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## Late Miocene hominin teeth from the Gona Paleoanthropological Research Project area, Afar, Ethiopia



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## ABSTRACT

Since 2000, significant collections of Latest Miocene hominin fossils have been recovered from Chad, Kenya, and Ethiopia. These fossils have provided a better understanding of earliest hominin biology and context. Here, we describe five hominin teeth from two periods (ca. 5.4 Million-years-ago and ca. 6.3 Ma) that were recovered from the Adu-Asa Formation in the Gona Paleoanthropological Research Project area in the Afar, Ethiopia that we assign to either *Hominina, gen. et sp. indet.* or *Ardipithecus kadabba*. These specimens are compared with extant African ape and other Latest Miocene and Early Pliocene hominin teeth. The derived morphology of the large, non-sectorial maxillary canine and mandibular third premolar links them with later hominins and they are phenetically distinguishable and thus phylogenetically distinct from extant apes.

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## Introduction

With the announcement of the 3.9–4.2 million-year-old (Ma) *Australopithecus anamensis* (Leakey et al., 1995, 1998; White et al., 2006), the 4.4 Ma *Ardipithecus ramidus* (White et al., 1994, 1995, 1996; WoldeGabriel et al., 1994; Renne et al., 1999; White et al., 2009; Suwa et al., 2009) fossils, and the discovery of even more ancient Late Miocene age hominins (6–7 Ma *Sahelanthropus tchadensis* (Brunet et al., 2002, 2005; Lebatard et al., 2008), 5.6–6.0 Ma *Orrorin tugenensis* (Senut et al., 2001; Pickford and Senut, 2004;

Sawada et al., 2002), the 5.2–5.8 Ma *Ardipithecus kadabba* (Haile-Selassie, 2001a,b; Haile-Selassie et al., 2004; WoldeGabriel et al., 2001), and the Late Miocene fossils from Lothagam (Leakey and Walker, 2003)), our understanding of the earliest hominin biogeography, ecological context, and anatomy has improved substantially. These collections, while highly informative, are still quite few in number and additional information of the biology and context of the hominins from this period post-dating the human-chimpanzee divergence (Chen and Li, 2001) is necessary.

The discovery of these Late Miocene teeth has raised a number of taxonomic and phylogenetic questions. For example, the presence of three Late Miocene named groups (*S. tchadensis*, *O. tugenensis*, and *Ardipithecus kadabba*) raises the issue of whether there is a 'bushiness' to the origins of our lineage or whether they are part of a common lineage. The identification of *Ardipithecus* (White et al., 1994, 1995; Haile-Selassie et al., 2001a,b) as a hominin has also been challenged (Sarmiento, 2010), with some (e.g., Senut

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et al., 2001) linking it uniquely with the extant chimpanzees. Here, we describe five recently recovered hominin teeth from two time periods (ca. 5.4 Ma and 6.3 Ma) within the Adu-Asa Formation in the Gona Project area in Ethiopia. These teeth provide additional evidence for the hominin status of *Ardipithecus*.

