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Hominin lower limb bones from Sterkfontein Caves, South Africa (1998–2003 excavations)

We describe late Pliocene and early Pleistocene hominin fossils from Sterkfontein Caves (South Africa), including two femoral specimens, as well as a partial tibia and a partial fibula. The fossils are likely assignable to *Australopithecus africanus* and/or *Australopithecus prometheus* and the morphology of each corroborates previous interpretations of Sterkfontein hominins as at least facultative bipeds.

Significance:

- A recent series of papers by our research team describes the morphology of a hominin skeleton from Sterkfontein Caves (South Africa), nicknamed ‘Little Foot’. Based on its unique skull morphology, R.J. Clarke, the skeleton’s discoverer, places it in the species *Australopithecus prometheus*, as distinct from the better-known and co-occurring *Australopithecus africanus*. Here we describe additional hominin thigh and leg fossils from Sterkfontein that, when considered in a comparative context, support the hypothesis that there was significant (probably interspecific) variation in South African hominin postcranial morphology during the late Pliocene and early Pleistocene.

Introduction

A long history of palaeoanthropological research at Sterkfontein Caves (Gauteng, South Africa), starting in 1936, has yielded a massive store of hominin fossils.^{1–5} As one in a series of papers, we report here on four previously undescribed hominin fossils excavated by R.J.C. between 1998 and 2003. Those other papers present descriptions and interpretations of sizeable samples of teeth⁶ and of axial and upper limb bones^{7,8}. The sample described here comprises fewer materials, representing two femur specimens, a partial tibia and a partial fibula. All four specimens preserve sufficient anatomy to indicate that the individuals from which they derived were bipeds, but more comprehensive functional interpretations of the fossils are limited by their fragmentary nature. Each also preserves taphonomic information that we report.

Two of the fossils derive from Member 4 of the Sterkfontein Formation, the site’s most hominin-rich deposit, which is probably slightly greater than 2.6 to around 2.5 million years old (Ma) (Figure 1).^{9–13} The other two are part of the Jacovec Cavern fossil assemblage, which includes a modest sample of hominin specimens, previously described by Clarke¹⁴. The original interpretation of the Jacovec stratigraphy identified several generations of cave fill, including three sedimentary units identified as ‘orange’, ‘brown’, and ‘stony’.¹⁴ More recent research demonstrates multigenerational infilling and reworking of the chamber’s sediments, which created several secondary deposits and a talus composed of orange and brown units.¹⁵ Dating of the Jacovec deposits is still in progress. Based on the presence of a fossil attributed to *Equus*, Kibii¹⁶ proposed a relatively young age of 2.34 Ma for the recovered faunal assemblage. However, Partridge et al.¹⁴ provided an age of 4.02 ± 0.27 Ma for orange sediments exposed on the chamber ceiling, which yielded a partial hominin cranium cataloged as StW 578. It is concluded that all hominin fossils thus far recovered from the chamber floor derive from this in-situ orange unit.^{14,15} Accordingly, we propose that until such time as multiple, stratigraphically associated, and dateable proxies contradict this radiometric date, it remains the best plausible estimate for the age of the Jacovec fossils. Based on craniocentral analyses, Clarke^{5,17–19} has argued for the presence of two coeval hominin species in Member 4: *Australopithecus africanus* and *Australopithecus prometheus*. Additionally, analysis of hominin teeth from Jacovec indicate that both taxa also occur in that deposit.

Methods

We provide information on each fossil’s spatial context, its relative completeness and condition, and its morphology and osteometrics. The legend to Figure 1 summarises the excavation coordinate system employed at Sterkfontein. As to condition, we recorded the degree to which a specimen suffered subaerial weathering, using Behrensmeyer’s²⁰ well-known weathering stage system, and noted its degree of staining by manganese dioxide. Bone surface modifications were also identified using 10x power magnification.²¹ All fractured bone surfaces were assessed with reference to the ‘angle formed by the fracture surface and bone cortical surface’^{22 (p.34)}. Typically, fracture angles on long limb bones that were created when the bone was ‘green’ (i.e. before significant loss of a bone’s organic fraction and its desiccation) are usually either acute or obtuse, while those created on dry long limb bones are usually right angles.^{22–24} We used Mitutoyo™ digital calipers to collect standard osteometric linear measurements and collected standard osteometric angular measurements with SPI™ 0–180° protractors.^{25–27} We followed recently published methods²⁸ in order to derive femoral neck anteversion on the single proximal femur specimen in the analysed sample.

Results

StW 598 (Jacovec Cavern)

This proximal left femur was described preliminarily by Clarke¹⁴. It is an exquisite specimen, stained uniformly by manganese dioxide but essentially unweathered (stage 0) and preserving the head and nearly half of the diaphysis (maximum length = ~153.0 mm) (Figure 2). The fossil is truncated distally along a relatively straight, right-angled breakage plane, indicating that the bone was leached of much, if not all, of its organic content when it was fractured.

