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 (Bayle 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). 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).

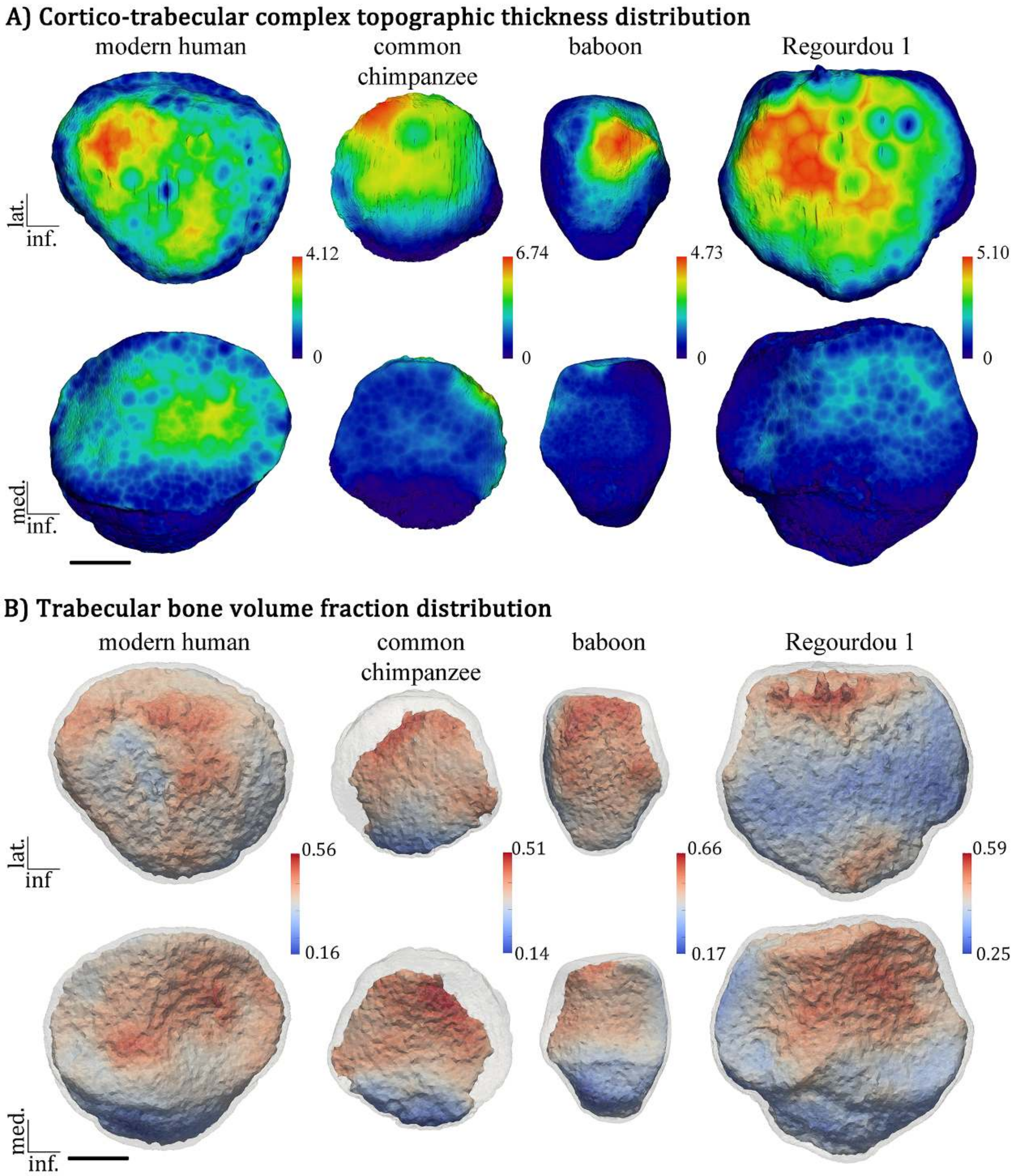

Figure 1. (A) Microtomography-based maps of cortico-trabecular complex (CTC) thickness (in mm) topographic distribution in anterior (upper row) and posterior (lower row) views, measured for each pixel of the periosteal surface as the shortest distance to the CTC inner limit and rendered by a chromatic 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 néanderthalienne de Regourdou 1 (présentée ici comme droite). Barre d'échelle : 10 mm*

