular
area can be fully
substantiated, the
remains appear to
be most
compatible with a
male morphology
in this region.”
(Trinkaus, 1983)

M Iraq 50 (Trinkaus, 1983)S1 Published data

Shanidar 3

“The right -
preauricular -
surface possesses -
a smooth surface
with slight
ligamentous

M Iraq 50 (Trinkaus, 1983)- -

roughening but without the pitting or sulcus usually associated with pregnancy in the female” (Trinkaus, 1983)

Shanidar 4

“Yet an inferior portion of the left ilium has been preserved with the sciatic notch intact. The Shanidar 4 sciatic notch is a tightly curved semicircle similar to those of males and quite distinct from the posteriorly more open notches of females.” (Trinkaus, 1983)

- - - M Iraq 70 (Trinkaus, 1983)- -

SH Pelvis 1

“The SH Pelvis 1 is sexed as a male because of its extreme robustness, its large cotylosciatic breadth, the triangular shape of

Absence of the composite arc (Bonmatí et al., 2010)

“The SH Pelvis 1 is sexed as a male because of its extreme robustness, its large cotylosciatic breadth, the triangular shape of the pelvic inlet, the anterior position of the sacroiliac joint, the narrow ischial notch and its pubic

M Spain 430 (Arsuaga et al., 1999; Bonmatí et al., 2010) Published data

the pelvic inlet, the anterior position of the sacroiliac joint, the narrow ischial notch and its pubic morphology.”

(Arsuaga et al., 1999)

morphology.” (Arsuaga et al., 1999)

Tabun C1^d

“Tabūn I is the only specimen showing an exceptional (female) measurement; we estimate the width of the notch as having been 60 mm. [sic] and shallow, only 25 mm. [sic] deep.” (McCown and Keith, 1939)

F Israel

120

(McCown and Keith, 1939; Trinkaus, 1980)

T1

3D (reconstruction)

Abbreviations: GrSN, greater sciatic notch; CArc, composite arc; PrSu, preauricular sulcus; SH, Sima de los Huesos; M, male; F, female; I, indeterminate.

^a Descriptions are cited including grammatical errors present in the original text.

^b Specimens used in this study and a mode of their use is indicated in the last column (3D indicates a virtual surface scan or computed tomography scan). Other Neandertal pelvic remains from the Krapina site, Spy, or Vilafamés are not included as they are either not well preserved or they are not sufficiently described in the literature.

^c The only specimen that is also sexed genetically (Skoglund et al., 2013).

^d Reconstruction of Weaver and Hublin (2009) was used.

SOM Table S2

Reference sample used in the morphological method of Brůžek (2002) and revised by Santos et al. (2019).

Sample	Region	Period	Number of females	Number of males
Tamagnini collection	Coimbra, Portugal	early 20 th century	66	54
Hamann-Todd collection	Cleveland, Ohio	1910–1940	57	56
Spitalfields	London, England	1729–1852	43	30
Olivier collection	Paris, France	early 20 th century	32	48
Terry collection	Washington, DC	19 th and 20 th century	106	100

SOM Table S3

Definition and scoring of morphological traits (Brůžek, 2002; Santos et al., 2019) that were evaluated in this study.

Trait	Definition and scoring		
PrSu1	Development of a negative relief on the preauricular surface f: well-delimited deep depression	i: intermediate form	m: smooth surface or very slightly negative relief
PrSu2	Aspect of grooves or pitting f: closed circumference of pit(s) or groove(s) when a depression is present	i: intermediate form	m: absent depression or open circumference of depressions
PrSu3	Development of a positive relief f: lack of positive relief or tubercle	i: intermediate form	m: tubercle present or clear protuberance
GrSN1	Proportion of the length of sciatic notch chords f: posterior chord segment (AC) longer than or equal to the anterior chord (CB)	i: intermediate form	m: posterior chord (AC) shorter than the anterior chord (CB)
GrSN2	Form of contour notch chords f: symmetry of chords contours in the basal portion of the sciatic notch relative to its depth	i: intermediate form	m: asymmetry of chords contours in the basal portion of the sciatic notch relative to its depth
GrSN3	Retroversion of the posterior notch chord relative to the line from point A perpendicular to the sciatic notch breadth f: lack of retroversion, contour (outline) of the posterior chord does not cross the perpendicular line	i: intermediate form, contour tangent the perpendicular	m: contour of posterior chord crosses the perpendicular line
CArc	Form of the composite arc f: double curve	i: intermediate form	m: single curve
IsPu	Visual relationship between pubis and ischium lengths ^a f: pubis visually longer than ischium	i: intermediate form	m: ischium visually longer than pubis