### Gona Paleoanthropological Research Project overview

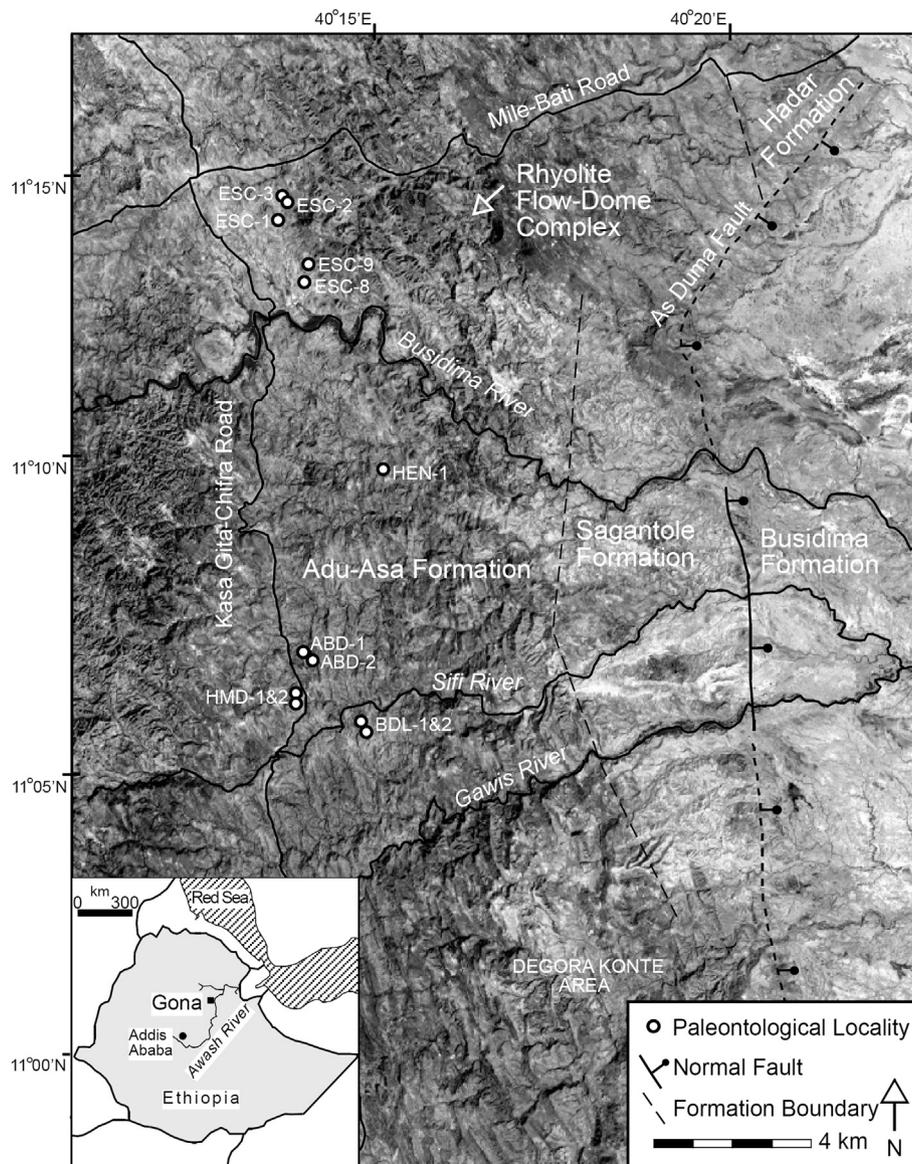
In 2001, Gona Paleoanthropological Research Project members began surveying sedimentary deposits interbedded with serial basalt flows at the edge of the Western Ethiopian Escarpment in the Afar, Ethiopia (Fig. 1). Research goals for this area were to document the presence of hominins and other fauna in these deposits, collect data for paleoenvironmental reconstruction, and develop chronometric control of the sediments. During the course of nine field seasons, 26 paleontological sites were discovered and approximately 1000 fossil specimens were collected, including five hominin teeth from four localities. These hominin teeth are all surface finds. At the time of discovery, all hominin sites were crawled by

the team and all of the fossils at those areas collected. Locality ESC2 had the surface lag removed to facilitate erosion. These sites have been visited annually (through February 2013).

Collecting regions in the Gona Project area are assigned two or three letter designations describing them (e.g., ESC = Escarpment, and ABD = Asbole [pronounced 'as-bō-lee'] Dora). Each locality in the named regions is numbered serially as it was found. Individual fossils were assigned catalogue numbers in sequence within a site with the preface 'P' to indicate it is a paleontological specimen. All sites are mapped on 1:60,000 air photos and 1:50,000 topographic maps, both provided by the Ethiopian Mapping Authority. GPS coordinates for the fossil sites are recorded using the UTM coordinate system based on the Adindan datum.

### Geology

The fossil sites described here come from the Adu-Asa Formation, which crops out across the western third of the Gona Paleoanthropological Research Project area (Fig. 1). Our current estimate



**Figure 1.** Figure showing geologic formations, paleontologic localities, and key geographic features of the western part of the Gona Paleoanthropological Research Project area.

of the thickness of the Adu-Asa Formation is  $\geq 185$  m (Kleinsasser et al., 2008). This formation is dominated by fine-grained fluvial and lacustrine sediments, intercalated with stacked basaltic lava flows, and a single rhyolite flow–dome complex near the top of the section in the northern Gona Project. To the east, the formation is capped by a series of topographically high-standing basalt flows that divide the Adu-Asa Formation from the younger and apparently conformable Sagantole Formation (Quade et al., 2008). Extensive basalt flows underlie the Adu-Asa Formation and form the functional lower limit for the Adu-Asa Formation at Gona. The beds are tilted 5–20°E, and hence deposits tend to become younger eastward. The Adu-Asa Formation is extensively faulted with small-scale normal faults, producing much repetition of section. This makes correlation between exposed sections difficult, and the use of tephra composition has proved vital for correlation between fossil-bearing sections. A detailed discussion of the geology of Gona has been presented in Quade et al. (2008), and of the Adu-Asa Formation at Gona in Kleinsasser et al. (2008).

All fossil sites are located within the sedimentary intervals of the Adu-Asa Formation. The dates given for each hominin site in the composite stratigraphic section (see Kleinsasser et al., 2008 for details) assume a constant rate of sedimentation between units of known age. Of chief importance to constraining the hominin sites are the dates on samples of the Bodele Tuffs ( $6.24 \pm 0.19$  Ma;  $6.48 \pm 0.22$  Ma) and the Kobo'o Tuff ( $5.44 \pm 0.06$  Ma) (Appendix 1). The oldest site, ABD1, lies atop the Bodele Tuffs and below the Sifi Tuff in sandstones below a diatomite layer. As the mean ages from the Bodele Tuffs average slightly older than 6.3 Ma, we assign an age of ca. 6.3 Ma to the ABD1 locality.

