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## Functional insights from an exploration of the inner structure of the patella: new perspectives for the study of the hominin fossil record

### *Informations fonctionnelles dans l'exploration de la structure interne de la patella : nouvelles perspectives pour l'étude du registre hominine fossile*

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**Abstract** – This contribution is a short review of the functional significance of the patella in extant catarrhines and extinct hominins and of current functional, adaptive and evolutionary-related questions concerning the fossil hominin record. The patella plays a key functional role in the knee joint and thus reflects habitual postural and locomotion modes. However, patellar remains are rare in the hominin fossil record and it is still unclear whether and how their differences in shape and proportions compared to extant humans affect knee kinesiology. Here, we illustrate with a first example from a sample of human, *Pan*, *Papio* and Neanderthal patellae that the development of a "whole-bone" endostructural analysis has the potential to provide relevant functional information for reconstructing the knee loading environment in fossil taxa, combined, whenever necessary, with a subsampling approach. This method relies on the plastic nature of the cortical and trabecular bony tissues and the modelling and remodelling dynamics during life to adjust structurally to the site-specific loading environment. This kind of information would bring new contributions not only to ongoing discussions on the evolutionary forces that shaped the knee joint in association with postural and locomotor adaptations, but also to the tentative taxonomic identification of isolated fossil specimens.

**Keywords** – patella, cortical bone, trabecular bone, fossil hominins, "whole-bone" analysis

**Résumé** – Cette contribution est une courte revue littéraire sur le rôle fonctionnel de la patella chez les catarrhiniens actuels et les hominines fossiles et les questions fonctionnelles, adaptatives et évolutives concernant le registre des hominines fossiles. En effet, la patella joue un rôle clé dans

l'articulation du genou, reflétant postures et modes locomoteurs. Cependant, les vestiges patellaires sont rares dans le registre des hominines fossiles et l'impact possible sur la kinésiologie du genou des différences de formes et de proportions par rapport à la condition humaine actuelle reste toujours incertain. Illustré par le premier exemple sur un échantillon d'une patella d'un humain, d'un chimpanzé, d'un babouin et d'un représentant Néanderthal, étant donné le caractère plastique des tissus cortical et trabéculaire et les dynamiques de modelage et remodelage osseux au cours de la vie pour s'adapter à l'environnement local des charges, le développement d'une étude holistique de l'endostructure de la patella, ponctuellement accompagnée d'une approche de sous échantillonnage lorsque nécessaire, pourrait permettre de révéler des informations fonctionnelles pour la reconstruction de l'environnement des charges du genou chez les taxons fossiles. De telles informations peuvent enrichir la discussion sur les forces évolutives ayant configuré l'articulation du genou en relation avec les modes posturaux et locomoteurs. Elle pourrait également contribuer à l'identification taxinomique de spécimens fossiles isolés.

**Mots clés** – patella, os cortical, os trabéculaire, hominines fossiles, analyse intégrale de l'os

### Introduction

This brief review compiles and summarises the information currently available on the functional significance of the patella in extant catarrhines and extinct hominins, and presents current functional, adaptive and evolutionary-related questions concerning the fossil hominin record. Based on these sources, we propose a new methodological

approach for the analysis of this so far neglected bone, which have the potential to provide relevant information to bring answers to these recurrent questions.

### The patella in extant catarrhines and extinct hominins

The patella (kneecap) is functionally analogous to the fused olecranon of the proximal ulna (Herzmark, 1938; Samuels et al., 2017) and plays a key functional role in the knee joint, thus reflecting habitual postural and locomotor modes (e.g., Ward et al., 1993; 1995; Pina et al., 2020). In catarrhine primates, a number of differences in the outer morphology of this bone have been related to knee function. More specifically, the kneecap morphology reflects adaptation to full extension (as seen in humans/hominins), to predominant excursion of the joint from a fully flexed knee to an extended position (as seen in taxa relying on leaping and galloping), or to a more versatile knee (as seen in great apes; Harrison, 1986; Ward et al., 1995; Pina et al., 2014). The proximodistally short and anteroposteriorly thin patellae of the great apes have been associated with a more versatile knee that allows a wider range of positions but no habitual full flexion of the knee. In contrast, a proportionally long, narrow and thick patella, as in the cercopithecoids especially, would increase the quadriceps moment arm in knee extension during walking, galloping, climbing and leaping (Ward et al., 1995; Isler, 2005; Crompton et al., 2010; Pina et al., 2014). In addition, variation between human and ape patellae in the shape of the articular surface has been specifically related to knee function in full extension and bipedalism (Aiello and Dean, 1990; Lovejoy, 2007; Cazenave et al., 2019a).

