Current events

A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus*

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Introduction

Stw 514a and Stw 514b are, respectively, the proximal and distal ends of a right hominoid tibia recovered together from Sterkfontein Member 4 in 1989 from the ''Type site'', grid square J/42 at a depth of 20′4″–21′5″. The specimen was excavated from *in situ* hard breccia near the areas of discovery of Sts 5 (''Mrs. Ples''), the partial skeleton Sts 14 and the Stw 505 cranium, all currently attributed to the hominid species *Australopithecus africanus*. The tibia is associated with large numbers of other *A. africanus* craniodental fossils. By association with these elements and by the absence of any non-hominid ape remains, it can be assumed that this tibia is australopithecine, and most probably of the species *A. africanus*. The Member 4 deposits have until recently been dated to 2·4–2·8 mya by faunal, geomorphological and geophysical dating methods (Vogel *et al.*, 1984; Butzer, 1984; Delson, 1984; 1988; Vrba, 1985*a,b*; Schwarcz *et al.*, 1994), but recent recalibration has narrowed the dating of Member 4 to 2·6–2·8 mya (Partridge cited by Clarke and Tobias, 1995). The Member 4 specimens, thus, represent some of the oldest hominid fossils from southern Africa. All measurements of the specimens described below are standard and recorded in millimetres.

Description

The proximal tibial fragment Stw 514a (Figure 1) is 66·7 mm in length (from the most proximal to the most distal point). The specimen is extremely small, being only slightly larger than the AL 288-1aq (Lucy) specimen. Mediolateral (ML) breadth of the tibial plateau is 52·3. The ML breadth of the lateral condyle is ca. 20, while its anteroposterior (AP) diameter is 16·8. The ML breadth of the medial condyle is ca. 20·5, but the AP diameter is not determinable. The intercondylar area is damaged but the estimated distance between the intercondylar tubercles, as assessed by the positions of the bases of the tubercles is 6 mm. A fossilization crack runs anteroposteriorly through the specimen bisecting the lateral edge of the medial condyle. The most striking feature of the tibial plateau is the ape-like, extremely curved convex surface of the lateral condyle, especially when viewed in sagittal section [Figures 1(a), (b) and (d)], in contrast with the slightly more flattened surface of the medial condyle [Figure 1(b)]. In

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addition, although slightly damaged in the area, the posteromedial edge of the lateral condylar surface is straight and un-notched, being ape-like in this regard. The most proximal part of the tibial shaft is supero–inferiorly shallow, giving the tibial plateau a shelf-like appearance [Figure 1(a) and (b)]. This appearance is accentuated by the extreme hollowing of the proximal shaft lateral to the tibial tuberosity. As in apes, the attachment area for semi-membranosus forms a marked circular depression situated on the posteromedial margin of the condyle immediately below the medial condylar surface [Figure 1(e)]. On the anterior surface, a curved, superomedially oriented groove separates the tibial tuberosity from the intracapsular area above it. The tibial tuberosity itself is pronounced and supero–inferiorly elongated. There is a shallow groove just below, and medial to, the tibial tuberosity. On the posterior surface the soleal line is pronounced. The specimen ends before the full outline of the area of insertion of the common tendon of sartorius/gracilis/semitendinosus is visible. It is, however, clearly present as a marked depression, but in general, the markings in the superior part of this area are not as strong as those observed in the AL 288-1aq tibia.

The distal tibial fragment Stw 514b (Figure 2) is poorly preserved and only a small part of the distal articular area and medial malleolus are present. The greatest ML breadth of the specimen is 31·3, although no other measurements can be estimated. On the medial surface, part of the fibular notch is visible as a slight, ovoid depression. On the anterior surface there is a slight squatting facet located centrally at the inferior edge of the bone. The distal articular surface, although damaged posteriorly, appears to have a posterior tilt in the sagittal plane, although accurate assessment of this feature is difficult.