The fossils from the ESC sites (–2, –3, and –8) are stratigraphically equivalent and are exposed ca. 7 m below the porphyritic basalt (see Kleinsasser et al., 2008). At ESC3, there is an altered tuff below the level of the fossils, while the fossils from ESC8 are from a stratigraphic level between an aphanitic basalt flow below and the overlying porphyritic basalt flow. Kleinsasser et al. (2008) speculate that the altered tuff below ESC3 may be the Kobo'o Tuff, which would place the ESC sites between the level of the Kobo'o Tuff and the porphyritic basalt. Multiple outcrops of the Kobo'o Tuff occur near many of the ESC sites, so this scenario is

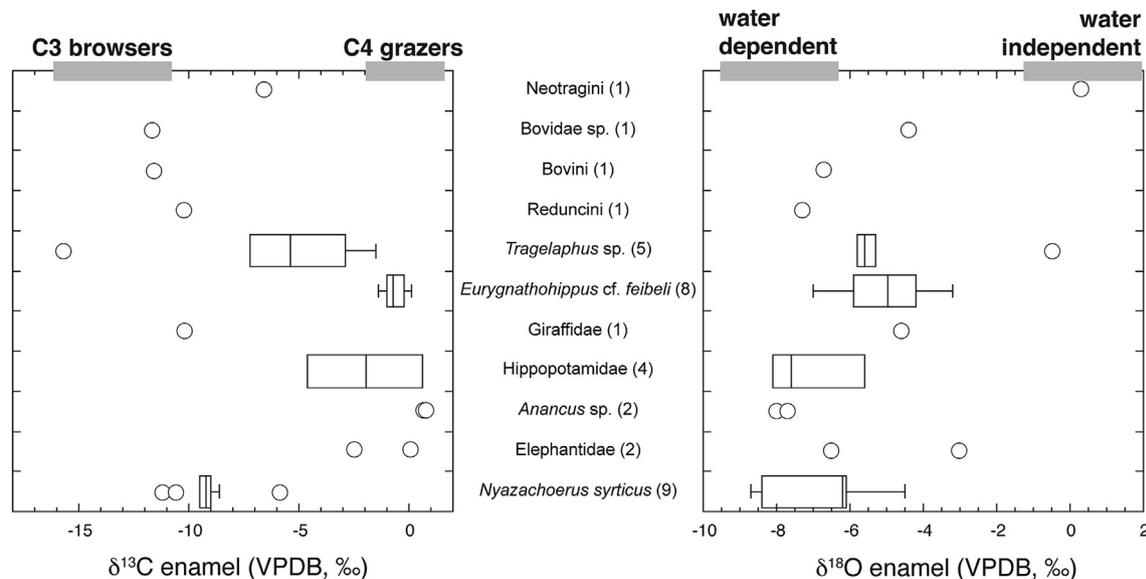
plausible. Based on this evidence, we estimate the age of the ESC sites to be 5.4 Ma (Kleinsasser et al., 2008).

The majority of fossil accumulations in the Adu-Asa Formation are associated with fluvial deposits and outcrop on deflationary surfaces. The concentrations of fossils are commonly localized to areas less than 600 m<sup>2</sup>. The faunal assemblages of the Adu-Asa Formation are dominated by isolated teeth, although cranial and postcranial fragments, tooth rows, and horn cores are present in the assemblages. Preservation of fossils is good with some signs of weathering from recent surface exposure. The fossils do not show signs of fluvial transport.

### Habitat and paleoecology

Combined sedimentologic and isotopic evidence depict a paleoenvironmental setting for the Adu-Asa Formation of woodlands or grassy woodlands in a well-watered landscape associated with low-energy streams and small lakes set among the volcanic centers and basalt flows in the dynamic rift margin (Quade et al., 2008; Kleinsasser et al., 2008; Levin et al., 2008). This area lacks calcareous paleosols, precluding the use of their isotopic composition in paleoenvironmental reconstruction. The lack of soil carbonate formation suggests the short residence time of land surfaces and a relatively mesic setting. These short-lived surfaces were depositional corridors that likely provided a unique set of resources (e.g. water and vegetation) relative to what would have been available on the volcanic terrains in the immediate vicinity. The fauna associated with the rivers and shallow lakes in these depositional corridors indicate both terrestrial and aquatic elements. A list of the preliminary faunal identifications is provided below (Appendix 2). The identified fauna support the Late Miocene age estimate.