In humans, in full flexion, the small medial facet comes into contact with the anterolateral portion of the medial femoral condyle, and the highest portion of the wider lateral facet with the anterior part of the lateral condyle. In extension, patellofemoral contact is limited to the lowest portions of both facets (Goodfellow et al., 1976; Aglietti and Menchetti, 1995; Lovejoy, 2007). Compared to the multifaceted human kneecap bearing several distinctly angulated planes, a simpler articular morphology is found in *Pan*, where the posterior surface is smooth and fits the similarly flatter trochlear surface (patellar groove) of the distal femur (Aiello and Dean, 1990; Lovejoy, 2007; Cazenave et al., 2019a). The extension of the quadriceps complex (smaller in *Pan*, where flexion prevails) and the topography of the insertion of the vastus medialis (which in apes does not insert onto its extreme medial edge) also distinguish humans from *Pan* (Mariani et al., 1978; Aiello and Dean, 1990; Taylor et al., 2004; Lovejoy, 2007; Standring, 2008; Masouros et al., 2010).

Patellar remains are rare in the hominin fossil record and it is still unclear whether their differences in shape and proportion compared to extant humans affect knee kinesiology. For instance, Ramirez and Pontzer (2015) have suggested that patellar dimensions can be used in extant primates and fossil hominin taxa as proxies for the physiological

cross-sectional area of the quadriceps muscle, the primary extensor of the knee (see also Trinkaus, 1983a; Pina et al., 2014, and the review in Pina, 2016). They showed that an increase in quadriceps size, relative to body size, occurred with the emergence of the genus *Homo* (Ramirez and Pontzer, 2015). However, it remains uncertain whether the relatively small size of the patellae attributed to *Paranthropus robustus*, *Australopithecus sediba*, *H. floresiensis* and *H. naledi* (Jungers et al., 2009; DeSilva et al., 2013; Berger et al., 2015; Marchi et al., 2017) corresponds to a small quadriceps and whether these fossil taxa experienced a limited home range size compared to that commonly expected for *Homo* (Antón, 2013; Antón et al., 2014; Ramirez and Pontzer, 2015; Cazenave et al., 2019a). Interestingly, the posterior articular surface of the *A. sediba* kneecap is human-like in being strongly convex mediolaterally and displaying a high central keel separating the condylar facets medially and laterally. Accordingly, DeSilva and colleagues (2013) hypothesized that these human-like features reflect an adaptation to resist injurious lateral translation of the knee region during foot hyperpronation and the resulting internal rotation of the tibia and femur during the late stance phase. The authors also suggested that *A. sediba* might have had a reduced or absent vastus medialis obliquus in counteracting lateral translation of the patella (DeSilva et al., 2013). However, this interpretation still requires confirmation.

The Neanderthal patellar morphology also differs from that of recent humans in being anteroposteriorly thicker, having more symmetrical articular facets associated with wider angles, and showing displacement of the lateral and medial masses (e.g., Trinkaus, 1983a; 2000; Trinkaus and Rhoads, 1999; Trinkaus et al., 2017; Rosas et al., 2020). The hypothesis of an exceptionally powerful knee extension in Neanderthals compared to the extant human condition, previously suggested because of differences in the anteroposterior patellar thickness (Trinkaus, 1983b; Miller and Gross, 1998; see also Chapman et al., 2010), has been questioned given the lack of any close relationship between the degree of patellar facet asymmetry and the distal femoral configuration (Trinkaus and Rhoads, 1999). In this respect, it is also unclear to what extent this variation in patellar articular proportions affects knee kinesiology (Trinkaus, 2000). Given also the displacement of the masses compared with their position in extant humans, the hypothesis of a distinct rotation of the tibia relative to the position of the proximal femur has been put forward. This would imply a medial or lateral displacement of the patellar ligament, respectively increasing the contact force of the medial or lateral surface of the patella with the respective femoral condyle (thus affecting the functional space for the expansion of its facets, and therefore influencing the size of the contact area of the patella with the femur condyles). However, this hypothesis still remains to be tested (Rosas et al., 2020; see also Lee et al., 2003).

