INTERNAL BONE ARCHITECTURE IN THE CAPITATE OF EXTANT HOMINIDS

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Introduction

The capitate sits centrally in the wrist (Fig.1). Its morphology plays a key role proximally as the 'ball' component of the mobile mid-carpal joint, where it articulates with the loosely tethered proximal row[1]. Distally, it articulates with the tightly bound distal row and is loaded in tension by the attaching extrinsic and intrinsic ligaments[1]. Morphological differences in the bone across hominids are linked to variation in habitual hand postures and locomotor modes and as such, has been an important carpal bone for drawing inferences about fossil hominin locomotor and behavioural capacities[1-3]. However, it has yet to be determined whether the epigenetically sensitive internal bone tissue may also reflect locomotor and behavioural repertoires. An holistic analysis of the proximal and distal portion of the capitate allows for an investigation into potential locomotor signals as well as a better understanding of the divergent joint environment on functional adaptation.

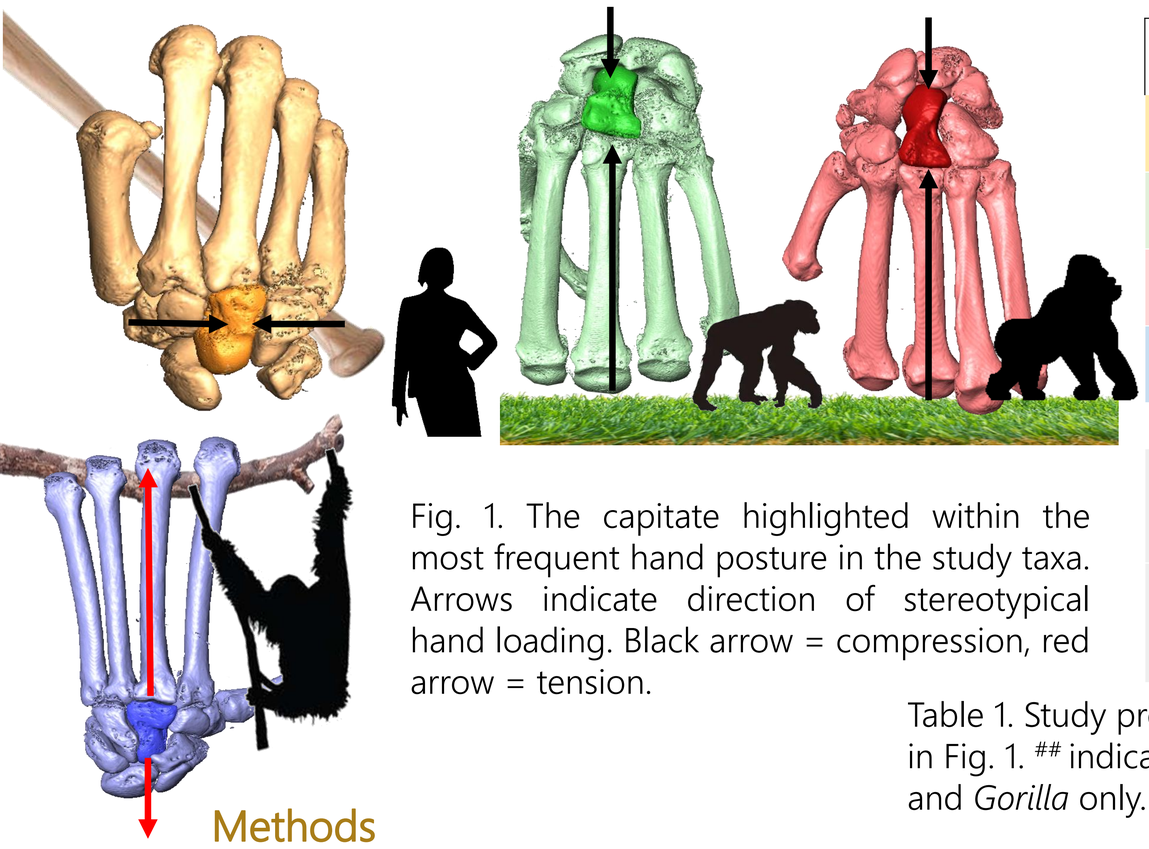

Fig. 1. The capitate highlighted within the most frequent hand posture in the study taxa. Arrows indicate direction of stereotypical hand loading. Black arrow = compression, red arrow = tension.

