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THE NEANDERTAL (KRAPINA AND REGOURDOU 1), FOSSIL MODERN HUMAN (CHANCELADE 1) AND EXTANT HUMAN PATELLA : AN INSIGHT FROM INSIDE

Marine Cazenave[a],
Davorka Radovčić[b],
Jakobus Hoffman[c],
Roberto Macchiarelli[d]

a. *Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent - Canterbury, UK; Department of Anatomy and Histology, School of Medicine, Sefako Makgatho Health Sciences University - Pretoria, South Africa - marine.cazenave4@gmail.com*
b. *Department of Geology and Paleontology, Croatian Natural History Museum - Demetrova 1, 10000 Zagreb, Croatia - davorka.radovcic@hpm.hr*
c. *South African Nuclear Energy Corporation SOC Ltd. - Pelindaba, South Africa - Jakobus.Hoffman@necsa.co.za*
d. *Département Homme et Environnement, UMR 7194 CNRS, Muséum national d'histoire naturelle, Musée de l'Homme FR - 75013 Paris; Unité de Formation Géosciences, Université de Poitiers FR - 86073 Poitiers - roberto.macchiarelli@univ-poitiers.fr*

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KEY-WORDS Knee joint, patella, endostructure, biomechanics, Neandertals, anatomically modern fossil humans.

ABSTRACT

Evolutionary endostructural patterns of the cortical and cancellous tissues of the postcranial skeleton are commonly investigated for inferring functional behaviours in extinct hominin taxa and past human populations. Information on the endostructural arrangement of the patellar bone has the potential of revealing individual- and/or taxon-specific aspects of the knee biomechanics. However, evidence on its inner conformation extracted from human fossil specimens is nearly non-existent. The present pilot study aims at characterising the endostructural pattern of two Neandertal (from Krapina, Croatia, and Regourdou, France) and one anatomically modern fossil human (from Chancelade, France) adult patellae and to compare their signal with the recent human condition. In the context of the gracilisation trend of the human skeleton occurred from the late Pleistocene, we expect (i) the two Neandertal patellae showing a higher amount of cortical bone compared to the fossil modern and the recent human conditions, (ii) the fossil modern patella showing a higher amount of cortical bone compared to the comparative sample, (iii) the cancellous network being relatively homogeneous between the two Neandertal individuals but distinguishable from that of the fossil modern human representative and of the comparative sample, and that (iv) the structural organisation revealed by the fossil modern patella is distinguishable from the recent human condition. For assessing the endostructural organisation of the selected patellae, we used non-invasive techniques of high resolution virtual imaging. The results do not support the first hypothesis, as marked differences have been found between the two Neandertal specimens. The second hypothesis is supported for the anterior surface, but not for the posterior surface. The third hypothesis is supported for the superior and the lateral regions of the patellar bone but for the inferior and medial portions. Finally, the fourth hypothesis is supported, but the cancellous organisation of the two Neandertal representatives is closer to the extant human pattern than to the Magdalenian specimen. Despite the generalised lack of comparable information from the human fossil record, we consider the present results of potential interest for future research of paleobiomechanical, paleobiological, and perhaps taxonomic interest, on the evolutionary structure of the human knee joint.

RÉSUMÉ

La patella néandertalienne (Krapina et Regourdou 1), humaine moderne fossile (Chancelade 1) et humaine actuelle: une perspective interne.

Les patrons d'évolution de l'endostructure des tissus cortical et trabéculaire du squelette postcrânien sont communément analysés pour reconstruire les activités fonctionnelles des homininés fossiles et des populations humaines anciennes. Les informations sur l'arrangement endostructural de la patella ont le potentiel de déceler des aspects de la biomécanique du genou spécifiques à l'individu ou caractéristiques d'une espèce. Cependant, les témoins de la conformation interne extraits de spécimens humains fossiles sont quasi-inexistants. Cette étude pilote a pour objectif de caractériser le patron de l'endostructure de deux patellae néandertaliennes (de Krapina, Croatie, et Regourdou, France) et d'une patella d'un humain moderne fossile (Chancelade, France) et de le comparer à la condition humaine récente. Dans le contexte d'un processus de gracilisation du squelette humain de la fin du Pléistocène, nous formulons les hypothèses suivantes: (i) les deux patellae néandertaliennes présentent un cortex plus épais par rapport aux conditions moderne fossile et récente, (ii) la patella moderne fossile présente un cortex plus épais que mesuré dans l'échantillon comparatif, (iii) le réseau trabéculaire est relativement homogène entre les Néandertaliens mais distinct de celui du fossile moderne et de l'échantillon comparatif et (iv) l'organisation structurale de la patella moderne fossile est distincte de la condition humaine récente. Pour analyser l'endostructure des patellae sélectionnées nous avons utilisé des techniques non-invasives d'imagerie virtuelle à haute résolution. Les résultats ne soutiennent pas la première hypothèse car des différences importantes ont été montrées entre les deux spécimens néandertaliens. La seconde hypothèse est vérifiée pour la surface antérieure mais pas pour celle postérieure. La troisième hypothèse est vérifiée pour les régions supérieure et latérale de la patella mais pas pour celles inférieure et médiale. Finalement, la quatrième hypothèse est vérifiée mais l'organisation trabéculaire des deux Néandertaliens est plus proche de la condition humaine récente que celle du spécimen magdalénien. Malgré le manque généralisé d'informations comparatives issues du registre humain fossile, nous estimons que les résultats de cette étude pilote ont un intérêt potentiel pour des recherches futures d'intérêt paléobiomécanique, paléobiologique et, peut-être, taxinomique sur l'évolution de la structure de l'articulation du genou humain.

MOTS-CLÉS Articulation du genou, patella, endostructure, biomécanique, Néandertaliens, humains modernes fossiles.

INTRODUCTION

In the postcranial skeleton, subchondral and cancellous bone tend to respond to the loading environment of the complementary joint surface. Indeed, besides the influence of a number of genetically-related factors affecting bone endostructural patterning during growth (e.g., Lovejoy *et al*. 1999; Judex *et al*. 2004; Demssie *et al*. 2007; Bonewald and Johnson 2008; O'Neill and Dobson 2008; Havill *et al*. 2010; Wallace *et al*. 2012; Agostini *et al*. 2018), the mechanosensitive bone tissues remodel during life to adjust the site-specific mechanical loads (e.g., Huiskes 2000; Pearson and Lieberman 2004; Mittra *et al*. 2005; Ruff *et al*. 2006; Skerry 2008; Barak *et al*. 2011; Gosman *et al*. 2011; Su 2011). At different skeletal sites, such as the proximal femur and tibia, a functional relationship between the local arrangement and topographic distribution of the underlying cortico-trabecular bone and cancellous architecture and the pattern(s) of articular load dissipation has been shown (e.g., Ryan and Ketcham 2002; Mazurier 2006; Fajardo *et al*. 2007; Volpato 2007; Mazurier *et al*. 2010; Ruff and Higgins 2013). Accordingly, bone evolutionary endostructural patterns are used for inferring functional behaviours in extinct hominin taxa and past human populations (e.g., Ruff 2008a,b, 2009; Carlson and Marchi 2014; Raichlen *et al*. 2015; Kivell 2016; Ruff *et al*. 2016; Saers *et al*. 2016; Ryan *et al*. 2018; Komza and Skinner 2019). In the anatomical context of the hominin knee joint, whose characteristics are part of a suite of derived traits intimately related to habitual bipedal locomotion (e.g., Aiello and Dean 1990; Tardieu 1999; Lovejoy 2007; Masouros *et al*. 2010; Sylvester 2013), the patellar bone covers and protects the anterior articular surface of the joint, expands the area of contact between the patellar ligament and the distal femur, and acts as a pulley for the quadriceps muscle, the largest muscle of the thigh and primary extensor of the knee (Standring 2008; Hartigan *et al*. 2011; White *et al*. 2012; Pina 2016). Accordingly, information on its subtle endostructural arrangement has the potential of contributing to the assessment of the knee-joint loading environment and to reveal individual- and/or taxon-specific functional behaviours. However, while the endostructural conformation of the extant human patella has been extensively considered in a clinical perspective (e.g., Raux *et al*. 1975; Townsend *et al*. 1975; van Kampen and Huiskes 1990; Katoh *et al*. 1996; Toumi *et al*. 2006, 2012), comparable information from the human fossil record is nearly non-existent (Beaudet *et al*. 2013; Cazenave 2018; Cazenave *et al*. 2019).