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References

Aglietti P, Menchetti PPM (1995) Biomechanics of the patellofemoral joint. The Patella. Springer, New York, pp 25-48

Aiello L, Dean C (1990) An Introduction to Human Evolutionary Anatomy. Academic Press, New York

Allen MR, Burr DB (2014) Bone modeling and remodeling. In: Burr DB, Allen MR (eds) Basic and Applied Bone Biology. Academic Press, New York, pp 75-90

Antón SC (2013) *Homo erectus* and related taxa. In: Begun DR (ed) A Companion to Paleoanthropology. Blackwell Publisher, Chichester, pp 497-516

Antón SC, Potts R, Aiello LC (2014) Evolution of early *Homo*: An integrated biological perspective. Science 345 (6192):45-58 [https://www.science.org/doi/10.1126/science.1236828]

Arias-Martorell J, Zeininger A, Kivell TL (2021) Trabecular structure of the elbow reveals divergence in knuckle-walking biomechanical strategies of African apes. Evolution 75(11):2959-2971 [https://doi.org/10.1111/evo.14354]

Barak MM (2019) Bone modeling or bone remodeling: That is the question. American Journal of Physical Anthropology 172(2):153-155 [https://doi.org/10.1002/ajpa.23966]

Bayle P, Bondioli L, Macchiarelli R et al (2011) Three-dimensional imaging and quantitative characterization of human fossil remains. Examples from the NESPOS database. In: Macchiarelli R, Weniger G-C (eds), Pleistocene Databases. Acquisition, Storing, Sharing. Wissenschaftliche Schriftendes Neanderthal Museums 4, Mettmann, pp 29-46

Berger LR, Hawks J, de Ruiter DJ et al (2015) *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 4:1-35 [https://doi.org/10.7554/eLife.09560]

Bird EE, Kivell TL, Skinner MM (2021a) Cortical and trabecular bone structure of the hominoid capitate. Journal of Anatomy 239(2):351-373 [https://doi.org/10.1111/joa.13437]

Bird EE, Kivell TL, Skinner MM (2021b) Patterns of internal bone structure and functional adaptation in the hominoid scaphoid, lunate, and triquetrum. American Journal of Biological Anthropology 177(2):266-285 [https://doi.org/10.1111/joa.13437]

Böhme M, Spassov N, Fuss J et al (2019) A new Miocene ape and locomotion in the ancestor of great apes and humans. Nature 575(7783):489-493 [https://doi.org/10.1038/s41586-019-1731-0]

Cazenave M, Oettlé A, Thackeray JF et al (2019a) The SKX 1084 hominin patella from Swartkrans Member 2, South Africa: An integrated analysis of its outer morphology and inner structure. Comptes Rendus Palevol 18(2): 223-235 [https://doi.org/10.1016/j.crpv.2018.06.002]

Cazenave M, Radovčić D, Hoffman J et al (2019b) The Neandertal (Krapina and Regourdou 1), fossil modern human (Chancelade 1) an extant human patella: an insight from inside. Paleo 30(2):76-91 [https://doi.org/10.4000/paleo.5167]

Chapman T, Moiseev F, Sholukha V et al (2010) Virtual reconstruction of the Neandertal lower limbs with an estimation of hamstring muscle moment arms. Comptes Rendus Palevol 9(6-7):445-454 [https://doi.org/10.1016/j.crpv.2010.07.011]

Crompton RH, Sellers WI, Thorpe SKS (2010) Arboreality, terrestriality and bipedalism. Philosophical Transactions of the Royal Society B 365(1556):3301-3314 [https://doi.org/10.1098/rstb.2010.0035]

DeMars LJ, Stephens NB, Saers JP et al (2021). Using point clouds to investigate the relationship between trabecular bone phenotype and behavior: An example utilizing the human calcaneus. American Journal of Human Biology 33(2):e23468 [https://doi.org/10.1002/ajhb.23468]

