

Anterior Knee Pain from the Evolutionary Perspective

Monk AP, Gill HS, Gibbons CLMH, Price AJ, Vollrath F, Rees JL, Murray DW

Abstract

Background

This paper describes the evolutionary changes in morphology and orientation of the PFJ using species present through our ancestry over 340 million years.

Methods

37 specimens from the Devonian period to modern day were scanned using a 64-slice CT scanner. 3D geometries were created following routine segmentation and anatomical measurements taken from standardised bony landmarks.

Results

Findings are described according to gait strategy and age. The adoption of an upright bi-pedal stance caused a dramatic change in the loading of the PFJ which has subsequently led to changes in the arrangement of the PFJ.

From Devonian to Miocene periods, our sprawling and climbing ancestors possessed a broad knee with a shallow, centrally located trochlea. A more rounded knee was present from the Paleolithic period onwards in erect and bipedal gait types (aspect ratio 0.93 vs 1.2 in late Devonian), with the PFJ being placed lateral to the midline compared to the medial position in quadrupeds. The depth of the trochlea groove was maximal in the Miocene period of the African ground apes with associated acute sulcus angles in Gorilla (117°) becoming more flattened towards the modern human (138°).

Conclusions

The evolving bipedal gait lead to anteriorisation of the patellofemoral joint, flattening of the trochlea sulcus, in a more lateral, dislocation prone arrangement.

Ancestral developments might help explain the variety of presentations of anterior knee pain and patellofemoral instability.

Introduction

Anterior knee pain (AKP) is common and remains poorly understood. AKP is the reason behind around 30% of all orthopaedic and sports medicine outpatient referrals, both for the native knee and following knee joint replacement [1, 2]. Despite musculoskeletal disorders representing an increasing global problem that account for one third of the entire burden of disability in the UK, much of the information available in contemporary knee literature regarding AKP and the PFJ is surprising and contradictory [2]. In many cases AKP is thought to be related to patellofemoral subluxation and instability [3], a condition for which there is no consensus for treatment with over one hundred described techniques for the surgical correction of patellofemoral dysplasia [4, 5]. With modern designs of knee replacement up to 20% of arthroplasty patients remain dissatisfied with the outcome, the PFJ being the leading source of complications [6, 7]. Despite this, there is no clear evidence to guide whether or not to replace the patellar articulating surface at operation [8-13]. Similarly, recent literature has suggested that neither PFJ degeneration as found at operation, or pre-operative AKP compromise the outcome of unicompartmental knee replacement (UKR), and therefore can largely be ignored [14].

Treatment strategies for patellofemoral joint problems must be based on a fundamental understanding of the PFJ, which currently does not exist.

The basic structure of the knee has been conserved for over 300 million years. The knee of all terrestrial tetrapods and bipeds is derived from the analogous structure of the sarcopterygian lobe-finned fish from the early Devonian period, 370 million years ago (Mya) [15, 16]. The earliest fossil evidence of a load-bearing knee is that of *Ichthyostega* (360 Mya), in which the femur, tibia and fibula are all present, with the bicondylar shape of the distal femur already evident [17]. This feature is common to all knees in the human lineage, but is qualitatively different between species with different locomotive strategies. The first traces of bipedalism can be seen around 6 million years ago, representing a key stage in human evolution, the result of multi-factorial selection pressures. The adoption of an upright stance greatly altered both the internal loading environment and the kinematics of the knee.

In humans, normal knee kinematics is the result of a complex interaction between joint surface morphology and soft tissue constraints. Hominin bipedal gait requires, in addition to loading in extension and flexion, loading during axial rotation of the knee, features not present throughout our non-bipedal ancestry.

Darwinian theory suggests that the process of natural selection has led to modern-day knee morphology having evolved to best suit its environment. However, this appears counter-intuitive considering the precarious, dislocation-prone arrangement of the human PFJ; with the trochlear groove orientated in valgus, being shallow and having a poor lateral buttress. To date, there has been no specific report to chronicle the changes that brought about the precarious arrangement of the modern human knee joint. Morphological analysis of the human lineage will highlight developmental trends that might be related to AKP.

Aim

This study set out to describe the evolution of the PFJ in terms of its changing *morphology* (trochlear depth and sulcus angulation) and *orientation* (medio-lateral and antero-posterior) by analyzing knee joints throughout human lineage to provide insights into anterior knee pain and patellofemoral instability.

Materials and Methods

A collaboration with the Smithsonian Institute (Washington DC), the Natural History Museums of London and Oxford, and the Department of Zoology, University of Oxford provided access to distal femora, including fossil and bony specimens from the Devonian, Triassic, Jurassic, Cretaceous, Miocene, Paleolithic, Pleistocene periods to the modern day. Specimens included amphibious reptiles (eg. Hellbender), dinosaurs, shrews, tupaiae, lemurs, African ground apes, Lucy (*A afarensis*), Turkana Boy (*H erectus*), *H neanderthalis* and modern man.