Discussion

The proximal part of the tibial fragment Stw 514 exhibits five important morphological features that serve to distinguish this specimen from the proximal tibiae of humans, and it exhibits one feature that suggests that this knee-joint was more mobile and more ape-like than any other early hominid tibia yet recovered. First, the articular surface of the lateral tibial condyle of Stw 514 is markedly convex from anterior to posterior. The shape of the lateral condyle in the modern human tibiae examined is most commonly slightly concave or flat, but sometimes slightly convex, whereas that of apes is more markedly convex (Martin & Saller, 1959). This feature has been associated with the potential for a greater rotational ability, more extreme flexion of the knee-joint and a more mobile lateral meniscus in apes (Trinkaus, 1975; Tardieu, 1983; Aiello & Dean, 1990). When convexity of the lateral tibial condyle occurs in humans it has been associated with hyperflexion in squatting postures (Trinkaus, 1975). In such cases, the form of the articular surface is similar to that observed in the AL 288-1aq tibia in having a slight depression of the anterior part of the condylar surface near the lateral intercondylar tubercle. This differs markedly from the condition observed in Stw 514a (Figure 3), in which the lateral condylar articular surface exhibits no pronounced depression at any point across its entire surface, and the greatest curvature lies in the posterior third of the condyle. The degree of convexity observed in the lateral condyle of Stw 514a is thus extreme, and chimpanzee-like, and indicates that the lateral femoral condyle and its meniscus would have been capable of a large amplitude of movement on the lateral tibial plateau during rotation of the knee.

Second, the posteromedial border of the lateral condyle of Stw 514a lacks a notch, its straightness indicating a single attachment of the lateral meniscus and, thus, an ape-like morphology (Tardieu, 1983; Senut & Tardieu, 1985). Humans have been shown to possess a

Figure 1. Stw 514a, right proximal tibia. (a) posterior view; (b) anterior view; (c) superior view; (d) lateral view; (e) medial view. Scale in centimetres.

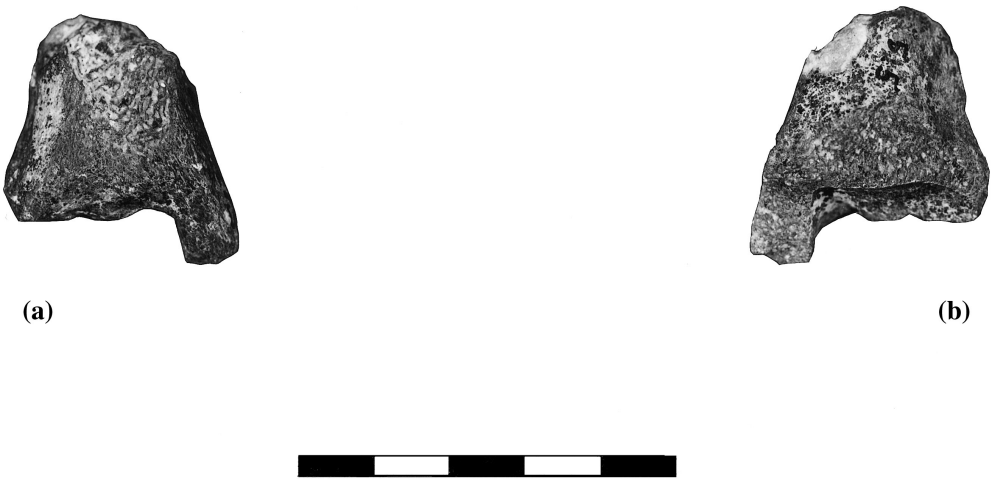

Figure 2. Stw 514b, right distal tibia. (a) anterior view; (b) posterior view. Scale in centimetres.

Figure 3. Sections through the lateral condyles of (a) AL 288-1Laq (——) and Stw 514a (– – –) comparing the curvatures of the articular surfaces and (b) through the lateral condyles of a typical human (——) and a typical chimpanzee (– – –). Outlines of early hominids are approximately × 1·5 natural size.

