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New fossils of *Australopithecus anamensis* from Kanapoi, West Turkana, Kenya (2003–2008)

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ABSTRACT

Renewed fieldwork from 2003 through 2008 at the *Australopithecus anamensis* type-site of Kanapoi, Kenya, yielded nine new fossils attributable to this species. These fossils all date to between 4.195 and 4.108 million years ago. Most were recovered from the lower fluvial sequence at the site, with one from the lacustrine sequence deltaic sands that overlie the lower fluvial deposits but are still below the Kanapoi Tuff. The new specimens include a partial edentulous mandible, partial maxillary dentition, two partial mandibular dentitions, and five isolated teeth. The new Kanapoi hominin fossils increase the sample known from the earliest *Australopithecus*, and provide new insights into morphology within this taxon. They support the distinctiveness of the early *A. anamensis* fossils relative to earlier hominins and to the later *Australopithecus afarensis*. The new fossils do not appreciably extend the range of observed variation in *A. anamensis* from Kanapoi, with the exception of some slightly larger molars, and a canine tooth root that is the largest in the hominin fossil record. All of the Kanapoi hominins share a distinctive morphology of the canine–premolar complex, typical early hominin low canine crowns but with mesiodistally longer honing teeth than seen in *A. afarensis*, and large, probably dimorphic, canine tooth roots. The new Kanapoi specimens support the observation that canine crown height, morphology, root size and dimorphism were not altered from a primitive ape-like condition as part of a single event in human evolution, and that there may have been an adaptive difference in canine function between *A. anamensis* and *A. afarensis*.

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Introduction

From 2003 to 2008, a field team from the National Museums of Kenya led by one of us (FKM) recovered several new hominin fossils from Kanapoi, Kenya. These specimens are attributed to *Australopithecus anamensis*, because not only is this the only hominin known from Kanapoi, but their morphology matches previously described Kanapoi *A. anamensis* fossils (Leakey et al., 1998; Ward et al., 1999a, 2001). The new fossils presented here include three associated partial dentitions and several isolated teeth. They expand the hypodigm of *A. anamensis* and provide an opportunity to evaluate the variation and dental morphology and proportions within this taxon. The new fossils include the largest canine tooth root currently known in the hominin fossil record.

Australopithecus anamensis was originally announced in 1995 by Leakey et al. based on fossils from Kanapoi, and additional specimens were described subsequently (Leakey et al., 1998; Ward et al., 1999a, 2001). Kanapoi is the type-site for *A. anamensis*, and has yielded the majority of the fossils attributed to this species ($n = 69$ including the new specimens presented here). The published Kanapoi *A. anamensis* sample includes three mandibles, a partial temporal bone, a maxilla, at least eight associated partial juvenile and adult dentitions, more than 20 isolated teeth, a partial humerus, manual phalanx, capitate and tibia (Ward et al., 2001). In addition, Kanapoi has yielded more than 3800 other micro- and macrofaunal specimens (Harris et al., 2003; Winkler, 2003; Manthi, 2006, 2008).

The *A. anamensis* hypodigm as originally described also includes slightly younger specimens from Allia Bay, Kenya (3.9 Ma [millions of years ago]), including a nearly complete radius, as well as some maxillary fragments and isolated teeth (Heinrich, 1993; Coffing et al., 1994; Ward et al., 1999a, 2001). Thirty additional *A. anamensis* fossils were announced more recently from the

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Ethiopian site of Asa Issie (4.12 Ma, White et al., 2006), including a partial maxilla, two associated dentitions, mandible fragment, isolated teeth, plus a partial metatarsal, eroded distal pedal phalanx, manual phalanx, four vertebral fossils and partial femur. Most of these postcranial fossils have not yet been figured or described. A partial heavily worn dentition and isolated lower fourth premolar from Fejej, Ethiopia (Fleagle et al., 1991) is dated from about 4.1 (4.2–3.7) Ma and in preserved morphology more closely resembles those of *A. anamensis* than any other species (see Ward et al., 2010; Manthi et al., 2012, also discussions in; Delson et al., 2000; White, 2002; MacLatchy et al., 2010; Wood and Leakey, 2012). Hominins from the 3.76–3.72 Ma site of Woranso-Mille, Ethiopia (Deino et al., 2010) have also provisionally been attributed to *A. anamensis* (Haile-Selassie, 2010; Haile-Selassie et al., 2010).

Kanapoi is the earliest occurrence of *A. anamensis*, making the Kanapoi hominins the earliest *Australopithecus*. The sediments at Kanapoi were initially dated radiometrically to between 4.17 and 4.07 Ma (Leakey et al., 1995; Feibel, 2003; Leakey and Walker, 2003) but were revised to between 4.195 and 4.108 Ma (McDougall and Brown, 2008). With only one exception (mandible KNM-KP 29287) (Leakey et al., 1998; Ward et al., 2001), most published Kanapoi hominin fossils date to the earliest part of this sequence (McDougall and Brown, 2008).