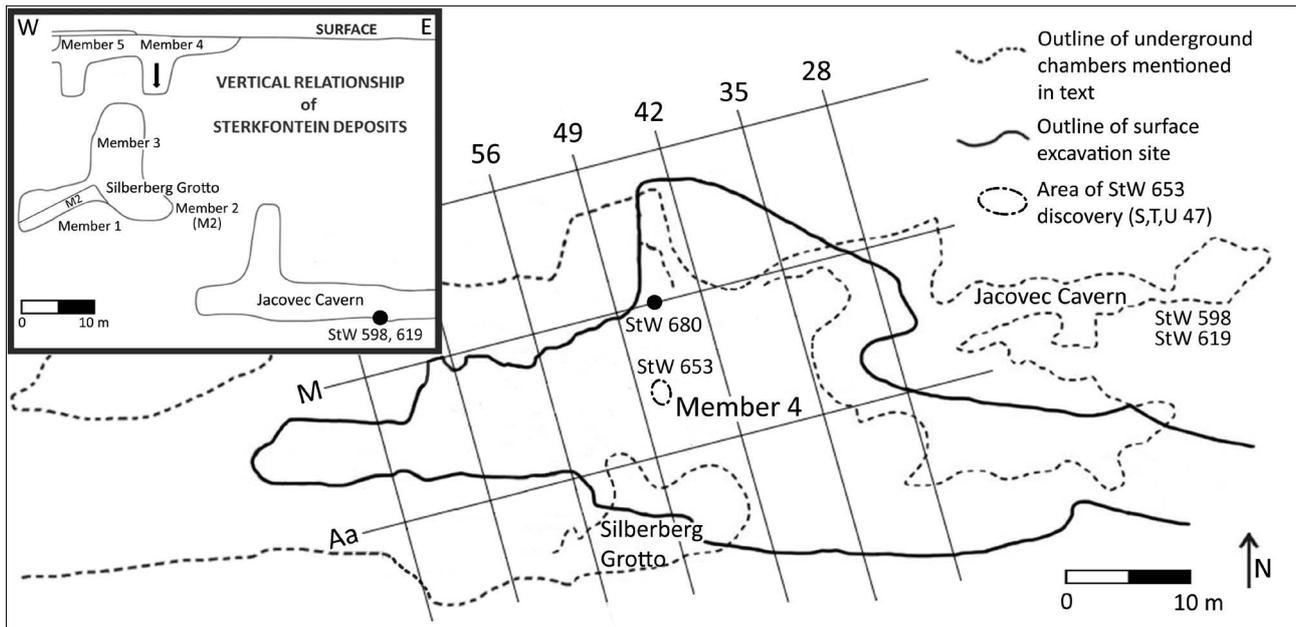


Figure 1: Composite plan view of the eastern portion of the Sterkfontein fossil site, with surficial deposits indicated by solid lines and underground deposits delimited by dashed lines (main image) (modified from Reynolds and Kibii⁶⁴ Figure 2 and references therein), and a schematic ~EW profile illustrating the vertical relationships of some of the site’s major deposits (inset) (modified from Clarke⁶⁵ Figure 6). All fossils described in this paper derive from Member 4 and Jacovec Cavern. Sterkfontein sediments are excavated in spits of 3’ x 3’ x 1’ volume under an alpha (NS coordinate)-numerically (EW coordinate) labelled grid; values in feet and inches listed in fossil specimen descriptions indicate depths below site datum.⁶⁶

Further, the fracture surface is partially coated by breccia, attesting to the antiquity of the breakage event that created it. A crack emanates from the middle of the anterior edge of this fracture surface and travels proximally, along the middle of the anterior surface of the diaphysis, for a length of ~80.0 mm. The crack is wider mediolaterally for its distal ~two-thirds than it is proximally. A similarly constructed longitudinal crack courses the middle of the posterior diaphysis (along the medial lip of the linea aspera), starting distally in the middle of the dorsal edge of the specimen’s distal fracture surface and terminating ~78.0 mm proximal to that point, near the junction of the base of the lesser trochanter and the proximal terminus of the pectineal line. Both cracks are infilled by breccia, which caused their mediolateral expansions, especially distally. Other ancient modification to StW 598 occurs at its proximolateral corner. Unlike the previously described incidences of damage, this alteration of the fossil was most likely inflicted when the bone was still fresh and its trabeculae were packed with nutritionally attractive red marrow and grease. The crenulated surface³ of the base of the largely missing greater trochanter, as well as several deeply invasive tooth gouges in the exposed trabeculae at the anterolateral portion of the distal margin of that damaged surface, indicate that the trochanter was chewed away by a prehistoric carnivore(s). This carnivore-inflicted damage continues superomedially across the anteroproximal femoral neck, where several layers of lamellae were peeled away in a dorsoventrally wide strip (maximum width = ~14.0 mm) that terminates ~11.0 mm from the superior rim of the femoral head. The head of StW 598 is small and spherical, with a relatively large fovea capitis that is placed dorsally on the medial aspect of the joint surface (Table 1). The fovea capitis is deep, with a superior and dorsal margin that is contiguously sharply raised. The femoral head is hafted to the bone’s diaphysis at a neck-shaft angle of 121°, via a mediolaterally elongated and anteroposteriorly compressed neck (Table 1). StW 598 has a fairly marked femoral anteversion angle of 102° (Figure 3). The obturator externus groove of the specimen is not palpable superiorly and just barely so dorsolaterally. Likewise, the specimen’s intertrochanteric crest and intertrochanteric and spiral lines are underdeveloped. In contrast, the fossil shows a small but robust, superoinferiorly elongated (maximum superoinferior length = ~16.3 mm; maximum mediolateral width = ~10.4 mm) lesser trochanter, a well-developed pectineal line and an especially rugose gluteal tuberosity.

The lesser trochanter projects slightly medially beyond the medial margin of the proximal diaphysis, so that it (the tubercle) is just visible when viewing the anterior aspect of the bone. The gluteal marking is a well-developed, posterolaterally placed ridge that merges with the pectineal line ~49.0 mm distal to the inferior margin of the lesser trochanter, at a small, distally opening nutrient foramen, to form the superior terminus of the mediolaterally broad linea aspera. Viewed medially or laterally, the subtrochanteric diaphysis appears relatively flat anteriorly (especially proximally) and only slightly more convex posteriorly, forming a gentle posterolaterally placed angle along the course of the linea aspera (Table 1). The shaft cross-section is roughly circular at the distal fracture edge, with an anteroposterior diameter of 20.5 mm and mediolateral diameter of 21.1 mm at that level (these dimensions are uncorrected for the slight mediolateral gaps in the antero- and posterodistal diaphysis described above). The thickest portion of the cortex at this natural fracture surface is posteriorly, at the position of the linea aspera (7.4 mm). Because the diaphyseal midpoint cannot be determined precisely on the broken specimen, we cannot report a pilasteric index (midshaft anteroposterior diameter divided by midshaft mediolateral diameter, multiplied by 100²⁹). However, an index of 97 is calculated using these measurements taken from the distalmost edge of the fossil.

