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Hypothesis: Brain size and skull shape as criteria for a new hominin family tree

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ABSTRACT

Today, gorillas and chimpanzees live in tropical forests, where acid soils do not favor fossilization. It is thus widely believed that there are no fossils of chimpanzees or gorillas. However, four teeth of a 0.5-million-year (Ma)-old chimpanzee were discovered in the rift valley of Kenya (McBrearty and Jablonski, 2005), and a handful of teeth of a 10-Ma-old gorilla-like creature were found in Ethiopia (Suwa et al., 2007), close to the major sites of *Homo* discoveries. These discoveries indicate that chimpanzees and gorillas once shared their range with early *Homo*. However, the thousands of hominin fossils discovered in the past century have all been attributed to the *Homo* line. Thus far, our family tree looks like a bush with many dead-branches. If one admits the possibility that the australopithecines can also be the ancestors of African great apes, one can place *Paranthropus* on the side of gorilla ancestors and divide the remaining *Australopithecus* based on the brain size into the two main lines of humans and chimpanzees, thereby resulting in a coherent family tree.

Introduction

The complete genomes of humans and chimpanzees have been sequenced, which indicates that the divergence of the two lines must be approximately 4.1–6.3-Ma old, and the split leading to the

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gorillas occurred 7–8 Ma ago (Hobolth et al., 2007; Patterson et al., 2006). The analyses of Curnoe and Thorne (2003), examining the estimates of genetic distance, indicate there may have been only four species on the direct line to modern humans and five species in total, contrasting with some current taxonomies, which recognize up to 23 species. Fossils of the proto-chimpanzee and early gorillas must be in the range of 1–8-Ma old, i.e., the same range as australopithecine fossils. The short distance between humans and chimpanzees also places a strict limit on the number of possible evolutionary 'side branches' that might be recognized on the human lineage. It would therefore be surprising if among the thousands of hominin fossils, there are not also some chimpanzee and gorilla ancestors.

Paranthropus as gorilla ancestors

If one admits the possibility that some of the hominid fossils are also gorilla ancestors, then the first candidates are the *Paranthropus*, a group of robust australopithecines that are 1.2–2.7-Ma old. There are three main classes of *Paranthropus*: *P. aethiopicus* (2.7–2.5-Ma old), *P. boisei* (2.5–1.2-Ma old) and *P. robustus* (2.0–1.2-Ma old). Once classified as robust *Australopithecus* or *Zinjanthropus*, these three main classes are now grouped in their own genus *Paranthropus*. It is widely believed that *Paranthropus* are not direct *Homo* ancestors but are a dead branch that disappeared for unknown reasons that might be related to an over-specialization for eating tough food, i.e., they were not adapted to a mixed savannah habitat.

The best way to describe *Paranthropus* is to say "gorilla-like". On their skull, they have a sagittal crest and very robust chewing apparatus, including very large molars and jaw-muscles that extend all the way up to attach to the crest. Broom and Robinson (1950) noted that the molar teeth resembled those of a gorilla more than those of a human. *P. boisei* in eastern Africa had a C4 diet, whereas *P. robustus* in southern Africa had the same C3 diet as gorillas (Cerling et al., 2011; Why *P. boisei* differs is still controversial). *P. robustus* was sexually dimorphic, with males (1.2 m, 54 kg) being larger than females (1.0 m, 40 kg). *P. boisei* was the largest in the family, and it was also sexually dimorphic, with males (1.3 m, 68 kg) being larger than females (1.05 m, 45 kg), which is a sexual dimorphism not yet as strong as in today gorillas, where males can reach twice the weight of females. A recent study has shown that male *Paranthropus* continued to grow well into adulthood, accounting for the sexual dimorphism (Lockwood et al., 2007). To summarize, *Paranthropus* fossils have a gorilla-like skull and very strong chewing apparatus, are robustly built, and exhibit a strong sexual dimorphism that is similar to gorillas. Although these many similarities were noted in original papers, the logical conclusion that *Paranthropus* could be the ancestors of gorillas was not reached. Bridging this gap provides both some descendants for a branch previously considered as a dead-end and ancestors for the gorillas, thereby increasing the coherence of our family tree.

Australopithecus, chimpanzees and humans

The same analysis can be performed for chimpanzees, but it is more difficult to do that than in the case of gorillas. Despite the remarkable developments in molecular biology, over the past three decades, anthropological genetics has had only a limited impact on the systematics in human evolution. It is important to take into account the basic principles of evolutionary genetics: for example, the chimpanzee/human last common ancestor (CHLCA) had as many human-like traits as chimpanzee-like traits and it is difficult to predict which traits were chimp-like, which were human-like and intermediate or different. Evolution progresses by short discrete steps, thus progressing along the chimp line means losing some human-like traits and gaining some chimpanzee traits. Conversely, as we progressed along the human line, we lost chimp-like traits and gained human traits (Jobling et al., 2004). Applied to the question of our family tree, it means that a 4.4-Ma-old fossil such as *Ardipithecus ramidus*, which is very close to the CHLCA (5.2-Ma old), will be very difficult to place in the human line, in the chimp-line or in the common line, just before the split (Lovejoy, 2009). A 5.6-Ma-old fossil such as *Ardipithecus kadabba* or a 6-Ma-old fossil such as Orrorin are presumably before the split, but could be very early on either the chimp-line or on the human line if one refers to the oldest values of 6–7-Ma old for the CHLCA. "*A. ramidus*" means "ape, close to the roots", which is the safest description (Suwa et al., 2009). Toumaï, at 7-Ma old, is also close to the common ancestor with gorillas, as it can be