

1 *Comptes Rendus Palevol*

2 **Thematic issue: Hominin biomechanics, virtual anatomy and inner structural morphology:**

3 **From head to toe - A tribute to Laurent Puymeraul**

4

5 Cortical bone mapping: An application to hand and foot bones in hominoids

6

7 *Distribution topographique de l'os cortical: une application aux os de la main et du pied chez les*

8 *hominoïdes*

9

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28

29 ABSTRACT

30 Bone form reflects both the genetic profile and behavioural history of an individual. As cortical
31 bone is able to remodel in response to mechanical stimuli, interspecific differences in cortical
32 bone thickness may relate to loading during locomotion or manual behaviours during object
33 manipulation. Here, we test the application of a novel method of cortical bone mapping to the
34 third metacarpal (Mc3) and talus of *Pan*, *Pongo*, and *Homo*. This method of analysis allows
35 measurement of cortical thickness throughout the bone, and as such is applicable to elements
36 with complex morphology. In addition, it allows for registration of each specimen to a canonical
37 surface, and identifies regions where cortical thickness differs significantly between groups.
38 Cortical bone mapping has potential for application to palaeoanthropological studies, however,
39 due to the complexity of correctly registering homologous regions across varied morphology,
40 further methodological development would be advantageous.

41

42 RÉSUMÉ

43 La forme d'un os reflète simultanément le profil génétique et l'histoire comportementale d'un
44 individu. L'os cortical est capable de remodelage en réponse à des stimuli mécaniques. Les
45 différences interspécifiques dans l'épaisseur de l'os cortical peuvent donc être corrélées avec la
46 charge mécanique exercée durant la locomotion ou la manipulation d'objets. Ici, nous présentons
47 l'application d'une méthode novatrice pour cartographier la distribution de l'os cortical du
48 troisième métacarpien et du talus chez *Pan*, *Pongo* et *Homo*. Cette méthode permet d'analyser
49 l'épaisseur corticale sur toute la longueur de l'os et est applicable à tous les éléments osseux
50 ayant une morphologie complexe. En outre, cette méthode permet de recalibrer chaque spécimen
51 sur une surface canonique et d'identifier les régions où l'épaisseur corticale diffère
52 significativement entre les groupes. Ce procédé peut être appliqué à des études
53 paléanthropologiques. Cependant, du fait de la complexité du recalage correct des régions
54 homologues, des progrès méthodologiques futurs sont envisagés.

55

56 1. Introduction

57

58 Identifying skeletal variables that relate to functional patterns is essential for reconstructing
59 the behaviour of extinct species. However, it is often unclear which morphological features are
60 most functionally relevant, as some researchers focus on novel, derived features, with the
61 intention of understanding evolutionary change, while others are interested in the entire
62 morphological complex of features, aiming to reconstruct the way in which a species lived
63 (Ward, 2002). This is a common problem in palaeoanthropology, and has led to differing
64 interpretations of skeletal morphology in fossil hominins (e.g., Latimer, 1991; Stern, 2000;
65 Ward, 2002). In this debate, more plastic morphological features that can adapt in response to an
66 individual's behaviour are of critical importance.

67 As cortical bone is able to remodel during life in response to mechanical load - a concept
68 known as bone functional adaptation - it has the potential to hold a signal of an individual's
69 behaviour (see Ruff et al., 2006, and references therein). Bone adapts to loading in several ways,
70 for example by increasing/decreasing mineralisation to adapt its stiffness, changing shape to alter
71 load transmission, or increasing thickness (Currey, 2003, 2010). However, this is a complex
72 process that is likely to vary depending on skeletal location and systemic factors such as age,
73 hormones and genes (e.g., Lovejoy et al., 2003; Pearson and Lieberman, 2004). Moreover,
74 individual factors such as the magnitude and frequency of strain and the previous loading history
75 of the bone cells can also affect cortical remodelling (e.g., Frost, 1987; Pearson and Lieberman,
76 2004; Ruff et al., 2006). Experimental studies are not always able to demonstrate that bone
77 structure is well adapted to withstand strains (Demes et al., 1998, 2001; Lieberman et al., 2004)
78 or that bone morphology changes in the expected way (Wallace et al., 2015a). However, in
79 general, studies have shown that cortical bone is able to respond to behaviour during an
80 individual's lifetime (Carlson and Judex, 2007; Christen et al., 2014; Robling et al., 2002; Ruff et
81 al., 2006), and thus analysis of cortical bone thickness holds potential for reconstructing
82 behaviour in extinct species.