StW 619 (Jacovec Cavern)

This partial distal epiphysis of a left femur is heavily mottled by deposits of manganese dioxide but shows little subaerial weathering (stage 0) (Figure 4). All areas of damage on the fossil are ancient, as evidenced by the fact that the exposed trabeculae are smoothed and polished and are filled by red cave sediments. The specimen is broken proximally, along a relatively straight transverse plane, at the inferior margin of the distal metaphysis. The edge of this fracture surface is roughly right-angled for its entire circumference; two short but deep, probable carnivore, tooth scores emanate in an inferoanterior direction from the medial margin of this fracture edge. Most of the lateral condyle and lateral epicondyle of StW 619 are missing, although much of a roughened impression for the lateral head of the gastrocnemius is preserved. The lateral patellar lip of the specimen is broken away laterally and proximally but it is obvious from an inferior view that the lateral lip projected significantly anteriorly (Figure 4). The region of the lateral meniscal groove is missing.

Table 1: Metric comparisons of South African early hominin proximal femora^a

Specimen/ Taxon	Head SI (mm)	Neck SI (mm)	Neck AP (mm)	Neck shape ^b	Neck length (mm)	Subtrochanteric diaphysis AP (subAP) (mm)	Subtrochanteric diaphysis ML (subML) (mm)	Meric Index ^c
MLD 46 ^d	[38.4]	30.1	19.8	65.8	36.5	–	–	–
SK 82 ^e	34.4	27.2	19.2	70.6	41.7	24.8	30.4	81.6
SK 97 ^e	37.1	26.2	19.6	74.8	46.8	23.3	35.3	66.0
SK 3121 ^e	28.6	19.1	16.0	83.8	–	–	–	–
SKW 19 ^e	30.2	–	–	–	–	–	–	–
SWT1/LB-2 ^e	34.4	25.9	17.7	68.3	35.3	–	–	–
Sts 14 ^d	–	22.6	13.4	59.3	–	–	–	–
StW 25 ^d	[31.3]	[22.9]	–	–	–	–	–	–
StW 99 ^d	[34.6]	29.6	18.5	62.5	[49.9]	–	–	–
StW 311 ^d	35.8	26.4	20.5	77.7	–	–	–	–
StW 392 ^d	31.4	[21.4]	–	–	–	–	–	–
StW 403 ^d	–	24.9	17.3	69.5	–	–	–	–
StW 479 ^d	–	[23.5]	17.7	75.3	–	–	–	–
StW 501 ^d	[31.8]	[23.8]	[16.5]	69.3	–	–	–	–
StW 522 ^d	30.8	20.9	15.5	74.2	31.3	–	–	–
StW 527 ^d	[33.3]	–	–	–	–	–	–	–
StW 598	32.1	25.5	16.5 ^f	64.7	40.4	20.2	22.3	90.6

^aStandard linear measurements from McHenry and Corruccini²⁷. Abbreviations: SI = superoinferior; AP = anteroposterior (all SIs and APs are diameters); MLD = Makapansgat Limeworks Dump (South Africa); SK, SKW and SWT1/LB = Swartkrans (South Africa); Sts and StW = Sterkfontein. Measurements in brackets are estimates; dash in a cell indicates that the measurement was unobtainable.

^bNeck shape = neck AP divided by neck SI, multiplied by 100.

^cMeric index = subAP divided by subML, multiplied by 100.

^dHead SI, neck SI, neck AP and neck length values from Harmon⁴⁶.

^eHead SI, neck SI, and neck AP values from Pickering et al.⁶⁷; subAP and subML values from Robinson⁹⁰.

^fUncorrected for missing cortical bone on anteroproximal aspect of neck.



Figure 2: The StW 598 hominin left proximal femur from Jacovec Cavern, Sterkfontein, shown in, from left to right, superior view (anterior facing up) and anterior, medial, posterior, and lateral views (superior facing up in all views). Bar scale = 1 cm.

