Comment

An early ape shows its hand

When Charles Darwin, Thomas Huxley, and Sir Arthur Keith pondered how and why humans had evolved, they did so without much knowledge of genetics, evolutionary theory or even observations of the behaviour of extant apes. Nevertheless, these deficiencies were dwarfed by their lack of a hominoid fossil record—the single element without which interpreting our own evolution would be simply impossible. For example, only owing to *Australopithecus afarensis* do we now know that at one point our direct ancestor's locomotor skeleton had become fully adapted to upright walking even though its brain was still ape-sized (*contra* Stern 2000; Lovejoy 2005*a*,*b*, 2007). Despite the remarkably extensive insights that such fossils have provided, our ultimate genesis still remains shrouded in the mysterious and enigmatic Miocene—the epoch that preceded the Pliocene and Pleistocene, with their luxuriant human fossil records (White 2002).

The Miocene was pivotal in human evolution. Stretching from approximately 23 to 5 Myr ago, it witnessed an amazing saga: the appearance, florescence and then near disintegration of our ancestral stock. In their heyday, apes (one of which must have been our lineal ancestor) were everywhere—in Africa, Europe and Asia. They came in all sizes, from tiny *Micropithecus* (Harrison 2002) to the enormous *Gigantopithecus* (Kelley 2002). They lived in Turkish and Indopakistani woodlands, in Chinese forests and above Italian swamps. Then nearly all disappeared, leaving behind only a few isolated remnants (today's chimpanzees, gorillas, orang-utans and gibbons) barely eking out survival in tiny forest refugia (Lovejoy 1981; Andrews 1993). And, of course, some itinerant hominid bipeds who would eventually inherit the Earth.

One impressive thing about the fossil record is that even small parts of animals can sometimes reveal a great deal about how and where they lived. A case in point is the report by Almécija *et al.* (2007) in this issue on the fascinating structure of the hand of *Hispanopithecus*, a critically important fossil from the Late Miocene of Spain (Moyà-Solà & Köhler 1996; approx. 9.5 Myr). Obviously, hand structure is a key element in the lives of all primates, especially arboreal apes (Napier 1993), and *Hispanopithecus* was no exception. Its hands, however, prove to be unlike those of any living ape, and in ways that are every bit as unpredicted and surprising as the brain/postcranium mismatch in *A. afarensis*.

At the base of each finger in the primate hand lies a metacarpal. The thumb's metacarpal is mobile and can be pressed against the other four which act more or less as a unit. Each finger is completed by three phalanges (only two in the thumb). When flexed as in grasping, the joints between the finger bones manifest as knuckles. Both the non-thumb metacarpals and phalanges are quite long in

apes—from being only somewhat longer than those of humans in the mostly terrestrial modern gorilla to being enormously so in orang-utans, who live almost exclusively in the higher canopy. No surprise there. All have become elongated to some degree in apes for grasping and hanging as they climb and swing their way through different parts of the canopy (see Begun *et al.* (1994) for thorough discussion).

But not in *Hispanopithecus*. When Almécija *et al.* (2007) compared its hand bones with the specimen's probable body mass, its metacarpals were proportionally as short or even shorter than those of gorillas; yet its phalanges were almost as long as those of orang-utans. This kind of 'disproportion' does not occur in any living ape (or in humans; Schultz 1930). And there is another surprise. The metacarpal heads are markedly constricted, and the small pits where the knuckle joints' collateral ligaments attach (the ones that guide the adjacent phalanx through its range motion much like those of our knees guide our shins) are perched up on the dorsal aspect of the bone. This is yet another unpredicted configuration that permitted the joint to *extend*—to bend in the direction opposite the one we use when we make a fist (flexion). Why?

One possibility, as these authors suggest, is that *Hispanopithecus* still constituted an intermediate step on an apparently somewhat bumpy ride towards becoming orang-utan-like. The Spanish ape's Early Miocene ancestors had been much more monkey-like—smaller and more cursorial, usually negotiating the canopy by running atop large stiff branches and jumping between any gaps—although their loss of a tail, which can serve as a balancing organ, tells us that they had already become more deliberate in such activities than are modern Old World monkeys (Ward *et al.* 1993).

During the Miocene, at least some larger-bodied apes began to rely increasingly on suspension and reaching across such gaps (known as 'bridging'; Cartmill 1985) to avoid difficulties in balancing their greater mass atop compliant limbs. Longer phalanges enabled their fingers to completely encircle smaller secondary supports, and this allowed them to suspend themselves and to negotiate gaps by grasping nearby branches of similar size. But why had they not also elongated their metacarpals as living apes have? Apparently, these 'intermediate apes' had kept the bones of their palms short so that they could still walk atop larger branches as their ancestors had, relying on palmigrady, the practice of supporting one's weight using the wrist and metacarpal heads. Only later did the descendants of *Hispanopithecus* abandon this practice and add long metacarpals to their suspensory arsenal.

Other scenarios of morphological evolution seem equally feasible, however, especially given the fact that no extant hominoid shows any evidence of this metacarpal–phalangeal disproportion. It is therefore possible that the

direct ancestors of living great apes became adapted to suspensory locomotion more directly—by elongating both their metacarpals and phalanges at the same time, and thereby skipping a '*Hispanopithecus* stage'. If so, the Spanish fossil might not preserve a step in the evolution of modern apes. That would make its locomotor behaviour entirely unique—a special adaptation that left no modern descendants. Not unlikely at all, considering that by the end of the Miocene, the Earth had become littered with extinct hominoid lineages and had ceased to be the Planet of the Apes.

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