Supported by the evidence that «*variation in trabecular structure is our best source of morphological information that is preserved in the fossil record, particularly when analysed in conjunction with cortical bone, for reconstructing actual, rather than potential, behaviours in fossil hominoids and hominins*» (Kivell 2016: 587), a recent exploratory study provided the first endostructural information extracted from two fossil hominin patellae: the specimen SKX 1084 from Swartkrans, South Africa, likely representing a *Paranthropus robustus*, and the Neandertal patella Regourdou 1 (Cazenave 2018; Cazenave *et al*. 2019; see also Beaudet *et al*. 2013).

In the present study, we aim at assessing the endostructural pattern of two European Neandertal (from Krapina, Croatia, and Regourdou, France) and one

anatomically modern fossil human (from Chancelade, France) patellae and to compare their signal with the extant human condition.
Neandertal skeletal morphology at the knee differs in some ways from that of the anatomically modern fossil and extant humans. Among other details, these differences include a thicker patella, a more prominent tibial tuberosity and tibial condyles, and associated knee joint capsule and ligament attachments posteriorly displaced relative to their diaphyseal axes (e.g., Vandermeersch 1981; Heim 1982; Trinkaus 1983a,b, 2006; Trinkaus and Ruff 1989; Miller and Gross 1998; Trinkaus and Rhoads 1999; Trinkaus *et al*. 2017). Accordingly, given the gracilisation trend in postcranial skeletal robusticity occurred from the late Pleistocene through the Holocene (e.g., Chirchir *et al*. 2015, 2017; Ruff *et al*. 2015; Ryan and Shaw 2015; Scherf *et al*. 2016), in principle we expect (i) the two Neandertal patellae showing a relatively higher amount of cortical bone compared to both the fossil modern representative and the recent human comparative sample, and (ii) the fossil modern patella showing a higher amount of cortical bone compared to the extant human figures, at least as documented by the comparative sample used in this study. For the textural properties of the cancellous network, we predict that (i) the signature is relatively homogeneous between the two Neandertal patellae but somehow distinguishable from that of the fossil modern human representative and, to a greater extent, from that of the recent human sample, and that (ii) the structural organisation revealed by the fossil modern patella is distinguishable from the recent human condition.

MATERIALS

The investigated fossil specimens consist of two Neandertal and one fossil (late Upper Paleolithic) modern human patellae, all from adult individuals. The two Neandertal specimens, labelled 216.1-Pa 5. (Radovčić *et al*. 1988) and Regourdou C3 90 (Madelaine *et al*. 2008), are respectively form the early OIS 5e Croatian site of Krapina (Radovčić *et al*. 1988; Rink *et al*. 1995) and the OIS 5 partial skeleton Regourdou 1 discovered in 1957 in the homonym rock shelter in Dordogne, France (Vandermeersch and Trinkaus 1995; Couture 2008; Madelaine *et al*. 2008; Maureille *et al*. 2015). The fossil modern human patella is from the fairly complete skeleton of Chancelade (hereafter referred to Chancelade 1 to distinguish it from other human remains from the same site deposits; Taborin and Thiébault 1988) discovered in 1888 in a burial context in the OIS 2 cave site of Raymonden, also in Dordogne (Hardy 1888, 1891a,b). Firstly described by Testut (1889; among other studies, see in particular Vallois 1941-1946; Billy 1969; Dastugue 1969), it is chronologically referred to the Magdalenian III or IV period (Sonneville-Bordes 1959; Soubeyran 1965).

The three fossil specimens are imaged in figure 1 (A-C).
The left patella Krapina 216.1-Pa 5. (**fig. 1A**; hereafter referred to Krapina) shows abrasion limited to the upper, lateral and medial articular margins, the medial facet, and the posterior rim of the apex (Radovčić *et al*. 1988; Kricum *et al*. 1999). Its anterior surface, including around the base, is relatively smooth, with faint vertical striations but spread nutrient foramina. Posteriorly, the articular facets are intact but along the lateral margin, and rise from a rather developed and moderately anteriorly sloped articular crest. Both facets are concave at their most lateral and, to a lesser extent, medial part, respectively. A 3 mm-high supero-lateral vastus notch is present. The maximum height of this specimen measures 42.0 mm, the maximum breadth 48.4 mm and the maximum thickness 23.4 mm (Radovčić *et al*. 1988); its medial and lateral facet breadths measure 24.5 mm and 28.0 mm, respectively (Trinkaus 2000). The fossil is housed at the Croatian Natural History Museum in Zagreb.
Regourdou C3 90 (**fig. 1B**, hereafter referred to Regourdou 1) is a nearly perfectly preserved left patella for its outer (Madelaine *et al*. 2008) and inner structure (Bayle *et al*. 2011; Cazenave *et al*. 2019). Limited periosteal erosion and immediately underlying cancellous bone appearance is found around the base, at the lower portion of the articular surface and at the apex. A small notch of unknown (compressive?) origin is present along the lower rim of the medial articular facet. Approximately at its middle, the base shows a shallow medio-laterally oriented groove-like mark, slightly eroded along its upper rim, related to the insertion of the rectus femoris. The anterior surface is vascularised and displays several vertical striae from the fibres of the quadriceps tendon. Posteriorly, the articular crest raises moderately and the articular facets, both showing a concave shape, slope slightly anteriorly. A distinct lateral vastus notch is present. Maximum height and breadth in this specimen measure 42.1 mm and 44.7 mm, respectively, while maximum thickness is 21.0 mm (Vandermeersch 1981; Cazenave *et al*. 2019). According to Trinkaus (2000), its lateral facet breadth measures 23.5 mm and its medial articular breadth 22.5 mm. In 2008, its likely right counterpart, labelled Reg 4C 3848/D2-54, has been identified among the faunal remains collected during the field work run at the site between 1961 and 1964 (Madelaine *et al*. 2008). The sex of Regourdou 1, whose age at death is tentatively estimated at c. 23-30 years (in Volpato *et al*. 2012), is still a matter of discussion (Volpato *et al*. 2012; Plavcan *et al*. 2014; Pablos *et al*. 2019). Regourdou 1 is stored at the Musée d'Art et d'Archéologie du Périgord, Périgueux.
Among the three fossils examined in this study, Chancelade 1 is the least, but still relatively well preserved specimen (**fig. 1C**). Together with its counterpart, this right patella was firstly described by Testut (1889) and then re-examined by (Billy 1969). Part of its medial portion is missing and the upper and lower articular margins are locally abraded, thus showing some limited spots of cancellous bone. Its concave upper lateral edge is nearly intact. As noted by Testut (1889), the rough anterior surfaces of the Chancelade 1's patellae bear some developed markings («*La face antérieure des deux rotules présente un système de stries verticales qui lui donnent un aspect ligneux*»; Testut 1889: 208). A similar comment on their wrinkled anterior aspect was later provided by Billy («*La face antérieure de la rotule possède par ailleurs un relief vigoureux constitué de stries verticales très saillantes et de fortes empreintes tendineuses qui traduisent un développement certain du muscle quadriceps*»; 1969: 234). With special reference to the left patella, the presence of some accentuated markings was also briefly mentioned by Dastugue (1969), but considered of no pathological relevance («*…quelques bavures marginales de la rotule gauche; le fait est bien banal et ne peut guère être tenu*

— FIGURE 1 —

Anterior (upper row) and posterior (lower) views of the left Neandertal patella Krapina 216.1-Pa 5., Croatia (A), the left Neandertal patella Regourdou C3 90, France (B), the right Magdalenian patella Chancelade 1, France (C), and an extant human right patella from the Pretoria Bone Collection, South Africa (D) (according to the South African rules, in order to keep individual identity confidential, the label number of this specimen has been partially masked). All specimens are from adult individuals. Scale bar: 1 cm.