83 Within palaeoanthropology, numerous studies have investigated how cortical bone
84 properties relate to behaviour in both extant and fossil taxa. These can be broadly separated into
85 three methodologies: (1) analysis of cross sectional geometric properties either at mid-shaft or at
86 several points throughout the length of the shaft (e.g., Carlson, 2005; Carlson et al., 2006, 2008;

87 Davies and Stock, 2014; Marchi, 2005; Ruff, 2002, 2008; Ruff et al., 2013, 2015; Sarringhaus et
88 al, 2005; Shaw and Stock, 2013); (2) generating 2D colour maps of cortical thickness throughout
89 the diaphysis, with potential for application to non-cylindrical, irregularly shaped elements,
90 although as yet this has only been tested on tooth roots, and not the epiphyses of long bones (e.g.,
91 Bondioli et al., 2010; Jashashvili et al., 2015; Puymerrail et al., 2012a, b, 2013); and (3) analysis
92 of bone profiles at the articular surfaces, some of which include both cortical bone and also the
93 underlying trabecular structure (Carlson et al., 2013; Mazurier et al., 2010; Patel and Carlson,
94 2007). These analyses have been conducted using both clinical and micro-computed tomography
95 (microCT) (e.g., Lillie et al., 2015). Several studies have focused specifically on cortical bone of
96 the hands (e.g., Lazenby, 1998; Marchi, 2005) and feet (e.g., Griffin and Richmond, 2005;
97 Jashashvili et al., 2015; Marchi, 2005). Recent studies that have analysed cortical bone thickness
98 identified subtle differences both between African apes and modern humans, and between
99 modern and fossil *Homo* species (Jashashvili et al., 2015; Puymerrail et al., 2012a, b, 2013).

100 Here we investigate the potential applications of a novel method of cortical thickness
101 analysis, developed for medical research, which allows for statistical comparison between groups
102 (Poole et al., 2011, 2012; Treece et al., 2010, 2012). The main advantage of this method is that,
103 unlike previous methods, it allows measurement of cortical bone thickness throughout the entire
104 bone, i.e., including the diaphysis, metaphysis and epiphyses, and as such is applicable to both
105 long bones and to more complex elements. Moreover, in contrast to existing methods which
106 require registration to a 2D map (e.g., Bondioli et al., 2010), it enables generation of 3D colour
107 maps for each taxon/group, as well as quantification and visualization of regions whose
108 difference in cortical thickness between groups can be assessed for statistical significance.

109 We test the application of this method on comparative samples of hand (third metacarpal)
110 and foot (talus) bones of extant hominoids and, in order to test the applicability of this method in
111 specimens with taxonomic alteration, one early Holocene human (Arene Candide 2, third
112 metacarpal). As the hands and feet are the direct contact between an individual and the substrate,
113 they are likely to experience the initial forces of both locomotion and object manipulation. As
114 such, the skeletal elements in these regions are likely to reflect loading from these behaviours.
115 However, many bones of the hands and feet, particularly carpals and tarsals, have irregular and
116 complex shapes. As such, existing methods of analysis may not be applicable because complex

117 bones cannot be modelled as simple beams and their morphology cannot be easily mapped to a
118 2D plane for between-group comparisons.

119 In sum, we assess the utility of this method in an anthropological context for: (1)
120 comparing cortical thickness differences amongst taxa where there are also consistent differences
121 in shape, (2) comparing cortical thickness between taxa with systemic differences in cortical
122 thickness between species, (3) conducting statistical comparisons across small sample sizes,
123 common in palaeoanthropology and (4) applicability to taphonomically-altered fossil specimens.

124 2. Methods

125

126 2.1. Sample and microCT scanning

127

128 This study tests application of a cortical bone thickness analysis to the third metacarpal
129 (Mc3) and talus. The study sample for the Mc3 consists of *Homo sapiens* (N = 21), *Pan*
130 *troglydtes verus* (N = 5), *Pongo* sp. (N = 5), and a subfossil *H. sapiens* individual, Arene
131 Candide 2 (N = 1), from the early Holocene (9,900-10,850 Uncal BP) (Sparacello et al., 2015).
132 For the talus the sample includes two species: *H. sapiens* (N = 9) and *P. t. verus* (N = 13).
133 Details of the study samples are shown in Table 1. All non-human apes were wild-caught
134 individuals and the modern human sample is composed of nine individuals from Nubian Egypt
135 (6th-11th century) (Paoli et al., 1993; Strouhal and Jungwirth, 1979), eight individuals from
136 Tiera del Fuego (19th century) (Marangoni et al., 2011), and four individuals from Syracuse
137 (20th century).

138 High resolution microCT scans of the sample were collected using a SkyScan1173 scanner
139 at 100-130kV and 61-62 μ A and a BIR ACTIS 225/300 scanner at 130kV and 100-120 μ A. Both
140 CT scanners are housed at the Department of Human Evolution, Max Planck Institute for
141 Evolutionary Anthropology (Leipzig, Germany). All scans were reconstructed as 2048 x 2048
142 16-bit tiff stacks. All specimens were analysed at an isotropic voxel size of around 33 microns
143 (mean: 33 μ m, range: 30 - 42 μ m).

