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Using the morphology of the hominoid distal fibula to interpret arboreality in *Australopithecus afarensis*

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ABSTRACT

The fibula has rarely been considered in anthropological studies. However differences in morphology — and inferred function — of the fibula between human and non-human apes have been noted in the past and related to differences in locomotor behavior. Recent studies have pointed out the correlation between diaphyseal rigidity of the fibula and tibia and locomotor behavior in living hominids, and its possible application for inferring early hominin locomotor behavior. The problem with the application of the method proposed in these studies is the extreme rarity of associated early hominin fibula and tibia. Additionally, previous studies investigating morphological traits of fibulotalar articular facets to infer the degree of arboreality in fossil australopiths were often qualitative. In the present study, articular measurements of the distal fibula of living great apes and humans (*Pongo*, *Gorilla*, *Pan* and *Homo*) are quantified and compared to *Australopithecus afarensis* distal fibulae. Quantitative analysis is carried out for articular areas and breadths of the fibulotalar articular facets, for the angles formed by the fibulotalar articular facets and the longitudinal axis of the fibula, and for the angle between the proximal fibulotalar articular facet and the subcutaneous triangular area. Results show that the fibula of *A. afarensis* bears some traits consistent with modern terrestrial bipedalism, like a more laterally facing lateral malleolus, in association with more ape-like traits, like the smaller distal fibulotalar articular facet area and the more inferiorly oriented fibulotalar articular facets, consistent with *A. afarensis* being a terrestrial hominin adapted for some form of arboreality.

1. Introduction

Despite a relatively extensive hominin postcranial fossil record, there is still no consensus on the manner of bipedalism in the earliest hominins, with considerable debate specifically about the relative amount of arboreal versus terrestrial locomotion (Stern and Susman, 1983; Latimer et al., 1987; Latimer and Lovejoy, 1990a,b; Berge, 1994; Stern, 2000; Ward, 2013). Hands and feet directly contact the substrate and the study of the morphology and biomechanics of these body sections offers an invaluable clue to the locomotor adaptations of early hominins (Susman and de Ruiter, 2004; Ward et al., 2011; Zipfel et al., 2011), but are scarce in the fossil record compared to long bones. The long bones that are usually used to infer mobility patterns in early hominins and prehominin ancestors are the femur and the tibia, while studies on the fibula are comparatively rare. The femur and tibia have been the preferred elements of study both because they are mainly involved in the function of load bearing in humans, and they are more numerous in the fossil record. The fibula, in contrast, is generally overlooked in anthropological research (but see Marchi, 2004, 2007, 2015).

The distal fibula, together with the distal tibia and talus, form the ankle joint. The fundamental architecture of the ankle joint in the tetrapod ancestors of mammals involved a weight-bearing articulation between the fibula and the calcaneus (Schaeffer, 1941). The key event in transforming the pre-mammal foot into a mammalian one was the superimposition of the talus upon the calcaneus. This modification introduced new flexibility into the foot by permitting eversion and inversion at the subtalar joint (Lewis, 1980).

In non-human mammals, the fibula is an important supporting structure of the leg (Walmsley, 1918; Carleton, 1941; Barnett and Napier, 1953; Lambert, 1971). Early studies, focusing primarily on primates, documented the link between variation in mammalian

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fibular morphology and function (Carleton, 1941; Barnett and Napier, 1953). In jumping mammals a progressive approximation of the lower ends of the two bones has been observed, leading to a partial fusion (Fig. 1a). This fusion is seen in tarsiers among primates and in many insectivores. When the limb is habitually used in action against a resistant medium, such as water or earth, a powerful bony base is necessary for the insertion of the muscles acting on the paws, as in for example moles and armadillos (Fig. 1b), where the fibula is fused to the tibia at both the proximal and distal extremities. A third variant of the immobile fibula is the one observed in animals specialized for fast running, like ungulates. In these animals, the fibula is completely fused with the tibia and only a small distal portion remains free (Fig. 1c). The mobile fibula is less common within mammals and is limited to carnivores and primates (Fig. 1d). A further distinguishing feature present in mammals is the relative proportions of the tibia and fibula: the fibula being large (i.e. more robust) relative to the tibia in the burrowing and swimming mammals, small (i.e. less robust) and more flexible in saltatorial mammals, and intermediate in size in those mammals adapted for progression over uneven surfaces in the trees or on the ground such as primates and carnivores (Barnett and Napier, 1953).

The degree of robusticity and the general morphology of the fibula of primates and carnivores are associated with the high mobility of the bone. High fibular mobility is found in animals moving on uneven terrain, like carnivores, and especially in primates living in an arboreal setting (Walmsley, 1918; Carleton, 1941; Barnett and Napier, 1953). It is the low robusticity of the human fibula (compared to the tibia) that led scholars to classify the fibula as a bone mainly involved in forming the lateral border of the ankle joint but very marginally involved in weight bearing in humans (White and Falkens, 2000). Some have even described the human fibula as vestigial (Moore and Dalley, 2006). However, studies conducted on human samples (Lambert, 1971; Takebe et al., 1984; Goh et al., 1992; Wang et al., 1996; Funk et al., 2004) indicate that the fibula has a weight-bearing function, carrying 6.4–19.0% (depending on the study and ankle position) of the load borne by the leg.