Stable carbon isotope analyses of dental enamel of the major herbivores indicate that the Adu-Asa fauna had access to a range of C<sub>3</sub> (browse) and C<sub>4</sub> (graze) resources (Fig. 2), as discussed by Levin et al. (2008). The carbon isotopes results for some taxa, such as *Eurygnathohippus* cf. *feibeli* and the proboscideans, indicate diets that were restricted to C<sub>4</sub> graze. In particular, a large sample ( $n = 8$ ) from *Eurygnathohippus* cf. *feibeli* shows little variation (average  $\delta^{13}\text{C} -0.6 \pm 0.5\text{‰}$ ) and suggests that there was enough C<sub>4</sub> grass on



**Figure 2.** Box plots of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of fossil teeth from the Adu-Asa Formation. Median values are marked by a vertical line within the box, the edges of the boxes represent quartile values, the horizontal lines indicate the range, and outliers are plotted as circles.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for taxa with three or fewer samples are plotted as circles. Number of teeth sampled is indicated in parentheses next to taxon name.

the landscape to support committed grazers. Other fauna, such as *Nyanzachoerus syrticus* and some bovids indicate a reliance on C<sub>3</sub> vegetation, which is typical of East African suids and bovids from the late Miocene (Harris and Cerling, 2002; Cerling et al., 2003). The presence of herbivores with both C<sub>3</sub> and C<sub>4</sub> dominated diets suggests that a woodland or grassy-woodland, not a closed-canopy forest, was prevalent during the deposition of the Adu-Asa Formation (Levin et al., 2008).

Oxygen isotope ratios from the Adu-Asa fauna are reported but not discussed by Levin et al. (2008). The oxygen isotopic results of tooth enamel from the Adu-Asa fauna are plotted in Fig. 2. There are not enough samples to quantitatively estimate aridity as proposed by Levin et al. (2006), however the results are worth noting and suggest the potential for continued work. As with most modern and fossil assemblages from East Africa (e.g., Bocherens et al. 1996; Cerling et al., 2003; Levin et al., 2006), isotopic results from hippopotamids and proboscideans in the Adu-Asa Formation yield values that are among the lowest oxygen isotope values for the assemblage and indicate their dependence on water. *N. syrticus*, also plots at the lower end of this oxygen isotope spectrum, making it comparable to modern bushpigs (*Potamochoerus larvatus*) which yield oxygen isotope values similar to hippopotamids from the same environment, but unlike modern warthogs (*Phacochoerus africanus*) which yield oxygen isotope values that are elevated relative to hippopotamids (Levin et al., 2006). Oxygen isotopic results from the Adu-Asa bovid and giraffid samples are not yet conclusive, given the smaller number of samples from each taxon represented. The high oxygen isotopic values of two bovid individuals suggest that at least some animals in the assemblage tolerated considerable water stress, although additional data are needed to understand the full implications of these results.

### Descriptions of hominin teeth

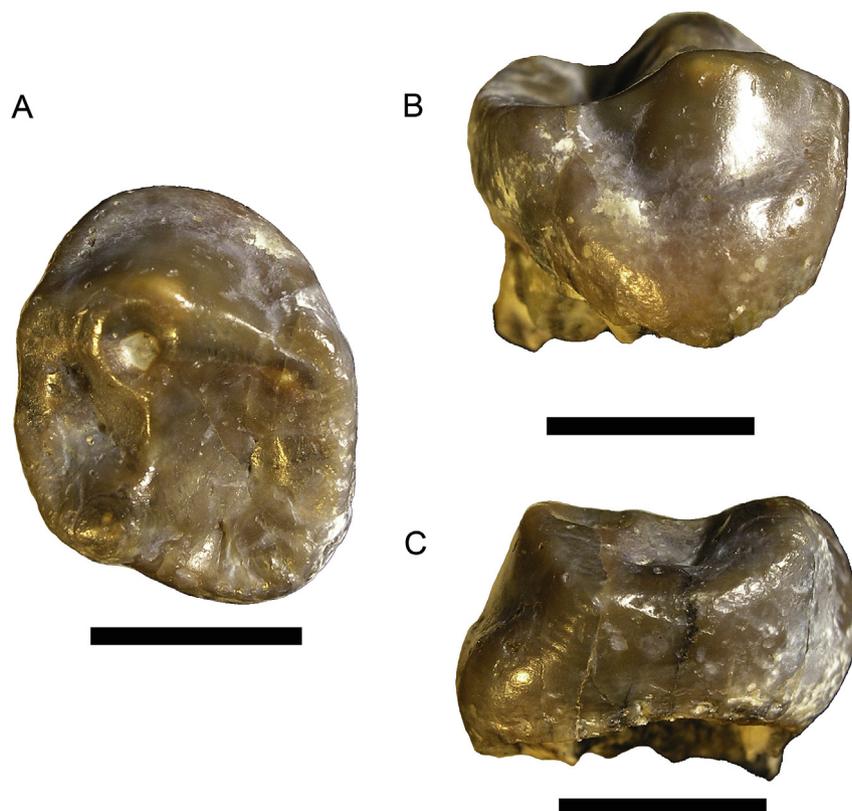
Abbreviations used in this paper are: BL – buccolingual; BLdis – buccolingual distal half (metacone – hypocone breadth on maxillary molars); BLmes – buccolingual mesial half (paracone – protocone breadth on maxillary molars); DEJ – dentino-enamel junction; DMR – distal marginal ridge; HY – hypocone; IPCF – interproximal contact facet; LL – labiolingual; MD – mesiodistal; ME – metacone; MED – metaconid; MMR – mesial marginal ridge; PA – paracone; PR – protocone; PRD – protoconid; nd – no data. All measurements are in millimeters. Measurements in parentheses are estimates.