Genus	Presumed force magnitude	Bone volume / total volume (BV/TV)	Degree of Anisotropy (DA)	Cortical thickness (Ct.Th)
Homo n=26	Lowest	Lowest##	Intermediate	Lowest##
Pan n=14	High	Highest##	High	High##
Gorilla n=16	Highest	Highest##	High	Highest##
Pongo n=13	Moderate	Intermediate#	Lowest	Intermediate
Joint	**Joint loading**	**BV/TV**	**DA**	**Ct.Th**
Mid-carpal (proximal capitate)	Compression	Lower#	Lower^	Lower##
Carpometacarpal (distal capitate)	Compression + tension	Higher#	Higher^	Higher##

Table 1. Study predictions. Presumed force magnitude correlates with the most frequent hand postures outlined in Fig. 1. ## indicates strong and # some support was found for prediction. ^ indicates support was found in *Pan* and *Gorilla* only.

Methods

- **Bone structure related to strength** was analysed in the capitate of extant apes to **test whether bone architecture correlates with variation in joint and hand loading** (Table 1).
- Capitates were µCT scanned (30-50 microns) (Fig.2A) then segmented and partitioned into the proximal and distal portion (Fig.2B). The cortical (Fig.2C) and trabecular (Fig.2D) region was analysed holistically in 3D using medtool[4] within the proximal and distal portion of the bone (Fig.2E).
- **Interspecific mean differences** in bone variables were tested in *R* using Kruskal-Wallis and pairwise rank-sum tests with the Holm p adjust method.
- **Intraspecific ratios** were calculated as the distal variable relative to proximal variable. Differences were tested for significance with a Wilcoxon signed-rank test with the Holm p adjust method.

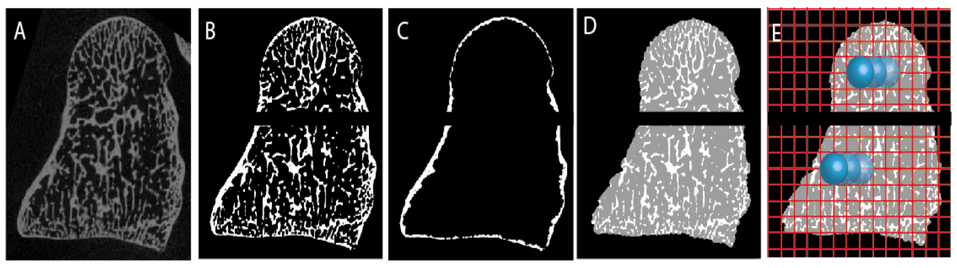

Fig. 2. Steps of trabecular and cortical bone analysis using medtool. Proximal is up, distal is down.