144

145 2.2. Cortical thickness measurement

146

147 Segmentation of the outer surface of the bone and measurement of cortical thickness were
148 conducted using Stradwin v5.1a (<http://mi.eng.cam.ac.uk/~rwp/stradwin>) (following Treece et
149 al., 2010, 2012). Contours were automatically segmented using a threshold-based segmentation
150 at 20-30 slice intervals along the length of the bone, with minor manual correction of errors in
151 contour definition (Fig. 1A and B). Interpolation of these contours enabled creation of an outer
152 surface of the bone (Fig. 1C). Using this surface as a guide, around 10000 - 15000 independent
153 measures of cortical bone thickness were made at each vertex, which were based on the grey
154 value profile of the CT data (Fig. 1D). As the vertices were placed at similar geometric

155 separations, the number of measurements was dependent on the size of the bone. These thickness
156 values were mapped onto the surface to generate a colour map of cortical thickness for each
157 individual, which could be smoothed in order to minimise the effect of erroneous measurements
158 (Fig. 1E).

159

160 2.3. *Specimen registration*

161

162 For comparison of cortical bone thickness maps between specimens, an average
163 (canonical) surface was created to which each individual surface was registered using
164 wxRegSurf v13 (<http://mi.eng.cam.ac.uk/~ahg/wxRegSurf/>) (following Gee et al., 2015). To
165 create the canonical surface, an initial specimen was chosen to which every surface in the sample
166 was then registered to create an average of all individuals (Fig. 2A). For both the Mc3 and talus,
167 the specimen chosen to begin creation of an average surface was an individual of *H. sapiens*.
168 Each specimen was registered to the canonical surface in order to compare cortical thickness
169 between specimens (Fig. 2B).

170

171 2.4. *Protocol for processing fossil specimens*

172

173 A common problem encountered with archaeological and fossil specimens is the presence
174 of unwanted inclusions within the bone. In some of the samples included here we found such
175 inclusions were of a higher density than the bone, which may affect measurement of cortical
176 thickness. The protocol for segmentation was therefore modified for these samples, with those
177 steps taken during the processing of the Arene Candide 2 Mc3 being used as an illustration (Fig.
178 3). Non-bone inclusions were corrected by either removing the bright inclusions or reducing the
179 brightness of the bone in these regions. Both were achieved by creating a label field within
180 Avizo 8.1, where the magic wand tool was used to select the high density materials. Those that
181 were to be removed were subtracted from the original image with an arithmetic operation (i.e.
182 original – label-field), while those areas constrained along the exterior of the cortical bone were
183 first multiplied by a fraction of their grey values and then subtracted from the original (i.e.
184 (original data - (label field x .05)). This resulted in an even grey value range that would permit an
185 accurate estimate of the cortical thickness for each measured point.

186

187 *2.5. Statistical parametric mapping*

188

189 Mean cortical thickness maps were generated for each taxon and between-group
190 comparisons were conducted using statistical parametric mapping (Friston et al., 1995) in the
191 SurfStat package (Worsley et al., 2009). In order to generate mean cortical thickness maps for
192 each species, the species mean was calculated for each vertex of the registered surfaces. As the
193 surfaces are registered to a canonical surface, these vertices are at equivalent locations. Statistical
194 parametric maps, commonly used in neuroimaging, are in essence the mapped results of
195 univariate comparisons at multiple points. In essence this is a “mass-univariate” analysis in that
196 univariate comparisons are made at each of the many vertices of the registered surface (Friston et
197 al., 1995). We applied statistical parametric mapping to the registered surfaces in order to
198 conduct interspecific comparisons. A general linear model (GLM) was fitted to the data to
199 determine whether cortical thickness can be explained by covariates of interest (species/taxa) and
200 confounding covariates. In order to minimise the effect of shape differences on systematic
201 misregistration, we incorporated information about shape as a confounding covariate in the GLM
202 (Gee and Treece, 2014; Gee et al., 2015). Specifically, we included non-rigid shape coefficients,
203 which were generated from a statistical shape model via principal component analysis of the
204 movement of each vertex during registration, as described in Gee and Treece (2014). The most
205 dominant mode of shape variation, which largely captured bone size, was disregarded since this
206 was highly correlated with taxa. Statistical parametric maps were generated using F statistics for
207 pairwise comparisons (t_{al}) or T statistics for multiple comparisons (Mc₃), and the
208 corresponding p-values were corrected for multiple comparisons using random field theory, in
209 order to control for the chance of false positives (Fig. 2C) (Friston et al., 1995; Worsley et al.,
210 2009). For statistical tests a p-value of $p < 0.05$ was considered significant. These statistical tests
211 are conducted both for each vertex of the registered surface (Fig. 2C: yellow-red colour scale)
212 and for localised regions, or clusters, on the registered surface (Fig. 2C: blue colour scale)
213 (Friston et al., 1995). For the t_{al}, relative thickness values were calculated for each individual
214 by subtracting the individual mean value from all of the thickness measurements then dividing
215 by the standard deviation, so as to test a method for standardising values when there are
216 considerable interspecific differences in mean cortical thickness.