Gait Type	Specimen	Million Years Ago	Period	N
Sprawling	Cryptobranchus	340	Devonian	2
	Iguana tuberculata	310	Permian	2
	Varanus flavascens,			1
	Caiman crocodilus,			2
	Crocodylus porosus,			4
	Tupaia minor	70	Cretaceous	1
Climbing	Perodicticus potto	63 - 70		1
	Pachylemur insignis,			1
	Palaeopropithecus ingens			1
	Callithrix jacchus	40		1
	Pongo pygmaeus	14		1
Erect	Gorilla	7		2
	Pan troglodytes	6	Miocene	2
	Australopithecus aferensis	3.5		1
Bi-pedal	Australopithecus africanus	2	Paleolithic	1
	Homo ergaster	0.5		1
	Homo erectus	0.5		1
	Homo neanderthalis	0.3	Pleistocene	2
	Homo sapiens	0		10
			Total	37

Table 1: List of specimens organised chronologically.

As the interest for this analysis concerns the potential morphological changes associated with changing locomotion strategy specimens are broadly classified into four gait categories, namely sprawling, climbing, erect and bi-pedal; detailed in Table 1. The earliest locomotion methods shown by the reptiles involved movement primarily with both the hip and knee flexed (sprawling gait) [18]. Normal locomotion is slow and accompanied by very small excursions at the hip and knee joint, both of which remain essentially in a fixed flexion position and are dependent on lateral flexion of the spine. A notable exception is in the rare event of reptilian running, which demonstrates larger flexion and extension movements at the hip and knee.

The subsequent gait pattern of our arboreal ancestors (climbing gait) demonstrates a large range of motion at the knee joint utilised for climbing and jumping. When stationary the knee is predominantly held in flexion, allowing for ground foraging and rest, whilst at other times the hind legs are used for jumping and swinging, in combination with a well developed tail. To accommodate these movements, the range of movement at the knee joint is from full extension to approximately 160 degrees of flexion.

During the period of the African ground apes and the running monkeys, the knee is held in extension during static stance. Although these species are habitually quadrupedal, a considerable amount of time is spent 'erect' with the legs in full extension, due to their ability to walk upright for short periods.

By the time of the Australopithecines and subsequent hominins, the majority of the time is spent upright on both feet, and the 'bi-pedal' gait strategy is well established. At this stage, the knee functions as a weight-bearing, modified hinge joint.

Geometry Measurement

Computed Tomography (CT) data of each specimen was obtained using a 64 slice CT scanner (GE Light speed CT-1, GE Healthcare, Buckinghamshire, United Kingdom). Data sets were obtained using a helical scan with an inter-slice distance of 0.625 mm. Raw CT DICOM images were imported into MIMICS software (MIMICS Version 12.0.1, Materialise, Leuven, Belgium) for three dimensional reconstruction. Automated CT segmentation was performed to generate the three-dimensional (3D) geometries of the distal femur, Figure 1.

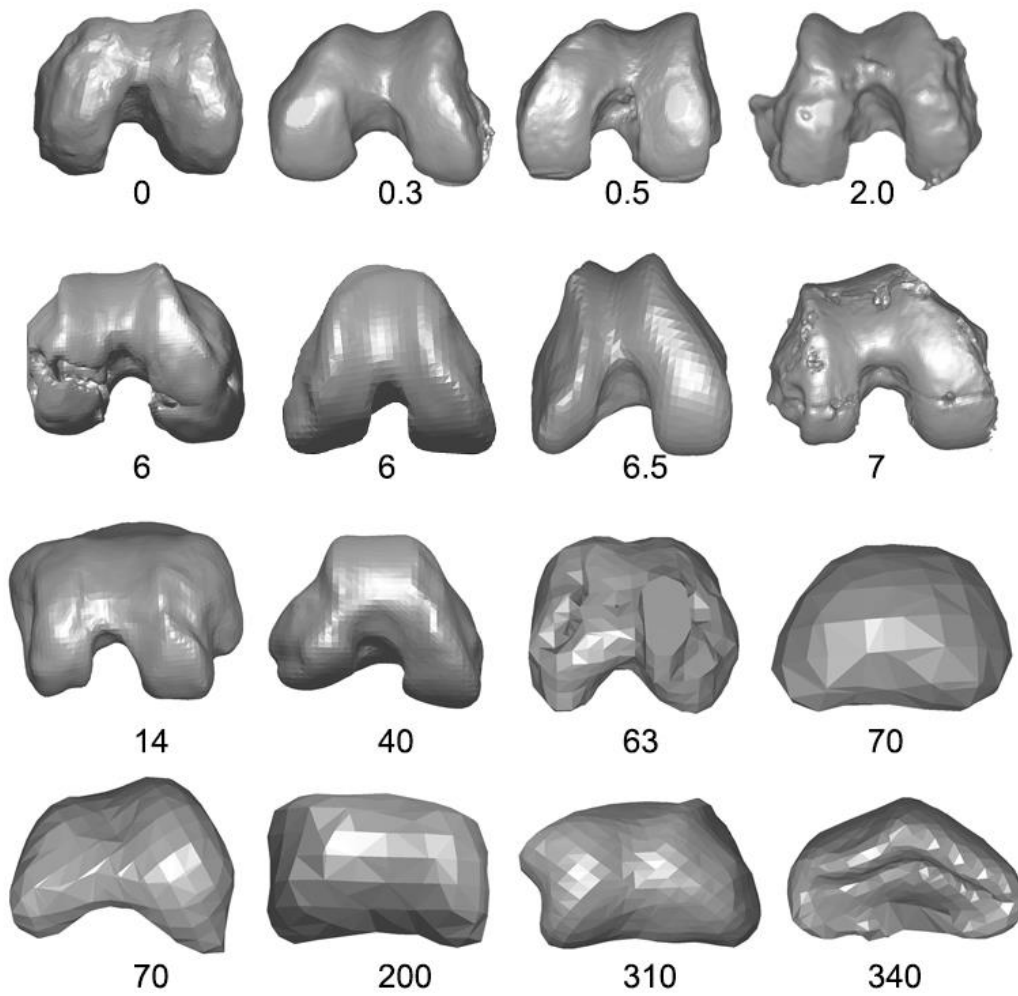


Figure 1: Showing examples of distal femora of selected specimens ordered in Millions of years of age.