**ABD1/P1:** Mandibular right fourth premolar crown (Fig. 3).

Taxonomic assignment: cf. *Ardipithecus kadabba*.

This tooth is a lightly weathered, somewhat worn, nearly complete crown with the roots broken off at the cervix. The MD maximum length is 8.3 mm and the BL breadth is 9.9 mm. In occlusal view, this tooth looks like a rounded parallelogram and the major axis passes through the mesio-buccal and disto-lingual corners. The transverse ridge (protocristid) is a well defined crest sharpened by wear that connects the PRD and MED and divides the crown into two unequal portions. The PRD shows horizontally oriented wear with cupping of the cusp apex exposing a <1 mm dentinal window. The MED is less worn (apically rounded) and now projects occlusally to the same degree as the PRD. The slightly worn MMR is quite broad (ca. 1.3 mm). The distal fovea has a short transverse linear depression forming its floor.

The buccal surface has mesial and distal vertical ridges that pass towards the cervix where they join forming a buccal cervical bulge (small buccal cingulum). In buccal view, it is clear that there are separate mesial and distal occlusal wear planes and that the distal



**Figure 3.** Mandibular fourth premolar. ABD1/P1: Mandibular Right Fourth Premolar crown. A. Occlusal view. B. Buccal view. C. Mesial view. Scale bar is 10 mm. For color images of the fossils, see the online version.

plane (talonid) is lower forming a step between the two. The mesial and distal margins are oriented vertically and the buccal margin is angled slightly supero-lingually.

A root fragment ca. 2.5 mm long is retained on the distolingual corner. The cervical cross-section is a MD flattened triangle in outline. Three pulp apices are visible on the superior surface of the pulp chamber. Although broken, the root fragment orientation and pulp chamber roof are suggestive of a divergence of the roots perhaps reflecting a multiple root system.

The fragmentary state and paucity of similarly aged materials requires caution in making a taxonomic assignment of this specimen.

**ESC2/P76:** Maxillary right canine (Fig. 4)

Taxonomic assignment: *Ardipithecus kadabba*

This large tooth was found in three conjoining fragments within a one meter square area. Surface preservation is very good although there has been some post-fossilization damage to the tooth including small etching pits and chipping of the occlusal margins. A series of shallow hypoplastic lines are present across the labial face and, except where removed by polishing, perikymata are present throughout. The basal crown dimensions are 10.8 mm (maximum) and 9.3 mm (minimum) with cervical dimensions of 10.2 mm and 7.7 mm. This tooth has an oblique, distally oriented wear facet (8.5 mm × 5.0 mm) on the distolingual marginal face of the crown. This wear has removed a significant amount of the crown height and the wear plane nearly intersects the distal cervix of the crown removing most of the distal tubercle. An enamel chip on the labial surface of the crown has removed the external cortex of the enamel revealing the underlying transverse enamel structure. Adjacent to this on the lingual occlusal surface are two premortem chips with polished margins. Polish is found on the more occlusal portions of the labial face and throughout the

lingual surface. There is a distal IPCF but no mesial IPCF indicating a C–I<sup>2</sup> diastema.

In occlusal view, the cervical outline is shaped like a rounded rectangle. The tooth has the characteristic primitive hominin trait of a very low mesial ‘shoulder’ – slightly lower than in *Ar. ramidus* (see below). Occlusal to this mesial ‘shoulder’, the mesial cuspal ridge angles disto-occlusally indicating that the crown would have been projecting but not to the same degree as in extant female chimpanzees. The mesial occlusal ridge shows polish but no defined wear facet. There is a mesial marginal ridge that contributes to the ‘shoulder’ that encloses a small lingually positioned pit. This small pit is perhaps comparable to the mesial fissure in the African apes but it is substantially reduced in size and more lingually positioned in the ESC2/P76 canine and as in other hominins. A well-defined mesially positioned lingual bulge (lingual pillar) is present. Along the lingual cervical margin there is a small well-defined swelling. The nature and extent of the distal ‘shoulder’ is incompletely known due to marked occlusal wear.