Vues antérieure (rangée supérieure) et postérieure (rangée inférieure) de la patella gauche néanderthalienne Krapina 216.1-Pa 5., Croatie (A), la patella gauche néandertalienne Regourdou C3 90, France (B), la patella magdalénienne droite Chancelade 1, France (C) et d'une patella droite humaine actuelle de la Pretoria Bone Collection, Afrique du Sud (D) (selon les règles sud-africaines, afin de préserver l'anonymat de l'individu, le numéro du spécimen a été partiellement masqué). Tous les spécimens sont issus d'individus adultes. Barre d'échelle: 1 cm.

pour important»; Dastugue 1969: 251). Actually, in association to an enthesophyte formation likely resulting from the ossification of fibres of the quadriceps femoris tendon, in the right patella used in this study some relatively large but poorly branched bone outgrowths of moderate relief are present at the upper and lower margins of its anterior surface, notably around the base rim. However, no evidence of alterations such as bone overgrowth with articular grooving, pitting, lipping, spur formation or eburnation typical of degenerative joint disease (i.e., osteoarthritis; Steinbock 1976; Zimmerman and Kelley 1982), can be found neither on its articular surface, such as for example in the left patella Pavlov 35 from the homonym Mid Upper Paleolithic Moravian site, Czech Republic (Trinkaus *et al*. 2017), or on/around the patellar surface of its corresponding distal femur. The anterior surface also displays well spread and relatively large nutrient foramina, especially on the middle third of the specimen. Superiorly, the groove-like area of attachment of the quadriceps tendon is especially wide and proportionally deep, and the attachment area of the apex for the ligamentum patellae is also well developed and rough. Posteriorly, the concave articular facets slope moderately anteriorly. A marked lateral vastus notch is present. The maximum height in this specimen is 44.0 mm, the maximum breadth 52.0 mm, and the maximum thickness 25.0 mm (Billy 1969; Testut 1889; Vandermeersh 1981), with minimum asymmetry between the two sides. The geometric mean of the maximum dimensions is 38.8 mm (Trinkaus *et al*. 2017). While the skeleton is traditionally regarded as representing an adult (c. 35-40 year old) male individual (e.g., Vandermeersch 1971), besides some classical descriptions mainly focussing on the skull (e.g., Boule 1925; Keith and Knowles 1926; LeGros Clark 1926; Morant 1926; Sollas 1927; Vallois 1941-1946), a morphoscopic and a probabilistic study based on the hip bone, as well as a discriminant analysis on a combination of 14 measurments of the humerus, femur and talus suggest that the skeleton Chancelade 1 represents a female individual (Villotte 2008). As Regourdou 1, Chancelade 1 is stored at Périgueux, in the Musée d'Art et d'Archéologie du Périgord.

The comparative material used in this study (**fig. 1D**) consists of a whole of 18 perfectly preserved right adult patellae from recent individuals of both sexes, all lacking macroscopic evidence of alteration or pathological change. The assemblage represents six individuals of African ancestry (3 males and 3 females aged 22-32 years) and four of European ancestry (1 male and 3 females aged 22-50 years) selected from the Pretoria Bone Collection stored at the Department of Anatomy of the University of Pretoria (L'Abbé *et al*. 2005), and 8 patellae (from 3 likely males and 5 likely females whose estimated age at death ranges between c. 20 and c. 50 years) from the Imperial Roman graveyard of Velia, Italy, stored at the National Prehistoric Museum of Rome (rev. in Beauchesne and Agarwal 2017). Average size and standard deviation of the comparative sample (n = 18) are as follows: maximum height = 32.6 ± 4.0 mm; maximum breadth = 41.4 ± 4.2 mm; maximum thickness = 19.8 ± 2.2 mm.

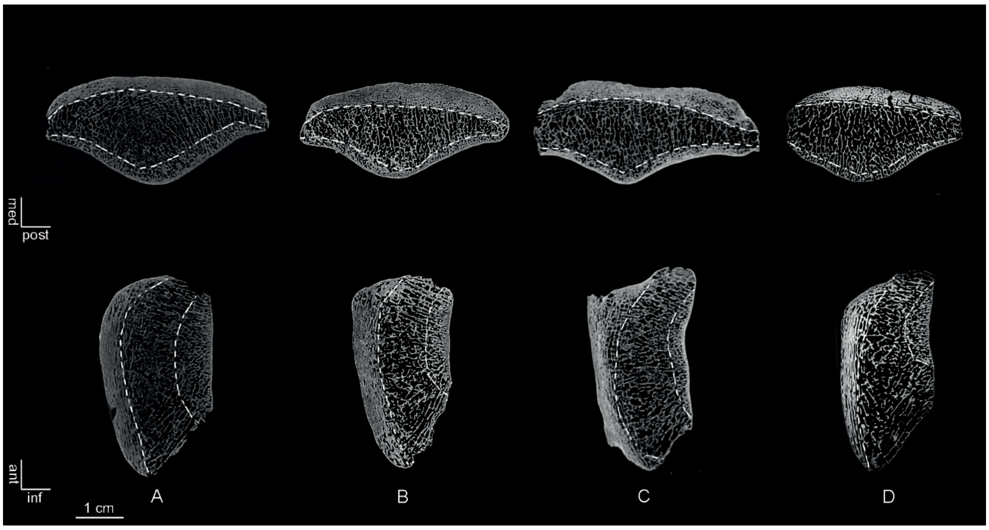
METHODS

Krapina was imaged in 2012 by X-ray microtomography (µXCT) at the Multidisciplinary Laboratory of the International Centre for Theoretical Physics (ICTP) of

Trieste, Italy (Tuniz *et al*. 2013), at an isotropic spatial resolution of 33.0 µm. Regourdou 1 was imaged in 2004 by SR-µCT at the beamline ID 17 of the European Synchrotron Radiation Facility (ESRF) of Grenoble, France (Mazurier *et al*. 2006), at an isotropic spatial resolution of 45.5 µm (Bayle *et al*. 2011; Cazenave *et al*. 2019), while the patella from Chancelade 1 was scanned in 2007 at the analytical platform set at the University of Poitiers, France, by a Viscom X8050-16 AG system at an isotropic spatial resolution of 53.2 µm.
The comparative extant human sample from the Pretoria Bone Collection was scanned in 2016 at the South African Nuclear Energy Corporation (Necsa), Pelindaba, using a Nikon XTH 225 ST equipment with an isotropic voxel size ranging from 24.0 µm to 50.0 µm, while the archaeological specimens from Velia were imaged in 2012 at the ICTP at an isotropic voxel size ranging from 25.0 µm to 30.0 µm. Following the acquisitions, a virtual transformation of each dataset was necessary to coherently orient all specimens by using Avizo v.8.0.0. (Visualization Sciences Group Inc.). For the purposes of the comparative analyses, in each specimen we firstly defined the cortico-trabecular complex (CTC, in mm), i.e., the subchondral component which includes the cortical shell (lamina) and the intimately related adjoining portions of the supporting trabecular network (**fig. 2**), which mostly consists of plate-like structures (Mazurier 2006; Volpato 2007; Mazurier *et al*. 2010; Cazenave *et al*. 2019). Once virtually isolated, the mean cortico-trabecular thickness of the anterior (aCTT) and posterior (pCTT) surfaces were measured by the routine MPSAKv2.9 (in Dean and Wood 2003) on the sagittal and transversal slices extracted at the midpoint of the maximum medio-lateral breadth and maximum antero-posterior thickness, respectively. To allow size-independent inter-taxic comparisons, in each specimen the measures were standardised with respect to the medio-lateral diameter of the patella and provided as % values.

