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 anamensis, 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 hominoids (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 symphysis outline), nor the other four craniodental 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 shared-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, 13). Moreover, attempts to link Ar. ramidus to an exclusive human lineage by pointing to suspected facultative bipedal characters in the foot (16) 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 basioccipital) (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 entognathous/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 molecular 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).

References and Notes
14. This character is quantified as the mid sagittal distance from basil to a frontal plane passing through the two carpoid foramina in percentage of bicoronal foramina.
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.


16. Authors also note pelvic and femoral bipedal characters (8), but given a very fragmentary femur and a markedly crushed os coxa, these are open to interpretation.


29. Two incisors and a molar fragment from Homo bearing deposits ~500,000 years in age have been assigned to *Pan* (20) without any diagnostic hominoid morphology and based only on their cursory similarity to *Pan* and distinctiveness from contemporary *Homo*. Had these fragments come from older deposits where the human lineage was not as easily recognizable and could be confused with nonhominid catarrhines, they could have been labeled human ancestors, as has been done at different times with many Miocene hominoid fossils (13).

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