notched posteromedial border indicating two areas of attachment, which connotes a smaller amplitude of rotation of the knee than in African apes (Tardieu, 1983; Senut & Tardieu, 1985). Third, the area of the distal attachment for semi-membranosus in Stw 514a, as in *Australopithecus afarensis* tibiae, is ape-like in being a marked circular depression. This contrasts with the condition in modern humans, where the attachment area for semi-membranosus is in the same position, but forms a large, indistinct horizontal groove (Aiello & Dean, 1990). Fourth, the curved groove that separates the tibial tuberosity from the intracapsular area above it is superomedially oriented. Aiello & Dean (1990) have noted that in humans, this bursal groove is horizontal, whereas in apes it is superomedially inclined. In other early hominids this feature has been noted as horizontal and has thus been termed ''human-like'' (Johanson *et al.*, 1982). Thus this feature accords with a more ape-like bursal attachment in Stw 514a. Finally, the proximal shaft lateral to the tibial tuberosity is hollowed, and is very similar in appearance to those of chimpanzees, indicating that the attachment of tibialis posterior is positioned on the lateral surface of the shaft, rather than on the posterior surface as in humans. The lateral aspect of the Stw 514 tibial tuberosity further has a sharp edge and creates a proximodistally shallow lateral tibial plateau very similar in appearance to those of apes. In contrast, human tibiae are more robust in this region and generally lack a sharp, shelf-like distinction between the shaft and the condyles. The *A. afarensis* tibiae demonstrate similar lateral hollowing to that observed in Stw 514a.

The lack of distinct localization of the tibial tuberosity is the only feature that might serve to distinguish Stw 514a from the tibiae of chimpanzee. Chimpanzee tibiae are said to possess more localized tibial tuberosities; however, the appearance of the tuberosity in the apes we have observed is highly variable and we suggest that this feature does not clearly separate human tibiae from those of chimpanzee.

Very little functional information can be gleaned from the distal tibial fragment Stw 514b, except that, if the articular surface in fact possesses a posterior tilt when viewed in the sagittal plane, such a tilt is generally associated with quadrupedal or ape-like forms of locomotion although there is disagreement concerning the importance of this feature in interpreting locomotor behaviour (Latimer *et al.*, 1987).

The total morphological pattern of the Stw 514 tibia is certainly the most ape-like of any Pliocene or Pleistocene hominoid tibia yet recovered, being even more ape-like than those of *A. afarensis*. The whole morphology implies that the proximal tibial joint is less stable and more mobile than that of a human. We, thus, question the ability of this tibia to function in the same way as in a human obligately terrestrial biped. The morphology of the proximal tibia of Stw 514 would, however, offer a great deal of rotational capacity of the knee as in the extant African apes.

The very chimpanzee-like morphology of Stw 514 highlights the question of whether this is in fact a hominid tibia. Is this the first non-hominid ape fossil recovered from the Plio-Pleistocene of southern Africa? This possibility is strongly contraindicated by the close association of Stw 514 with large numbers of craniodentally-identified australopithecine fossils. The lack of any craniodental or other remains of recognizable apes in the deposit, and recent studies of other postcranial bones that suggest that *A. africanus* was extremely ape-like in its morphology, and possibly arboreally adapted (Berger, 1994; Clarke & Tobias, 1995). The recent discovery of of the Stw partial foot in Member 2, with its highly mobile first metatarsal (Clarke & Tobias, 1995), surprisingly does not appear to be an incompatible morphology for a hominid possessing a tibia like Stw 514. Furthermore, recent discoveries of fossil plant material (Clarke & White, 1994) have indicated that the Sterkfontein environment during the deposition of Member 4 was far more wooded than has previously been suggested (Vrba, 1985*a*,*b*), showing that *A. africanus* may have been living in and adapted to a tropical woodland or even forest environment. We are struck by the fact that no single feature can be used to separate this tibia unequivocally from that of a chimpanzee. If Stw 514 is from an *A. africanus* individual, the presence of ape-like tibial morphology begs a re-analysis of the phylogenetic relationships of *A. africanus* and *A. afarensis*. Because the tibial morphology in Stw 514a is more ape-like, and apparently more primitive than that observed in *A. afarensis*, it is difficult to reconcile these features with the interpretation of White *et al*. (1983) that *A. afarensis* was ancestral to *A. africanus*. We are at present examining other *A. africanus* postcranial bones and our provisional results show that the tibia is not the only bone which indicates *A. africanus* is more primitive than the Hadar homologues.

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