Partial hominin tibia (StW 396) from Sterkfontein, South Africa

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Comparison of a proximal hominin tibial fragment, StW 396 from Sterkfontein Member 4, South Africa, with the StW 514a tibia, also from Member 4 and attributed to *Australopithecus africanus,* indicates a degree of morphological variability that may represent the extremes of intraspecific variability or even exceed what one would expect from intraspecific variation alone. The morphology of StW 396 is human-like which suggests adaptations towards stability at the knee, whilst that of StW 514a is interpreted as being more mobile and ape-like (Berger & Tobias 1996). Four features separate the two morphological patterns. In StW 514a the attachment area of m. semimembranosus is strongly localized, whereas in StW 396 the posteromedial border is notched near the base of the lateral intercondylar tubercle; thirdly, the lateral tibial condyle of StW 514a is supero-inferiorly thin, whereas in StW 396 the lateral condyle is supero-inferiorly thickened and the contrast between the condyle and the shaft is less pronounced; lastly the articular surface of the medial condyle of StW 396 is anteroposteriorly broad and highly concave as opposed to the narrower, flatter surface of StW 514a. The degree of variability of the two specimens possibly suggests differing functional adaptations and may thus support an hypothesis suggesting that two hominin species may be represented within Sterkfontein Member 4.

Keywords: hominin, tibia, Sterkfontein, *Australopithecus africanus.*

INTRODUCTION

The fossil tibia StW 514a from the Sterkfontein Formation, Gauteng, South Africa, is argued to possess ape-like proximal tibial morphology (Berger & Tobias 1996). The specimen is regarded as belonging to an australopith from Member 4, which has been estimated to be 2.4–2.8 Ma (Vrba 1985; Delson 1988; Partridge & Watt 1991; McKee *et al.* 1995; Kuman & Clarke 2000; Pickering *et al.* 2004). Berger *et al.* (2002), in a revision of the *Australopithecus*-bearing deposits of Sterkfontein, interpreted Member 4 more likely to fall between 1.5–2.5 Ma. These revised age estimates have been refuted by Clarke (2002).

StW 514a has a close association with large numbers of cranio-dental remains attributed to australopiths (Moggi-Cecchi *et al.* 2006), suggesting a high probability that the tibia should be assigned to this taxonomic group, and most probably to the species *Australopithecus africanus* (Berger & Tobias 1996). More recently we have analysed another proximal tibial fragment from Member 4 (StW 396) and we find that, in certain functionally important features, this specimen differs from StW 514a. Berger & Tobias (1996) described the convex anteroposterior curvature of the lateral tibial condyle of StW 514a as possibly being associated with a more chimpanzee-like locomotor function when compared to the flatter lateral tibial condyle of *A. afarensis.* Latimer *et al.* (1987) have observed that joints become flatter as size increases as a result of a response to increased transarticular loads accompanied by larger body mass. They suggest that variation observed among hominins, both within and between species, reflects size alone rather than function (Latimer *et al.* 1987). Recently, Organ & Ward (2006) in a detailed study, compared the three-dimensional surface areas of the lateral tibial condyle of humans and apes with those of *A. afarensis* (A.L. 129b, A.L. 288-1aq, A.L. 333–42, A.L. 333X-26) and *A. africanus* (StW 514a). Their results neither support the hypotheses that *A. africanus* and *A. afarensis* differ in condylar topology or that joint surfaces become flatter with increased transarticular load accompanying increased body size. Organ & Wards' (2006) arguments are compelling and their methods would have been useful in solving the problem of the StW 396 proximal tibial fragment if a lateral condyle was present. However, the remainder of this specimen appears to vary enough from StW 514a to justify further consideration. Following is a description of StW 396 and a comparison of its morphology with that of StW 514a that highlights the morphological differences between these two specimens. The implications of the differences are discussed, with special reference to the claim of Clarke (1985, 1994, 2009) that two different hominin taxa may possibly be represented in Sterkfontein Member 4.

