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Structure and composition of the Trinil femora: Functional and taxonomic implications

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ABSTRACT

The original hominin femur (Femur I) and calotte discovered at Trinil, Java by Eugene Dubois in 1891/1892 played a key role in the early history of human paleontology by purportedly demonstrating the contemporaneity of archaic cranial form with modern human erect (bipedal) posture. On this basis, both specimens were subsequently assigned to *Pithecanthropus erectus*, later transferred to *Homo erectus*. However, chronological and phylogenetic links between the two have been questioned from the beginning. Four additional hominin partial femora (Femora II–V) from Trinil were subsequently described but have played a relatively minor part in evolutionary scenarios. Here we present the results of a new analysis of structural and density characteristics of the Trinil femora obtained using computed tomography. Trinil Femur I shows none of the characteristics typical of early *Homo* femora from elsewhere in Asia or Africa, including a relatively long neck, increased mediolateral bending rigidity of the mid-proximal shaft, or a low position of minimum mediolateral breath on the shaft. In contrast, Femora II–V all demonstrate features that are more consistent with this pattern. In addition, material density distributions within the specimens imply more recent and less complete fossilization of Femur I than Femora II–V. Thus, it is very likely that Trinil Femur I derives from a much more recent time period than the calotte, while the less famous and less complete Femora II–V may represent *H. erectus* at Trinil. The morphological variation within the Trinil femora can be attributed to broader changes in pelvic morphology occurring within the *Homo* lineage between the Early and late Middle Pleistocene.

Introduction

The discovery by Eugene Dubois in 1891/2 of a fossilized hominin calotte and femur (and two molars) from the site of Trinil next to the Solo River, Java was one of the most significant events in the history of human paleontology. The calotte was markedly more primitive than any other hominin fossil found to date—Dubois himself originally considered it to be more closely related to chimpanzees and only later assigned it to the human lineage (Dubois, 1894), a viewpoint that was initially questioned by a number of scientists but eventually widely accepted (Theunissen, 1989; de Vos, 2008). In contrast, the femur was remarkably similar to those of modern humans (see Fig. 1). It was also remarkable for the large exostosis on its proximal shaft, which has been given various explanations (see Discussion). Its overall similarity to modern humans was immediately recognized by Dubois, who noted its length and relative slenderness (indicating a long lower limb relative to body weight), bicondylar angle, and other human-like features, concluding that "It follows with complete certainty from this examination of the thigh bone that the Javanese *Anthropopithecus* stood and walked in the same upright position as man" (Dubois, 1893, p. 13). On this basis he assigned the species name *erectus* to both the calotte and femur, later transferring them to *Pithecanthropus erectus* (Dubois, 1894), which 50 years afterwards was subsumed into *Homo erectus* (Mayr, 1944, 1950).

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Figure 1. Anterior photographs of the original Trinil Femora I–V specimens. Femora I, III, and V are left sides, and Femora II and IV are right sides. Femora I and II are shown oriented in approximate anatomical position, while the others are oriented with the shaft positioned vertically.

However, from the outset questions were raised regarding the association between the calotte and femur. Dubois did not carry out the excavations himself and was not present at the site when the calotte and femur were discovered (nine months apart; Shipman, 2001). He included no stratigraphic diagrams or site maps in his initial publications (Dubois, 1893, 1894), only producing these in later presentations (Dubois, 1895, 1896). He argued from the beginning, however, that the calotte and femur were found at the same level or layer in the site, although some 15 m apart (later amended to 10–12 m; Dubois, 1932). However, on the basis of other contemporary documentary evidence, Bartsiokas and Day (1993) questioned the attribution of the two specimens to the same stratum, noting that because of a downward inclination of lower beds in the site, the femur, although at the same absolute level relative to the river, may have come from a stratigraphically more recent layer. The later demonstration of much more recent (Late Pleistocene) deposits at the Trinil site (Barstra, 1982), along with other chemical evidence (see below), also lent weight to the viewpoint that the original Trinil femur derived from a later time period than the calotte.

The very modern morphology of the femur—more modern than other hominin fossils known at the time (i.e., European Neandertal specimens)—also raised questions about its antiquity (Cunningham, 1895; Pearson and Bell, 1919). Dubois seems to have anticipated this issue and took pains to point out several features that, while not changing his overall functional interpretation, purportedly distinguished the femur from those of modern humans, including in particular a more convex popliteal surface (Dubois, 1894, 1896, 1926). His statement at a meeting in 1895 reflects this potential conflict: "It [the femur] has a *human character* … but that does not mean that it is a *human femur*" (italics original; Dubois, 1895: 159). However, other researchers demonstrated that these features could in fact commonly be found among modern humans (Hepburn, 1896; Pearson and Bell, 1919).

The discovery of the Zhoukoudian femora, associated with crania similar to the Trinil calotte but showing a different morphology, also called into question the age and association of the Trinil femur (Weidenreich, 1938). Weidenreich described several characteristics of the Zhoukoudian femora that together set them apart from those of modern humans, including marked mediolateral (M-L) widening of the shaft (platymeria), a distal position of minimum M-L breadth (well below midshaft), and thick cortices. None of these features characterized the Trinil femur, leading him to conclude that the femur was most likely "one of recent man and with no close relationship to the skull cap" (Weidenreich, 1938: 615; see also von Koenigswald and Weidenreich, 1939). Le Gros Clark (1939) questioned this assertion, arguing that the features described by Weidenreich for the Zhoukoudian femora represented variable and developmentally plastic features (basing this in part on the comparative studies of Buxton [1938]). However, Weidenreich defended his position with more detailed analyses of both the Zhoukoudian and Trinil specimens (Weidenreich, 1941). Day (1971) extended these comparisons to the (African) *H. erectus* OH 28 femur, which exhibited many of the same features as the Zhoukoudian femora, and again called into question the age and taxonomic status of the Trinil femur. He later incorporated these features into a "femoropelvic complex" that characterized Early and early Middle Pleistocene *Homo* specimens from East Africa, Europe, and Asia (but not the original Trinil femur; Day, 1984, 1986a). The more recently discovered late Early Pleistocene femora from Bouri, Ethiopia, also fit this pattern (Gilbert, 2008).

In a series of papers in the 1930s, Dubois described five other partial femora excavated at Trinil in 1900 and discovered in collections of the Leiden Museum (Dubois, 1932, 1934, 1935). The sixth femoral specimen may not be hominin and is not from the Trinil locality (Day and Molleson, 1973), so is not further considered here. The others, referred to as Femora II, III, IV, and V, are shown in Figure 1 along with the original Femur I. None is complete, although Femur II preserves much of the neck as well as shaft, and Femora III and IV preserve most of the shaft, while Femur V is more fragmentary. All are also more weathered than Femur I. Their stratigraphic provenience is not certain, although they came out of the collection of fossils from the Trinil site, and chemical evidence associates them with the calotte (see below). Weidenreich considered