Alignment

The distal femoral geometry for each specimen was aligned using 3D manipulation software, Geomagic (Geomagic Studio 11, Geomagic Inc., North Carolina, USA). All measurements were taken relative to a coronal plane defined using the medial and lateral (posterior) femoral condyles, and the shaft of the femur as shown in Figure 2a. Three points were defined using the centres of spheres fitted to the posterior articulating surface of the medial and lateral femoral condyles and the midpoint of the femoral shaft was used; centre of the femoral canal at an estimated height halfway between the proximal surface of the greater trochanter and the most distal part of the articular surface of the femoral condyles. The posterior femoral condyle boundary subtended a 90° arc beginning halfway between the anterior and posterior edges of the femur, to the most posterior extent of the posterior condyle [19] (figure 2).

A line drawn between the centres of the posterior condyles represented the posterior intercondylar line, PICL (Figure 2b).

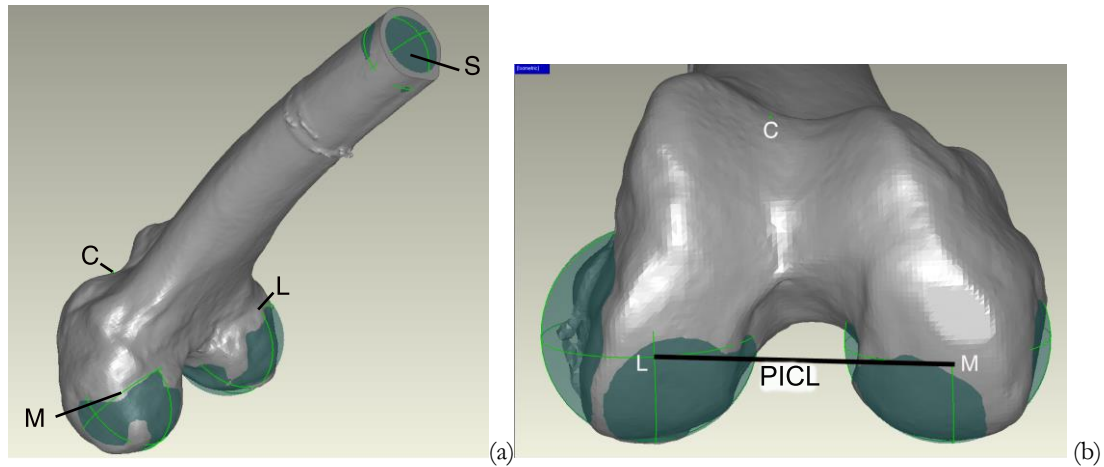


Figure 2: Oblique (a) and Distal (b) views of a Homo Neanderthal right femur. Showing spheres fitted to postero-medial (M); postero-lateral (L) condyles; midpoint of the femoral shaft (S); centroid of the femoral trochlea (C); and the posterior intercondylar line (PICL).

The centre of the trochlea (C) was represented as the centroid of all points on the 3D reconstructed mesh within the boundary of the femoral trochlea, Figure 3b.

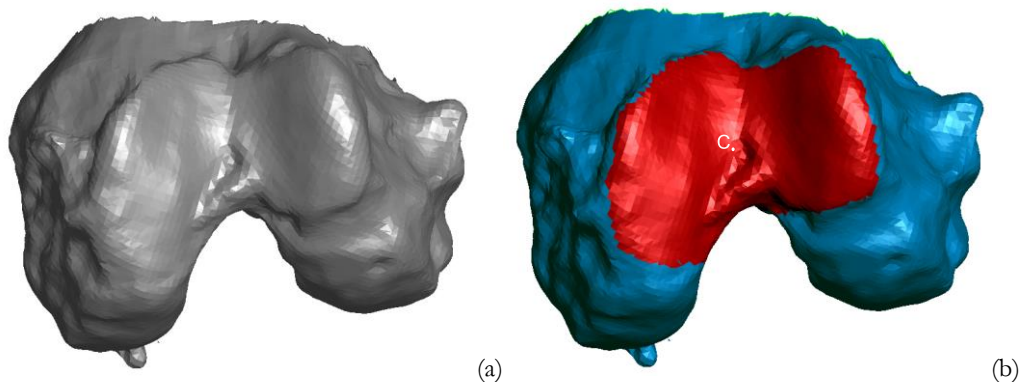


Figure 3: (a) Right distal femur of H. ergaster (b) showing the manually selected trochlear boundary (red) and automated centroid of the femoral trochlea (C).