DESCRIPTION

StW 396 is a fragment of the proximal epiphysis and diaphysis of a right hominoid tibia including the medial condyle and intercondylar eminence (Fig. 1). This tibial fragment was recovered in August 1986 by the Sterkfontein excavation team under A.R. Hughes, grid square O/45 at a depth of 18′4′–19′7′ (5.6–6.0 m) in partially decalcified sediments that Clarke (2006) attributes to the deepest fossil-bearing levels of Member 4. The specimen comprises a complete medial condyle, a small part of the lateral condyle, most of the intercondylar eminence, the posterior intercondylar area, and a short length of the posterior and medial parts of the shaft. The apices of both the medial and lateral intercondylar tubercles are damaged. The articular surface of the medial condyle is markedly concave, the greatest depth being located just lateral to

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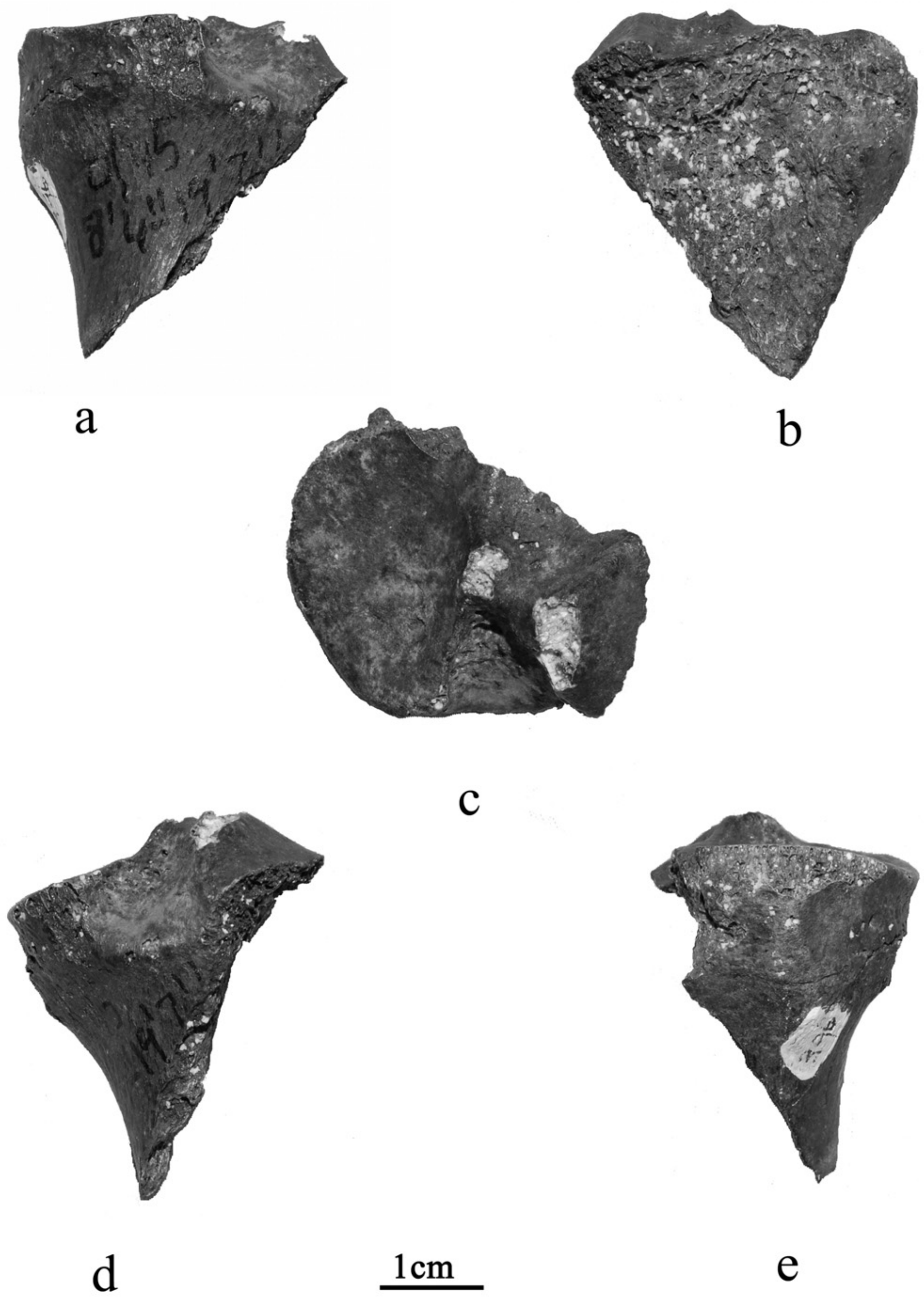
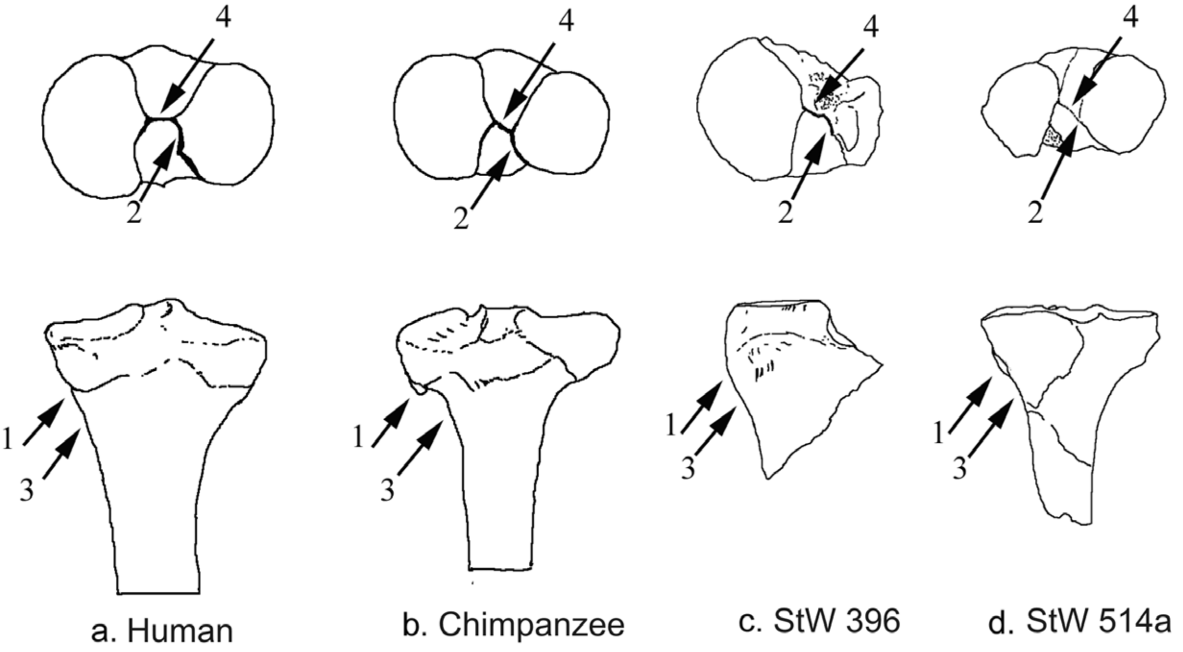


Figure 1. StW 396 proximal tibial fragment from Sterkfontein: **a**, posterior; **b**, anterior; **c**, superior; **d**, lateral; **e**, medial.