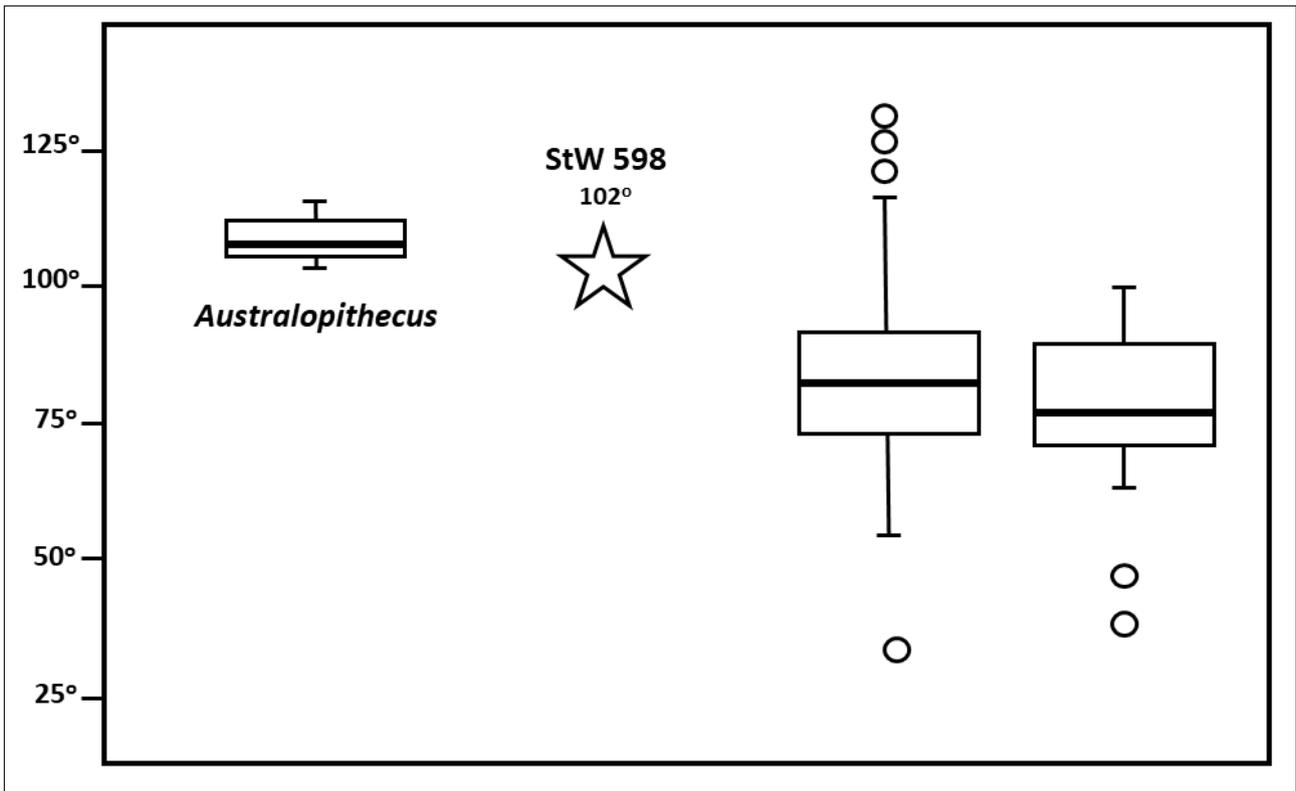


Figure 3: Head/neck anteversion of the StW 598 proximal femur from Jacovec Cavern, Sterkfontein, compared to that of other *Australopithecus* and extant hominoid femora. Modified from Marchi et al.²⁸ Figure 23. The box-and-whisker plot shows the median (dark horizontal line), upper and lower quartiles (boxes), range (whiskers), and outliers (circles). Comparative data from Marchi et al.²⁸: *Australopithecus* specimens include A.L. 288-1 and A.L. 333-95 (Hadar, Ethiopia), StW 99 (Sterkfontein, South Africa), and MH1 (Malapa, South Africa).

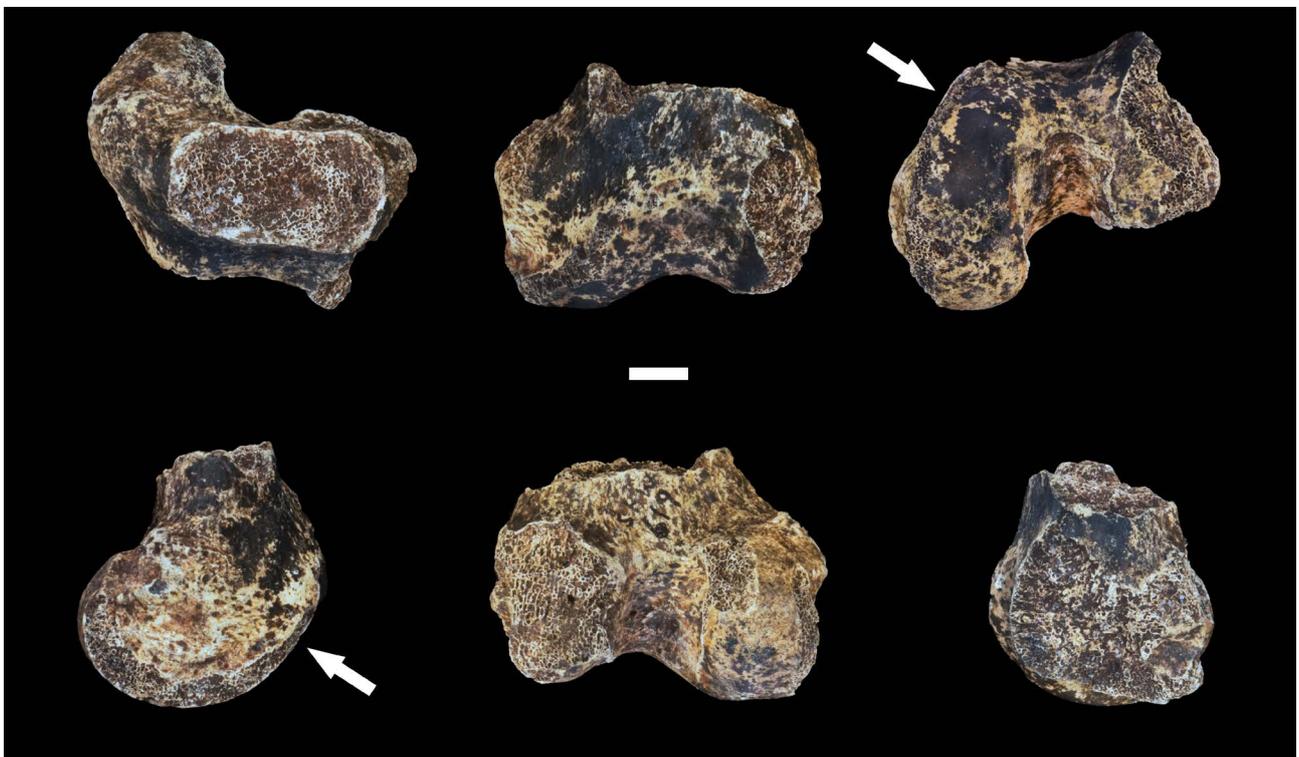


Figure 4: The StW 619 hominin left distal femur from Jacovec Cavern, Sterkfontein, shown in superior (posterior facing up), anterior (superior facing up), and inferior (anterior facing up) views (left to right, top row), and in medial, posterior and lateral views (superior facing up; left to right, bottom row) Arrows indicate the estimated position of the medial meniscal groove. Bar scale = 1 cm.

