Estimates of fossil hominin quadriceps physiological cross sectional area from patellar dimensions

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BACKGROUND

The fossil record almost exclusively leaves behind isolated osteological elements. While information on the morphology of the muscles would aid efforts to reconstruct locomotion and other aspects of fossil hominin biology, previous attempts to predict muscle parameters from bones have often failed (see Zumwalt, 2005). It is difficult to quantify the expanse of a muscle attachment site along long bone shafts, nor is there a significant relationship between long bone and muscle cross-sectional areas (Shaw, 2010).

The **patella**, a sesamoid bone in the quadriceps tendon, may provide an accurate measure of quadriceps morphology because of its intimate relationship with the extensor muscle complex of the knee. **Here, we test whether patellar dimensions are a reliable indicator of quadriceps physiological cross sectional area (PCSA) in extant primates and other mammals.** PCSA reflects a muscle's ability to produce force, and may be an important anatomical variable for locomotor performance. A strong functional relationship between patellar dimensions and quadriceps PCSA could allow for the estimation of muscle morphology and locomotor performance in fossil taxa.

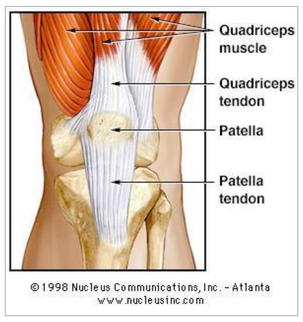

Figure 1. **Anatomical position of the patella.**

Reliable estimates of fossil hominin muscle parameters are critical for evaluating the transition from relatively smaller hominoid to relatively larger human lower limb musculature (Figure 4) likely related to an increase in home range size over the course of hominin evolution.

QUESTION

Is the patella a reliable predictor of quadriceps PCSA in extant and fossil taxa?

MATERIALS AND METHODS

Sample

Quadriceps PCSA for extant taxa was taken from the literature (Table 1). The availability of quadriceps PCSA data for primates and other mammals limited the sample of measured taxa for this study. Patellar and femoral linear measurements (Table 2) were taken from mixed-sex samples of wild shot , adult specimens with no evident pathologies.

Table 1.

Taxon	N	Collection*	Muscle Data Source
Lemur fulvus	5	AMNH	Anapol and Jungers, 1986
Hylobates sp.	32	AMNH, NMNH	Channon *et al.*, 2009
Symphalangus sp.	10	AMNH, NMNH	Channon *et al.*, 2009
Pongo pygmaeus	29	AMNH, NMNH	Payne *et al.*, 2008
Gorilla gorilla	21	AMNH, NMNH	Payne *et al.*, 2008
Pan troglodytes	39	AMNH, NMNH	Thorpe *et al.*, 1999; Payne *et al.*, 2008
Homo sapiens	28	AMNH	Alexander and Vernon, 1975
Oryctolagus cuniculus	9	NMNH	Lieber and Belvins, 1989
Felis catus	10	NMNH	Sacks and Roy, 1982

*AMNH = American Museum of Natural History, New York, NY; NMNH = Smithsonian National Museum of Natural History, Washington, DC.

Measurements

Patella

- Superior-Inferior Height (SI)*
- Medial-Lateral Width (ML)*
- Anterior-Posterior Thickness (AP)*

Femur

- Superior-Inferior Head Diameter (FHSI)*
- Bicondylar Length (FBL)+

*Digital Caliper (mm) +Osteometric Board (mm)

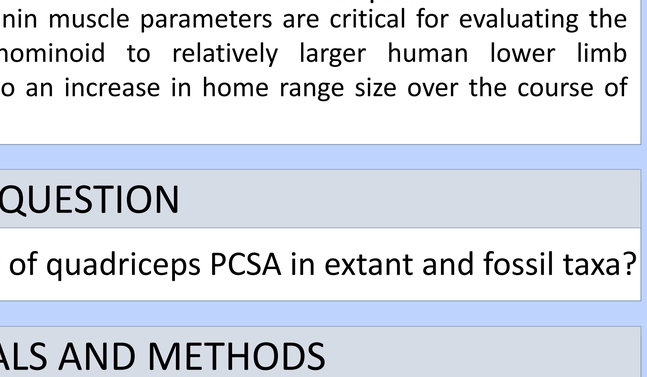

Figure 2. **Measurements taken on the patella and femur.**

Calculated Patellar Planes

- Sagittal Cross Sectional Area (SCSA) = AP*SI
- Transverse Cross Sectional Area (TCSA) = AP*ML

Analyses

Published quadriceps PCSA were regressed against species-averaged patellar and femoral dimensions using Ordinary Least Squares (OLS) (Fig. 3, Table 2) and Phylogenetic Generalized Least Squares (PGLS) (Table 3) regressions. Analysis of variance (ANOVA) was used to identify the metrics most related to quadriceps PCSA (Table 2). The best regressions were used to predict fossil hominin quadriceps PCSA (Table 4).