Results

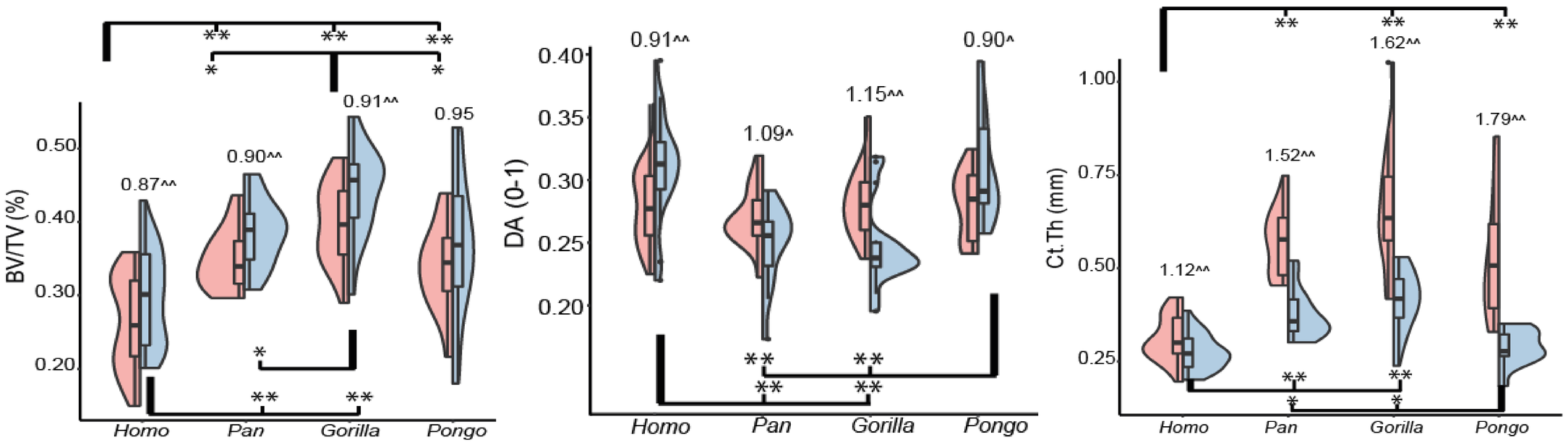

Fig 3. Boxplots of the mean distal and proximal bone variable and results of the inter- and intraspecific statistical tests. Pink plots are distal results and blue plots are proximal. Ratios are written above boxplots with Wilcoxon signed-rank results: ^ p=≤0.005; ^^ p=≤0.001. Pairwise rank-sum tests indicated with square brackets: distal tests top of graph; proximal tests bottom of graph * p=≤0.005 ** p=≤0.001.

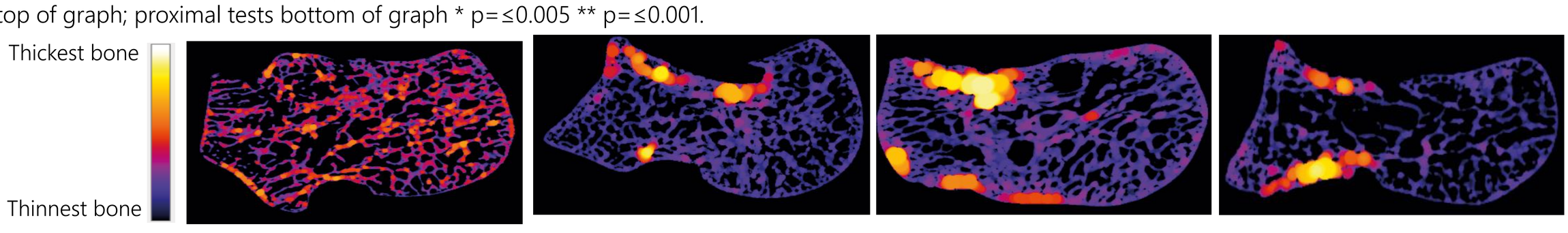

Fig. 4. Visualisation of the internal structure of the capitate. From left to right: *Homo, Pan, Gorilla, Pongo*. Proximal is right, distal is left.

Conclusions

The non-human apes are differentiated from *Homo* principally by thick distal cortical bone. *Pan* and *Gorilla* are further differentiated from *Pongo* and *Homo* by a more isotropic capitate head.

Distal DA was the only bone parameter that was not differentiated among the genera. This may indicate that the limited mobility at the distal region results in a similar DA, irrespective of hand use.

Partitioning of 'cortical' and 'trabecular' regions in carpals (and likely tarsals) **may obscure functionally relevant information in the carpus of hominids.**

Divergent bone parameters between the proximal and distal capitate suggest that **force and functional adaptation differs across the bone**. Biomechanically meaningful sub-regions may be more informative than whole bone or single VOIs for future research.

Tensional strain, which has a lower failure load than compressive[5], is induced during vertical climbing[6]. The distal Ct.Th increase coincides with the attachment sites for several ligaments and as they load the capitate in tension, **may represent a climbing signal in the capitate**. The intergeneric differences suggest that **the hand of bipedal *Homo* may not experience a similar magnitude of tensional strain**.

References: **[1]** Lewis OJ (1989) *Functional morphology of the evolving hand and foot* **[2]** Kivell TL, Schmitt D (2009) *PNAS* 106 **[3]** Richmond BG, Begun DR, Strait DS (2001) *Am J Phys Anthropol* 116. **[4]** Pahr, D. http://www.dr-pahr.at/medtool/ **[5]** Pattin CA, Caler WE, Carter DR (1996) *J Biomech* 29 **[6]** Hanna JB, Rana P, Schmitt D. (2017) *J Exp Biol*. 220

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