By taking into account the inner preservation conditions of the three fossil patellae, notably that of Chancelade 1, in order to quantitatively assess the textural properties of their cancellous network we identified four homologous cubic volumes of interest (Ryan and Ketcham 2002) respectively sampling the superior (sVOI), inferior (iVOI), medial (mVOI) and lateral (lVOI) aspects (**fig. 3**). The geometric centre of the sVOI and iVOI was respectively placed at the middle of the medio-lateral breadth and antero-posterior thickness, and at ¼ of the supero-inferior articular height from the superior and inferior margins. The mVOI and lVOI were positioned at the middle of the supero-inferior articular height and antero-posterior thickness, and at ¼ of the medio-lateral breadth from the medial and lateral margins, respectively. The same analytical protocol was systematically applied to the specimens used for comparison.

By definition, in this study each VOI has an edge length equal to 10% of the medio-lateral breadth, which corresponds to a VOI of 113.4 mm^3 in Krapina, 89.3 mm^3 in Regourdou 1, and 140.6 mm^3 in Chancelade 1. Accordingly, the structural conformation of a whole of 453.6 mm^3, 357.3 mm^3 and 562.4 mm^3 of cancellous network have been assessed in the three fossil patellae, respectively. This value ranges from 142.0 mm^3 to 503.2 mm^3 in the recent comparative sample, where the unitary VOIs fluctuate between 35.5 mm^3 and 125.8 mm^3.



— FIGURE 2 —

Transversal (upper row) and sagittal (lower) virtual sections respectively extracted at the midpoint of the medio-lateral breadth and the maximum antero-posterior thickness in Krapina 216.1-Pa 5. (A), Regourdou C3 90 (B), Chancelade 1 (C), and in an extant human right patella (D). In each section, the dashed line delimits the cortico-trabecular complex (CTT) assessed for its average anterior (aCTT) and posterior (pCTT) standardised thickness. Scale bar: 1 cm.

Sections virtuelles transversale (rangée supérieure) et sagittale (rangée inférieure) extraites respectivement au milieu de la largeur medio-latérale et de l'épaisseur antéro-postérieure maximales pour Krapina 216.1-Pa 5. (A), Regourdou C3 90 (B), Chancelade 1 (C) et pour une patella droite humaine actuelle (D). Pour chacune des sections, la ligne en pointillés délimite le complexe cortico-trabéculaire (CTT) considéré pour sa moyenne d'épaisseur standardisée antérieure (aCTT) et postérieure (pCTT). Barre d'échelle: 1 cm.

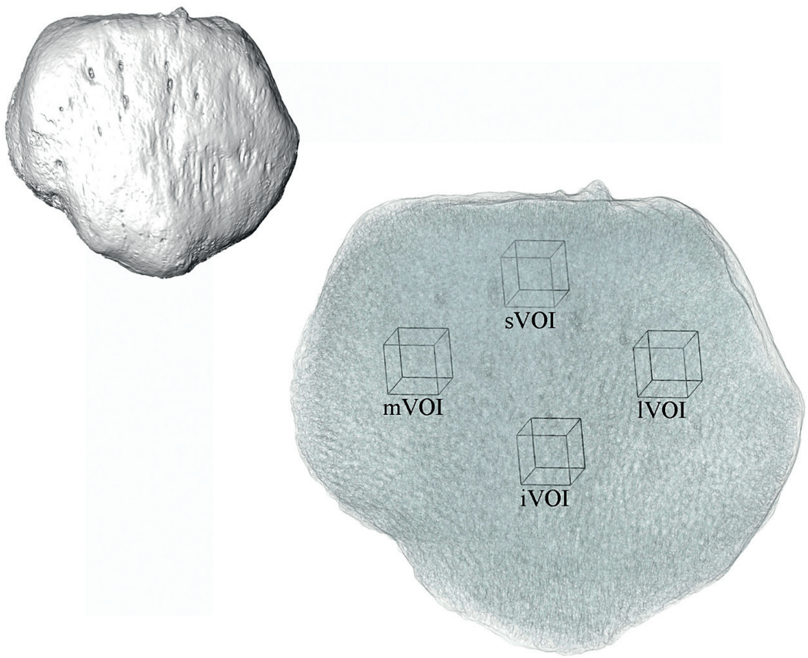


FIGURE 3

Microtomographic-based 3D reconstruction in slightly oblique anterior view of Regourdou C3 90. The enlarged image in semi-transparency shows the position of the superior (s), inferior (i), medial (m) and lateral (l) cubic volumes of interest (VOI) extracted for assessing cancellous bone properties. The virtual reconstruction of the outer surface of the specimen (not to scale) is provided for orientation.

Reconstruction microtomographique en 3D en vue antérieure oblique de Regourdou C3 90. L'image agrandie en semi-transparence indique la position des volumes cubiques d'intérêt (VOI) supérieur (s), inférieur (i), médial (m) et latéral (l) extraits pour quantifier les propriétés de l'os trabéculaire. La reconstruction virtuelle de la surface externe du spécimen (non à l'échelle) est présentée pour orientation.

To assess their properties, the cubic VOIs were binarised into bone and non-bone using the «Half Maximum Height» (HMH) quantitative iterative thresholding method (Spoor *et al*. 1993) and the region of interest protocol (ROI-Tb; Fajardo *et al*. 2002) by taking repeated measurements on different slices of the virtual stack (Coleman and Colbert 2007) using Avizo v.8.0.0. and ImageJ (Schneider *et al*. 2012). By using the star volume distribution (SVD) algorithm in Quant3D (Ryan and Ketcham 2002), on each virtually extracted VOI we measured the following variables: (i) the trabecular bone volume fraction (BV/TV), given as the ratio of the number of bone voxels to the total number of voxels; (ii) the trabecular thickness (Tb.Th., in mm), which is the mean thickness of the trabecular struts; and (iii) the degree of anisotropy (DA), a fabric characteristic of trabecular bone assessed following Ryan and Ketcham (2002) by dividing the eigenvalue representing the relative magnitude of the primary material axe of the bone structure ($\tau1$) by the eigenvalue representing the relative magnitude of the tertiary material axe of the bone structure ($\tau3$) (see also Ryan and Walker 2010; Shaw and Ryan 2012).

For all variables, a number of intra- and inter-observer tests for accuracy run by three independent observers revealed differences less or near 5%, which is compatible with the estimates from other similar studies (e.g., Tsegai *et al*. 2018; Cazenave *et al*. 2019).

Due to small sample sizes, only non-parametric statistical tests were performed using R v3.4.4 (R Core Team, 2019). In the comparative sample, the significance of the differences between the VOIs for BV/TV, Tb.Th. and DA was tested using the Mann-Whitney U-test.

RESULTS

Endostructural preservation and conformation of the fossil specimens

All three fossil patellae Krapina, Regourdou 1 and Chancelade 1 show a quality of the endostructural signal fully compatible with the specific purposes of the present study (**fig. 4A-C**). As frequently observed while investigating the inner structural conformation in fossil remains (e.g., Skinner and Sperber 1982; Kricum *et al*. 1999; Macchiarelli *et al*. 1999; Cazenave *et al*. 2017; Cazenave 2018), in this case also cortical and cancellous bone appearance are relatively unrelated to the outer preservation conditions, in the sense that the inner signal may sometimes topographically vary in a hardly predictable way among distinct areas within the same specimen.