DeSilva JM, Holt KG, Churchill SE et al (2013) The lower limb and mechanics of walking in *Australopithecus sediba*. Science 340(6129):54-78 [https://doi.org/10.1126/science.1232999]

Dunmore CJ, Kivell TL, Bardo A et al (2019) Metacarpal trabecular bone varies with distinct hand-positions used in hominid locomotion. Journal of Anatomy 235(1):45-66 [https://doi.org/10.1111/joa.12966]

Dunmore CJ, Bardo A, Skinner MM et al (2020a) Trabecular variation in the first metacarpal and manipulation in hominids. American Journal of Physical Anthropology 171(2): 219-241 [https://doi.org/10.1002/ajpa.23974]

Dunmore CJ, Skinner MM, Bardo A et al (2020b) The position of *Australopithecus sediba* within fossil hominin hand use diversity. Nature Ecology & Evolution 4(7):911-918 [https://doi.org/10.1038/s41559-020-1207-5]

Dunmore CJ, Wollny G, Skinner MM (2018) MIA-Clustering: a novel method for segmentation of paleontological material. PeerJ 6:e4374 [https://doi.org/10.7717/peerj.4374]

Finestone EM, Brown MH, Ross SR et al (2018) Great ape walking kinematics: Implications for hominoid evolution. American Journal of Physical Anthropology 166(1):43-55 [https://doi.org/10.1002/ajpa.23397]

Fourvel JB, Thackeray JF, Brink JS et al (2018) Taphonomic interpretations of a new Plio-Pleistocene hominin-bearing assemblage at Kromdraai (Gauteng, South Africa). Quaternary Science Reviews 190:81-97 [https://doi.org/10.1016/j.quascirev.2018.04.018]

Georgiou L, Dunmore CJ, Bardo A et al (2020) Evidence for habitual climbing in a Pleistocene hominin in South Africa. Proceedings of the National Academy of Sciences 117(15):8416-8423 [https://doi.org/10.1073/pnas.1914481117]

Georgiou L, Kivell TL, Pahr DH (2019) Trabecular architecture of the great ape and human femoral head. Journal of Anatomy 234(5):679-693 [https://doi.org/10.1111/joa.12957]

Georgiou L, Kivell TL, Pahr DH et al (2018) Trabecular bone patterning in the hominoid distal femur. PeerJ 6: e5156 [https://doi.org/10.7717/peerj.5156]

Goodfellow J, Hungerford DS, Zindel M (1976) Patellofemoral joint mechanics and pathology. Journal of Bone Joint Surgery 58(3):287-290 [https://doi.org/10.1302/0301-620X.58B3.956243]

Gross T, Kivell TL, Skinner MM et al (2014) A CT-image-based framework for the holistic analysis of cortical and trabecular bone morphology. Palaeontologia Electronica 17(3):1-13 [https://doi.org/10.26879/438]

Hammond AS (2013) 3D analysis of hip joint mobility and the evolution of locomotor abilities in Miocene hominoids. PhD Dissertation, University of Missouri-Columbia

Harrison RN, Lees A, McCullagh PJ et al (1986) A bioengineering analysis of human muscle and joint forces in the lower limbs during running. Journal of Sports Sciences 4(3): 201-218 [https://doi.org/10.1080/02640418608732119]

Harrison T (2011) Hominins. Paleontology and Geology of Laetoli: Human Evolution in Context (Fossil Hominins and the Associated Fauna, vol. 2). Springer, Dordrecht, pp 141-188

Hartigan E, Lewek M, Snyder-Mackler L (2011) The knee. In: Levangie PK, Norkin CC (eds) Joint structure and function, 5th ed. F.A. Davis, Philadelphia, pp 395-439

Heegaard J, Leyvraz PF, Curnier A et al (1995) The biomechanics of the human patella during passive knee flexion. Journal of Biomechanics 28(11):1265-1279 [https://doi.org/10.1016/0021-9290(95)00059-q]

Herzmark MH (1938) Evolution of the knee joint. Journal of Bone and Joint Surgery 20(1):77-84