217 3. Results

218

219 Cortical thickness mean values and standard deviations are shown in Table 2. In the talus
220 *Pan* has thicker cortical bone than *Homo*. This is similar to the cortical bone in the Mc3, where
221 both *Pongo* and *Pan* have thicker cortical bone than *Homo*. Within *Homo*, the Arene Candide 2
222 Mc3 has the thickest cortical bone, approaching the average of *Pongo*.

223

224 3.1. Cortical thickness maps: Mc3

225

226 Cortical thickness maps for the Mc3 are shown in Fig. 4. Both *Pan* and *Pongo* have much
227 thicker cortical bone in the shaft compared with *Homo*, and in *Pongo* the regions of greater
228 thickness extend further proximally and distally than in *Pan*. The non-human specimens also
229 have greater cortical thickness than *Homo* at the epiphyses, however no visible differences
230 between the species can be discerned from the mean cortical thickness maps.

231 Quantitatively, the overall greater thickness of the Mc3 of Arene Candide 2, compared
232 with modern humans, is in line with previous assessments of increased gracility of the skeleton
233 in recent, more sedentary modern humans (Chirchir et al., 2015; Ryan and Shaw, 2015, but see
234 Wallace et al., 2015b). Qualitatively, however, the local thickness pattern is largely comparable
235 to that of recent *Homo*, where the thickest point of cortical bone is at the palmar aspect of the
236 midshaft, while the cortex thins at the epiphyses. Interestingly, there is also thickening
237 observable along the presumed attachment site of the second and third dorsal interosseous
238 (Cashmore and Zakrzewski, 2013, but see Rabey et al., 2015; Williams-Hatala et al., 2016).

239 Fig. 5 shows the overall cortical thickness differences and statistically significant
240 differences by region. A comparison between *Pongo* and *Homo* reveals that *Pongo* has thicker
241 cortex along the majority of the diaphysis (Fig. 5, left), and this difference is statistically
242 significant (Fig. 5, right), with further cortical differences at the palmar and dorsoulnar aspect of
243 the Mc3 head. Less dramatic differences exist between *Pan* and *Homo*, with *Pan* demonstrating
244 significantly thicker cortical bone primarily along the dorsal aspect of the diaphysis and head, as
245 well as a prominent region at the radial and ulnar aspects of the base that extends distally to the
246 Mc2/Mc4 articular surfaces. *Pongo* and *Pan* differ in regions in which the cortical bone is both
247 thicker and thinner; *Pongo* is relatively thinner than *Pan* along the dorsal aspect of the Mc3

248 diaphysis and head, but comparatively thicker along the palmar aspect of the diaphysis and
249 dorsal aspect of the base. However, none of these differences in cortical thickness were
250 statistically significant (Fig. 5).

251

252 3.2. *Cortical thickness maps: talus*

253

254 Cortical thickness maps for the talus are shown in Fig. 6A. The mean maps for each
255 species, based on the absolute thickness values, show that *Homo* and *Pan* both share thicker
256 cortical bone on the medial and lateral malleolar surfaces and on the medial aspect of the talar
257 neck. *Pan*, but not *Homo*, has a region of thicker cortical bone on the posterior subtalar articular
258 surface. However, the absolute thickness map (Fig. 6A) shows that overall *Homo* has thinner
259 cortex throughout the talus compared with *Pan*. There are several regions of significant
260 differences in cortical bone thickness between the species, which generally represent the regions
261 in which *Pan* has the thickest cortical bone compared with *Homo*.

262

263 3.3. *Relative means*

264

265 To account for the significantly thicker cortex throughout the *Pan* talus, relative thickness
266 maps were produced and are shown in Fig. 6B. Relative cortical thickness was calculated for
267 each specimen by subtracting the individual mean value from each thickness measurement and
268 dividing by the standard deviation. The regions in which the mean colour maps show relatively
269 thicker cortical bone are similar to the absolute thickness maps. The comparison between the two
270 species, however, shows a different pattern. There are regions in which *Pan* has relatively thicker
271 cortical bone compared with *Homo*, particularly on the medial and lateral malleolar surfaces and
272 on the medial aspect of the talar neck. In contrast, *Homo* has relatively thicker bone at the
273 posterior talar tubercles, the posterior surface of the talar trochlea, and in some regions of the
274 talar head. The regions in which cortical thickness differs significantly between the two species
275 also differ between the absolute and relative colour maps.