The whole inner structure of Krapina is very well preserved, with limited matrix infilling the inter-trabecular spaces (**fig. 4A**). There is only a c. 3 mm deep thin crack running from its infero-medial surface towards the core of the specimen. A denser cancellous area, likely related to the attachment of the quadriceps muscle, is found at its supero-lateral margin, and a number of radially-oriented trabeculae are also noticeable in the peripheral medial region and around the apex. A vertically-oriented anterior bundle (Standring 2008), mostly consisting of plate-like trabeculae (Gibson 1985; Dalstra and Huiskes 1995; Ding *et al*. 2002; Stauber and Müller 2006) runs from the base towards the apex. In sagittal view, the outline of its posterior limit is slightly convex anteriorly, thus following the shape of the anterior cortico-trabecular complex. At the upper and distal margins, two obliquely-oriented bundle-like structures running from the anterior to the posterior endosteal surfaces are also discernible. Both mostly consist of relatively thicker struts and/or plate-like structures, but the upper one is proportionally thicker. The remaining cancellous network mostly displays

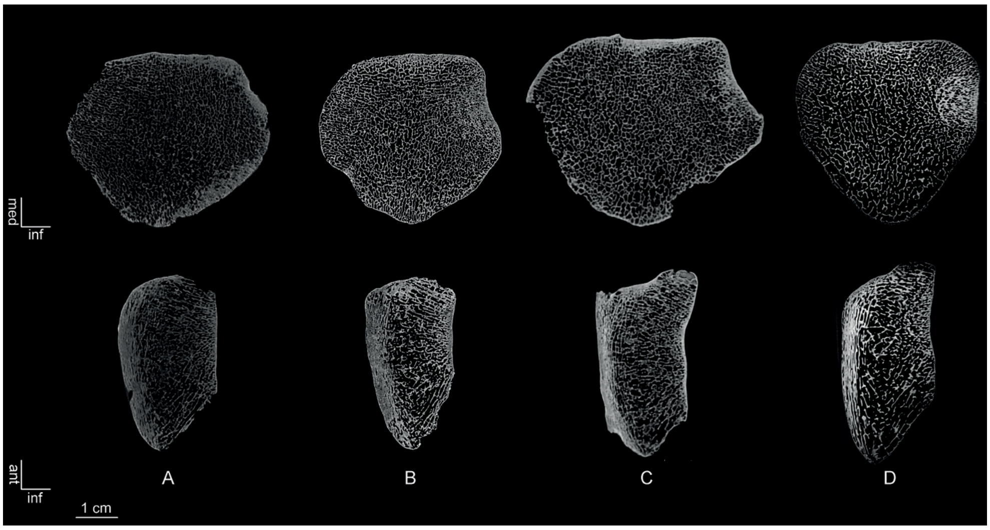


FIGURE 4

Coronal (upper row) and sagittal (lower) virtual sections extracted across the centre of Krapina 216.1-Pa 5. (A), Regourdou C3 90 (B), Chancelade 1 (C), and of an extant human right patella (D). Scale bar: 1 cm.

Sections virtuelles coronale (rangée supérieure) et sagittale (rangée inférieure) extraites au centre des patellae Krapina 216.1-Pa 5. (A), Regourdou C3 90 (B), Chancelade 1 (C) et d'une patella droite humaine actuelle (D). Barre d'échelle: 1 cm.

a typically honeycomb-like appearance, especially at the medial aspect, while around the core the struts are relatively more structured and oriented (**fig. 4A, 5**).

Among the investigated fossil specimens, Regourdou 1 revealed the most finely preserved inner structure, with mineralized struts arranged in a distinctly appreciable network and no evident matrix infilling the inter-trabecular spaces (**fig. 4B**). Limited cracking and lacunae are only found across the upper portion of the anterior cortex. A trabecular reinforcement, likely related to the attachment of the vastus lateralis, is noticeable around it supero-lateral margin; many radially-oriented trabeculae are also present in the medial peripheral area and around the apex. As seen in the patella from Krapina, a vertically-oriented bundle displaying a slightly anteriorly convex outline and mostly consisting of plate-like trabeculae runs across the anterior portion in both sagittal and transversal views from the base towards the apex. Here also, the two upper and lower bundle-like structures obliquely moving from the anterior to the posterior endosteal surfaces are evident. However, while in Regourdou 1 they are poorly distinguishable in terms of relative unitary strut thickness, the superior bundle is anyhow lager. Around the core, the cancellous network displays a rather vermiculate appearance.

Despite the missing bony chunks and local erosion, Chancelade 1 shows a relatively well-preserved endostructure (**fig. 4C**), its cancellous network being only punctually filled by a consolidated sediment whose density is anyhow distinct from that of the surrounding bone. Importantly for the present study, despite the ossification of fibres of the quadriceps femoris tendon and some bone outgrowths evident on its anterior surface (**fig. 1C**), the structural organisation of the corresponding subchondral bone does not appear locally altered with respect to the evidence provided by the other investigated specimens (**fig. 6A**). Nonetheless, compared to the fossil and recent patellae used in this study, at nearly all sites across its anterior surface, the antero-posterior virtual sections of Chancelade 1 reveal a variably wavy anterior rim (**fig. 6A-B**) suggesting a locally thickened periosteal contour which could locally affect the estimates of its cortico-trabecular anterior thickness (aCTT). Additionally, the specimen reveals an especially developed blood supply system originally derived from the superior and inferior genicular vessels forming the anastomosis around the front of the knee joint (Cunningham *et al*. 2016). For example, in correspondence of its largest nutrient foramen opening appearing laterally on the middle third of the anterior surface, the Magdalenian patella has a 0.4-1.1 mm-large vessel track which obliquely penetrates infero-superiorly the body for c. 8.6 mm towards the posterior surface (**fig. 6B**). A denser trabecular area is present at the supero-lateral margin. Radially-oriented trabeculae are essentially limited to the upper medial peripheral area of the specimen, but the vertically-oriented anterior bundle (Standring 2008) is well distinguishable. Conversely, while present, the two oblique bundle-like reinforcements obliquely running antero-posteriorly around the upper

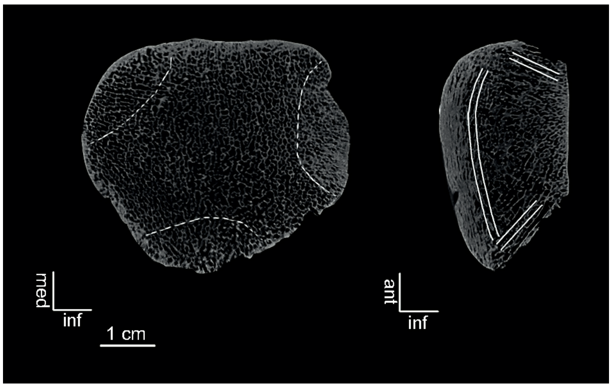
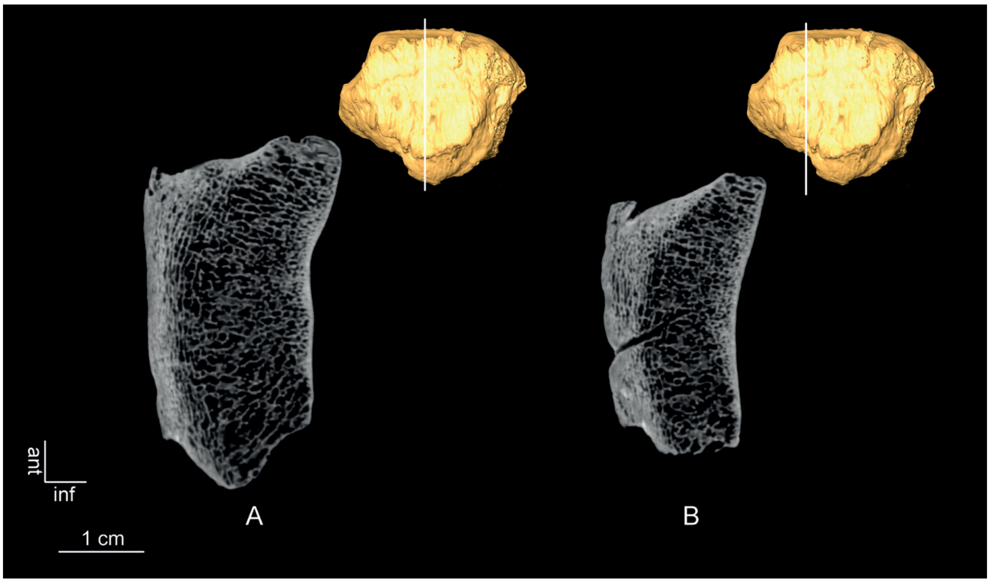


FIGURE 5

Coronal (A) and sagittal (B) virtual sections extracted across Krapina 216.1-Pa 5 showing the denser cancellous area in the supero-lateral margin, the peripheral medial and the apical regions with radially-oriented trabeculae (A), the vertically-oriented anterior bundle and the two obliquely-oriented bundle-like structures at the upper and distal margins (B). Scale bar: 1 cm.