Hoechel S, Schulz G, Müller-Gerbl M (2015) Insight into the 3D-trabecular architecture of the human patella. Annals of Anatomy-Anatomischer Anzeiger 200:98-104 [https://doi.org/10.1016/j.aanat.2015.02.007]

Houssaye A, de Perthuis A, Houée G (2021) Sesamoid bones also show functional adaptation in their microanatomy–The example of the patella in Perissodactyla. Journal of Anatomy 240:50-65 [https://doi.org/10.1111/joa.13530]

Isler K (2005) 3D-kinematics of vertical climbing in hominoids. American Journal of Physical Anthropology 126 (1):66-81 [https://doi.org/10.1002/ajpa.10419]

Jungers WL, Larson SG, Harcourt-Smith W et al (2009) Descriptions of the lower limb skeleton of *Homo floresiensis*. Journal of Human Evolution 57(5):538-554 [https://doi.org/10.1016/j.jhevol.2008.08.014]

Katoh T, Griffin MP, Wevers HW et al (1996) Bone hardness testing in the trabecular bone of the human patella. Journal of Arthroplasty 11(4):460-468 [https://doi.org/10.1016/S0883-5403(96)80037-4]

Kivell TL (2016) A review of trabecular bone functional adaptation: What have we learned from trabecular analyses in extant hominoids and what can we apply to fossils? Journal of Anatomy 228(4):569-594 [https://doi.org/10.1111/joa.12446]

Kivell TL, Davenport R, Hublin JJ et al (2018) Trabecular architecture and joint loading of the proximal humerus in extant hominoids, *Ateles*, and *Australopithecus africanus*. American Journal of Physical Anthropology 167(2): 348-365 [https://doi.org/10.1002/ajpa.23635]

Kivell TL, Skinner MM, Lazenby R et al (2011) Methodological considerations for analyzing trabecular architecture: an example from the primate hand. Journal of Anatomy 218(2):209-225 [https://doi.org/10.1111/j.1469-7580.2010.01314.x]

Lazenby RA, Skinner MM, Kivell TL et al (2011) Scaling VOI size in 3D μCT studies of trabecular bone: A test of the over-sampling hypothesis. American Journal of Physical Anthropology 144(2):196-203 [https://doi.org/10.1002/ajpa.21385]

Lee TQ, Morris G, Csintalan RP (2003) The influence of tibial and femoral rotation on patellofemoral contact area and pressure. Journal of Orthopaedic & Sports Physical Therapy 33(11):686-693 [https://www.jospt.org/doi/10.2519/jospt.2003.33.11.686]

Lovejoy CO (2007) The natural history of human gait and posture: Part 3.The knee. Gait & Posture 25(3):325-341 [https://doi.org/10.1016/j.gaitpost.2006.05.001]

Maga M, Kappelman J, Ryan TM et al (2006) Preliminary observations on the calcaneal trabecular microarchitecture of extant large-bodied hominoids. American Journal of Physical Anthropology 129(3):410-417 [https://doi.org/10.1002/ajpa.20276]

Marchi D, Walker CS, Wei P et al (2017) The thigh and leg of *Homo naledi*. Journal of Human Evolution 104:174-204 [https://doi.org/10.1016/j.jhevol.2016.09.005]

Mariani PP, Puddu G, Ferretti A (1978) Jumper's knee. Italian Journal of Orthopaedics and Traumatology 4: 85-93

Masouros SD, Bull AMJ, Amis AA (2010) Biomechanics of the knee joint. Orthopaedics and Trauma 24(2):84-91 [https://doi.org/10.1016/j.mporth.2010.03.005]

Maureille B, Gómez-Olivencia A, Couture-Veschambre C et al (2015) Nouveaux restes humains provenant du gisement de Regourdou (Montignac-sur-Vézère, Dordogne, France). Paleo 26:117-138 [https://doi.org/10.4000/paleo.2937]

Mazurier A (2006) Relations entre comportement locomoteur et variation cortico-trabéculaire du plateau tibial chez les Primates: analyse quantitative non invasive à haute résolution (SR-CT) et applications au registre fossile. PhD dissertation. Université de Poitiers, Poitiers

