

On the cross-sectional form of the patella in several primates

Christopher David Stanford Jones

MAppSc, BAppSc

A thesis submitted for the degree of Doctor of Philosophy at the University of Adelaide,
Department of Anatomical Sciences

June 2003

Table of Contents

Table of Contents	ii
List of Figures	xii
List of Tables	xv
Abstract	xxii
Declaration	xxiv
Acknowledgments	xxv
Chapter 1 Introduction	1
Chapter 2 Review of the Literature	3
2.1 Structure, Function, Development and Variation	3
2.1.1 Gross Anatomy	3
2.1.1.1 Patella.....	3
2.1.1.2 Distal femur	6
2.1.1.3 Quadriceps femoris	8
2.1.1.4 Fibrous tissues.....	11
2.1.1.5 <i>Q</i> -angle.....	11
2.1.2 Biomechanics of the Patella.....	14
2.1.2.1 Kinematics of knee function	15
2.1.2.2 Role of the patella	17
2.1.2.3 Kinetics of patellar function.....	18
2.1.2.4 Stability of the patella	21
2.1.2.5 Primate knee function	22
2.1.2.6 Mechanical properties of bones	24
2.1.3 Development of the Patella.....	27
2.1.3.1 Limb bone morphogenesis	28

2.1.3.2 Patellar morphogenesis	29
2.1.3.3 Growth, modelling and remodelling.....	31
2.1.3.3.1 growth.....	31
2.1.3.3.2 modelling.....	31
2.1.3.3.3 remodelling.....	34
2.1.3.4 Knee joint evolution.....	35
2.1.4 Phenotypic Variation	35
2.1.4.1 Genetic, epigenetic and environmental influences	35
2.1.4.2 Structure-function association	38
2.1.5 Summary.....	41
2.2 Mathematical and Statistical Concepts	43
2.2.1 Morphometric Methods	43
2.2.1.1 Multivariate morphometrics.....	44
2.2.1.2 Coordinate morphometrics.....	44
2.2.1.3 Boundary morphometrics.....	45
2.2.1.3.1 the conventional Fourier method.....	46
2.2.1.3.2 the elliptic Fourier method	48
2.2.1.3.3 methodological considerations	48
2.2.1.4 Comparison of methods – landmark versus outline methods	50
2.2.2 Mathematical and Statistical Methods.....	52
2.2.2.1 Principal component analysis	52
2.2.2.1.1 description	53
2.2.2.1.2 methodological issues	55
2.2.2.1.2.1 covariance or correlation matrix?.....	55
2.2.2.1.2.2 raw or logarithmic data?.....	55
2.2.2.1.2.3 how many principal components?.....	56
2.2.2.1.2.4 distinctness of eigenvalues	56

2.2.2.1.3 interpretation of principal components	57
2.2.2.2 Cluster analysis	58
2.2.2.2.1 description	58
2.2.2.2.2 methodological issues	58
2.2.3 Summary	60
Chapter 3 Preliminary Investigations	61
3.1 Background.....	61
3.2 Aims and Hypotheses.....	63
3.3 Materials and Methods	64
3.3.1 Materials	64
3.3.2 Methods	64
3.3.2.1 Specimen preparation/data capture	64
3.3.2.2 Reliability.....	67
3.3.2.3 Power spectra	68
3.3.2.4 Ordination	69
3.4 Results	71
3.4.1 Specimens	71
3.4.2 Reliability	74
3.4.2.1 Conventional data	74
3.4.2.2 Fourier data	75
3.4.3 Power	77
3.4.4 Ordination	82
3.4.4.1 Principal component analysis	82
3.4.4.1.1 <i>Homo</i>	82
3.4.4.1.1.1 conventional data.....	82
3.4.4.1.1.2 Fourier data.....	84
3.4.4.1.2 <i>Cercopithecus</i>	86

3.4.4.1.2.1 conventional data.....	86
3.4.4.1.2.2 Fourier data.....	87
3.4.4.1.3 <i>Colobus</i>	89
3.4.4.1.3.1 conventional data.....	89
3.4.4.1.3.2 Fourier data.....	90
3.4.4.1.4 <i>Gorilla</i>	92
3.4.4.1.4.1 conventional data.....	92
3.4.4.1.4.2 Fourier data.....	93
3.4.4.2 Cluster analysis.....	104
3.4.4.2.1 conventional data.....	104
3.4.4.2.1.1 females distal.....	104
3.4.4.2.1.2 females proximal.....	105
3.4.4.2.1.3 males distal.....	105
3.4.4.2.1.4 males proximal.....	105
3.4.4.2.2 Fourier data.....	107
3.4.4.2.2.1 females distal.....	107
3.4.4.2.2.2 females proximal.....	107
3.4.4.2.2.3 males distal.....	108
3.4.4.2.2.4 males proximal.....	108
3.5. Discussion.....	110
3.5.1 Reliability.....	110
3.5.2 Power.....	110
3.5.3 Ordination.....	111
3.5.3.1 Principal component analysis.....	111
3.5.3.2 Cluster analysis.....	114
3.5.4 Comparative Discussion.....	118
3.5.4.1 Principal component analysis versus cluster analysis.....	118