The mechanosensitive cortical and trabecular bony tissues model and remodel during the course of a life (Allen and Burr, 2014; Barak, 2019) as they adjust structurally to

the site-specific loading environment (e.g., Raux et al., 1975; Townsend et al., 1975; Takechi, 1977; Van Kampen and Huiskes, 1990; Katoh et al., 1996; Mazurier, 2006; Toumi et al., 2006; 2012; Mazurier et al., 2010; Kivell, 2016; Georgiou et al., 2018; Sukhdeo et al., 2020). Therefore, a detailed assessment of how the patellar cortical thickness and the structural arrangement of its underlying cancellous network vary topographically has the potential to provide valuable functionally-related information, including on extinct taxa (Cazenave et al., 2019a; 2019b; Houssaye et al., 2021). However, except for some studies focusing on extant humans (Raux et al., 1975; Townsend et al., 1975; Toumi et al., 2006; 2012; Hoechel et al., 2015), only very few investigations have been conducted on the endostructural organisation of the patella in fossil hominins (Cazenave et al., 2019a; 2019b).

### Comprehensive insights into endostructure

Besides the classic radiographic and invasive studies (Raux et al., 1975; Townsend et al., 1975; Toumi et al., 2006; 2012), the three-dimensional endostructural analyses of the patellar bone performed so far rely upon the virtual extraction of Volumes of Interest (VOIs; Hoechel et al., 2015; Cazenave et al., 2019a; 2019b). However, despite the advantages in terms of the amount and complexity of the information retrieved compared to classic two-dimensional observations, this methodological approach also has several inherent limitations (see details and review in Kivell, 2016). First, a VOI must be large enough to provide an exploitable signal, but small enough to include only trabecular bone. Also, while Lazenby et al. (2011) supported the use of scaled VOIs, Kivell et al. (2011) warned that the scaling factor chosen would also influence some trabecular values. In addition, and importantly, the definition of the position of the VOIs is challenged by determining anatomically and/or biomechanically homologous VOIs across a sample, especially in the case of anatomical regions displaying a wide range of morphological and dimensional variation (Maga et al., 2006; Kivell et al., 2011; Lazenby et al., 2011).

Following a generation of virtually-based endostructural studies focussing on specific VOIs, some so-called “whole-epiphyses/bone” analytical methods have been developed (e.g., Pahr and Zysset, 2009; DeMars et al., 2021; Veneziano et al., 2021) and applied to characterize the entire endostructural organisation of several regions/elements of the extant primate skeleton and also to tentatively assess some hominin fossil specimens. Such an approach has been applied, for instance, to investigate the upper limb elements (Kivell et al., 2018; Arias-Martorell et al., 2021), the hand bones (Tsegai et al., 2013; Skinner et al., 2015; Stephens et al., 2016; 2018; Dunmore et al., 2019; 2020a; 2020b; Bird et al., 2021a; 2021b), the femur (Georgiou et al., 2018; 2019; 2020; Sukhdeo et al., 2020), the distal tibia and the foot bones (Tsegai et al., 2013; 2017), as well as to directly compare different skeletal parts (Tsegai et al., 2018).

A comparative endostructural analysis of the distal femur allowed Georgiou et al. (2018) to point out that, while it is true that the trabecular architecture of humans, *Pan*, *Gorilla* and *Pongo* holds a functional signal reflecting habitual postural and locomotor behaviours, there was more similarity and greater intraspecific variability across the taxa than expected on the basis of differences in knee postures. Notably, the study also revealed that the trabecular organisation of the human distal femur is not as distinct from the structural arrangement of the great apes as suggested by previous studies. From a different sample, Sukhdeo et al. (2020) showed that, typically of their locomotor behaviours, *Pan*, *Pongo*, and *Papio* show evidence of flexed knee postures in the distribution of trabecular bone density (BV/TV) at the distal femur, and that while the pattern in humans is unique, it is associated with a high BV/TV in the patellar groove area, the latter being a feature also observed in *Papio*. Again in the distal femur, but also in the region of the proximal tibia, functional relationships have been identified in some primates between the local arrangement and the topographic distribution of the underlying cortico-trabecular complex (CTC) – i.e., the component which includes the cortical shell (the lamina) and the closely related adjoining portions of the supporting trabecular network, which mostly consists of plate-like structures (in Cazenave et al., 2019a) – the cancellous bone architecture and the pattern(s) of locomotor-related articular load dissipation (Mazurier, 2006; Volpato, 2007; Mazurier et al., 2010).