Several areas of the medial condyle are also eroded, including the entirety of its superior border from that feature's anterior point of connection with the medial patellar lip to its dorsal termination. This arc of damage extends laterally into the region in which the medial meniscal groove was positioned, obliterating the medial extent of that feature. We are, however, able to discern what we judge to be the lateralmost extremity of the groove as indicated by arrows in Figure 4. This probable groove remnant is quite shallow. StW 619 lacks a well-developed medial condylar boss. The distal medial condyle does not drop appreciably inferiorly dorsal to the presumed meniscal groove; instead, the distal medial condyle is fairly smooth across its extent, except for a low and mediolaterally narrow, anteroposteriorly elongated elevation along the length of its lateral edge. The adductor tubercle of StW 619 projects only modestly in superior direction, away from the solid mass it forms in connection medially with the blunt, strongly projecting medial epicondyle. In medial view, the medial condyle is elliptical in shape. Maximum (non-anatomical; taken mediolaterally) linear length of StW 619 is 55.5 mm. In general form and size, StW 619 is very similar to Sts 34 and TM 1513 – two hominin distal femora from Sterkfontein Member 4 that also preserve medial condyles (Table 2).³⁰

Table 2: Metric comparisons of hominin distal femora (preserving medial condyles) from Sterkfontein^{a,b}

Femur specimens			
Standard linear measurement	Sts 34	StW 619	TM 1513
Anteroposterior diameter of the distal shaft	29.0	25.5	27.5
Anteroposterior diameter of the medial condyle	45.5 ^c	[43.0]	[45.0]
Mediolateral (transverse) diameter of medial condyle	–	[20.0]	[22.1]
Condylar notch width	16.7 ^c	[13.5]	13.4 ^d

^aStandard linear measurements from McHenry and Corruccini²⁷. Sts and StW = Sterkfontein; TM = Kromdraai (South Africa).

^bAll measurements in mm; measurements in brackets are estimates; dash in a cell indicates that the measurement was unobtainable.

^cAgrees with measurement in Robinson³⁰.

^dDisagrees with measurement in Robinson³⁰ (12.4 mm), which was taken anteriorly (contra recommendation in McHenry and Corruccini²⁷).

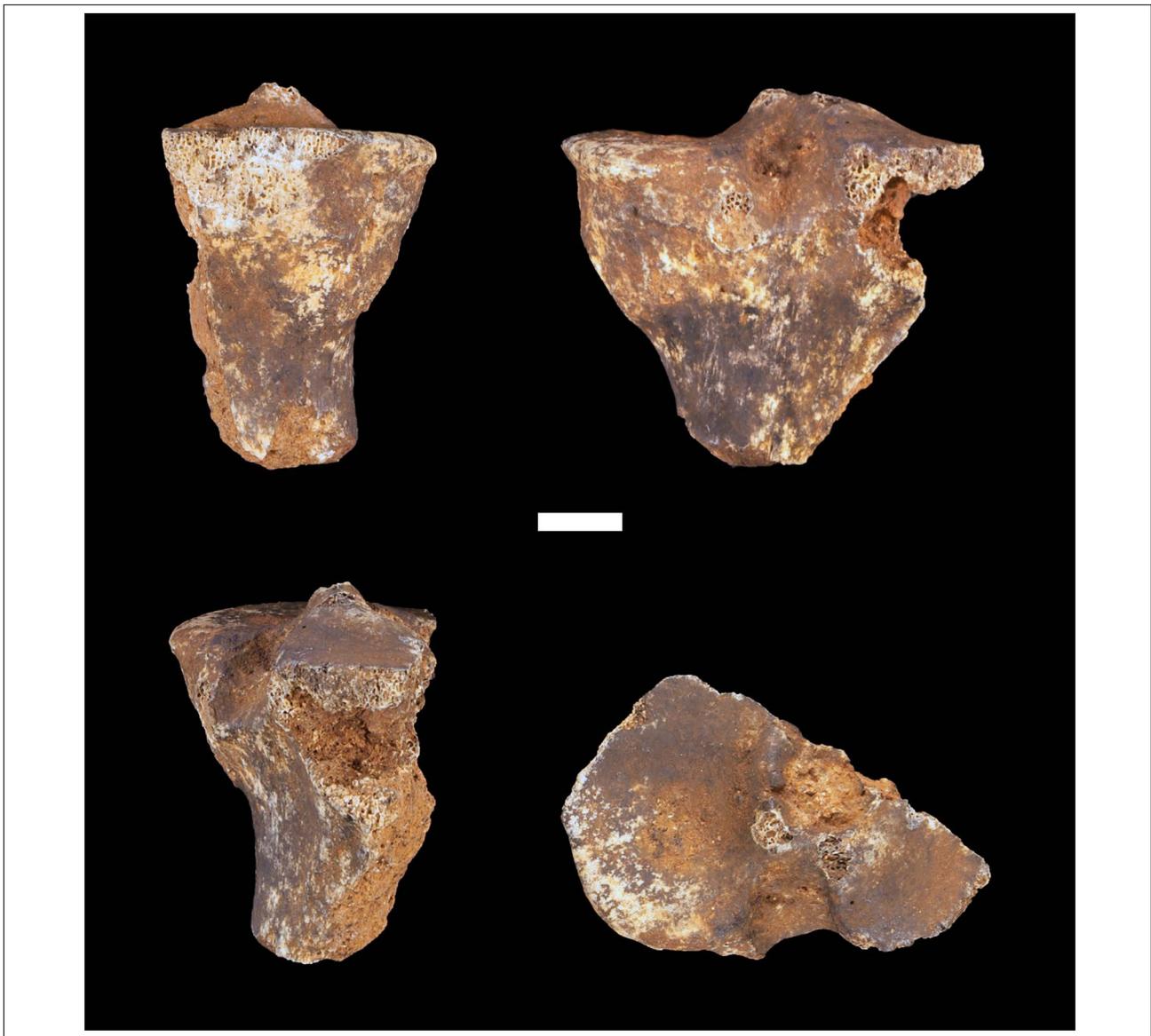


Figure 5: The StW 653 hominin right proximal tibia from Sterkfontein Member 4 shown in medial and posterior views (superior facing up in both; left to right, top row) and in lateral (superior facing up) and superior (anterior facing up) views (left to right, bottom row). Bar scale = 1 cm.

StW 653 (Member 4, mixed S,T,U/47)

This partial proximal epiphysis and extreme proximal metaphysis of a right tibia is well stained by manganese dioxide and is unweathered (stage 0) (Figure 5). Its maximum length is mediolateral at 49.7 mm. The anterolateral aspect of the specimen is missing and the exposed trabeculae in that area are filled with lightly calcified breccia. Dorsolaterally, the specimen's proximal end preserves damage reminiscent of ragged edge chewing imparted by carnivores (cf. Brain³), but there is no independent indication of feeding damage on the rest of the specimen in the form of tooth scores or pits. The distal fracture surface of StW 653 is obscured by adhering breccia but appears to be right-angled.