Mazurier A, Nakatsukasa M, Macchiarelli R (2010) The inner structural variation of the primate tibial plateau characterized by high-resolution microtomography. Implications for the reconstruction of fossil locomotor behaviours. Comptes Rendus Palevol 9(6-7):349-359 [https://doi.org/10.1016/j.crpv.2010.07.020]

Miller JA, Gross MM (1998) Locomotor advantages of Neandertal skeletal morphology at the knee and ankle. Journal of Biomechanics 31(4):355-361 [https://doi.org/10.1016/s0021-9290(98)00031-1]

Milz S, Eckstein F, Putz R (1995) The thickness of the subchondral plate and its correlation with the thickness of the uncalcified articular cartilage in the in the human patella. Anatomy and Embryology 192(5):437-44 [https://doi.org/10.1007/BF00240376]

Pahr DH, Zysset PK (2009) From high-resolution CT data to finite element models: development of an integrated modular framework. Computer Methods in Biomechanics and Biomedical Engineering 12(1):45-57 [https://doi.org/10.1080/10255840802144105]

Pina M (2016) Unravelling the positional behaviour of fossil hominoids: Morpho functional and structural analysis of the primate hindlimb. PhD dissertation, Universidad Autònoma de Barcelona, Barcelona

Pina M, Almécija S, Alba DM et al (2014) The middle Miocene ape *Pierolapithecus catalaunicus* exhibits extant great ape-like morphometric affinities on its patella: Inferences on knee function and evolution. PLoS One 9: e91944 [https://doi.org/10.1371/journal.pone.0091944]

Pina M, DeMiguel D, Puigvert F et al (2020) Knee function through finite element analysis and the role of Miocene hominoids in our understanding of the origin of antipronograde behaviours: the *Pierolapithecus catalaunicus* patella as a case study. Palaeontology 63(3):459-475 [https://doi.org/10.1111/pala.12466]

Ramirez KR, Pontzer H (2015) Estimates of fossil hominin quadriceps physiological cross sectional area from patellar dimensions. American Journal of Physical Anthropology 156:261

Raux P, Townsend PR, Miegel R et al (1975) Trabecular architecture of the human. Journal of Biomechanics 8 (1):1-17 [https://doi.org/10.1016/0021-9290(75)90037-8]

Rook L, Bondioli L, Köhler M et al (1999) *Oreopithecus* was a bipedal ape after all: evidence from the iliac cancellous architecture. Proceedings of the National Academy of Sciences 96(15):8795-8799 [https://doi.org/10.1073/pnas.96.15.8795]

Rosas A, Agustina BL, García-Martínez D et al (2020) Analyses of the Neandertal patellae from El Sidrón (Asturias, Spain) with implications for the evolution of body form in *Homo*. Journal of Human Evolution 141: 102738 [https://doi.org/10.1016/j.jhevol.2019.102738]

Samuels ME, Regnault S, Hutchinson JR (2017) Evolution of the patellar sesamoid bone in mammals. PeerJ 5:e3103 [https://doi.org/10.7717/peerj.3103]

Skinner MM, Stephens NB, Tsegai ZJ et al (2015) Human-like hand use in *Australopithecus africanus*. Science 347 (6220):395-399 [https://doi.org/10.1126/science.1261735]

Standring S (2008) Gray's Anatomy: The Anatomical Basis of Clinical Practice. Elsevier Health Sciences, London

Stephens NB, Kivell TL, Gross T et al (2016) Trabecular architecture in the thumb of *Pan* and *Homo*: implications for investigating hand use, loading, and hand preference in the fossil record. American Journal of Physical Anthropology 161(4):603-619 [https://doi.org/10.1002/ajpa.23061]

Stephens NB, Kivell TL, Pahr DH et al (2018) Trabecular bone patterning across the human hand. Journal of Human Evolution 123:1-23 [https://doi.org/10.1016/j.jhevol.2018.05.004]

Sukhdeo S, Parsons J, Niu XM et al (2020) Trabecular bone structure in the distal femur of humans, apes, and baboons. The Anatomical Record 303(1):129-149 [https://doi.org/10.1002/ar.24050]

