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Journal of Human Evolution 50 (2006) 534–539

Hallucial convergence in early hominids

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Received 14 June 2005; accepted 19 December 2005

Abstract

There is a richly documented fossil record of the evolutionary transition from ape-sized brains that are less that one-third the size of modern humans through a series of intermediate-sized brains up to the modern range. The first report on the discovery of the foot of the Stw 573 skeleton emphasized the apparent transitional nature of its great toe [Clarke, R.J., Tobias, P.V., 1995. Sterkfontein Member 2 foot bones of the oldest South African hominid. Science 269, pp. 521–524]. The hallux appeared to be intermediate in its divergence between human-like adduction and ape-like abduction. A major part of this evidence is the medial encroachment of the metatarsal I facet on the medial cuneiform. This study quantifies the variability of this feature in extant hominoids and fossil hominids. The results are consistent with the view that all currently known hominids were specialized for bipedality and lacked the ape-like ability to oppose the great toe.

Keywords: Australopithecus; Foot; Bipedalism; Locomotion; Early *Homo*

Introduction

A profound shift occurred in the evolutionary history of apes and people when the foot lost its divergent and grasping great toe (Huxley, 1863; Darwin, 1872; Haeckel, 1879). Bipedalism may have been relatively common in ancient apes as it is in the lesser apes today. *Oreopithecus* apparently had a bipedally adapted hip (Harrison, 1991; Köhler and Moyà-Solà, 1997; Rook et al., 1999). But as of yet there is no evidence of any ape living or extinct that gave up hallucial divergence. How did this transformation happen? Perhaps Stw 573 holds the answer (Clarke and Tobias, 1995).

The first report of Stw 573 stressed both its humanness and its primitiveness. The primitive features of this specimen that might be as old as 3.5 Ma may provide the link needed to understand the transition from an arboreal ape-like foot to the specialized terrestrial foot of humans.

A key primitive feature stressed by Clarke and Tobias (1995) is the partially abducted hallux of Stw 573. Several features of the fossil appear to indicate a divergent great toe, but of particular significance is the extent to which the facet for the first metatarsal extends proximally over the medial surface of the medial cuneiform.

The original description reported this as proximal encroachment of the metatarsal one facet on the medial cuneiform that extended 33% (projected distance) of the proximodistal surface diameter. In a small sample of gorillas, the value was 35% to 40% and nearly 50% in *Pan*. Clarke and Tobias (1995) note that "OH 8 and humans show virtually no such encroachment" (p. 524).

The purpose of this study is to place this important fossil in a larger comparative context and to quantify the extent of hallucial divergence in Stw 573 reflected by its proximal facet on the medial cuneiform. The degree of hallucial divergence varies among extant apes but there is no overlap with living humans (Schultz, 1936, 1968). The evolutionary transition must have involved a complex sequence of genetic changes affecting the ontogeny of the foot. The adult manifestation of these changes is dichotomous in living Hominoidea, but fossil discoveries have the potential of documenting intermediate stages. These intermediate stages may appear as modifications of the medial cuneiform-first metatarsal joint where it becomes less medially oriented and flatter through time.

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doi:10.1016/j.jhevol.2005.12.008

Materials and methods

This study measures the extent of proximal encroachment of the metatarsal I facet on the medial surface of the medial cuneiform by comparing the total area of the medial side of the medial cuneiform with the area taken up by the metatarsal I facet. This is accomplished by photographing the medial cuneiform with the plane of its medial surface held parallel to the focal plane of the camera. A 135 mm telephoto lens with a ring attachment minimized distortion due to parallax. The focal plane of the 35 mm camera rested 68 cm from the plane of the medial surface of the medial cuneiform. A millimeter scale lay close to the bone at the same level as the medial surface. A light pencil mark followed the border between the articular and nonarticular portions of the medial surface of the medial cuneiform to clarify the precise limits of each surface.

The comparative sample consists of 17 female and 14 male *Homo sapiens* from North America (Terry Collection, Smithsonian Institution, Washington, D.C.) of known body weight; 2 very small-bodied female *Homo sapiens* (Akaka Pygmy and Andaman Islander, Museum of Natural History, London); 1 male and 2 female *Pan paniscus*; 5 male, 5 female, and 5 unknown sex *Pan troglodytes*; 7 male and 5 female *Gorilla gorilla*; 7 male and 8 female *Pongo pygmaeus*; 1 male siamang; and 1 male gibbon. The ape specimens derive from the Smithsonian, Museum of Comparative Zoology (Harvard), and Powell-Cotton Museum.