The only study conducted so far with specific reference to the mammal kneecap investigated its trabecular bone organization using a “whole-bone” approach (Houssaye et al., 2021). The qualitative and quantitative analyses concerned the microanatomy of the whole bone in extant Perissodactyla displaying a wide range of body morphologies and masses and locomotor modes, and were conducted in order to investigate how their knee adapts to a variety of functional constraints. Applying this new approach, the authors (Houssaye et al., 2021) concluded that various morphologies of the patellofemoral joints in the three perissodactyl families (Equidae, Tapiridae and Rhinocerotidae) are associated with distinct stresses at the knee, pointing to the interest of further biomechanical investigations.

In the study of fossil patellar specimens, including from hominin taxa, an analytical VOI approach adapted case by case is commonly necessary given the frequent discovery of incomplete remains and the limited amount of preserved cortical and cancellous bone suitable for reliable quantitative assessment as a result of taphonomic dynamics and diagenetic changes (Cazenave et al., 2019a; 2019b). Whenever the preservation of a fossil specimen allows holistic analysis, an analytical approach allowing a complementary assessment of the distribution of topographical thickness across the whole CTC and of the three-dimensional arrangement of the entire cancellous network would enable highly sensitive functional information to be extracted to reconstruct the knee loading environment in extinct taxa.



## First example of application of the whole bone microstructural analysis to the patella of extant and fossil catarrhines

A “whole-bone” comparative analysis was applied here for the first time to a sample of three perfectly preserved adult patellae (all right) from three non-pathological skeletons representing a 49 year-old extant human male individual from the Pretoria Bone Collection (PBC) stored at the Department of Anatomy of the University of Pretoria, South Africa; a wild adult *Pan troglodytes* from the osteological collections at the Muséum national d’Histoire naturelle (MNHN) in Paris, France; and a wild adult *Papio ursinus* also from the PBC. Based on this initial evidence, we also tentatively investigated the left patella from the partial Neanderthal skeleton Regourdou 1, stored at the Musée d’Art et d’Archéologie du Périgord, Périgueux, France (Bailey et al., 2011; Maureille et al., 2015; Cazenave et al., 2019a; 2019b).

All the specimens were detailed by high-resolution microtomography (resolutions ranging from 22 to 50 microns). In all cases, the bone was segmented using MIA-Clustering segmentation (Dunmore et al., 2018) and the CTC was automatically isolated from the trabecular bone using Medtool 4.5 ([www.dr-pahr.at](http://www.dr-pahr.at)). The topographic distribution of cortico-trabecular thickness, measured for each pixel of the periosteal surface as the shortest distance to the CTC inner limit, was rendered virtually with Avizo v. 9.0.0 (Visualization Sciences Group Inc., <https://www.fei.com/software/amira-avizo/>) using a chromatic scale from dark blue (thin) to red (thick) (figure 1a). The trabecular bone volume fraction (BV/TV) was quantified throughout the entire bone using Medtool 4.5 and rendered in 3D following Gross et al. (2014) (see also Tsegai et al., 2017) (figure 1b).

In the knee region, loads on the anterior patellar surface are directly transferred from the quadriceps (Heegaard et al., 1995; Toumi et al., 2012). In humans, the posterior aspect of this bone is covered by a thick hyaline cartilage, among the thickest in the human body as it is able to withstand intermittent compressive stresses occurring locally at a high frequency (Milz et al., 1995; Standring, 2008; Hartigan et al., 2011). It has therefore been suggested, from parasagittal and transversal cross sections of the patellar bone, that in humans the anterior plate is thicker than measured at the articular surface (Cazenave et al., 2019b).

By using the “whole-bone” analysis method described above, this preliminary observation is confirmed in both the extant and the fossil (Neanderthal) human representatives. However, here this structural characteristic is also revealed for the first time in the *Pan* and *Papio* patellae, bringing evidence that no longer allows this pattern to be considered as a human autapomorphy (figure 1a). Conversely, our analysis of the whole bone confirms that the reinforcement across the superior and lateral regions underlying the CTC (figure 1) does represent a feature so far evidenced only in the human kneecap (Toumi et al., 2012; Cazenave et al., 2019a; 2019b).