The root is long (labial cervical margin to apex: 26.5 mm) and robust (cervical maximum breadth: 10.4 mm; cervical minimal breadth: 8.1 mm). The mesial and distal surfaces of the longitudinally curved root are flat. The labial surface has a groove running throughout much of its length and the lingual surface is rounded. The root apex is blunt. Discoloration and surface erosion around the radicular cervix is clearly present and this is associated with alveolar and gingival recession in extant hominoids.

**ESC2/P430:** Maxillary left third molar (Fig. 5).

Taxonomic assignment: *Ardipithecus kadabba*.

This is a weathered tooth including portions of both the crown and root. The crown exhibits areas of demineralization and pits from root etching throughout although the crown has a small area of black-colored occlusal enamel on the protocone that retains



**Figure 4.** ESC2/P76 Maxillary Right Canine. A. Labial view. B. Disto-lingual view. C. Mesial view. D. Oblique labial view. In C, note both the bulge on the lingual face of the tooth and the highly invaginated course of the mesial dentino-enamel junction. In A & D, note the cervical placement of the distal ‘shoulder’.



**Figure 5.** ESC2/P430 Maxillary Left Third Molar. Left: Occlusal view. Buccal side is up and mesial surface is to the left. Middle: Mesial view. The buccal surface is to the left. Right: Radicular view. The buccal surface is up and the mesial surface faces to the right. Scale bar is 5 mm.

**Table 1**  
The late Miocene Adu-Asa Formation (Gona Project area) teeth.

Specimen number	Tooth	MD max	BL max	Age (Ma)	Taxon	Finder
ABD1/P1	RP <sub>4</sub>	8.3	9.9	ca. 6.3	cf. <i>Ar. kadabba</i>	Mohammed Ahmedin
ESC2/P76	RC <sup>x</sup>	10.8*	9.3**	ca. 5.4	<i>Ardipithecus kadabba</i>	Yasin Ismail Mohammed
ESC2/P430	LM <sup>3</sup>	(10.4)	(11.6)	ca.5.4	<i>Ardipithecus kadabba</i>	Yasin Ismail Mohammed
ESC3/P50	LP <sub>3</sub>	8.3**	9.2*	ca. 5.4	<i>Ardipithecus kadabba</i>	Wegenu Amerga
ESC8/P1	LM <sup>1/2</sup>	10.6	12.5	ca. 5.4	<i>Ardipithecus kadabba</i>	Wegenu Amerga

Position: L = Left, R = Right, C=Canine, P=Premolar, M = Molar, Superscript = maxillary, Subscript = mandibular. MD (mesio-distal) and BL (bucco-lingual) measurements in millimeters. For canine and mandibular P3, \*maximum and \*\*minimum basal crown dimensions are reported. Age is in million years (Kleinsasser et al., 2008).

some shiny wear facets. Most of the marginal enamel has been lost so crown dimensions (Table 1) are estimates. The crown has a triangular occlusal plan. The talon has a small cusplet in the distal fovea and the talon's margin is composed of four small cusplets. The low relief occlusal surface is worn nearly flat with wear on all of the cusps and the central basin. The intercuspal fissures are poorly represented and the cusps are poorly delimited. There is evidence of occlusal crenulation throughout. The crown is low relief exacerbated by wear. The only dentin exposure is a small round window on the protocone. Maximum radial enamel thickness was about 1 mm thick as measured on a naturally fractured surface on the unworn buccal side of the hypocone.

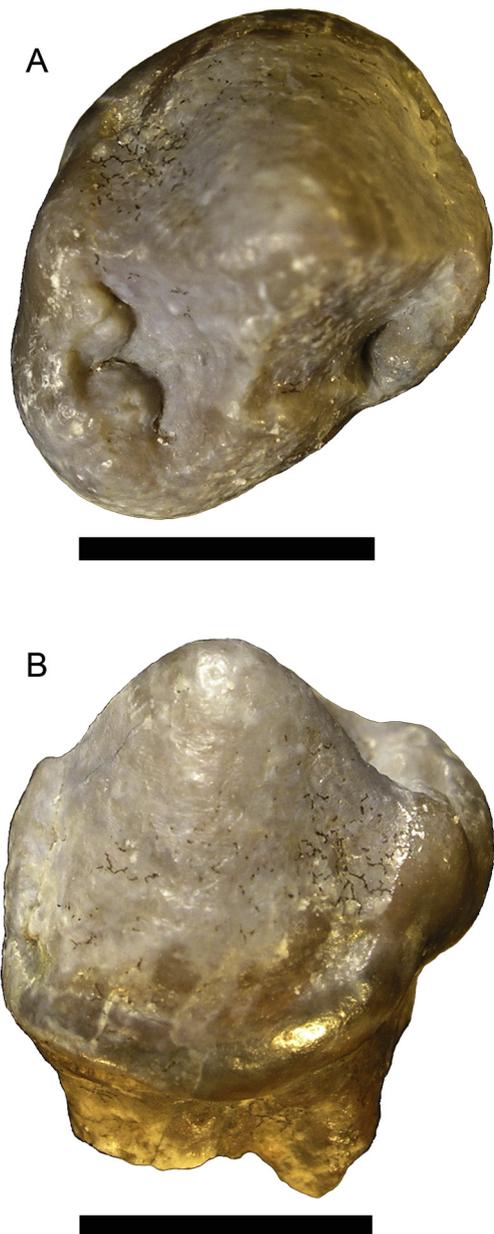
The roots are broken about 3–4 mm below the cervix. The lingual root is large with an oval cross-section. Two smaller buccal roots are present separated by a fissure and the disto-buccal root is smaller than the mesio-buccal root.