276 4. Discussion

277

278 We sought to augment and expand upon well-established methods of cortical bone analysis
279 for palaeoanthropological research by adapting an imaging technique originally designed for low
280 resolution diagnostic medical CT scans. This 3D cortical mapping method (using freeware
281 Stradwin v5.1a and wxRegSurf v13) is attractive because it allows for the rapid acquisition of
282 thousands of independent measurements of cortical thickness using unsegmented CT data of
283 relatively simple (e.g., femoral) and complex (e.g., vertebral) morphologies within a stand-alone
284 and freely available software package. Such measurements may then be mapped onto a canonical
285 bone of mean shape for qualitative and quantitative comparison (i.e., using statistical parametric
286 mapping; Friston et al., 1995; Gee and Treece, 2014). Within the present study we found that this
287 method is capable of analysing and visualizing cortical thickness data from high resolution
288 microCT scans of hominoid metacarpals and tali, which present two distinctly different
289 morphologies.

290 Broadly speaking we found that the average cortical thickness of both the Mc3 and talus
291 was relatively thinner in modern *Homo* when compared to *Pan*, *Pongo*, and the subfossil Mc3 of
292 Arene Candide 2. Within the Mc3 of *Pan* and *Homo*, regions of greater thickness were
293 concentrated in a band along the proximal-midshaft with the thinnest portion being found at the
294 palmar surface of the proximal and distal articular surfaces. However, the greatest thickness in
295 *Homo* is apparent along the palmar aspect of this band. *Pongo* differed from the other two groups
296 in a noticeable absence of a thick band at midshaft, with thickening instead being found along
297 the palmar aspect of the shaft and head. Although there were no statistically significant
298 differences between *Pongo* and *Pan*, subtle variations in thickness are apparent along the dorsal
299 aspect, where *Pongo* is relatively thinner at the head and dorsal aspect of the shaft but thicker at
300 the base. It would be interesting to see if these differences reach significance with increased
301 sample sizes. Within the talus, we found regions of greater thickness in both *Homo* and *Pan* on
302 the medial and lateral malleolar surfaces and on the medial surface of the talar neck. In *Pan*, but
303 not *Homo*, the posterior subtalar articular surface has very thick cortical bone. Statistically
304 significant differences between *Pan* and *Homo* were then found and visualized using both raw
305 and equalized data that supported the qualitative observations. Although not the goal of the
306 present study, these results illustrate the potential of this method for identifying differences in

307 cortical thickness between species that can be used to test hypotheses founded upon bone
308 functional adaptation and known variation in behavioural loading.

309 Inherent to any method seeking to evaluate interspecific comparisons is the necessity of
310 identifying homologous anatomical regions. The “whole bone” approach of this 3D cortical
311 mapping method helps to overcome some challenges associated with identifying homologous
312 subsamples (e.g., a single slice) of cortical bone. However, this method does suffer from two
313 shortcomings when comparing morphology that differs across samples. First, the automated
314 method finds it challenging to register morphologically ambiguous regions, such as the relatively
315 simple morphology of the shaft that lacks clearly identifiable features. Within
316 palaeoanthropology, homology is often ensured by first selecting shared diagnostic features that
317 can be easily and reproducibly identified, i.e., by using landmarks (e.g., Arias-Martorell et al.,
318 2015; Knigge et al., 2015; Rein et al., 2015). This is not the case here, where correspondence is
319 driven by proximity within a predefined search region. The method of registration applied here
320 registers prominent morphological features, which would be appropriate for landmark placement,
321 fairly effectively. However in more featureless regions, such as the Mc3 shaft, the registration is
322 not constrained by clear shape differences. Often in such transformations there are ambiguous
323 regions, such as the shaft, where multiple registrations could be argued to be valid resulting in a
324 systematic misattribution of the mapped thickness. Even though we allowed for shape in the
325 GLM, we were not able to allow for the dominant shape mode since it was highly correlated with
326 group. It must therefore be kept in mind that the thickness differences identified may be the
327 result of some systematic misregistration, especially since the lengths and widths of the Mc3
328 shafts across the hominoids in this sample are very different.

329 The second challenge with this method arises when morphology across the comparative
330 sample differs substantially. For example, *Homo* has a styloid process at the base of the Mc3 that
331 is absent in non-human primates and most fossil hominins (Marzke and Marzke, 1987; Ward et
332 al., 2013). However, the current method requires registering the entire comparative sample to a
333 single surface, in this case an average mesh of the entire sample. In this study, the average mesh
334 has a styloid process, and so the *Pan* and *Pongo* Mc3s are deformed during registration to a more
335 *Homo*-like morphology. Thus information taken from the base of the Mc3 is obscured and
336 complicates interpretations of the potential differences in function, loading, and bony response.
337 This has clear implications for testing hypotheses generated under the bone functional adaptation

338 paradigm and will likely be an issue for other comparisons of skeletal elements that possess
339 highly variable anatomical regions. Thus, with this method it would be necessary to mask or
340 disregard such anatomical regions.