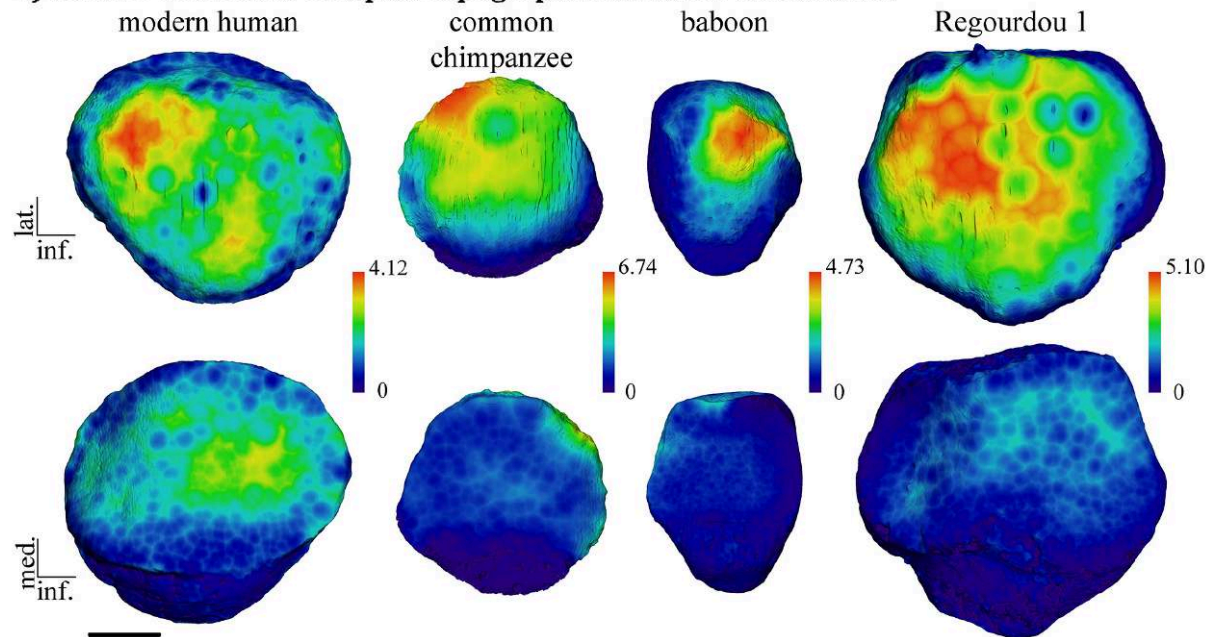
The modern human-like endostructural pattern revealed here by Regourdou 1 (figure 1) is consistent with the site-specific signal provided by a number of cross sections and VOIs extracted virtually from the same fossil in a previous comparative analysis with a Neanderthal patella from Krapina, Croatia, and a Late Pleistocene (Magdalenian) modern human specimen from Chancelade, France (Cazenave et al., 2019b). However, the “whole-bone” approach highlights some previously unreported differences between the Regourdou 1 Neanderthal patella and the extant human endostructural condition, at least as represented by the single specimen used in this study. Specifically, these differences include a higher BV/TV in the anterior part of the base of the fossil patella vs. a more centrally-set anterior configuration probably related to differences in the insertion and/or action of the rectus femoris. This previously unreported finding is of biomechanical significance and deserves additional investigations in a broader comparative context.

The present test on the patellar bone highlights the potential of the “whole-epiphyses/bone” analytical approach to contribute to our understanding of the evolutionary forces that have shaped the hominin/hominid knee joint in conjunction with postural and locomotor adaptations. In this context, the functional reasons for the less structurally heterogeneous CTC thickness and BV/TV distributions characterising the articular regions of the patella in *Pan* compared with the human reference (figure 1; cf. Cazenave et al., 2019a) have yet to be investigated by also considering the endostructural signal from the hip joint (notably, the proximal femur) indicating a higher degree of articular mobility in great apes (e.g., Isler, 2005; Hammond, 2013; Finestone et al., 2018) compared to the derived human condition. Similarly, the functional implications of a CTC reinforcement localised in the anteromedial region of the patella, identified here in *Papio*, remain to be clarified. It is nevertheless important to point out that future quantitative investigations should conduct statistical analyses on standardised values of CTC and BV/TV to avoid including differences related to body size.