Most of the medial condyle of StW 653 is still intact, as is the approximate dorsal third of the lateral condyle. The medial condyle is dorsoventrally elongated (estimated anteroposterior diameter = 34.5 mm; estimated mediolateral diameter = 22.5 mm) and slightly concave, bounded by a blunt but superiorly projecting rim dorsomedially (the rest of the rim is missing so we cannot comment on its original form). The concavity of the medial condyle is accentuated by the acute manner in which the medial intercondylar tubercle rises from it superiorly. The intercondylar eminence and the posterior and most of the anterior intercondylar areas are also preserved, as is the lateral intercondylar tubercle. The last falls less severely distolaterally toward the lateral condyle than does the medial intercondylar eminence fall distomedially toward the medial condyle. The superior apices of both intercondylar eminences are chipped, exposing their underlying trabeculae. The small portion of lateral condyle is convex dorsally, appears moderately concave ventrally, and is positioned more superiorly than is the medial condyle; its dorsomedial corner appears to be marked by a small 'meniscal notch' (cf. Tardieu³¹). In sum, the morphology of the tibial plateau is reminiscent of those of 'typical' modern human tibiae. Distal to the plateau, the proximolateral branch of the soleal line shows a degree of development that is also comparable to those of modern human tibiae; the groove for the semimembranosus is humanlike in morphology (i.e. deep and circular ventrally; superoinferiorly shorter and anteroposteriorly elongated dorsally) and position, immediately at the base of the dorsomedial corner of the medial condyle. The attachment area for the medial collateral ligament is very rugged, projecting strongly medially from the proximal metaphysis, inferior to it.

StW 680 (Member 4, M/46 18'5'–19'5')

This partial diaphysis of a hominin fibula, measuring 84.3 mm in maximum length, is well stained by manganese dioxide but is unweathered (stage 0) (Figure 6). It lacks surficial tooth scores or pits, but one of its ends terminates in an irregular break reminiscent of carnivore-induced ragged-edge chewing. This end is densely packed with trabeculae, indicating that it is metaphyseal. This region lacks a diagonal curve of an anterior border or crest toward the position of a lateral malleolus, as would be predicted for a distal fibula portion. Accordingly, we conclude that this part of the specimen is from the proximal end of the bone. Superiorly, the cross-section of the fossil is roughly triangular, with two sides of the triangle being slightly convex and divided by a low ridge, while the third side is flat-to-concave, and bounded on each side by sharply defined crests. When viewed in standard anatomical position, the lateral and posterior sides of a typical hominin fibula are convex, while its medial side, lying between well-defined crests, is concave. Following this understanding, it is clear that StW 680 is a left fibula. In addition, the specimen compares favourably to two other hominin left fibulae from Sterkfontein, StW 356 (Member 4) and StW 573 (Member 2).

The distal termination of the specimen is spiral but its fracture edge is right-angled, indicating that the break was probably induced by static loading (e.g. sediment compaction) and when the specimen was at least partially degreased. Its diaphysis is more robust than those of the two other Sterkfontein fibula mentioned above, and its fibular neck is round in cross-section. Martin and Saller²⁶ recommend that diameters of the fibular neck be taken at that feature's smallest circumference. Following that guideline, the anteroposterior diameter of the neck of StW 680 is 11.0 mm and its mediolateral diameter is 10.5 mm. Distal to the neck,

the medial and lateral surfaces diverge from each other at an acute angle formed by a low anterior border that is more elevated (i.e. anteriorly projecting) distally than it is proximally; the medial surface is flat proximally to very slightly concave distally for its preserved length, while the lateral surface bulges convexly for most of its length superiorly along a rounded ridge and is flat inferiorly. The posterior border, for its whole length, takes roughly the same rounded form as the lateral surface. In contrast, the interosseous border is sharp but still does not project all that markedly from the main body of the diaphysis.



Figure 6: The StW 680 hominin left fibula from Sterkfontein Member 4 shown in, left to right, posteromedial and lateral views (superior facing up). Bar scale = 1 cm.

Discussion

Neotaphonomic research, utilising modern baboon carcasses as proxies for early hominin cadavers, shows that the knee joint is especially susceptible to destruction by feeding carnivores.³² In this context, it is worth mentioning that taphonomic studies have also concluded that carnivores played at least some role in the creation of the hominin fossil assemblages from Sterkfontein Member 4 and Jacovec.^{4,7,14} We also note the following general characteristics of the South African hominin fossil record: proximal femora are more common than are distal specimens; proximal tibiae are rarer than are distal specimens; and, fibular specimens of any completeness are exceedingly exceptional.²⁻⁵ In sum, it thus seems especially fortunate that the chewed (and possibly chewed) thigh and leg specimens described here survived to become part of the Sterkfontein fossil record.

Member 4 fossils

Bipedalism is a defining hominin characteristic and the knee obviously plays a central role in mammalian locomotion, so it is no surprise that palaeoanthropologists have paid particular attention to that joint. More specific to Sterkfontein, Berger and Tobias³³ claimed that the anteroposterior convexity of the lateral condyle of StW 514a, a hominin proximal tibia from Member 4, as well as the fossil's lack of

a ‘meniscal notch’ might indicate that (at least one) *Australopithecus* at the site locomoted in a ‘chimpanzee-like’ manner. However, a study that compared digital, three-dimensional surface areas of the lateral tibial condyles of various extant African hominoids, South African *Australopithecus*, and East African *Australopithecus afarensis* to two-dimensional surface area and arc and chord length measurements of the same feature concluded ‘that tibial condylar curvature is a weak discriminator of locomotor variation in extant, and presumably fossil, hominoids’^{34(p.124)}. Further, Tardieu³⁵ showed earlier that the lateral condyles of other early hominin tibiae – none of which would otherwise be characterised as ‘chimpanzee-like’ – also lack notches; more recently, the absence of lateral condylar notches has even been documented in some tibiae of fully bipedal modern humans.³⁶ Zipfel and Berger³⁷ acknowledged these observations in a study comparing StW 514a to another hominin proximal tibia from Sterkfontein Member 4, StW 396, but still emphasised, as did Berger and Tobias^{33(p.343)} before them, that the semimembranosus attachment site of StW 514a ‘forms a marked circular depression situated on the posteromedial margin of the condyle immediately below the medial condylar surface’, implying that this enthesis morphology is distinctly chimpanzee-like. Our own observations of modern human tibiae disagree with this insinuation; in our experience, many modern human tibiae show large, strongly indented semimembranosus attachment sites with distinct borders, such as is illustrated in Figure 7. In sum, it thus seems that the StW 541a is not, in fact, particularly ‘chimpanzee-like’, but instead simply expresses a combined morphology that falls within the bounds of normal variation for hominin tibiae.