Measurements

The evolution of patellofemoral joint was measured in terms of:

Evolving depth of the trochlea; measured as the ratio of depth of the trochlea to depth of the distal femur in the axial plane. Following alignment of the specimen, the depth of the trochlea was measured as the maximum AP distance from the most anterior point of the distal femur to the deepest part of the trochlear groove (A) and the depth of the distal femur was defined as the maximum AP distance occupied by the distal femur (B), shown in Figure 4.

Trochlear sulcus angles (S); the angle subtended by three points; the apex of the medial and lateral walls of the trochlea and the deepest part of the trochlear groove. This was measured at a height midway between the proximal trochlea and the roof of the intercondylar notch (Figure 5).

Displacements of the trochlea position throughout evolution; in the antero-posterior direction, (a) and medio-lateral direction, (b) (Figure 6).

Furthermore: the antero-posterior position of the trochlea (a) was defined as the aspect ratio of the perpendicular A-P distance from the posterior intercondylar line (PICL) to the centroid of the trochlea (C) / the length of the PICL. The medio-lateral position of the trochlea (b) was established as the horizontal displacement of the trochlear centroid. Using the trochlear centroid (C) and the two condylar sphere centres (M + L), a triangle was formed. The length of the lines CM and CL were calculated as the scalar Euclidean distances between the two points. The medio-lateral position of the trochlea was represented by the ratio of CM/CL, a value of greater than one representing a more laterally placed trochlea and a value of less than one, more medial.

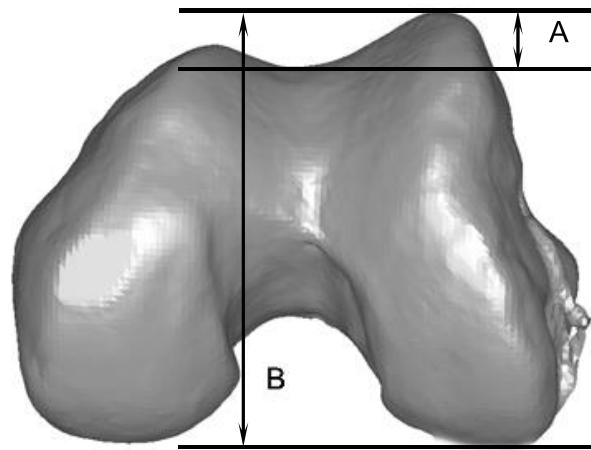


Figure 4: Showing measurements used for calculating the ratio of depth of trochlear groove (A) and depth of the distal femur (B). Ratio = A/B .

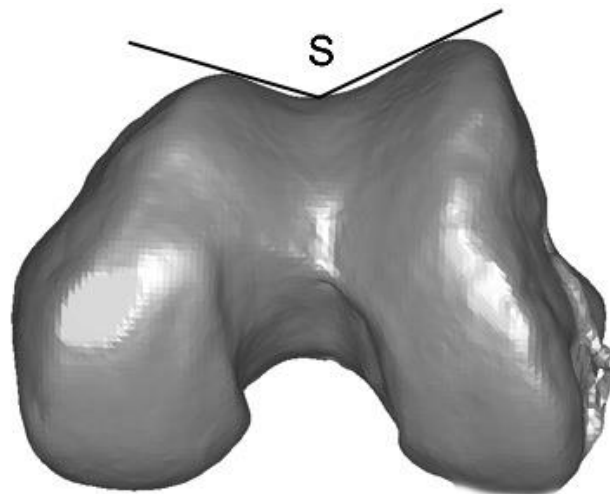


Figure 5: Showing measurement of sulcus angle, S.

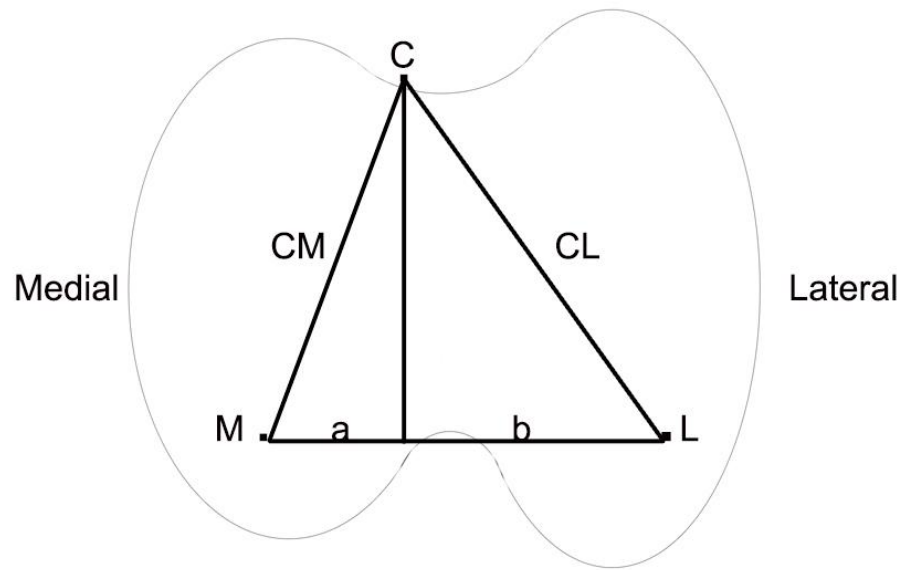


Figure 6: Showing measurements required to calculate displacements of trochlear groove. C = trochlear centroid, Posterior intercondylar line (PICL) is represented by the distance between the medial (M) and lateral (L) posterior condyles.

