

Comment on the Paleobiology and Classification of *Ardipithecus ramidus*

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White and colleagues (Research Articles, 2 October 2009, pp. 64–106 and www.sciencemag.org/ardipithecus) reported *Ardipithecus ramidus* as an exclusive member of the human lineage post–African ape divergence. However, their analysis of shared-derived characters provides insufficient evidence of an ancestor-descendant relationship and exclusivity to the hominid lineage. Molecular and anatomical studies rather suggest that *Ar. ramidus* predates the human/African ape divergence.

In a series of research articles in the 2 October 2009 issue of *Science* (1–11), *Ardipithecus ramidus*, a 4.4 million-year-old Pliocene fossil hominoid, is reported to be an exclusive member of the human lineage post-African ape divergence (a hominid in the classic sense). Sufficient support for this claim, however, is lacking. Table 1 in (1) lists the characters common to *Ar. ramidus*, *Australopithecus amanensis*, and *Au. afarensis*, including the character conditions in the hypothesized last common ancestor of humans and African apes (LCA). However, the authors fail to explain how they arrived at these LCA character conditions. In contrast to what the authors describe in other papers (7, 10, 11), the LCA character conditions listed appear to be guided not by systematic analyses, but by Lamarck's evolutionary interpretation of the scala naturae in which chimpanzees embody the primitive, and humans the derived. The authors also fail to show that the common *Ardipithecus/Australopithecus* characters provide evidence of an ancestor-descendant relationship and are exclusive to the hominid lineage and shared-derived with humans.

Fourteen of the 26 characters in table 1 in (1) common to *Ardipithecus* and *Australopithecus* are in the canine/premolar complex. However, reliance on the canine/premolar complex to diagnose hominids (in the classic sense) has misdiagnosed Miocene fossil apes (i.e., *Oreopithecus* and *Ramapithecus*) as early human ancestors (12, 13). Character polarity for this complex is not clear-cut, with many early hominoids, especially females, often showing a humanlike condition. The canine/premolar complex shows such a marked grade of character lability (e.g., conspecific males and females show the diagnostic character differences) that reversals in polarity could have occurred repeatedly over the evolutionary periods necessary for these fossil genera to differentiate (12). Approximation to the humanlike canine/premolar complex, therefore, does not indicate that *Ardipithecus* is a hominid or ancestral to *Australopithecus* any

more than it indicates that *Oreopithecus* and the orangutan-like females of *Sivapithecus*, both of which also share a humanlike premolar/canine complex, are hominids or represent a descendant-ancestor continuum.

Of the remaining characters listed as common to *Ardipithecus* and *Australopithecus*, none of the eight postcranial characters (sagittal iliac/isthmus orientation, slightly broadened iliac breadth, strong anterior inferior iliac spine formed by separate ossification center, robust second metatarsal base and shaft, dorsally domed second to fifth metatarsal heads, upwardly canted proximal foot phalanges, and short iliac isthmus and pubic symphysis outline), nor the other four cranio-dental characters [anterior basion position (14), advanced cranial flexion, and broad lower molars and mandibular corpus] are shown by systematic comparisons to be exclusive to humans or share-derived with humans. Nearly all are quantitative characters that appear in early hominoids (i.e., *Oreopithecus* and *Dryopithecus*) and have appeared independently in other primate lineages, and character simplicity is such that parallelisms or reversals in polarity cannot be demonstrated (12, 15). Moreover, attempts to link *Ar. ramidus* to an exclusive human lineage by pointing to suspected facultative bipedal characters in the foot (9) are not convincing (16). All of the *Ar. ramidus* bipedal characters cited also serve the mechanical requisites of quadrupedality, and in the case of *Ar. ramidus* foot-segment proportions, find their closest functional analog to those of gorillas, a terrestrial or semiterrestrial quadruped and not a facultative or habitual biped (17).

The diagnostic shared-derived characters of human and African apes have been well documented in the literature for more than a century (15, 18). The completeness of the *Ar. ramidus* wrist (7) and cranial remains (petrosal, ear, and basicrania) (5), where many of the exclusive hominid characters reside, could be used to show whether *Ar. ramidus* is or is not a hominid. A non-articular ulnar styloid process, a fused os centrale, and what appears from the photograph as a reduced triquetrum with a possible proximal articular surface (7) suggest that *Ardipithecus* belongs

to a common human/African ape lineage post-orangutan divergence. A continuous sphenopetrous/squamotympanic fissure preventing entoglenoid/tympanic fusion, a posteriorly placed occipital condyle relative to the condylar canal (5), a small dorsally disposed capitate head, short metacarpals relative to digital ray length, and palmigrade weight-bearing joint postures (7) further suggest that *Ar. ramidus* may be a primitive member of this lineage.

Over the past 40 years, a multitude of independent biomolecular studies based on different methods, some analyzing millions of DNA base-pair sequences, have arrived at a minimum human/African ape divergence date of ~3 to 5 million years before the present (19–26)—a date that accords well with those based on comparative anatomical studies of living and fossil hominoids (15). With a 4.4-million-year geologic age (1), *Ar. ramidus* probably predates the human and African ape divergence. Even if *Ar. ramidus* was an exclusive member of the human, chimpanzee, or gorilla lineages, given its proximity in time to this divergence date, it would be difficult to unambiguously recognize it as such (12, 27, 28). It therefore seems premature to use *Ar. ramidus* to directly infer LCA ecology and locomotor anatomy or the origin of supposed human social systems, selection strategies, and sexual behaviors. Human evolutionary studies are not a new science where every new find revolutionizes interpretations of our past. In fact, what is known of LCA anatomy and ecology is based largely on comparative studies of human and nonhuman primates. These same studies allow us to classify fossils and recognize ancestors. A purported fossil ancestor that must overturn nearly all we know about our evolution to fit into our lineage is unlikely to be such an ancestor. In this regard, it is curious that in a century-old race for superlative hominid fossils on a continent currently populated with African apes, we consistently unearth nearly complete hominid ancestors and have yet to recognize even a small fragment of a bona fide chimpanzee or gorilla ancestor (29).

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- diameter (5). As such, it is not clear if the high anterior basion values reported for *Ar. ramidus* and the low ones reported in chimpanzees are not the results of differences in bicarotid diameter. Unfortunately, the authors do not report the human condition or that of the other living and fossil apes.
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