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RESULTS

Figure 3. ***Quadriceps dimensions are more closely related to patellar size than to other measures of body size.***

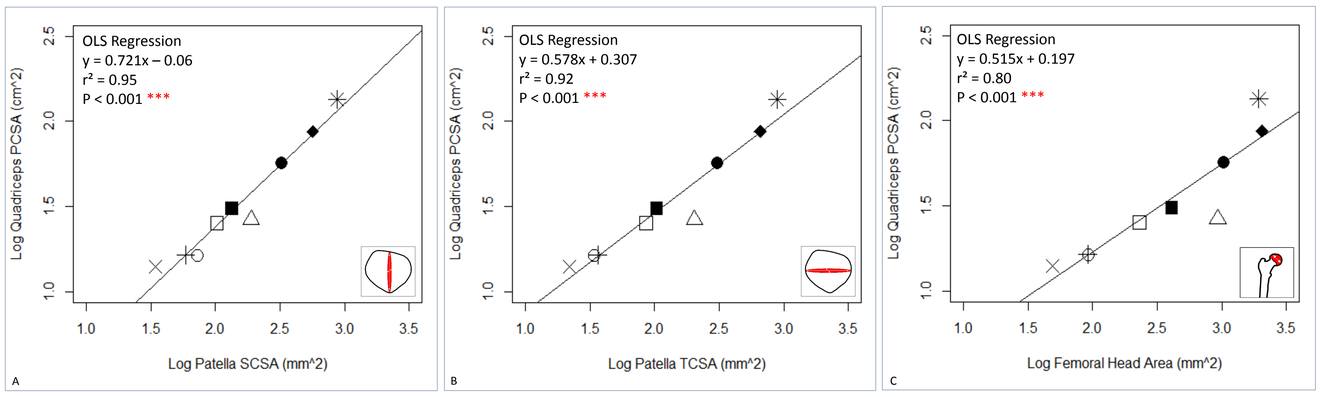


Figure 3 Legend

Felis	+	*Oryctolagus*	×	*Lemur*	○
Hylobates	□	*Symphalangus*	■	*Pongo*	△
Pan	●	*Gorilla*	◆	Human	✳

Table 2. ***ANOVA of OLS Models***

SCSA & Femoral Head Area		TCSA & Femoral Head Area	
	P		P
SCSA	**5.86E-08** ***	TCSA	**6.55E-07** ***
FH Area	0.1517	FH Area	**0.04088** *

Table 3. ***OLS vs. PGLS Regressions***

	OLS		PGLS			
	R^2	P	R^2	P	Wilks' λ	λ 95% CI
SCSA	0.95	**7.35E-06** ***	0.98	**3.17E-06** ***	0	(0, 0)
TCSA	0.92	**2.81E-05** ***	0.96	**6.44E-05** ***	0	(0, 0.868)

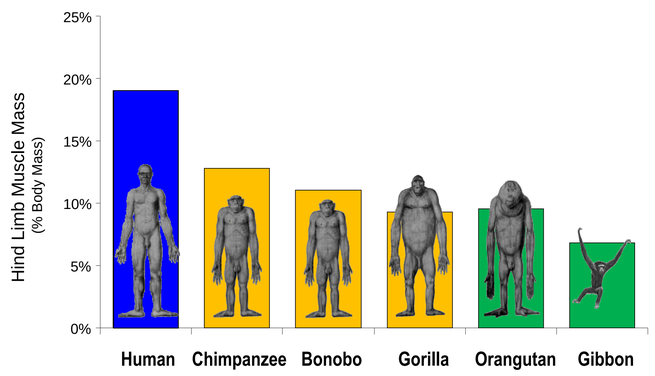
Fossil Hominin Predicted Quadriceps PCSA

Table 4.