341 Indeed, the above issues are likely exaggerated within a (palaeo)anthropological context
342 where small sample sizes are common and inter-species variation can be high. Although one
343 might be able to collect a statistically significant number of high resolution scans from *H.*
344 *sapiens* or Neanderthals to be studied in this manner, most fossil hominin taxa are frequently
345 only represented by one or two isolated and fragmentary specimens of any given anatomical
346 element. As such, we should always be on the lookout for methods that allow us to gain as much
347 data as possible from the available fossils (Zollikofer and Ponce de Leon, 2001). Although any
348 statistical analysis afforded by the present method will remain underpowered in regards to
349 fossils, the ability to create interactive 3D visualizations provides a novel and informative way to
350 compare morphology, and particularly morphological features that are attached to long-standing
351 functional hypotheses (e.g., the functional significance of the Mc3 styloid process within
352 humans, gracilization of the skeleton, or remodelling of bone at muscle attachment sites) and
353 even help to generate new ones (see Hermann and Klein, 2015).

354 In light of this, a potential advantage of this 3D cortical mapping method is that the
355 registration of individuals to a “mean mesh” produces information about shape differences across
356 the sample. Principal component analysis produces a compact set of eigenvectors that capture the
357 dominant modes of variation from the mean mesh. A statistical shape model of this nature can
358 potentially be used to quantify and explore shape differences (Joshi et al., 2016; Schneider et al.,
359 2015). In fact, the interactive visualization and deformation of the canonical model, by way of an
360 associated statistical shape model file, is a feature that is currently available within wxRegSurf.
361 This offers a quick and convenient way to visualise 3D shape/structure covariation, though
362 whether the variation is biologically meaningful depends on the accuracy of the homologies.

363 The value of being able to visually evaluate variation in cortical thickness across the entire
364 skeletal element is seen in comparison with previous cortical mapping techniques (Jashashvili et
365 al., 2015; Puymeraill et al., 2012a, b; Ruff et al., 2015; Zollikofer and Ponce de Leon, 2001) that
366 rely on the cylindrical shape of long-bones to digitally unroll the diaphysis and map thickness
367 values onto a uniform grid (Bondioli et al., 2010). In contrast, thickness values in our 3D cortical
368 mapping method are estimated on intact morphology using the width and height of the grey

369 value curve within the user-specified measurement line. This type of measurement allows for an
370 associated error range that is used to inform the weight of the smoothing algorithm and,
371 subsequently, the mean values mapped to the canonical bone. Although some subtle variation is
372 necessarily lost in this process, this allows for a reasonable estimation of cortical thickness in the
373 individual and mean model, which can then be visualised qualitatively and statistically on the
374 same mean model.

375 To conclude, the present method of cortical thickness measurement can be successfully
376 applied to comparative samples, and builds upon previous techniques in palaeoanthropology by
377 enabling cortical thickness measurement of more complex regions/elements, such as the
378 epiphyses of the metacarpals and the talus. Through registration to a canonical model, statistical
379 comparisons can be conducted between groups, which holds potential for applications to
380 archaeological and fossil samples. However, in applying this method to comparative samples, it
381 is important that the optimum morphology of the canonical mesh and the potential for
382 misregistration are considered.

383

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567

568 **Table captions**

569

570 **Table 1**

571 Study sample.

572 **Tableau 1**

573 L'échantillon étudié.

574

575 **Table 2**

576 Mean cortical thickness values and standard deviations for the third metacarpal and talus.

577 **Tableau 2**

578 Valeurs moyennes et écarts-types de l'épaisseur corticale pour le troisième métacarpien et le
579 talus.

580

581 **Figure captions**

582

583 **Fig. 1.** Overview of cortical thickness measurement protocol for a *Pan* talus. A: segmentation of
584 contours on an individual slice showing thresholded region in magenta (top) and subsequent
585 yellow contour around bone (bottom). B: contours are automatically drawn at 20-30 slice
586 intervals throughout the bone. C: contours are interpolated to generate a surface used as a guide
587 for cortical thickness measurements. D: measurement of cortical bone thickness along a line
588 running through the cortex (top), measurement is based on the grey values shown in the
589 interpolated data (graph, bottom). E: cortical thickness maps are subsequently generated (left),
590 which can be smoothed (right) to even out erroneous measurements. Thicker cortex is shown in
591 blue and thinner cortex in red.