The specimen was found within a meter of the ESC2/P76 canine and the relative wear of the canine and this molar, in addition to the state of preservation, suggest they belong to a single individual.

**ESC3/P50:** Mandibular left third premolar crown (Fig. 6).

Taxonomic assignment: *Ardipithecus kadabba*.

The slightly weathered crown is complete with some cervical enamel flaking and the slightly damaged root extends about 2–3 mm below the cervix. MD length of the tooth is 8.3 mm and maximum BL breadth is 9.2 mm. The crown has a large main cusp (PRD) with a sharp-edged transverse crest that originates slightly distal to the PRD apex and separates the mesial fovea from a distal fovea and connects the PRD to a very small triangular MED. The small slit-like mesial fovea is nearly enclosed by an incomplete MMR that communicates distally with a small MED mesial ridge. The mesio-lingually oriented face of the anterior fovea is large and



**Figure 6.** Mandibular third premolar. ESC3/P50 (Mandibular Left Third Premolar): A. Occlusal view. B. Buccal View. Note the well-defined tubercle at the base of the mesial cuspal crest (preprotocristid). Also note the cervical waisting visible beneath the talonid. Scale bar = 5 mm.

planar. In occlusal view, the crown is markedly asymmetrical having an oval plan with a very oblique major axis running mesio-buccally - distolingually. The slit-shaped distal fovea is surrounded by a DMR comprised of several small cusps. In buccal view, the mesial and distal occlusal PRD ridges are nearly the same length (ca. 5.1 mm) and the cusp apex is an asymmetric inverted 'V' with a slightly more vertical distal margin. Both ridges terminate in small tubercles that form mesial and distal 'shoulders'. In buccal view, the height of these 'shoulders' from the cervix is about 60% of the total crown height. In distal view, the crown appears like a symmetric inverted 'V' formed by the sloping buccal surface and transverse crest/MED.

The cervical enamel margin of the tooth projects peripherally forming a well-defined cervical waist. The cervix is markedly MD compressed (5.0 mm) relative to its BL breadth (9.0 mm). The root extends between 2 mm and 5 mm below the cervical dentino-enamel junction and its apical edge is tapered indicating that the root was incompletely formed. Two roots were present – a circular mesio-buccal root and a transversely oblong (MD compressed) distal root. IPCF's are not visible on this tooth. The degree of root formation, absence of interproximal wear, and apparent absence of occlusal wear indicate that this crown probably had not yet emerged.

**ESC8/P1:** Maxillary left molar crown (Fig. 7)

Taxonomic assignment: *Ardipithecus kadabba*

The apparently unworn tooth crown lacking a root is slightly weathered with pitting throughout although the major features of its anatomy are retained. Crown MD length is 10.6 mm, BLmes breadth is 12.5 mm, and the BLdis is 11.4 mm. It has four major cusps with the PR being the largest in area and the three remaining cusps are nearly equal in size. Each of the cusps has multiple

accessory ridges or crenulations enhancing the cuspal topography. Although the unworn cusps are salient, they lack the same degree of projection as in the African apes. The lingual cusp apices are more rounded than the buccal cusps. The cusp apices are not as peripherally positioned as in the African apes. The PR lacks a well defined ridge connecting the cusp apex with the basin. The hypocone is separated from the PR and ME by a well-defined fissure and a HY-ME crest is absent. In occlusal view, the PA has a greater buccal projection (BLmes: 12.5 mm) than does the ME (BLdis: 11.4 mm). The distances between the cusp apices are: PA–PR: 7.3 mm; PA–ME: 5.1 mm; PA–HY: 9.6 mm; PR–ME: 8.3 mm; PR–HY: 5.2 mm; and ME–HY: 6.6 mm. This fossil is most likely a first molar because of the simple cusp pattern and presence of a smaller hypocone. However, we cannot rule out that it is a second molar. The mesial and distal surfaces are nearly parallel with the lingual half of the crown very slightly broader than its buccal half. The buccal marginal groove is pronounced separating the PA and ME extends most of the distance to the cervix. There are shallow vertical grooves on the lingual surface of the PR mesial to the fissure that separates the PR and HY. The distal fovea, poorly defined distally by an incomplete DMR, is larger than the mesial fovea. This tooth also shows the presence of a small 'dimple' at the disto-buccal corner of the tooth at the junction of the DMR and the ME. The distal surface is slightly bilobate with the distal ME and HY cusps separated by a small marginal fissure. The crown lacks evidence of a cingulum. Wear details are difficult to discern although it appears that the PR and HY apices have slight amounts of polish although wear planes have not yet developed nor has dentin been exposed. There does not appear to be either a mesial or distal IPCF present.