the mediolateral midpoint of the condyle. A small area of pitting is present in the middle of the posterior part of the medial condyle that most likely represents slight osteoarthritic degeneration. The maximum mediolateral diameter of the medial condyle is 24.4 mm; the anteroposterior diameter cannot be determined. The intercondylar tubercles are high, and a line between their apices is oriented at an angle of approximately 30 degrees to the mediolateral line of the plateau. Most of the lateral condyle is missing except for a steeply sloping area applied to the lateral face of the lateral intercondylar tubercle. The steepness of this slope reflects the appreciable elevation of the intercondylar tubercles above the articular condylar surfaces. The posteromedial border of the lateral condyle is curved and slightly notched at the base of the lateral intercondylar tubercle and appears to have been long, although damage obscures its most posterior extent. On the posteromedial edge of the specimen, just below the most medial edge of the medial condyle, is an anteroposteriorly elongate, depressed area that represents the attachment of m. semimembranosus. The intracapsular area at this point is deep, extending almost 17.0 mm below the lip of the medial condyle. The transition between the intracapsular area of the medial condyle and the shaft is not marked and is distinguished only as a slight but definite lateral sloping of the shaft below the intracapsular area. The remainder of the lateral half and the anterior portion of the specimen are missing. The specimen is fully adult, with no traces of the epiphyseal plate remaining.

DISCUSSION

In descending order of importance, four features suggest a marked difference in morphology between



a. Human b. Chimpanzee c. StW 396 d. StW 514a

Figure 2. Dorsal and posterior views of proximal tibiae. The attachment area of m. semimembranosus is an indistinct, horizontal groove as in humans (**a**, '1'), whereas in StW 514a (**d**, '1') the attachment area is strongly localized as in apes (**b**, '1'). The posteromedial border of the lateral tibial condyle in StW 396 is slightly notched (**c**, '2'), whereas unnotched in StW 514a as in apes (**b**, **d**, '2'). In StW 396 the contrast between the condyle and the shaft is less pronounced as in humans (**a, c**, '3') whereas, the medial tibial condyle of StW 514a and chimpanzee is supero-inferiorly thin (**b, d**, '3'). An ape-like feature in StW 396 is that a line joining the intercondylar tubercles is oriented at a greater angle to the mediolateral centre-line of the plateau (**d**, '4') than one would expect in modern humans (**a**, '4'), similar to chimpanzees (**b**, '4') and StW 514a (**d**, '4').

the StW 396 and StW 514a tibiae (Fig. 2):

(1) In the StW 396 specimen, the attachment area of m. semimembranosus is an indistinct, horizontal groove as in humans, whereas in StW 514a the attachment area is strongly localized as in apes. Aiello & Dean (1990) have stressed the importance of this feature in distinguishing ape morphology from that of humans and the distinction appears consistent in our sample of comparative material consisting of humans, chimpanzees, gorillas, orangutans and a bonobo (Table 1).

(2) The posteromedial border of the lateral tibial condyle in StW 396 appears long and is slightly notched near the base of the lateral intercondylar tubercle, thereby indicating a semicircular lateral meniscus as is found in most humans (Senut & Tardieu 1985; Tardieu 1986; Holliday & Dugan 2003), whereas the posteromedial border is short, straight and unnotched in StW 514a as in apes. Senut & Tardieu (1985) pointed out that modern humans have two lateral meniscal insertions, differentiating them from apes and many earlier hominins. They also used this feature to differentiate fossil taxa, claiming two Plio-Pleistocene hominin taxa can be delimited, one modern (*Homo*), the other chimpanzee-like (*Australopithecus*). Holliday & Dugan (2003), however, in testing this feature's taxonomic utility in a much larger sample of human tibiae, found that some modern humans lack this notch, its absence cannot therefore be used to exclude a fossil tibia from *Homo.*

(3) In StW 396 the medial condyle is supero-inferiorly thickened and the contrast between the condyle and the shaft is less pronounced, thus creating a human-like appearance of this area, whereas the medial (and lateral) tibial condyle of StW 514a is supero-inferiorly thin, creating an ape-like shelved appearance of the tibial plateau. We recognize that we are dealing here with a possibly continuous variable, the assessment of which is thus highly subjective; moreover, it has previously been pointed out that variation of this feature in modern hominoids is extreme (Lovejoy *et al.* 1982; Berger & Tobias 1996), yet we are impressed by the fact that the two Sterkfontein proximal tibiae appear to represent opposite poles in the range of variation observed in humans and in apes.