Australopithecus anamensis predates *Australopithecus afarensis* by 600,000 years. *Australopithecus afarensis* is known from fossils dated to as early as 3.6 Ma, but is well known only starting at 3.4 Ma (for comprehensive review see Kimbel and Delezene, 2009). It appears likely that *A. anamensis* represents the ancestor to *A. afarensis*, and that these species represent portions of an anagenic lineage (Kimbel et al., 2006); see also (Haile-Selassie, 2010; Haile-Selassie et al., 2010). *Australopithecus anamensis* site samples are morphologically continuous with those of *A. afarensis* from Laetoli (3.6 Ma), Maka (3.4 Ma) (White et al., 1993), and Hadar (3.4–3.0 Ma) (Leakey et al., 1995; Wolpoff, 1999; Ward et al., 1999a, 2001; White, 2002; Kimbel et al., 2006; White et al., 2006, 2009; Haile-Selassie, 2010; Haile-Selassie et al., 2010). Because these samples are most parsimoniously interpreted as a single evolving lineage, it could be argued that *A. anamensis* be subsumed into the *A. afarensis* hypodigm (see discussions in Kimbel et al., 2006; Haile-Selassie et al., 2010). However, for pragmatic reasons we retain both species names to simplify discussion and provide a basis for comparison of fossils from different sites, and because *A. anamensis* is morphologically and perhaps adaptively distinct, especially in the earliest time periods (see also Leakey et al., 1995; Ward et al., 1999a, 2001; Grine et al., 2006; Kimbel et al., 2006; White et al., 2006; Haile-Selassie, 2010; Ward et al., 2010; Manthi et al., 2012).

In fact, although *A. anamensis* shares with *A. afarensis* the overall bauplan of *Australopithecus*, these species differ in many characters for which both species are known. Despite being known from several sites in two countries, *A. anamensis* remains “woefully underrepresented” (White et al., 2009: 84) in the fossil record, so that the extent of the similarities and differences between these species remain poorly understood. Thus, the new fossils are of particular significance in understanding the origins and early evolution of *Australopithecus*.

Little is known about the postcranial morphology of *A. anamensis*, although it appears to have been fully bipedal. The Asa Issie femur is described as equivalent to those attributed to *A. afarensis* (White et al., 2006), as is the Kanapoi tibia that bears the orthogonal shank characteristic of all hominins (Latimer et al., 1987; Ward et al., 1999a; DeSilva, 2009), differing from the somewhat verus shank of *Ardipithecus ramidus* (Lovejoy et al., 2009a) and that of apes. There may be some differences in upper limb morphology, however, that may hint at differences in locomotor and/or manipulatory function. While the Allia Bay radius and Kanapoi humerus and phalanx are long and curved like those of *A. afarensis* (Heinrich, 1993; Lague and Jungers, 1996; Ward et al., 2001; Patel, 2005), a middle phalanx from Asa Issie is described as being longer than those from Hadar (White et al., 2006), and the Kanapoi capitate has laterally-facing facets for MC2 as in extant African apes, unlike in *Proconsul*, *Ardipithecus* and all other hominins (Leakey et al., 1998; Lovejoy et al., 2009b; Macho et al., 2010, and see; McHenry, 1983; Beard et al., 1986; Ward et al., 1999b). Available data about forelimb morphology in *A. anamensis* are minimal, and at present, it appears that upright bipedal locomotion was indeed associated with the origins of *Australopithecus*, even pending the potential differences between *A. anamensis* and *A. afarensis* in the upper limb.

Unlike the postcrania, the jaws and teeth of *A. anamensis* and *A. afarensis* are well enough known to enable significant comparisons. Like *A. afarensis*, *Australopithecus anamensis* had larger, thicker-enameled, low-crowned molars than those of African apes or *Ardipithecus* (Suwa et al., 2009a,b; Ward et al., 2001; see also Ungar, 2004 for discussion of molar morphology and masticatory abilities), likely signaling the ability to process harder foods than these earlier hominins (Grine et al., 2012). This may have opened up wider ecological niches for australopiths, possibly related to exploiting more open habitats, which may in turn be related to the origins of the genus (White et al., 2000). *Australopithecus afarensis* appears to have been further specialized for increased masticatory strength with taller molar crowns and a more robust mandibular symphysis (Leakey et al., 1995; Ward et al., 1999a, 2001; Teaford and Ungar, 2000; Macho et al., 2005). *Australopithecus afarensis* also tends to have more posteriorly divergent toothrows than does *A. anamensis*, extant apes and *Ardipithecus* (Puech, 1986; Puech et al., 1986; Ward et al., 2001; Suwa et al., 2009a,b) that could potentially decrease symphyseal stresses during mastication (Hylander, 1984, 1985; Ravosa, 2000). It is notable then, that symphyseal robusticity is greater in *A. afarensis* than *A. anamensis*, despite its more divergent toothrows. Overall, dentognathic morphology would suggest that heavier mastication compared with earlier apes did characterize the origin of *Australopithecus* (see also Macho et al., 2005) but that this adaptation continued to be developed throughout the evolution of *A. afarensis*.

Despite the apparent morphological adaptations to heavier mastication in *A. anamensis* compared with earlier hominins, molar microwear taken from the occlusal surfaces of the teeth shows no evidence of the consumption of hard, brittle foods, so if the morphological adaptations to heavier mastication are indeed adaptations to consuming such items, the hominins may have done so as fallback foods only (Grine et al., 2012). *Australopithecus anamensis* has been reported to have a higher striation density on the buccal surfaces of its molar teeth than did *A. afarensis*, which was interpreted to indicate a greater proportion of hard and/or brittle foods in its diet than in *A. afarensis* (Estebaranz et al., 2012). However, as the nonocclusal surfaces of the teeth are not involved in food processing, the links between diet and buccal microwear are less well established than those involving occlusal microwear (review in Grine et al., 2012). *Australopithecus anamensis* and *A. afarensis* have been reported to display similar patterns of molar microwear, suggesting that the material properties of the foods commonly masticated were not very different; an observation that does not support the hypothesis that there was increasing adaptation to consuming hard foot items (Grine et al., 2006, 2012; Ungar et al., 2010). If microwear instead tracked the amount of grit in the diet, rather than the properties of foods themselves, however, it could be that similarities in microwear between these species tracked similarities in environment and terrestrial habitus (Lucas et al., 2013). Despite the similarities in molar microwear, the isotopic signatures in the tooth enamel differ between these species, with *A. anamensis*

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