Measurement of sulcus angles for all specimens were repeated by two independent observers at two separate time points (two months apart). Inter-observer error was assessed using correlation coefficients.

Results

Inter-observer variability measured using correlation coefficients was 0.987 indicating excellent agreement.

Evolving depth of the trochlea: Figure 7 shows the change in depth of the trochlea relative to the depth of the distal femur through evolution. From the amphibious reptiles in the Devonian period (340-410 Mya) to the tree dwelling lemurs of the Eocene epoch (38-23 Mya), a shallow trochlea of less than one twentieth of the overall depth of the distal femur is seen. A change in trend is most distinct from the period of the African Ground Apes (14 Mya) through to the Miocene period of running monkeys (6 Mya), when the trochlea occupied around a tenth the depth of the femur. By the hominin era of the Pliocene period the depth was at its greatest, with the trochlea depth being around one third that of the distal femur, followed by a progressive shallowing, and anteriorisation to the present day depth of one tenth of the distal femur, roughly similar to the chimpanzee.

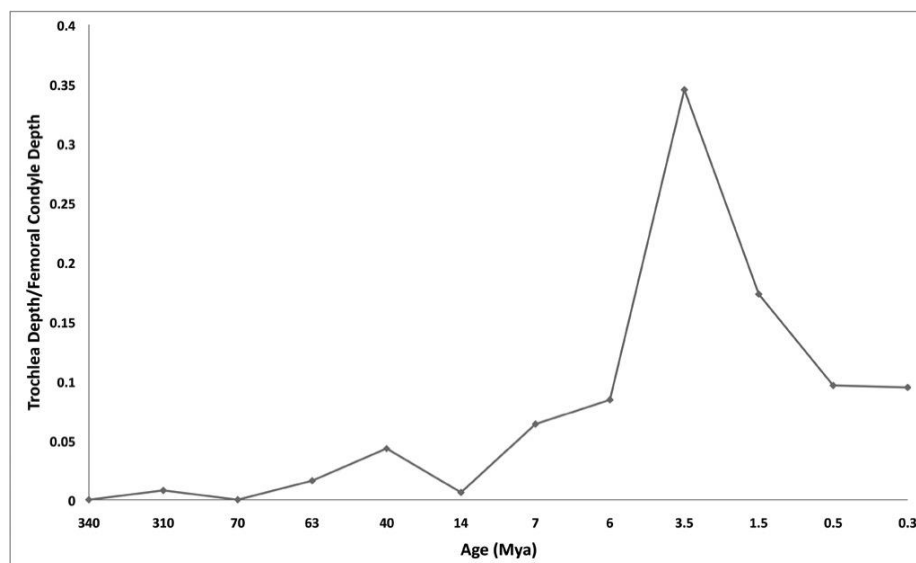


Figure 7: Showing the change in depth of the femoral trochlea relative to the maximum depth of the femoral condyle throughout evolution.

Sulcus angles: From the quadrupedal reptiles of the Devonian period (360 Mya) to the early lemurs of the Miocene period, the trochlea remained relatively flat with sulcus angles of 150 - 175°. A dramatic change can be seen during the time of human arboreal ancestors with orangutan, *Pongo Pygmaeus* (140°), followed by the gorilla (108°). This acute sulcus angle was maintained during the early homonins (3.5 Mya) of *A. Aferensis* (108°), *H. ergaster* (109°) and *H. erectus* (120°) before a flattening out to the current angulation in

H. sapiens of 138° (Figure 8).

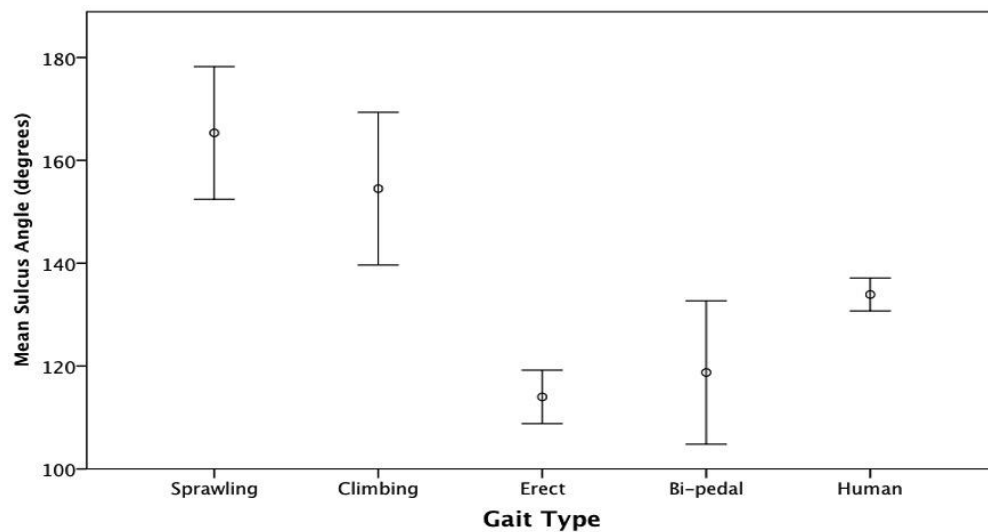


Figure 8: Showing the change in sulcus angle throughout evolution.