Sections virtuelles coronale (A) et sagittale (B) extraites de Krapina 216.1-Pa 5 illustrant la région supéro-latérale de renforcement osseux, la région périphérique médiale et la région de l'apex avec des trabeculae radialement orientées (A), le faisceau antérieur orienté verticalement et les deux faisceaux obliques des régions supérieure et distale (B). Barre d'échelle: 1 cm.



— FIGURE 6 —

Two parasagittal virtual sections extracted across Chancelade 1 showing the variably wavy anterior rim and the underlying subchondral bone and cancellous network (A, B). A 0.4-1.1 mm-large vessel track from the anterior surface opening obliquely penetrates the patella for c. 8.6 mm (B). The virtual reconstructions of the outer surface of the specimen (not to scale) are provided for orientation. Scale bar: 1 cm.

Deux sections virtuelles parasagittales extraites de Chancelade 1 présentant l'ondulation de la surface antérieure, l'os sous-chondrale sous-jacent et le réseau trabéculaire (A, B). Trace d'un vaisseau de 0.4-1.1 mm de large pénétrant obliquement la patella sur c. 8.6 mm depuis son ouverture de la surface antérieure (B). Les reconstitutions virtuelles de la surface extérieure du spécimen (non à l'échelle) sont présentées pour orientation. Barre d'échelle: 1 cm.

and lower margins are less dense, but proportionally larger than seen in both Krapina and Regourdou 1. Finally, in Chancelade 1 the core has a honeycomb-like structure similar to that of the Croatian patella.

The cortico-trabecular complex (CTT)

In the sagittal and transversal planes, Regourdou 1 and Chancelade 1 show a relatively thicker anterior cortico-trabecular complex (aCTT) than measured in the absolutely and relatively thin patella from Krapina and, on average, in the recent comparative sample (**tab. 1**). In this comparative context, Chancelade 1 shows the highest percentage value for the sagittal and Regourdou 1 for the transversal aCTT, respectively, both near or just above the upper limits of the variation range revealed by the comparative sample used in this study.
Following the transversal and, to a minor extent, the sagittal plane, such comparative structural heterogeneity is not found for the articular surface, where the values of the three fossil specimens fall within the variation range of the comparative sample. However, it should be noted the especially low percentage values respectively shown by Chancelade 1 for the sagittal and by Regourdou 1 for the transversal posterior cortico-trabecular complex (pCTT), both near the lower limits of the recent human variation (**tab. 1**).

It does not matter the orientation plan, in all three fossil patellae the cortico-trabecular complex is systematically thicker anteriorly than posteriorly, the greatest differences having been measured in Chancelade 1 for the CTT of the sagittal plan and in Regourdou 1 on the transversal plan. Conversely, such differences are very modest in Krapina for both slices. Within our comparative sample, an opposite pattern (pCTT > aCTT) is found anyhow in 22 % of the individuals for the sagittal plane and 17% for the transversal plane, respectively.

Cancellous bone structural organisation and topographic variation

The quantitative estimates of the cancellous network textural properties of the superior (sVOI) and lateral (lVOI) volumes of interests (**fig. 3**) do not appreciably differ among the three fossil specimens and, importantly, the values systematically fall within the variation range displayed by the recent comparative sample. Conversely, some structural differences among the fossils, as well as with respect to the recent human figures, are found for the variables of the inferior (iVOI) and medial (mVOI) volumes of interests (**tab. 2, fig. 7**). The greatest differences among the three fossil patellae concern the iVOI. Specifically, they are found between Krapina and Regourdou 1 for the degree of anisotropy (the adimensional DA: 0.34 vs. 0.64), and between Regourdou 1 and Chancelade 1 for both the bone volume fraction ratio (BV/TV: 0.24 vs. 0.44) and the trabecular thickness (Tb.Th.: 0.20 mm vs. 0.38 mm). In both VOIs, Chancelade 1 displays the absolutely thickest trabeculae (Tb.Th.) and the highest BV/TV ratio, while the highest DA is shown by the mVOI of the specimen from Krapina. However, the BV/TV of the two Neandertal patellae and the DA of Regourdou 1 and Chancelade 1 measured in the iVOI fall within the recent human variation range, and also the BV/TV of Chancelade 1 and the Tb.Th. of Regourdou 1 of the mVOI closely approach the upper limits of the comparative sample.

Specimen/sample	aCTT sagittal	pCTT sagittal	aCTT transversal	pCTT transversal
Krapina 216.1-Pa 5.	7.6	6.6	5.6	4.3
Regourdou C3 90	10.2	6.9	9.6	3.6
Chancelade 1	10.7	4.6	8.9	4.3
recent humans (s.d.)	8.2 (2.3)	7.0 (2.5)	6.6 (2.2)	4.9 (1.7)

— TABLEAU 1 —

Mean thickness of the cortico-trabecular complex (standardised % values) distinctly measured for the anterior (aCTT) and posterior (pCTT) patellar surfaces across the sagittal and transversal virtual slices respectively extracted at the midpoint of the maximum antero-posterior thickness and the medio-lateral breadth (see fig. 2) in Krapina 216.1-Pa 5., Regourdou C3 90, Chancelade 1 and in the recent human reference sample used for comparisons (n = 18); s.d., standard deviation.

Epaisseur moyenne du complexe cortico-trabéculaire (valeurs standardisées en %) mesurée pour les surfaces antérieure (aCTT) et postérieure (pCTT) de la patella sur des coupes sagittale et transversale extraites virtuellement au milieu du diamètre antéro-postérieure et de la largeur médio-latérale maximales (voir fig. 2) pour Krapina 216.1-Pa 5., Regourdou C3 90, Chancelade 1 et pour l'échantillon humain récent de référence utilisé pour comparaison (n = 18); s.d., déviation standard.

Specimen/sample	sVOI			iVOI			mVOI			lVOI		
	BV/TV	Tb.Th.	DA	BV/TV	Tb.Th.	DA	BV/TV	Tb.Th.	DA	BV/TV	Tb.Th.	DA
Krapina 216.1-Pa 5.	0.39	0.30	0.57	0.30	0.27	0.34	0.39	0.27	0.67	0.44	0.28	0.56
Regourdou C3 90	0.35	0.25	0.59	0.24	0.20	0.64	0.29	0.24	0.36	0.42	0.20	0.50
Chancelade 1	0.46	0.35	0.50	0.44	0.38	0.46	0.40	0.34	0.61	0.39	0.34	0.55
recent humans	0.40	0.28	0.52	0.30	0.23	0.56	0.28	0.23	0.51	0.40	0.31	0.50
(s.d.)	(0.10)	(0.11)	(0.18)	(0.13)	(0.05)	(0.17)	(0.07)	(0.05)	(0.14)	(0.11)	(0.14)	(0.17)

— TABLEAU 2 —

Bone volume fraction (BV/TV, in %), trabecular thickness (Tb.Th., in mm) and degree of anisotropy (DA) of the superior (sVOI), inferior (iVOI), medial (mVOI) and lateral (lVOI) volumes of interest of the patella (see fig. 3) assessed in Krapina 216.1-Pa 5., Regourdou C3 90, Chancelade 1 and in the recent human reference sample used for comparisons (n = 18); s.d., standard deviation.