Table 1. Approximate intercondylar tubercle angles of fossils, humans and apes measured between the mediolateral line of the tibial plateau to the highest point of the intercondylar tubercles. The great apes are of both wild shot and zoological garden origin.

Group	Intercondylar tubercle angle
StW 396	30°
StW 514a	40°
AL 288-1AQ[a]	45°
Homo sapiens (*n* = 24)	11.92° (S.D. = 9.8; range: 0–35°)
Pan troglodytes (*n* = 4)	33.75° (range: 30–40°)
Pan paniscus (*n* = 1)	30°
Gorilla gorilla (*n* = 3)	41.67° (range: 40–45°)
Pongo pygmaeus (*n* = 2)	37.5° (range: 35–40°)

[a] Good-quality cast (Cs 1573B) of 'Lucy' *Australopithecus afarensis.*

(4) The articular surface of the medial condyle of StW 396 is anteroposteriorly long and highly concave as opposed to the narrower, flatter surface in StW 514a. Again, while comparable measurements of StW 514a could not be made, the medial condylar articular surface of StW 396 is clearly relatively broader in relation to its estimated length.

The only 'ape-like' feature of the StW 396 tibia is that a line joining the intercondylar tubercles is oriented at a greater angle to the mediolateral centre-line of the plateau than one would expect in modern humans (Fig. 2).

Modern humans, however, vary a great deal in this morphology and in certain tibiae (e.g. A92, A330 and A757) in the Raymond Dart Collection of Human Skeletons, University of the Witwatersrand, we have observed angulation of the tubercles to a degree seen in StW 396 (Table 1) being about 30 degrees to the mesiolateral line of the plateau.

The morphology of the StW 396 tibia may be described as being more derived than primitive. The total morphology may be said to represent an adaptation to a human-like bipedal gait with the consequent ability to hyper-extend and 'lock' the knee. This morphology is in striking contrast to that described for the StW 514a tibia (Berger & Tobias 1996). In that specimen, it was concluded that the proximal tibial morphology indicated a knee joint which was less stable than those of humans, and more mobile with appreciable rotational capacity as in the extant African apes.

The degree of variation between the two Sterkfontein specimens may suggest differing functional adaptations, namely in the case of StW 514a, emphasis on mobility at the knee, and in the case of StW 396, emphasis on human-like stability. Both specimens have been obtained from seemingly *in situ* breccia in a deep part of Member 4 of the Sterkfontein Formation. Thus, the depth below datum of the ape-like StW 514a tibia was 5.6–6.0 m. In a 28 m total depth of the Sterkfontein Formation, these figures would place both tibiae in the second oldest bed (Bed B) of Member 4 (Partridge 1978; Stiles & Partridge 1979). Stratigraphically, therefore, the individuals represented by the two tibiae were near contemporaries, unless StW 396 proves after all to have been intrusive from younger sediments. Their discrepant morphological traits, albeit based on only two fragmentary specimens, compel us to consider whether the more human-like tibia StW 396 could possibly stem from the same taxon as that to which the chimpanzee-like tibia StW 514a belongs. At this stage, there is very little fossil evidence from which to infer the degree of intraspecific variability of the lower limb of *A. africanus,* or, for that matter, of any of the early hominin taxa.