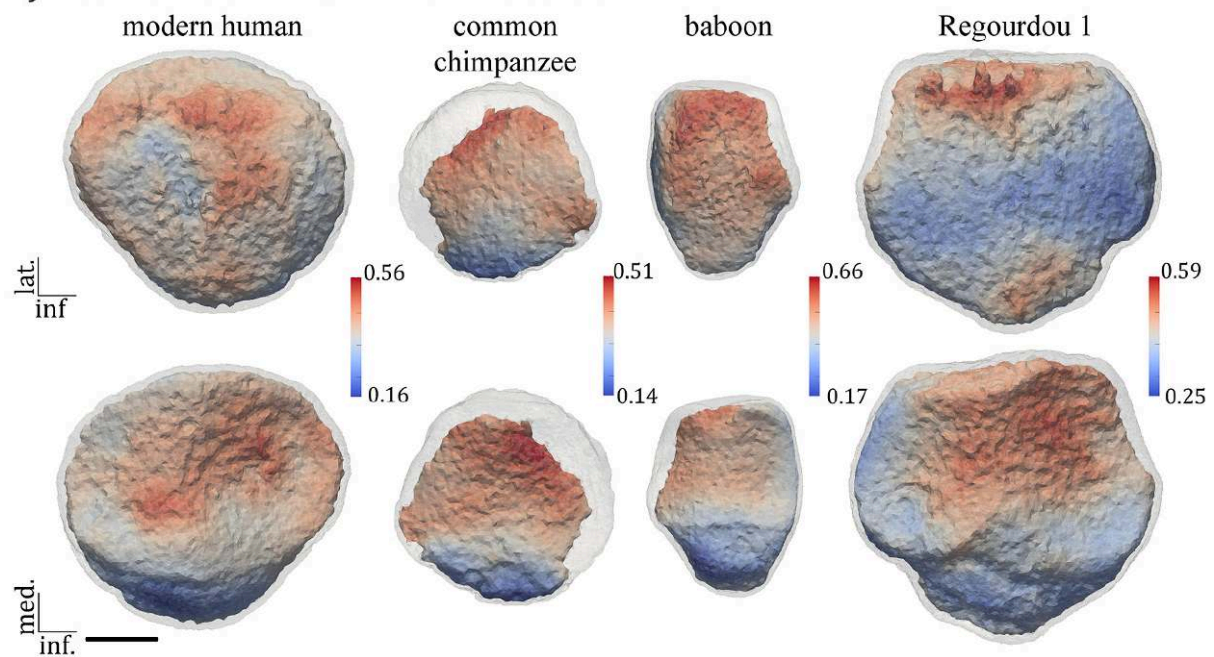
## Conclusions

In the current research context, characterised as it is by a notable paucity of qualitative and quantitative data on the functionally-related endostructural organisation of the patellar bone in extant and fossil primates, including in hominins/hominids, the combined VOI and “whole-bone” analytical approaches can contribute unique information about the biomechanical forces and constraints that have shaped the knee joint in conjunction with postural and locomotor adaptations. This is notably true with respect to the discussion on pronograde and antipronograde postural behaviours and to the identification of a bipedal component in Miocene great apes (e.g., Rook et al., 1999; Böhme et al., 2019; Pina et al., 2020). Importantly, these approaches could be used to tentatively assess the taxonomic identity of isolated specimens, which are common in the fossil record (e.g., Susman, 1989; Harrison, 2011; Fourvel et al., 2018).

### A) Cortico-trabecular complex topographic thickness distribution



### B) Trabecular bone volume fraction distribution



**Figure 1.** (A) Microtomography-based maps of cortico-trabecular complex (CTC) thickness (in mm) topographic distribution in anterior (upper row) and posterior (lower row) views, measured for each pixel of the periosteal surface as the shortest distance to the CTC inner limit and rendered by a chromatic scale increasing from dark blue to red; (B) morphometric maps of trabecular bone volume fraction (BV/TV) distribution in anterior (upper row) and posterior (lower row) surfaces at the limit with the CTC rendered by a chromatic scale ranging from light blue to light red in an extant human, a *Pan troglodytes* and a *Papio ursinus* patella and in the left patella from the partial Neanderthal skeleton Regourdou 1 (here imaged as right). Scale bar: 10 mm / (A) Reconstruction sur base microtomographique de la distribution topographique des variations d'épaisseur du complexe cortico-trabéculaire (CTC; en mm) en vues antérieure (ligne supérieure) et postérieure (ligne inférieure), mesurée pour chaque pixel de la surface périostée comme la distance la plus courte jusqu'à la limite interne du CTC, représentées selon une échelle chromatique variant du bleu foncé au rouge et ; (B) cartographies morphométriques sur base microtomographique de la distribution du volume de l'os trabéculaire (BV/TV) des surfaces antérieure (ligne supérieure) et postérieure (ligne inférieure) du tissu trabéculaire à la limite avec le CTC, représentées selon une échelle chromatique variant du bleu clair au rouge clair quantifié pour une patella humaine actuelle, *Pan troglodytes*, et d'un *Papio ursinus* et la patella gauche néanderthaliennne de Regourdou 1 (présentée ici comme droite). Barre d'échelle : 10 mm

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