Volume osseux (BV/TV, en %), épaisseur trabéculaire (Tb.Th., en mm) et degré d'anisotropie (DA) des volumes d'intérêts supérieur (sVOI), inférieur (iVOI), médial (mVOI) et latéral (lVOI) de la patella (voir fig. 3) mesurés pour Krapina 216.1-Pa 5., Regourdou C3 90, Chancelade 1 et pour l'échantillon humain récent de référence utilisé pour comparaison (n = 18); s.d., déviation standard.

In the patellae forming our comparative sample, a trabecular reinforcement is commonly found in the superior and lateral VOIs, both displaying a significantly denser cancellous network (higher BV/TV) resulting from thicker struts (higher Tb.Th. values) than measured in the inferior and medial VOIs (tab. 3). However, the differences for these variables between the sVOI and the lVOI, as well as those between the iVOI and the mVOI and among all four VOIs for the DA (tab. 2, fig. 7), are not statistically significant (**tab. 3**).

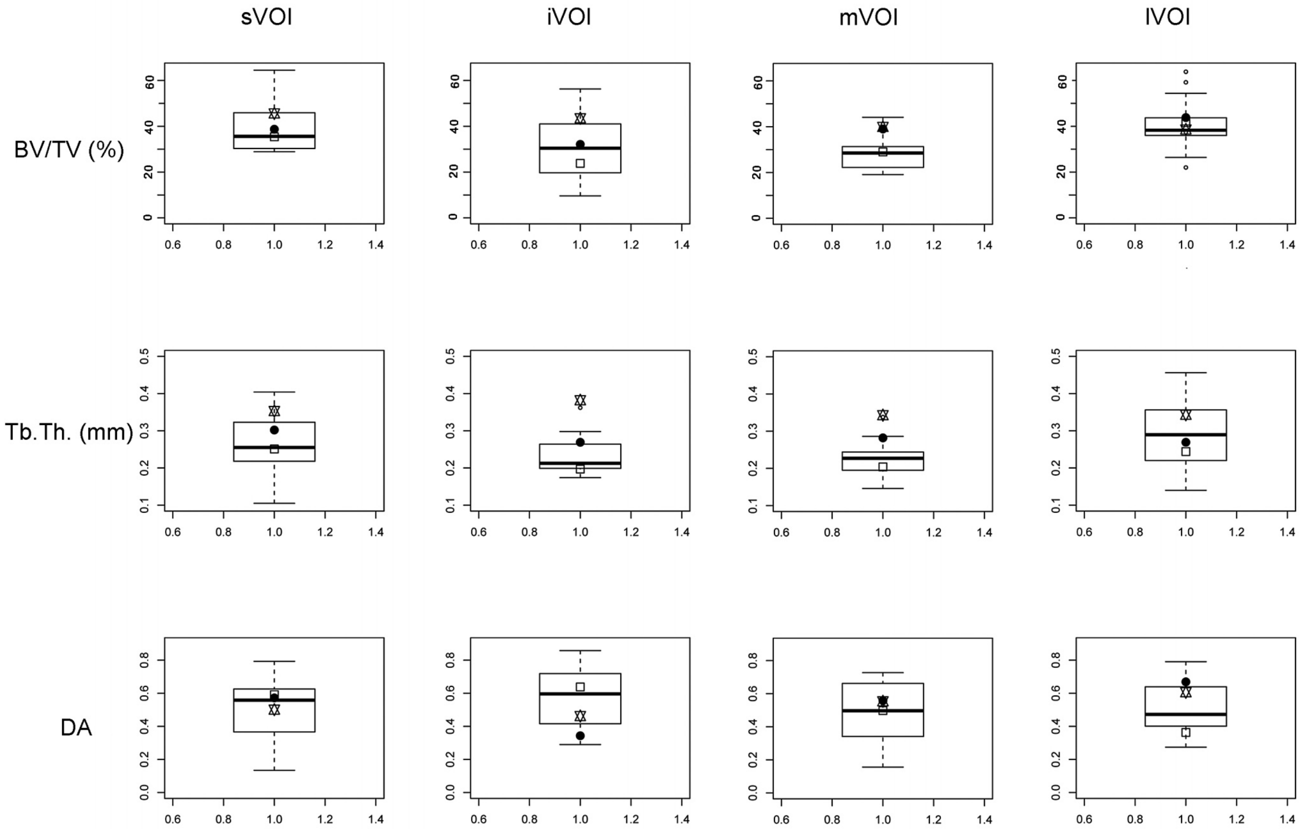
Among the fossil specimens, this extant distinct human pattern (sVOI-lVOI vs. iVOI-mVOI) is followed by Regourdou 1, but neither by Chancelade 1, where the superior and inferior spots show a denser network and thicker trabeculae than medially and laterally, nor Krapina, where a denser cancellous network is found in the lVOI and then in the sVOI and mVOI, and where the average differences in trabecular thickness between all four VOIs do not exceed 0.03 mm.

DISCUSSION AND CONCLUSIONS

Based on preliminary studies (Cazenave 2018; Cazenave *et al.* 2019; see also Beaudet *et al.* 2013) of potential interest in evolutionary knee paleobiomechanics (e.g., Chapman *et al.* 2010; DeSilva *et al.* 2013; Marchi *et al.* 2017), the present research aimed at: adding comparative evidence on another Neandertal individual (the specimen Krapina); documenting the still unreported condition displayed by an anatomically modern fossil human representative (the Magdalenian Chancelade 1); assessing the possible evidence for a still unreported time-related trend of endostructural gracilisation in bone tissue proportions also recorded by the patellar bone (e.g., Chirchir *et al.* 2015, 2017; Ruff *et al.* 2015; Ryan and Shaw 2015; Scherf *et al.* 2016). With this respect, we formulated four major hypotheses distinctly concerning the subchondral bone and the cancellous network.

(i) The two Neandertal patellae, Krapina and Regourdou 1, should display a relatively higher volume of cortico-trabecular complex (CTC) compared to both the Magdalenian Chancelade 1 and the recent-extant comparative sample of human patellae, and (ii) Chancelade 1 should display a thicker subchondral component compared to the extant human condition. They have been assessed by measuring the CTC mean thickness standardised by the patellar breadth on two virtual slices extracted across the anterior (aCTT) and posterior (pCTT) mid-sagittal and mid-transversal slices, respectively.

The results do not support the first hypothesis, as marked differences have been primarily found between the two Neandertal specimens, Krapina revealing an absolutely and relatively thin anterior complex across both planes, even thinner than compared to the average values of the recent comparative sample. Interestingly, this results is



— FIGURE 7 —

Box-and-whisker plots of the bone volume fraction (BV/TV, in %), trabecular thickness (Tb.Th., in mm) and degree of anisotropy (DA) of the superior (sVOI), inferior (iVOI), medial (mVOI) and lateral (lVOI) volumes of interest assessed in the recent human reference sample used for comparisons (n = 18) and in Krapina 216.1-Pa 5. (circle), Regourdou C3 90 (square) and Chancelade 1 (big star).