Specimen	Taxon	Prediction (SCSA)	Prediction (TCSA)	Patella Dimension Source
SKX 1084	*P. robustus*	——	64.09	Susman, 1989
MH 2	*A. sediba*	53.97	57.98	DeSilva *et al.*, 2013
D3481	*H. erectus*	95.54	98.36	unpublished
LB1/10	*H. floresiensis*	61.86	59.82	Jungers *et al.*, 2009
Shanidar 1	*H. neanderthalensis*	175.44	182.17	Trinkaus, 1983
Shanidar 4	*H. neanderthalensis*	164.5	170.81	Trinkaus, 1983
Shanidar 5	*H. neanderthalensis*	142.58	158.61	Trinkaus, 1983

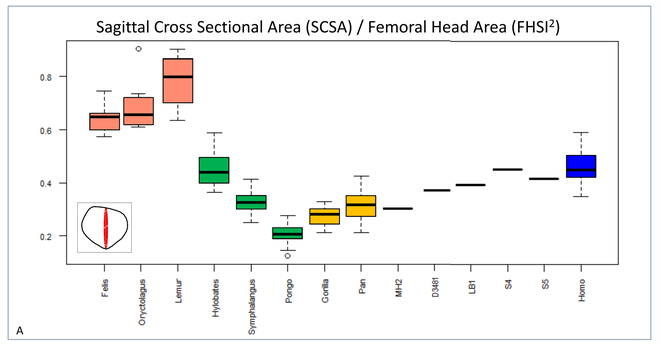
Predicted Quadriceps Physiological Cross Sectional Areas in cm^2

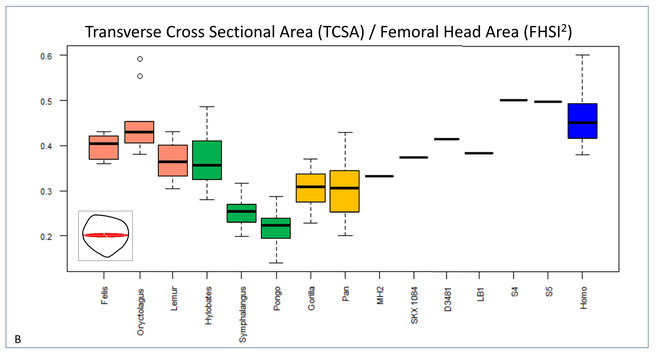
Figure 4. ***Extant Hominoid Relative Hind Limb Muscle Mass***



Source: Payne *et al.*, 2006; Thorpe *et al.*, 1999

Figure 5. ***Human-like relative patellar size is present in fossil members of the genus* Homo.**





*SKX 1084 patella is unassociated with a femur; the average of four *P. robustus* femoral head diameters (SK 19, SK 3121, SK 82, SK 97 (Susman *et al.*, 2001)) was used.
** S1 does not have a preserved femoral head (Trinkaus, 1983); it was omitted from these analyses as two other *H. neanderthalensis* specimens (S4, S5) do have associated femoral heads.

Figure 4 & 5 Legend
Locomotor Category — Bipedal; Knuckle-Walking/Suspensory; Suspensory/Quadrimanus; Quadrupedal Leaper/Saltorial

DISCUSSION AND CONCLUSIONS

The patella can reliably be used to estimate quadriceps size (Fig. 3, Tbl. 4).

- Patellar cross sectional dimensions (SCSA, TCSA) are better predictors of quadriceps physiological cross sectional area (r^2=0.95, 0.92 respectively) than femoral head size (as a body size proxy) alone (r^2=0.80) (Fig. 3, Tbl. 2). Phylogenetic relatedness does not significantly affect this relationship (Tbl 3).
- This relationship holds broadly across mammals, including hominoids and other primates (Tbl. 1, Figure 3). However, a larger sample is needed to determine whether the relationship holds in other groups.

Members of the genus *Homo* have relatively larger patellae and estimated quadriceps PCSA for their body size than *A. sediba* and *P. robustus* (Fig. 5, Tbl. 4).

- This has implications for locomotor reconstructions of extinct hominins. Relatively smaller patellae (and lower quadriceps PCSA) may suggest less terrestrial travel and smaller home range size. Muscle size is related to both strength and endurance in primates and other mammals (Weibel *et al.*, 2004).

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