Abbreviations: f, female; i, indeterminate; m, male.

^a Pubic and ischial lengths visually assessed from the inner boarder of the *facies lunata* where the axis of the superior pubic ramus crosses ischial axis.

SOM Table S4

Reference sample used in the metrical method DSP (Brůžek et al., 2017).^a

Skeletal collection	Geographical origin	Period	Number of females	Number of males
Olivier collection, Paris	France	early 20 th century	62 (29)	98 (43)
Tamagnini collection, Coimbra	Portugal	early 20 th century	130 (54)	102 (41)
Spitalfields, London	England	18 th and 19 th century	31 (3)	31 (3)
Garmus collection, Vilnius	Lithuania	20 th century	112 (55)	108 (53)
Dart collection, Zulu, Johannesburg	South Africa	early 20 th century	153 (72)	153 (75)
Dart collection, Soto, Johannesburg	South Africa	early 20 th century	58 (27)	52 (22)
Dart collection, Afrikaner, Johannesburg	Netherlands	early 20 th century	56 (22)	56 (26)
Hamann-Todd collection, Cleveland	Euroamerican	1910–1940	56 (24)	56 (24)
Hamann-Todd collection, Cleveland	Afroamerican	1910–1940	57 (22)	56 (25)
Terry collection, Washington	Euroamerican	19 th and 20 th century	102 (45)	94 (48)
Terry collection, Washington	Afroamerican	19 th and 20 th century	110 (54)	106 (50)
Chang-Mai collection, Chang-Mai	Thailand	late 20 th century	96 (43)	102 (49)
Maxwell collection, Albuquerque	USA	20 th century	59 (24)	61 (29)
Simon collection, Geneva	Switzerland	19 th and 20 th century	250 (30)	253 (38)

^aNumbers in parentheses indicate cases without missing values.

SOM Table S5

Comparison of DSP2 metric dimensions (Brůžek et al., 2017) for males and females.

Variable abbreviation	Variable name	Males			Females			U-statistics	p-value
		Mean	SD	n	Mean	SD	n		
PUM	Acetabulo-symphyseal pubic length (Novotný, 1986)	69.9	5.2	574	72.4	5.2	549	199112	<0.001
SPU	Cotylo-pubic width (Gaillard, 1960)	29.6	2.9	612	24.5	2.6	590	34871	<0.001
DCOX (M1)	Coxal length (Bräuer, 1988)	214.9	13.4	614	197.7	11.2	600	61911	<0.001
IIMT (M15.1)	Greater sciatic notch height (Bräuer, 1988)	40.0	5.7	652	45.6	5.6	654	323140	<0.001
ISMM	Postacetabular length (Schulter-Ellis et al., 1983)	113.1	6.8	620	101.3	5.4	608	33410	<0.001
SCOX (M12)	Coxal breadth (Bräuer, 1988)	157.0	10.9	582	152.8	10.5	580	131746	<0.001
SS	Spino-sciatic length (Gaillard, 1960)	74.3	5.8	649	68.1	4.9	651	87667	<0.001
SA	Spino-auricular length (Gaillard, 1960)	75.3	6.3	642	75.4	6.9	651	211290	0.730
SIS (M14.1)	Cotylo-sciatic breadth (Bräuer, 1988)	39.5	4.0	649	35.7	3.5	635	97245	<0.001
VEAC (M22)	Vertical acetabular diameter (Bräuer, 1988)	57.0	3.4	650	51.1	2.9	642	38698	<0.001

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