592 **Fig. 1.** Aperçu général du protocole de mesure de l'épaisseur corticale pour un talus de *Pan*. A:
593 segmentation des contours sur une coupe individuelle montrant la région seuillée en magenta (en
594 haut) et le contour jaune subséquent autour de l'os (en bas). B: les contours sont
595 automatiquement tracés par intervalles de 20-30 coupes sur toute la longueur de l'os. C: les
596 contours sont interpolés pour générer une surface utilisée comme un guide pour les mesures
597 d'épaisseur corticale. D: mesure de l'épaisseur de l'os cortical le long d'une ligne parcourant
598 l'épaisseur du cortex (en haut), la mesure est basée sur les valeurs de gris affichées dans les
599 données interpolées (graphique, en bas). E: la distribution de l'épaisseur de l'os cortical est
600 ensuite générée (à gauche) et peut être lissée (à droite) pour exclure de potentielles mesures
601 aberrantes. L'os cortical le plus épais est figuré en bleu et le plus fin est en rouge.

602

603 **Fig. 2.** Overview of registration to a canonical mesh and between-group comparisons of a *Pan*
604 and *Homo* talus. A: surface of one *Pan* (top left) and one *Homo* (bottom left) individual. Surface
605 files from the complete sample were used to generate an average, canonical surface (right). B: an
606 individual surface (green) and the canonical surface (red), before (left) and after (right) the
607 registration. C: mean cortical thickness maps of *Pan* (top left) and *Homo* (bottom left), both
608 expressed on the canonical surface, and a map showing regions where there are significant
609 differences between the two species (right). In the map of significant differences, regions in
610 yellow-red show significant differences at each vertex and regions in blue (extending from
611 yellow-red regions) show significant differences by cluster.

612 **Fig. 2.** Vue d'ensemble du recalage de talus de *Pan* et *Homo* sur un maillage canonique et
613 comparaisons entre groupes. A: surface d'un individu *Pan* (en haut à gauche) et d'un individu

614 *Homo* (en bas à gauche). Les fichiers de surface de l'échantillon entier ont été utilisés pour
615 générer une surface canonique moyenne (à droite). B: surface individuelle (en vert) et surface
616 canonique (en rouge), avant (à gauche) et après (à droite) le recalage. C: distribution moyenne de
617 l'épaisseur corticale chez *Pan* (en haut à gauche) et chez *Homo* (en bas à gauche), les deux étant
618 projetées sur la surface canonique, et distribution montrant les régions où les deux espèces
619 diffèrent significativement (à droite). Dans la carte montrant les différences significatives, les
620 régions en couleurs chaudes montrent les différences significatives au niveau de chaque vertex,
621 et les régions en couleurs froides (dépassant des régions en couleurs chaudes) montrent les
622 différences par cluster.

623
624 **Fig. 3.** Protocol for processing specimens with high density inclusions. Shown here is the Mc3 of
625 Arene Candide 2. Incorrect measurements on the original model (A) are due to high density
626 inclusions (B top) and differential preservation (B bottom) leading to artificially thick (orange
627 box) and thin (purple box) regions of the colour map. High density inclusions outside of the
628 cortex are selected in the CT data, shown in magenta (C) and removed (D top), while high
629 intensity grey values within the cortex are reduced with an arithmetic operation (D bottom) (see
630 text for explanation), to create the corrected model (E).

631 **Fig. 3.** Protocole pour traiter les spécimens avec des inclusions à haute densité. Le troisième
632 métacarpien d'Arene Candide 2 est ici illustré. Les mesures incorrectes sur le modèle original (A)
633 sont dues à des inclusions à haute densité (B, en haut) et à une préservation différentielle (B, en
634 bas) causant des régions artificiellement épaisses (encadré orange) et fines (encadré violet) sur la
635 carte colorée. Les inclusions à haute densité en dehors du cortex sont sélectionnées (en rouge)
636 dans les données CT (C) et enlevées (D, en haut), alors que les valeurs de gris correspondant aux
637 hautes densités de l'os cortical sont réduites par une opération arithmétique (D, en bas) (voir le
638 texte pour plus d'informations), pour créer le modèle corrigé (E).

639
640 **Fig. 4.** Mean cortical thickness maps of the Mc3 for each species, all mapped to the canonical
641 mesh. From top to bottom, *P. t. verus*, *H. sapiens*, *Pongo* sp. and archaeological *H. sapiens*
642 (Arene Candide 2). Thicker cortex in is blue, thinner cortex in red. Metacarpals are shown in
643 (left to right) lateral, palmar, distal (top), proximal (bottom), medial and dorsal views.

644 **Fig. 4.** Distributions moyennes de l'épaisseur de l'os cortical du troisième métacarpien pour
645 chaque espèce, toutes recalées sur le maillage canonique. De haut en bas, *P. t. verus*, *H. sapiens*,
646 *Pongo* sp. et un spécimen *H. sapiens* archéologique (Arene Candide 2). L'os cortical plus épais
647 est figuré en bleu, celui plus fin est en rouge. Les métacarpiens sont montrés, de gauche à droite,
648 en vues latérale, palmaire, distale (en haut), proximale (en bas), médiale et dorsale.