3.5.4.2 Proximal versus distal outlines	119
3.5.4.3 Conventional versus Fourier data	120
3.5.4.4 Comparison among genera	120
3.6 Conclusions	123
3.6.1 Reliability	123
3.6.2 Power	123
3.6.3 Ordination	123
Chapter 4 Size, Shape and Allometry.....	125
4.1 Background.....	125
4.1.1 Size-adjustment.....	126
4.1.1.1 Principal component analysis	127
4.1.1.2 Ratios	129
4.1.1.3 Methods for this investigation	131
4.1.2 Allometry	132
4.1.2.1 Functional relations.....	132
4.1.2.2 Biological scaling.....	135
4.1.2.3 Allometric methods.....	141
4.1.2.3.1 bivariate allometry.....	141
4.1.2.3.1.1 Model I (least-squares) regression.....	142
4.1.2.3.1.2 Model II (major axis) regression	143
4.1.2.3.1.3 comparison of methods.....	143
4.1.2.3.1.4 Mosimann's method	144
4.1.2.3.2 multivariate allometry	144
4.1.3 Summary	147
4.2 Aims and Hypotheses	149
4.3 Materials and Methods	151
4.3.1 Materials	151

4.3.2 Methods	151
4.3.2.1 Size-adjustment.....	151
4.3.2.1.1 principal component analysis	151
4.3.2.1.2 cluster analysis	152
4.3.2.2 Allometry	153
4.4 Results	156
4.4.1 Size-adjustment.....	156
4.4.1.1 Principal component analysis	156
4.4.1.1.1 <i>Homo</i>	156
4.4.1.1.1.1 conventional data.....	156
4.4.1.1.1.2 Fourier data.....	157
4.4.1.1.2 <i>Cercopithecus</i>	159
4.4.1.1.2.1 conventional data.....	159
4.4.1.1.2.2 Fourier data.....	160
4.4.1.1.3 <i>Colobus</i>	162
4.4.1.1.3.1 conventional data.....	162
4.4.1.1.3.2 Fourier data.....	163
4.4.1.1.4 <i>Gorilla</i>	164
4.4.1.1.4.1 conventional data.....	164
4.4.1.1.4.2 Fourier data.....	165
4.4.1.2 Cluster analysis	177
4.4.1.2.1 conventional data.....	177
4.4.1.2.2 Fourier data	177
4.4.2 Allometry.....	183
4.4.2.1 <i>Homo</i>	183
4.4.2.1.1 conventional data.....	183
4.4.2.1.2 Fourier data	184

4.4.2.2 <i>Cercopithecus</i>	186
4.4.2.2.1 conventional data.....	186
4.4.2.2.2 Fourier data	188
4.4.2.3 <i>Colobus</i>	191
4.4.2.3.1 conventional data.....	191
4.4.2.3.2 Fourier data	193
4.4.2.4 <i>Gorilla</i>	195
4.4.2.4.1 conventional data.....	195
4.4.2.4.2 Fourier data	196
4.5 Discussion.....	199
4.5.1 Size-adjustment.....	199
4.5.1.1 Principal component analysis	199
4.5.1.2 Cluster analysis	216
4.5.1.3 Comparative discussion	220
4.5.1.3.1 proximal versus distal outlines.....	220
4.5.1.3.2 conventional versus Fourier data.....	221
4.5.1.3.3 principal component analysis versus cluster analysis	225
4.5.1.3.4 comparison among genera.....	225
4.5.2 Allometry	226
4.5.2.1 Allometry	226
4.5.2.2 Comparative discussion	236
4.5.2.2.1 proximal versus distal outlines.....	236
4.5.2.2.2 conventional versus Fourier data.....	236
4.5.2.2.3 comparison among genera.....	237
4.6 Conclusions	240
4.6.1 Size-adjustment.....	240
4.6.2 Allometry	240

Chapter 5 Sexual Dimorphism.....	242
5.1 Background.....	242
5.1.1. Definitions	242
5.1.2 Causality	243
5.1.3 Body-part Dimorphism.....	245
5.1.4 Ontogeny.....	247
5.1.5 Primate Sexual Dimorphism.....	248
5.1.6 Review of Methods.....	251
5.1.6.1 Size dimorphism	251
5.1.6.1.1 ratios	252
5.1.6.1.2 differences	252
5.1.6.2 Shape dimorphism	253
5.1.6.3 Methods for this investigation	253
5.1.7 Summary.....	253
5.2 Aims and Hypotheses.....	255
5.3 Materials and Methods	258
5.3.1 Size Dimorphism	258
5.3.2 Shape Dimorphism	260
5.4 Results	262
5.4.1 Size Dimorphism	262
5.4.1.1 <i>Homo</i>	262
5.4.1.1.1 conventional data.....	262
5.4.1.1.2 Fourier data	262
5.4.1.2 <i>Cercopithecus</i>	263
5.4.1.2.1 conventional data.....	263
5.4.1.2.2 Fourier data	264
5.4.1.3 <i>Colobus</i>	265