3D migration of the trochlea.

Antero-Posterior position of trochlea: Aspect ratios (Antero-Posterior depth / Width) for the distal femur are demonstrated in Figure 9. The trochlear centroid remained anteriorly placed (AP distance greater than Medio-Lateral) until the hominin era (4 Mya) when the trochlear centroid moved more posteriorly, as the knee shape changed from being elongated in the medio-lateral plane to a more rounded shape (and defined trochlea groove) with an aspect ratio roughly equal to 1 (Figures 7 and 9).

Medio-lateral orientation of trochlea: Despite starting with a laterally orientated trochlea in the Devonian period (360 Mya), the majority of human evolution was spent with either a neutral or medially placed trochlea (310 - 4 Mya). From the time of the earliest hominins (A.afarensis, 3.5 Mya) the trochlea moved to a more lateral position, peaking in the Pleistocene period before moving to the less lateral, present day position. Notable exceptions to the general trend include the lemurs (63 Mya), running monkeys (14-6 Mya) and the iguana, V.flavascens (13 Mya) (Figure 10).

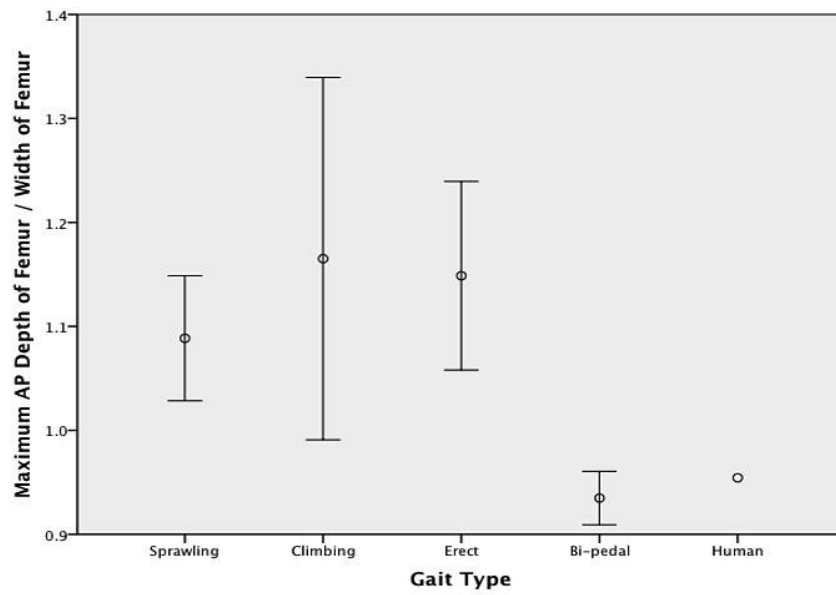


Figure 9: Showing the change in Antero-Posterior position of the trochlea throughout human evolution. A value greater than 1 represents an AP distance greater than the width of the distal femur.

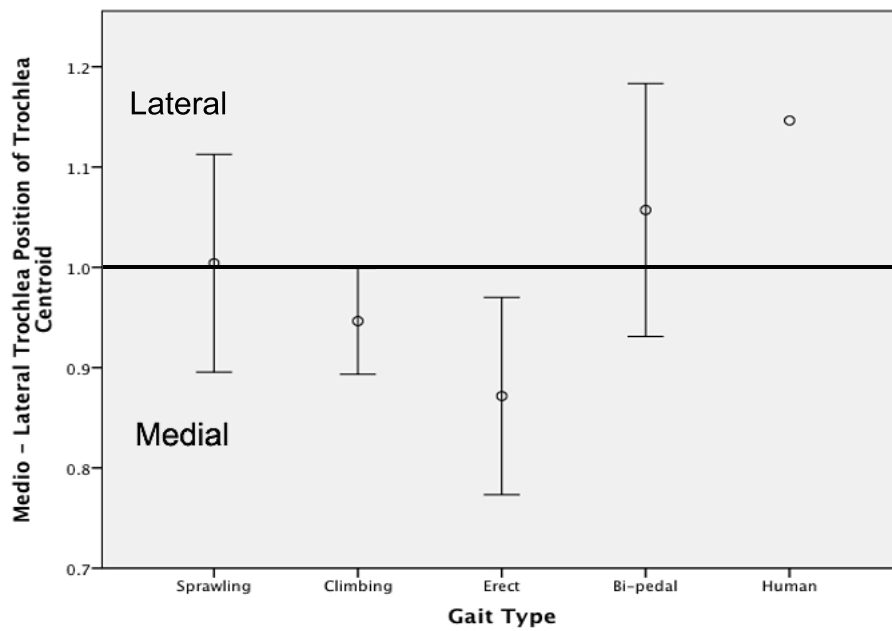


Figure 10: Showing the change in Medio-Lateral position of the trochlear groove throughout human evolution. A value greater than 1 represents a more lateral position; less than one, medial.