Boîtes à moustaches du volume osseux (BV/TV, en %), de l'épaisseur trabéculaire (Tb.Th., en mm) et du degré d'anisotropie (DA) des volumes d'intérêt supérieur (sVOI), inférieur (iVOI), médial (mVOI) et latéral (lVOI) mesurés pour l'échantillon humain récent de référence utilisé pour comparaison (n = 18) et pour Krapina 216.1-Pa 5. (cercle), Regourdou C3 90 (carré) et Chancelade 1 (grande étoile).

	iVOI	mVOI	lVOI
	p-value	*p*-value	*p*-value
BV/TV			
sVOI	**0.009**	**7.629e-05**	0.966
iVOI	-	0.757	**0.027**
mVOI	-	-	**1.068e-04**
Tb.Th.			
sVOI	**0.017**	**0.003**	0.214
iVOI	-	0.890	**0.018**
mVOI	-	-	**5.035e-04**
DA			
sVOI	0.417	0.459	0.702
iVOI	-	0.244	0.167
mVOI	-	-	0.963

— TABLEAU 3 —

P-values of the Mann-Whitney U-test between the superior (sVOI), inferior (iVOI), medial (mVOI) and lateral (lVOI) volumes of interest for the bone volume fraction (BV/TV, in %), the trabecular thickness (Tb.Th., in mm) and the degree of anisotropy (DA) assessed in the recent human reference sample used for comparisons (n = 18). Significant differences in bold.

Valeurs-p du test U de Mann-Whitney entre les volumes d'intérêts supérieur (sVOI), inférieur (iVOI), médial (mVOI) et latéral (lVOI) pour le volume osseux (BV/TV, en %), l'épaisseur trabéculaire (Tb.Th., en mm) et le degré d'anisotropie (DA) mesurés pour l'échantillon humain récent de référence utilisé pour comparaison (n = 18). Différences significatives en gras.

not size-dependent, as the Croatian patella, as tall as Regourdou 1 (42.0 mm vs. 42.1 mm), is larger (48.4 mm vs. 44.7 mm) and thicker (23.4 mm vs. 21.0 mm) than the French Neandertal representative, whose patellar thickness (21.0 mm) and articular breadth (Trinkaus 2000) is rather modest among the Upper Pleistocene human specimens and, differently from Krapina and Chancelade 1, falls within the variation range shown by our reference sample (17.6-22.0 mm). Conversely, comparative values have been found between Regourdou 1 and the Magdalenian specimen, the last showing the absolutely thickest CTC at least along the sagittal, but not the transversal, anterior surface. Even if the anterior sagittal signal from Chancelade 1 may be affected by a locally slightly thickened cortex bearing evidence of ossification of fibres of the quadriceps femoris tendon, the absolutely thick subchondral component does not appear structurally altered. The differences measured among the three fossil specimens across the posterior (articular) surface are modest and, mostly, the values hardly distinguishable from the recent human estimates. As expected, in all fossils and in the majority of recent human patellae, the anterior subchondral plate is variably thicker than measured at the articular surface. Indeed, while the loads at the anterior patellar surface are directly transferred from the quadriceps (Heegaard *et al*. 1995; Toumi *et al*. 2012), the posterior aspect is covered by a thick hyaline cartilage, among the thickest in the human body, able to withstand the intermittent compressive stresses locally occurring at a higher frequency (Hartigan *et al*. 2011; Milz *et al*. 1995; Standring 2008).

Concerning the second hypothesis (Chancelade 1's CTC thicker than measured in the comparative sample), it is supported for the anterior surface across both sagittal and transversal planes, but not for the posterior surface, whose thickness is lower than the recent mean estimates.

In terms of topographic organisation (i.e., bone volume fraction, trabecular thickness and degree of anisotropy of the network), following our *a priori* expectations, (iii) the cancellous pattern of the two Neandertal patellae should be qualitatively and quantitatively comparable, and at least locally distinguishable from the endostructural signal(s) of the Magdalenian, and especially of the extant human patellae and, accessorily, (iv) Chancelade 1's cancellous properties should be at least locally distinct from the recent human pattern. We tested such hypotheses by quantifying and comparing cancellous organisation at four homologous cubic volumes of interest (VOI) sampling the superior (sVOI), inferior (iVOI), medial (mVOI) and lateral (lVOI) portions of the patella.

In our study, the third hypothesis is supported for the superior and, to a lesser extent, the lateral cubic spots, where some structural concordances with the signals from Chancelade 1, but also with the recent comparative sample, are found. However, this is not the case for the inferior and medial VOIs, where the two Neandertals mostly, but not uniquely, differ for their fabric characteristics (DA). As a whole, Chancelade 1 is closer to the signature provided by Krapina than by Regourdou 1, but still rather distinct. In any case, the Croatian Neandertal and French Magdalenian share a honeycomb-like appearance of the cancellous network not observed in recent humans. Interestingly, in 75% of cases the estimates of the two Neandertal specimens fall within the variation range expressed by the comparative sample. In particular, at each topographic spot investigated in this study, the cancellous density and trabecular thickness of Krapina and Regourdou 1 fall within the recent human range, suggesting that the forces generated by the quadriceps travelling through the patella, thus the knee, were similar (cf. Miller and Gross 1998; Trinkaus 1983a,b, 1986; Trinkaus and Rhoads 1999). Compared to the signals from inferior and medial aspects, the evidence observed in our reference sample of a denser cancellous network and thicker trabeculae occurring in the superior and lateral regions of the patella fits the typical normal human pattern (Katoh *et al*. 1996).

The fourth hypothesis is supported, in the sense that in 33% of cases Chancelade 1's inner signature is distinct from that displayed by our comparative sample, and that the Magdalenian specimen also shows a less heterogeneous structural pattern than observed in extant humans (**tab. 3**). However, this result even exceeds the evidence from the two Neandertals, whose cancellous organisation is closer to the extant human pattern than that of the Magdalenian representative. At any rate, it is also noteworthy that all three fossils share with the patellae forming the reference sample a denser trabecular area at the supero-lateral margin; a higher number of radially-oriented trabeculae at the medial peripheral area and around the apex; a distinct vertically-oriented anterior bundle of plate-like trabeculae; and two obliquely-oriented superior and inferior bundle-like structures running from the anterior to the posterior endosteal surfaces (Standring 2008).

In tentatively assessing the value of the results summarised in the present pilot study, it should be noted that the major limiting factor of our research design primarily consists in the absolute lack of comparative information on the inner structural organisation of the patellar bone from any other human fossil representative, whatever its taxonomic status (Cazenave 2018; Cazenave *et al*. 2019). Two additional limits specifically concern the first assessment of the «anatomically modern fossil human condition», if any, by using Chancelade 1. The first of course consists in the use of a single specimen whose signal could reflect an idiosyncratic condition with respect to the «typical/average pattern», if any, characteristic of its reference population. The second limit deals with the presence in Chancelade 1 of some accentuated bony markings having altered the original morphology of its outer anterior cortex (Billy 1969; Dastugue 1969; Testut 1889). Even if we tend to minimise its impact on the structural arrangement of the subchondral bone and cancellous organisation, such periosteal alteration is nonetheless evident. However, ossification of the tendinous insertions of the quadriceps femoris and variably-sized bony spurs are commonly found on the anterior surface of fossil human patellae, notably among Neandertals, as they result from especially high levels of strain on the tendons related to muscular hyperactivity (Carretero *et al*. 1999; Trinkaus 1983a). In Chancelade 1, it is nonetheless noteworthy that its higher anterior CTT is associated with a general reinforcement of the cancellous density and to thicker trabeculae at all sites. Whatever the impact on Chancelade 1's endostructural organisation of its altered anterior cortex, the hypothesis of an alleged «anatomically modern fossil human condition» still deserves to be tested.

In conclusion, despite the obvious, and currently unavoidable, limits of the present study, notably the generalised lack of information on the endostructural pattern of the patella in any other fossil human representative besides the three analysed here, we nonetheless consider that the present results deserve attention to plan at the best for future research of paleobiomechanical, paleobiological, and perhaps taxonomic interest and for more accurately orient sampling strategies.

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