Figure 7: An approximate medial view of a modern human right proximal tibia showing a large, strongly indented and circular attachment site (circled), with a well-defined border, for the semimembranosus, contradicts the suggestion³³ that such morphology for that attachment site is uniquely ‘chimpanzee-like.’

The same is true of StW 653, the new Member 4 hominin tibia described here, which compares quite favourably to not only other *Australopithecus* tibiae but also to those of modern humans. For example, the new fossil’s strongly developed soleal line accords with those of fully bipedal modern humans. In no way does this suggest that StW 653 should be assigned to the genus *Homo*, but instead confirms the conclusions of others who question the efficacy of using certain morphological features to place early hominin tibia fossils into particular genera and/or species (see for example Dugan and Holliday³⁶).

In contrast, the new StW 680 fibula from Member 4 differs markedly from those of modern humans and is instead more like those of extant African apes and also compares favourably to the Sterkfontein *Australopithecus* fibula fossils, StW 356 and StW 573. It possesses a generally triangular neck and has a high neck robusticity index (mediolateral diameter/anteroposterior diameter *100)²⁸ of 95.4, compared to a mean for two other *Australopithecus* proximal fibulae of 95.7 and a mean for 23 modern human fibulae of 81.8±16.6 (range = 52.6–111.5) (comparative data from Marchi et al.²⁸). Moreover, the shape of the origin for the peroneus longus is convex, like those of other early hominin fibulae, including especially those attributed to *Australopithecus*, but unlike the origin on modern human fibulae.²⁸

Jacovec fossils

As first noted by Clarke¹⁴, in possessing a relatively small head and long neck, StW 598 resembles SK 82 and SK 97³⁰ – proximal femur fossils from Swartkrans (South Africa) that are usually assigned to *Paranthropus robustus*. StW 598 also resembles StW 99, a large femur specimen from Sterkfontein that is usually attributed to *Australopithecus*, but that – given its morphological continuity with the Swartkrans *Paranthropus* femur fossils and its possible origin from the *Paranthropus*-bearing Member 5 unit of the Sterkfontein Formation¹³ – is likely actually also *Paranthropus* (Table 1). With its long neck, StW 598 is, however, very similar to definitive *Australopithecus* femur specimens, StW 479 and StW 367, from Sterkfontein Member 4. StW 598 and StW 367 are, in fact, so similar that upon their cursory comparison, one could understandably conclude that the fossils are antimeres. Further detailed observations prove that conclusion erroneous, but the salient point made is that the morphology of StW 598 is not unique in the hominin fossil record. Adding to the comparative complexity, StW 522, a presumptive *Australopithecus* femur from Sterkfontein, shows a small head and short neck (Table 1).¹⁴

StW 598 has a remarkably high meric index of 90.6 (Table 1), compared to a mean meric index of 74.8±3.5 (range = 66.4–81.7) for 18 South and East African *Australopithecus* and *Paranthropus* femora.²⁸ The cause(s) of femoral shaft shape remain hypothetical, but biomechanical explanations include reference to the influences of both the vasti and gluteal complexes. However, the meric index ranges of both knuckle-walking African apes (mean meric index of 42 *Pan troglodytes* femora = 85.0±5.5 [range = 71.1–95.5]; mean meric index of 47 *Gorilla gorilla* femora = 83.2±4.0 [range = 76.5–93.8]²⁸) and terrestrial bipedal modern humans (mean meric index of 195 *Homo sapiens* femora = 80.8±6.8 [range = 56.1–96.6]²⁸) not only overlap but also encompass the index value of StW 598. Thus, we are currently reluctant to extrapolate any functional interpretations of the fossil based on its round diaphyseal cross-section.

Likewise, although the position and narrow, ridge-like form of StW 598’s gluteal entheses suggest a relatively humanlike insertion of its gluteal musculature³⁸, without a preserved greater trochanter, it would be unwise to place too much explanatory emphasis on that muscle scar. Indeed, in many other features, StW 598 is quite dissimilar to the proximal femora of modern humans. For instance, its anteroposteriorly compressed, superoinferiorly tall, and strongly anteverted neck is unlike the femoral necks of extant *H. sapiens* and, instead, mirrors the morphology of nearly every other known *Australopithecus* femur specimen.^{28,39}

Moving to the distal femur, the femora of bipedal hominins are/were adapted, via significant anterior projection (i.e. ‘elevation’) of the lateral patellar lip, to resist dislocation of the patella under the load of stance phase valgus. A simple way to visually assess the functional elevation of the lateral patellar lip of a femur is to view the specimen distally, with an

axis running through the condylar meniscal grooves oriented horizontal to the flat base over which the femur is positioned.⁴⁰ Unfortunately, because of the fragmentary nature of the fossil, the meniscal axis of StW 619 cannot be estimated with precision. However, placing the medial patellar surface of the specimen horizontally in distal view ‘corresponds closely to the orientation recommended by Lovejoy^{40,41} (p.1232999-1) (Figure 8). This view clearly illustrates the appreciable depth of StW 619’s patellar groove, as well as the significant functional elevation of its lateral patellar lip. Similarly, even though StW 619 lacks a discernible medial condylar boss, when the specimen is rotated into an estimated position of full extension and viewed distally, the anterior termination of the medial condyle assumes an ovoid shape. Lovejoy⁴⁰ emphasises that this shape, in this view, is an ancillary indication that the tibial contact area of a femoral condyle was elongated relative to those of the femora of quadrupedal mammals. Bipedal primates with such elongated, ellipsoid femoral condyles possess(ed) knees that are ‘tibial dominant’.⁴⁰