Discussion

The patellofemoral joint represents a source of pain and instability for many patients. From an evolutionary standpoint it is not clear whether these clinical entities are the result of inherited design from a previous gait strategy (sprawling/climbing) or a morphological adaptation from a recent ancestor. Whilst comparative anatomy studies have compared the overall knee structure between different species not restricted to the human lineage, to date no study has described the evolution of the PFJ in relation to PFJ pathology [15, 20]. Included here are various species, the ancestral origins of which span 400 million years, with their varying gait strategy including: sprawling, climbing, erect and bi-pedal. We have chronicled significant changes in the shape and orientation of the patellofemoral joint throughout human ancestry.

The earliest evidence of a patella is in tetrapods. Amphibians, reptiles and even some primitive tetrapods demonstrate upper leg muscles with a tendinous insertion to the proximal tibia [21]. The development of the trochlea however has followed a close association with gait type. During the time of our earliest ancestors (eg. *Cryptobranchus*, 340 Mya) the trochlea was shallow and flush with the anterior femur (with no patella). The sprawling gait of these amphibious reptiles rarely required extension beyond around 100° and these species demonstrate ‘semi-fixed flexion’ gait. By 13 Mya and the period of the African ground apes and running monkeys (gorilla, orangutan and chimpanzee), the trochlea is well formed and is accompanied by a bony patella. Interestingly, there is a similar arrangement to that of the apes shown 50 million years earlier demonstrated by certain species of lemur (with a cartilagenous patella), which is then not seen in intermediate species such as the marmoset and pongo. Of note in the cohort is the unique knee arrangement of the iguana, who has a PFJ which is more lateral, posterior and shallow compared to similar species with a sprawling gait, whose PFJ is characteristically medial and anterior. The explanation for this may lie in their unique gait strategies, which are in some ways akin to the hominin form [22]. The desert iguanas for example are traditionally considered to exhibit a sprawling gait pattern, but in reality are very able to sprint with full extension at the knee, a feature traditionally associated with bipedal gait. Similarly, the same trend seen in association with the lemurs (63 Mya) coincides with the appearance of a patella which most likely evolved to increase the lever arm to offset the enormous compressive stresses generated via the quadriceps tendon during the hyperflexed phase of leaping [23].

Offloading the PFJ reaction force

Throughout evolution, at certain key points, dramatic changes are noted in the development of the PFJ shape and morphology, which coincided with different loading environments within individual species. From a functional standpoint, the most poignant moment in our evolution was the adoption of upright stance and associated bipedal gait. With little or no weight bearing being performed by the arms, the entire body weight is carried through the hind limbs, through a total range of 130° flexion, and as a consequence the loading environment in the knee joint changed dramatically. The changing gait strategies from sprawling (through climbing) to erect species and the associated changes in the hind limb loading environment appear to be reflected in compensatory changes in PFJ morphology. We assert that the more recent bi-pedal adaptations have led to a compromise position. Early deepening of the trochlea groove seen with the great apes is seen to flatten more recently in hominins. This is likely to be due to the recent change in loading environment of the PFJ associated with bi-pedal gait. The deeper groove seen in the earliest erect species (gorilla and orangutan) is likely to reflect the requirement of increased knee stability in more 'top heavy' brachiates with proportionately larger forces being transmitted through the PFJ compared with later hominins. Subsequent species demonstrate flatter and more antero-laterally located PFJ. This is likely to represent an adaptation to avoid excessive load by improving the patellofemoral moment arm, a morphological compromise representing a trade-off between inherited design and current functional requirements.

Aspect ratios of the distal femur reveal that the shape of the distal femur (and proximal tibia) have changed from being triangular shaped to a more circular knee joint. Whilst there is no specific data regarding the development of the cruciate ligaments, it is likely that their influence on axial rotation altered the forces through the knee joint throughout the range of flexion. The cruciate ligaments would have caused a radial re-distribution of the line of action of the forces and over time, via altered biomechanics, created a more rounded knee. The key shift in trend towards the current human PFJ orientation was at the time of the African ground apes and especially, the gorilla. The gorilla, a habitual quadruped infrequently balances on two limbs, being top heavy with cumbersome arms. However, it is unique during this time in that a) it utilises a full range of movement at the knee from high flexion when seated to full extension during bipedal gait and b) is one of the earliest examples of periodic bipedal gait. It is at this point that this study has shown the deepest trochlear groove, with a sulcus angle of 109° , providing maximal stability whilst

accommodating loads being transmitted to the femur via the bony patella.

Lateralisation of the PFJ reaction force.

One of the striking changes associated with moving from quadrupedal to bipedal locomotion are the alterations in leg position required to support the centre of gravity throughout the gait cycle. During the swing phase, there is an adduction movement at the hip with the knee moving into a valgus posture, thereby pre-positioning the leg under the centre of gravity prior to the stance phase, a manoeuvre not required in the quadrupedal arrangement due to load sharing on the forelimbs. The associated loading of the PFJ with the bi-pedal valgus posture has created an increased resultant lateral force. Concurrently, since our first bipedal ancestors there has been a progressive lateralisation of the trochlea position, suggesting an 'evolutionary drift' over time. It follows that the associated anteriorisation of the PFJ is a consequence of providing a mechanical advantage for leg extension during lower limb weight bearing. Whilst the modern antero-lateral orientation of the PFJ is explicable through the trends of the data shown here, the resultant patellofemoral arrangement will inevitably render humans prone to lateral instability. It follows that patients suffering from anterior knee pain or painful subluxation, might be due in part to the increased lateral PFJ reaction force.