Susman RL (1989) New hominid fossils from the Swartkrans formation (1979-1986 excavations): Craniodental specimens. American Journal of Physical Anthropology 79(4): 451-474 [https://doi.org/10.1002/ajpa.1330790403]

Takechi H (1977) Trabecular architecture of the knee joint. Acta Orthopaedica Scandinavica 48(6):673-681 [https://doi.org/10.3109/17453677708994816]

Taylor WR, Heller MO, Bergmann G et al (2004) Tibiofemoral loading during human gait and stair climbing. Journal of Orthopaedic Research 22(3):625-632 [https://doi.org/10.1016/j.orthres.2003.09.003]

Toumi H, Higashiyama I, Suzuki D et al (2006) Regional variations in human patellar trabecular architecture and the structure of the proximal patellar tendon enthesis. Journal of Anatomy 208(1):47-57 [https://doi.org/10.1111/j.1469-7580.2006.00501.x]

Toumi H, Larguech G, Filaire E et al (2012) Regional variations in human patellar trabecular architecture and the structure of the quadriceps enthesis: A cadaveric study. Journal of Anatomy 220(6):632-637 [https://doi.org/10.1111/j.1469-7580.2012.01500.x]

Townsend PR, Raux P, Rose RM et al (1975) The distribution and anisotropy of the stiffness of cancellous bone in the human patella. Journal of Biomechanics 8(6):363-367 [https://doi.org/10.1016/0021-9290(75)90071-8]

Trinkaus E (1983a) The Shanidar Neandertals. Academic Press, New York

Trinkaus E (1983b) Neandertal postcrania and the adaptive shift to modern humans. In: Trinkaus E (ed) The Mousterian Legacy: Human Biocultural Change in the Upper Pleistocene. British Archaeological Reports, Oxford, pp 165-200

Trinkaus E (2000) Human patellar articular proportions: recent and Pleistocene patterns. Journal of Anatomy 196 (Pt3):473-483 [https://doi.org/10.1046/j.1469-7580.2000.19630473.x]

Trinkaus E, Rhoads ML (1999) Neandertal knees: power lifters in the Pleistocene? Journal of Human Evolution 37 (6):833-859 [https://doi.org/10.1006/jhev.1999.0317]

Trinkaus E, Wojtal P, Wilczyński J et al (2017) Palmar, patellar and pedal human remains from Pavlov. PaleoAnthropology 2017:73-101 [https://doi.org/10.4207/PA.2017.ART106]

Tsegai ZJ, Kivell TL, Gross T et al (2013) Trabecular bone structure correlates with hand posture and use in hominoids. PLoS One 8(11):e78781 [https://doi.org/10.1371/journal.pone.0078781]

Tsegai ZJ, Skinner MM, Gee AH et al (2017) Trabecular and cortical bone structure of the talus and distal tibia in *Pan* and *Homo*. American Journal of Physical Anthropology 163(4):784-805 [https://doi.org/10.1002/ajpa.23249]

Tsegai ZJ, Skinner MM, Pahr DH et al (2018) Systemic patterns of trabecular bone across the human and chimpanzee skeleton. Journal of Anatomy 232(4):641-656 [https://doi.org/10.1111/joa.12776]

Van Kampen A, Huiskes R (1990) The three-dimensional tracking pattern of the human patella. Journal of Orthopaedic Research 8(3):372-382 [https://doi.org/10.1002/jor.1100080309]

Veneziano A, Cazenave M, Alfieri F et al (2021) Novel strategies for the characterization of cancellous bone morphology: Virtual isolation and analysis. American Journal of Physical Anthropology 175(4):920-930 [https://doi.org/10.1002/ajpa.24272]

Ward CV, Ruff CB, Walker A et al (1995) Functional morphology of Proconsul patellas from Rusinga Island, Kenya, with implications for other Miocene-Pliocene catarrhines. Journal of Human Evolution 1:19 [https://doi.org/10.1006/jhev.1995.1045]

Ward CV, Walker A, Teaford MF et al (1993) Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. American Journal of Physical Anthropology 90(1):77-111 [https://doi.org/10.1002/ajpa.1330900106]