If our interpretation of the morphological and biomechanical patterns of the two tibiae is correct, it would seem most unlikely that the disparate patterns of knee-joint would occur in normal, healthy members of the same species. For example, neither gender dimorphism nor individual variation would be expected to be associated with two functional morphs of this nature. On the contrary, the studies of Senut & Tardieu (1985) indicate that precisely such differences as we believe are manifest between StW 398 and StW 514a occur between members of various hominoid taxa, extant and extinct.

We are drawn to the view that the two Sterkfontein Member 4 tibiae may indeed have belonged to members of two different taxa. The question is if there is any evidence from cranial and dental remains that more than one taxon is represented in the very large Member 4 sample of nearly 650 catalogued hominin specimens? A hypothesis of multiple hominin species at Hadar, Ethiopia, has arguably, been supported by the tibial condyle morphology of small *A. afarensis* fossils (Senut & Tardieu 1985; Zihlman 1985; Tardieu 1986, 1999). Organ & Ward (2006) draw attention to a number of studies that do not support this hypothesis, suggesting that the Hadar australopith assemblage represents a single species (e.g. Stern & Susman 1983; McHenry 1986; Jungers 1988; Richmond & Jungers 1995; Lockwood *et al.* 1996; Lague 2002). There is a growing impression that the inferred diversity of taxa suggests that there was also a considerable degree of locomotor diversity among early hominins (Harcourt-Smith & Aiello 2004).

Based on qualitative anatomical comparisons, Clarke (1985, 1994, 2009) has suggested that two species are present within the Sterkfontein Member 4 assemblage. One species is *A. africanus* Dart, while the other, as yet unnamed, presents a morphology that Clarke suggests is possibly ancestral to the robust australopithecine lineage. However, as yet no thorough statistical analysis of the craniodental subsets have been published, although such features as maxillary molar and pre-molar morphology are thought to play a major part in distinguishing the subsets (Clarke, 1994). At present, the case for two species being represented by the Member 4 hominin cranial and dental specimens can by no means be considered to be established. Furthermore, there appears to be no stratigraphic separation between Clarke's proposed two subsets; thus examples of his 'pre-*Paranthropus*' group stem from both Beds B and C (Partridge 1978).

Reason has previously been seen to recognize a mosaic of derived and primitive features in the fossil hominin specimens from Sterkfontein Member 4. These include traits in the cerebral cortex (e.g. Falk 1983, 1989; Tobias 1987), the basicranium (e.g. Tobias 1967; Dean & Wood 1982), the spinal column (Benade 1990), the shoulder region (Berger 1994), the hip (Häusler & Berger 2001) the knee (Berger & Tobias 1996; Organ & Ward 2006) and the foot (Deloison 2003; Zipfel *et al.* 2009).

Within this complex of regional morphological patterns, the tibia StW 514a with its chimpanzee-like traits can be comfortably accommodated. Only the human-like tibia StW 396 is difficult to place. On the prevailing single-species hypothesis, StW 396 may oblige us to extend the range of intraspecific variability of the proximal tibial morphology. On a two-species hypothesis, either of the Member 4 tibiae may need to be accommodated in a taxon other than *A. africanus.* Since mosaic evolutionary trends are evident in the lower limbs of early hominins (e.g. Lovejoy *et al.* 1982; Susman *et al.* 1984; Senut & Tardieu 1985; Harcourt-Smith & Aiello 2004; Clarke & Tobias 1995; Kidd & Oxnard 2005; Susman & deRuiter 2005; Zipfel & Kidd 2006; DeSilva 2008), it cannot be assumed that the more human-like StW 396 is necessarily the 'odd man out' requiring to be classified in a different taxon. In this regard, we strike a cautionary note; the two tibial specimens are incomplete and, on a two-species hypothesis, we should remain in the statistically and populationally invidious position of dealing with sample sizes of a single specimen in each of the putative subsets.

Although we are at present unable to link any specific Member 4 cranial or dental material directly with any postcranial specimens, our analysis of the StW 396 and

StW 514a tibiae suggests possible support for a two species hypothesis.

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