The Stw 573c medial cuneiform is damaged in the plantar area of the proximomedial corner and required a slight amount of reconstruction in clay. The geological age of this fossil is given as 3.3 Ma (Clarke and Tobias, 1995; Clarke, 1998, 1999) based on biostratigraphy, estimates of sedimentation rate, and magnetostratigraphy, although McKee (1996) and Berger et al. (2002) present evidence that it could be younger. Although one of us (HMM) has studied the original OH 8 specimen several times, the area measurements for this study derive from a cast.

The program MOCHA and its current upgrade as SPSS SigmaScan Pro allowed precise area measurements of the total medial surface of the medial cuneiform and the area of the metatarsal I facet visible from the medial surface. Figure 1 is a line drawing of six photographs that show what the total and facet areas look like. In the SigmaScan Pro program it is the trace measurement mode that provides an accurate means of defining the boundaries of areas.

One of us (ALJ) made all area measurements used in this study. Nineteen cuneiform images were picked at random and measured a second time by another observer to conduct a measurement error analysis. The frequency, magnitude, and direction of measurement error were calculated for these two sets of measurements on these 19 tarsal bones. Because the measurements are two-dimensional (mm^2), the square root of each area (total and facet) was used. The frequency was determined by using percentage agreement (Utermohle et al., 1983) taken to the nearest whole millimeter. The magnitude was represented by the mean absolute difference (Sokal and Rohlf, 1969; Utermohle et al., 1983). Fisher's nonparametric sign test was used to determine the directionality of error, if present (Hollander and Wolfe, 1973; Utermohle et al., 1983). Technical error of measurement was also calculated because this is a standard measurement in anthropological morphometrics and facilitates comparison between studies (Dahlberg, 1940; Utermohle et al., 1983), although technical error of measurement is strongly correlated with the mean absolute difference (Utermohle et al., 1983). These four measurement indices are not correlated with measurement size (Utermohle et al., 1983), so the variation in sizes of the cuneiforms within and between genera should not affect the error analysis.

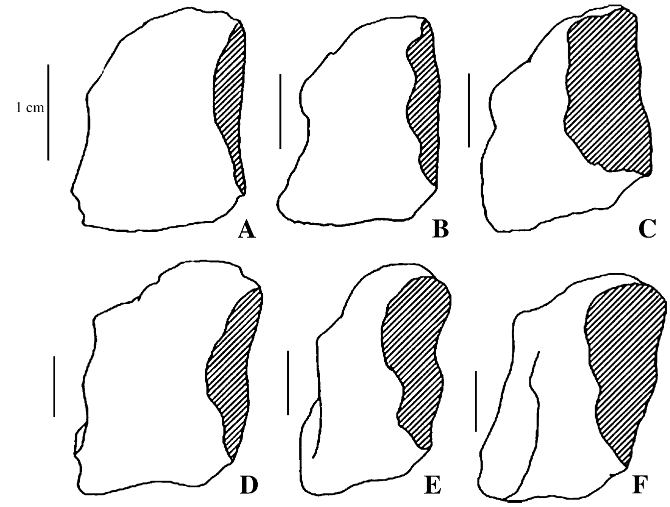

Fig. 1. Outline drawing of the medial cuneiform viewed from its medial surface. A = *H. sapiens*; B = Stw 573c; C = *P. paniscus*; D = *G. gorilla* male; E = *G. gorilla* female; F = *G. gorilla* male.

Results and discussion

The results of the measurement error analysis are listed in Table 1. Sixty-eight percent of all measurements by the two observers are equal at the level of the millimeter. The mean absolute differences and the technical error of measurement values are very low, so the measurement error can be judged to be low. Unless otherwise noted, the magnitude of the differences between the genera in this study are always greater than the absolute measurement error. The Fisher's sign test shows

Table 1
Measurement error analysis results[1]

	Percentage Agreement (%)	Mean Absolute Difference (mm)	Fisher's Sign Test[2]	Technical Error of Measurement (mm)
Total Area	68	0.38	0.00	0.336
Facet Area	68	0.25	2.45^{+}	0.198

$^{+}$Significant at the 0.01 level.
[1] See Utermohle et al. (1983) for definitions of measurement error techniques.
[2] "Distributed as a standard normal deviate (Z score)" (Utermohle et al., 1983:87).