5.4.1.3.1 conventional data.....	265
5.4.1.3.2 Fourier data	266
5.4.1.4 <i>Gorilla</i>	267
5.4.1.4.1 conventional data.....	267
5.4.1.4.2 Fourier data	267
5.4.2 Shape Dimorphism	268
5.4.2.1 <i>Homo</i>	268
5.4.2.1.1 conventional data.....	268
5.4.2.1.2 Fourier data	268
5.4.2.2 <i>Cercopithecus</i>	269
5.4.2.2.1 conventional data.....	269
5.4.2.2.2 Fourier data	270
5.4.2.3 <i>Colobus</i>	271
5.4.2.3.1 conventional data.....	271
5.4.2.3.2 Fourier data	271
5.4.2.4 <i>Gorilla</i>	272
5.4.2.4.1 conventional data.....	272
5.4.2.4.2 Fourier data	272
5.5 Discussion.....	274
5.5.1 Size Dimorphism	274
5.5.2 Shape Dimorphism	275
5.5.3 Comparative Discussion	279
5.5.3.1 Proximal versus distal outlines	279
5.5.3.2 Conventional versus Fourier data	280
5.5.3.3 Comparison among genera	280
5.6 Conclusions	281

Chapter 6 General Discussion, Limitations of This Study and Areas for Further Research, and Concluding Remarks.....	282
6.1 General Discussion.....	282
6.1.1 Summary of Findings	282
6.1.2 Function	283
6.1.3 Body Size.....	286
6.1.4 Sexual Dimorphism	290
6.1.5 Phylogeny	293
6.2 Limitations of this Study and Areas for Further Research.....	293
6.2.1 Limitations of This Study	293
6.2.2 Areas for Further Research	294
6.3 Concluding Remarks	295
Appendix.....	297
References.....	408

Abstract

This study was performed to investigate the patterns of morphometric variation of the primate patella in cross-section, in an attempt to understand further the influences upon bone morphology. Specimens were selected from *Homo*, *Gorilla*, *Cercopithecus* and *Colobus*. These genera were chosen to investigate variation in patellar form in primates that are (1) bipedal and quadrupedal, (2) large and small, and (3) closely and distantly related. Therefore, there was the potential to uncover morphometric patterns that reflected such influences as function, body size, sex differences and phylogeny, and the aims of this study were formulated to investigate these influences. Variables chosen for this study were based on the patellar outline on cross-sectional computed tomography images: elliptic Fourier amplitudes, and also the outline perimeter length and the area contained within the outline.

Ordination using principal component analysis and cluster analysis showed continuous distributions of specimens, and it appeared that the bulk of intragenus variation was based on patellar size differences. Although cluster analysis showed patellae from *Homo* and *Gorilla* on one hand, and *Cercopithecus* and *Colobus* on the other, to be clearly separated, there was no clear separation among genera: specimens at extremes on PCA tended to be clustered with the next genus. Given the large disparities in average body weights for these genera, it was expected that patellar size would differ widely. This pattern was present in nonhuman primates; humans represented a deviation from this pattern, having large patellae relative to average body weight; it was likely that this was due to larger forces associated with bipedal locomotion. Principal component analysis showed that morphometric variables were correlated to varying extents; there were strong correlations between the conventional variables, so that the specimens were linearly arranged, with an effective reduction in phenotype space from two dimensions to one. Although the dimension of Fourier variables could be reduced, two dimensions were required, which was in part reflective of the dominance of two of the ten variables; only seldom was reduction to one dimension possible. An inference of geometric similarity was made in some cases; in other cases, size differences were associated with shape differences, but no clear pattern of shape differences was seen. Specimens within genera were found to show sexual size dimorphism. Occasionally sexual shape dimorphism was found, but not so that results could be related to an influential factor (function, for example). Published average body weights suggested that patellar size dimorphism was a reflection of body weight dimorphism.

Thus, patellar size differences dominated the picture of morphological variation, and this reflected genus body weight averages, although function also prevailed, and human patellae were large considering body weight averages for *Homo*. Clear sexual size dimorphism reflected body weight dimorphism, but results for shape dimorphism did not appear to reflect functional differences assumed to exist between smaller and larger individuals. Although size and shape differences did follow a pattern that did not contradict phylogenetic relations, this was also explicable in terms of body size and function.