Recent studies have explored the relationship between fibulotibial diaphyseal rigidity ratio and different locomotor behaviors in extant hominoids (Marchi, 2007, 2015). In particular, hominoids which are more arboreal (chimpanzees, orangutans and gibbons) show, relative to the tibia, more robust fibula at midshaft and distally than more terrestrial hominoids (gorillas and humans). Results have been explained as consequence of both the greater load to which the fibula is subjected in arboreal primates (Schmitt, 2003; Carlson et al., 2005), and the greater mobility of the ankle joint (DeSilva, 2009) and fibula (Barnett and Napier, 1953) in arboreal primates compared to terrestrial primates. In another study, Marchi and Shaw (2011) found that within modern humans, groups where locomotor patterns require abrupt and repeated changes in direction (i.e. field hockey players) show, relative to the tibia, higher fibular diaphyseal rigidity compared with sedentary groups and groups where locomotor travel is generally in the parasagittal plane (i.e. cross-country runners). The relationship between fibulotibial diaphyseal rigidity ratio and ankle movements have been used to explain mobility patterns of bioarchaeological populations (Marchi et al., 2011; Sparacello et al., 2014). Overall, the studies performed by Marchi and colleagues on fibulotibial diaphyseal rigidity ratio provide a valuable additional perspective that complements traditional predictions of mobility patterns based on the femur and the tibia alone (Carlson and Marchi, 2014).

Although the method outlined above could be applied to the hominin fossil record to provide further clues on early hominin locomotor patterns, the rarity of associated australopith tibia and fibula prevents any exhaustive investigation at present. The only early australopith associated tibiae and fibulae are those from A.L. 288-1 (Johanson and Taieb, 1976), but the partial distal fibula is too fragmentary to apply the method developed by Marchi (2004, 2007). Though four additional distal fibula fragments of *Australopithecus afaresis* (i.e. A.L. 333-9a, A.L. 333-9b, A.L. 333-85, A.L. 333w-37) are present in the fossil record from the Hadar region of Ethiopia (Johanson and Taieb, 1976; Lovejoy et al., 1982), none is associated with a tibia.

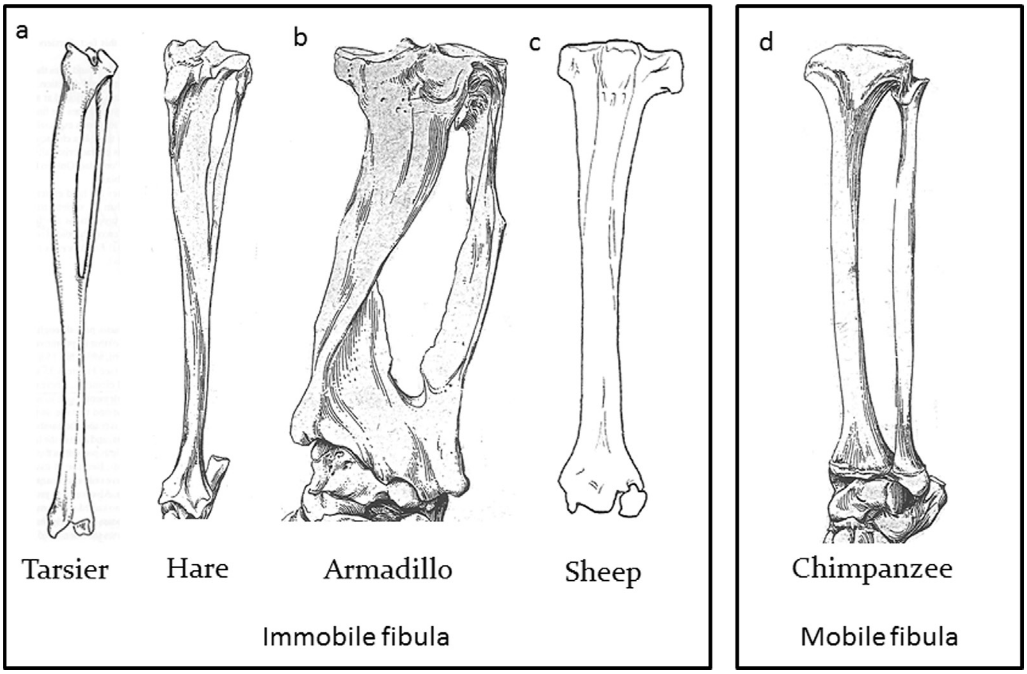

Figure 1. Different fibula morphologies in mammals.