649
650 **Fig. 5.** Colour maps of cortical thickness differences between each species (left) and statistical
651 comparisons (right) for the Mc3 in (top to bottom) *Pongo* sp. vs *H. sapiens*, *P. t. verus* vs *H.*
652 *sapiens*, and *Pongo* sp. vs *P. t. verus*. Differences in thickness between species (left) are blue
653 where the first species has a thicker cortex than the second and red where the first species has a
654 thinner cortex than the second. Statistical comparisons (right) show regions where there are
655 significantly different cortical thickness values at each vertex (yellow-red), and regions where
656 there are significant differences in cortical thickness at each cluster (blue). No significant
657 differences were found between *P. t. verus* and *Pongo* sp. Metacarpals are shown in (left to right)
658 lateral, palmar, distal (top), proximal (bottom), medial and dorsal views.

659 **Fig. 5.** Cartes chromatiques des différences de distribution d'épaisseur de l'os cortical entre
660 plusieurs paires d'espèces (à gauche) et comparaisons statistiques (à droite) pour le troisième
661 métacarpien de *Pongo* sp. et *H. sapiens*, *P. t. verus* et *H. sapiens*, et *Pongo* sp. et *P. t. verus* (de
662 haut en bas). Les différences d'épaisseur entre paires d'espèces (à gauche) sont figurées en bleu
663 lorsque la première espèce montre un cortex plus épais que la seconde, et en rouge en cas
664 d'épaisseur plus faible. Les comparaisons statistiques (à droite) montrent les régions pour
665 lesquelles les différences en épaisseur corticale sont significatives au niveau de chaque vertex
666 (couleurs chaudes), et de chaque cluster (couleurs froides). Aucune différence significative n'a
667 pu être identifiée entre *P.t.verus* et *Pongo* sp. Les métacarpiens sont montrés, de gauche à droite,
668 en vues latérale, palmaire, distale (en haut), proximale (en bas), médiale et dorsale.

669
670 **Fig. 6.** Mean cortical thickness maps for the *Pan* and *Homo* talus showing results for both A)
671 absolute cortical thickness measurements and B) relative cortical thickness comparisons. For
672 relative thickness comparisons, the mean was subtracted from every thickness measurement then
673 divided by the standard deviation for each individual before generating species averages and
674 conducting statistical comparisons. From top to bottom, mean cortical thickness maps for *Pan*,
675 mean cortical thickness maps for *Homo*, cortical thickness differences between *Pan* and *Homo*
676 and statistical comparisons between the two species. Talus is shown in (from left to right) lateral,
677 posterior and medial views.

678 **Fig. 6.** Distributions moyennes de l'épaisseur de l'os cortical pour le talus de *Pan* et *Homo*
679 montrant les résultats pour A) les mesures de l'épaisseur corticale absolue et B) les comparaisons
680 de l'épaisseur corticale relative. Pour ces dernières, la moyenne a été soustraite de chaque
681 mesure d'épaisseur puis divisée par l'écart-type, pour chaque individu, avant de générer des
682 moyennes par espèce et de conduire des comparaisons statistiques. De haut en bas, les
683 distributions d'épaisseur corticale moyenne chez *Pan*, chez *Homo*, les différences d'épaisseur
684 corticale entre *Pan* et *Homo*, et les comparaisons statistiques entre les deux espèces. De gauche à
685 droite, le talus est montré en vues latérale, postérieure et médiale.

686

687 **Table 1**
 688 Study sample.
 689 **Tableau 1**
 690 L'échantillon étudié.
 691

Taxon	Mc3	Talus	Locomotor mode	Mean body mass (kg) ¹
<i>Homo sapiens</i>	21	9	Bipedal	54.4-62.2
Early Holocene <i>Homo</i> (Arene Candide 2)	1	-	Bipedal	-
<i>Pan troglodytes verus</i>	5	13	Knuckle-walking	41.3-59.7
<i>Pongo sp.</i>	5	-	Suspensory, torso-orthograde	35.6-78.5

¹ Sex specific mean body mass (F-M). Body masses from Smith and Jungers (1997).

¹ Masse corporelle moyenne par espèce et par sexe (F-M). Les masses corporelles sont extraites de Smith et Jungers (1997).

692
 693
 694 **Table 2**
 695 Mean cortical thickness values and standard deviations for the third metacarpal and talus.
 696 **Tableau 2**
 697 Valeurs moyennes et écarts-types de l'épaisseur corticale pour le troisième métacarpien et le
 698 talus.
 699

Taxon	Mean cortical thickness (mm)	
	Mc3	Talus
<i>Homo sapiens</i>	1.03 (0.07)	0.45 (0.06)
Early Holocene <i>Homo</i> (Arene Candide 2)	1.40	-
<i>Pan troglodytes verus</i>	1.59 (0.19)	0.88 (0.19)
<i>Pongo sp.</i>	1.47 (0.10)	-

700