There are limitations with this study. Certain species in our study especially in the hominin group comprised only one sample, which clearly poses a limitation on any interpretation. Moreover, we did not know whether an individual represented a healthy specimen or perhaps suffered from a developmental abnormality, resulting in morphological dysplasia. Similarly, there was no indication of whether the specimen represented a young adult or elderly member of the species. Whilst the data tracking the centroid of the trochlea point towards a recent 'posteriorisation' of the trochlea during the hominin era, the actual position of the patellar tendon and quadriceps lever arm will be on the anterior aspect of the patella, which was not included in this study. Without patella specimens there can be no estimate of the extra distance from the bony trochlea to the patella tendon, which would include; trochlear cartilage; patellar cartilage and patella.

Conclusions

Human gait requires flexion, full extension and rotation necessitating a compromise of stability. It has required anteriorisation and lateralisation of the patellofemoral joint,

flattening of the trochlear groove and development of the cruciate ligaments to accommodate rotation. These alterations in position may have predisposed humans to AKP and PFJ kinematic abnormalities.

References

Uncategorized References

1. Butcher, J.D., et al., *Patient profile, referral sources, and consultant utilization in a primary care sports medicine clinic*. J Fam Pract, 1996. **43**(6): p. 556-60.
2. Murray, C.J., et al., *UK health performance: findings of the Global Burden of Disease Study 2010*. Lancet, 2013. **381**(9871): p. 997-1020.
3. Mehta, V.M., et al., *An algorithm guiding the evaluation and treatment of acute primary patellar dislocations*. Sports Med Arthrosc, 2007. **15**(2): p. 78-81.
4. Albuquerque, R.F., et al., *Appraisal of surgical treatment of 47 cases of patellofemoral instability*. Rev Hosp Clin Fac Med Sao Paulo, 2002. **57**(3): p. 103-7.
5. Xu, H., et al., *Arthroscopic medial retinacular imbrication for the treatment of recurrent patellar instability: a simple and all-inside technique*. Orthopedics, 2011. **34**(7): p. 524-9.
6. Rand, J.A., *Extensor mechanism complications following total knee arthroplasty*. J Knee Surg, 2003. **16**(4): p. 224-8.
7. Murray, D.W. and S.J. Frost, *Pain in the assessment of total knee replacement*. J Bone Joint Surg Br, 1998. **80**(3): p. 426-31.
8. Campbell, D.G., et al., *Patellar resurfacing in total knee replacement: a ten-year randomised prospective trial*. J Bone Joint Surg Br, 2006. **88**(6): p. 734-9.
9. Feller, J.A., R.J. Bartlett, and D.M. Lang, *Patellar resurfacing versus retention in total knee arthroplasty*. J Bone Joint Surg Br, 1996. **78**(2): p. 226-8.
10. He, J.Y., L.S. Jiang, and L.Y. Dai, *Is patellar resurfacing superior than nonresurfacing in total knee arthroplasty? A meta-analysis of randomized trials*. Knee, 2011. **18**(3): p. 137-44.
11. Li, S., et al., *Systematic review of patellar resurfacing in total knee arthroplasty*. Int Orthop, 2011. **35**(3): p. 305-16.
12. Mayman, D., et al., *Resurfacing versus not resurfacing the patella in total knee arthroplasty: 8- to 10-year results*. J Arthroplasty, 2003. **18**(5): p. 541-5.
13. Johnston, L., et al., *The Knee Arthroplasty Trial (KAT) design features, baseline characteristics, and two-year functional outcomes after alternative approaches to knee replacement*. J Bone Joint Surg Am, 2009. **91**(1): p. 134-41.
14. Beard, D.J., et al., *The influence of the presence and severity of pre-existing patellofemoral degenerative changes on the outcome of the Oxford medial unicompartamental knee replacement*. J Bone Joint Surg Br, 2007. **89**(12): p. 1597-601.
15. Dye, S.F., *Functional morphologic features of the human knee: an evolutionary perspective*. Clin Orthop Relat Res, 2003. **410**(410): p. 19-24.
16. Larson, R., *The Knee- the physiologic joint*. . The Journal of Bone and Joint Surgery. American 1983. **65**: p. 143-144.

17. Dye, S.F., *An evolutionary perspective of the knee*. J Bone Joint Surg Am, 1987. **69**(7): p. 976-83.
18. Lovejoy, C.O., et al., *Combining prehension and propulsion: the foot of Ardipithecus ramidus*. Science, 2009. **326**(5949): p. 72e1-8.
19. Monk, A.P., et al., *The shape of the distal femur: a geometrical study using MRI*. Bone Joint J, 2014. **96-B**(12): p. 1623-30.
20. Kingdon, J., *Lowly Origin*. 2nd Edition ed. 2003, Princeton: Princeton University Press.
21. Herzmark, M., *The Evolution of the Knee Joint*. J Bone Joint Surg Am, 1938. **20**: p. 77-84.
22. Irschick, D.J. and B.C. Jayne, *Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards*. J Exp Biol, 1999. **202 (Pt 9)**: p. 1047-65.
23. Jungers, W.L., F.K. Jouffroy, and J.T. Stern, Jr., *Gross structure and function of the quadriceps femoris in Lemur fulvus: an analysis based on telemetered electromyography*. J Morphol, 1980. **164**(3): p. 287-99.