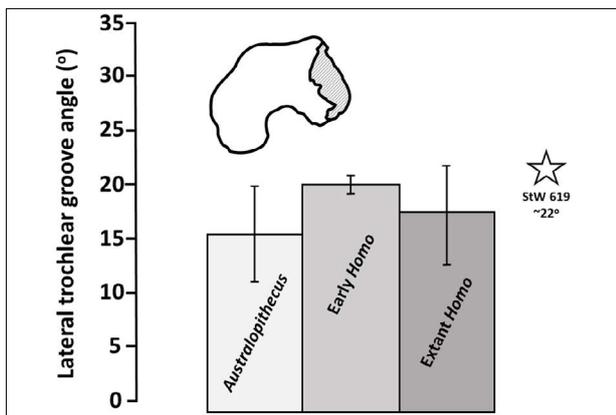


Figure 8: Comparison of the estimated lateral trochlear groove angle⁶⁸ of StW 619 to those of other hominin distal femora (modified from Desilva et al.⁴¹ Figure 1). The distal view outline of StW 619 shown on the graph is positioned so that its medial patellar surface is horizontal to the straight bottom edge of the image, which approximates the view recommended⁴⁰ for determining the functional elevation of the lateral patellar lip (see discussion in text). Comparative specimens include: Sterkfontein *Australopithecus* (specimens Sts 34 and TM 1513) plus Hadar, Ethiopia, *Australopithecus* (specimens A.L. 129-1, A.L. 333-4 and A.L. 333w-56); Lake Turkana, Kenya, early *Homo* (specimens KNM-ER 1472, KNM-ER 1481, KNM-ER 15000) and extant *Homo sapiens* (data from Desilva et al.⁴¹).

The conclusion that the knee of the StW 619 hominin – although not an exact morphological match for a modern human knee – was nonetheless capable of full, modern humanlike bipedal extension, is not unexpected given a broader view of the hominin fossil sample from Jacovec. As discussed above, the proximal femur StW 598 shows derived features, such as an elongated neck, a low neck-shaft angle and a relatively small head, observed in other proven bipedal hominins.^{38,41-48} In addition, Pickering et al.⁷ (see also Partridge et al.¹⁴) have also described two lumbar vertebrae from Jacovec that indicate the hominin(s) from which they derived possessed intrinsic lumbar lordosis. Lumbar lordosis is, of course, a critical component of hominid bipedality³⁰, as it functions to maintain orthogrady by ameliorating strain on the dorsal spinal ligaments and by absorbing shock emanating from upright activities on terrestrial substrates⁴⁹⁻⁵¹.

None of this is to suggest that all of the Jacovec hominins were necessarily as fully committed to terrestrial bipedalism as are modern humans. The StW 605 manual proximal phalanx from Jacovec is too damaged to quantify its included angle but it appears fairly curved longitudinally.⁸ Consensus posits a causal link between curved manual proximal phalanges and significant degrees of arboreal behaviour in primates.^{52,53} Similarly, the StW 606 hominin clavicle from Jacovec shows a mix of modern humanlike and apelike features, the latter of

which would have endowed the hominin from which it derived with good climbing abilities.^{7,14}

Conclusion

When added to results from previous studies of *Australopithecus* postcranial samples from Sterkfontein^{5,7,8,30,54-59}, this study corroborates that those samples include functionally heterogeneous mixes of elements, some of which indicate postural and locomotor behaviours that are ape-like and others of which indicate human-like adaptations. Starting from this basic understanding, there is, in our opinion, a fundamental problem that underlies many ensuing debates over the postcranial functional morphology of *Australopithecus*. Specifically, we are troubled by the fact that many disputants in these debates misunderstand or ignore the completely salient possibility (likelihood?) that the Sterkfontein Member 4 hominin postcranial collection samples at least two coeval species, *A. africanus* and *A. prometheus*, as is the case for the large craniodental sample of hominin fossils from that depositional unit.^{5,6,17-19} For instance, Harmon⁶⁰ detected significant variation in the shape of proximal femora typically assigned to *A. africanus*, which she considered intraspecific variation, but that might actually be an interspecific difference. In contrast, Clarke⁵ demonstrated that two hominin first metatarsals from Sterkfontein Member 4 show distinct morphologies indicative of different modes of locomotion and thus concluded that the fossils likely represent separate species (see also Deloison⁶¹). Additionally, Kibii and Clarke⁵⁷ suggested that the pelvis of the partial Sterkfontein Member 4 skeletons, Sts 14 and StW 431, do not necessarily sample the same species. This issue has been clarified recently with the cleaning and reconstruction of the StW 573 skeleton of a female *A. prometheus* from Sterkfontein Member 2⁶², which has a pelvis of similar size and morphology as that of the StW 431 male skeleton. Thus, it seems that StW 573 and StW 431 represent, respectively, female and male *A. prometheus*, while the much smaller female pelvis, Sts 14, seems to be that of *A. africanus*. In addition, the femur of *A. prometheus*, as exemplified by StW 573, possesses a short neck joined to a platymeric diaphysis⁶³, leading to the logical conclusion that the Jacovec femur, StW 598, with a long neck and rounded diaphysis (as described above), probably represents *A. africanus*. Last, both these femoral forms differ from presumptive *Paranthropus* femora from Swartkrans and that of StW 99, from Sterkfontein Member 4.^{14,30} Collectively, these results seem to indicate significant interspecific hominin postcranial morphological variability in late Pliocene and early Pleistocene South Africa.

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Competing interests

We declare that there are no competing interests.

Authors' contributions

T.R.P. conceived and designed the study, collected and analysed the data, and wrote the manuscript. J.L.H. conceived and designed the study and collected and analysed the data. R.J.C. conceived and designed the study and collected and analysed the data. D.S. collected and analysed the data. A.J.H. collected and analysed the data.

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