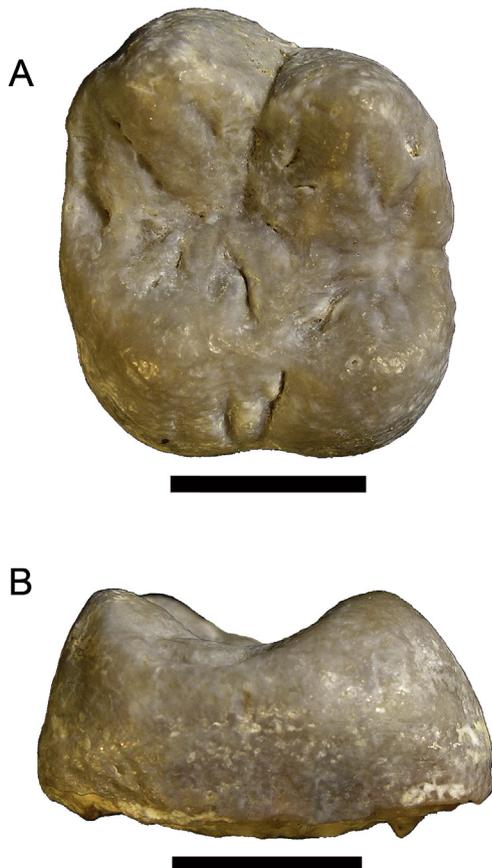
**Comparative analyses**

The paucity of Late Miocene aged fossil materials make comparative assessments somewhat opportunistic rather than systematic. Aside from the known hominins (*Sahelanthropus*, *Orrorin*, *Ardipithecus kadabba*, *Ar. ramidus*), the African Late Miocene is poorly represented by fossil apes and limited to 10.5–10.0 Ma *Chororapithecus abyssinicus* (Suwa et al., 2007), 9.88–9.80 Ma *Nakalipithecus nakayamai* (Kunimatsu et al., 2007), and 9.6 Ma *Samburupithecus kiptalami* (Ishida and Pickford, 1997; Pickford and Ishida, 1998). Another ape that has figured into discussions of hominin origins is the 9.6–9.3 Ma *Ouranopithecus macedoniensis* (Koufos and de Bonis, 2006) from Greece. Except for *Ouranopithecus* – none of these species has extensive dental remains. All of the Late Miocene samples are from populations that have teeth larger than any of the early hominins. *Chororapithecus* has been suggested to demonstrate derived features that align it with the gorilla clade (Suwa et al., 2007) precluding it from having any special relationship with later hominins or panins. Analyses of the *Nakalipithecus* fossils demonstrated some dental similarities with *Ouranopithecus* although the possibility of convergence rather than phyletic relatedness was not ruled out (Kunimatsu et al., 2007). *Samburupithecus* is considered to sample or predate the African ape and human stem (Pickford and Ishida, 1998).

Comparisons with extant common chimpanzees (*Pan troglodytes*) were conducted on specimens from the Hamann-Todd Osteological Collection housed at the Cleveland Museum of Natural History, Cleveland, Ohio, USA.

*Maxillary canine*

The thinly enameled maxillary canine of chimpanzees is dimorphic in size and to a lesser extent form. The female chimpanzee canine is smaller than the male in both basal dimensions and height (Swindler, 2002) and often lacks the distal tubercle and



**Figure 7.** Maxillary molar. A. (occlusal) and B. (mesial) views of ESC8/P1. Scale bar is 10 mm.

the mesial groove. The absence of a mesial tubercle or shoulder in chimpanzees is reflected in the near transverse course of the mesial enamel cervical margin. The ESC2/P76 maxillary canine is readily distinguishable from extant African apes in form by having a well-defined mesial shoulder, more lingually positioned mesial fovea, and invagination of the mesial enamel cervical margin. Chimpanzee males have a mesial groove that is located on the mesial surface rather than the lingual surface as in ESC2/P76 and other hominin canines. The ESC2 canine also has a lingual bulge that is absent in chimpanzees, a species that characteristically demonstrates lingual hollowing. In the ESC2/P76 canine, the lingual cervical tubercle is more distally located and closer to the distal tubercle as in extant apes and similar in position to *Ar. kadabba*. This distinguishes it from all subsequent hominins including *Ar. ramidus* where the lingual basal tubercle is positioned on the lingual face of the tooth. Although the cervical dimensions and root length in ESC2/P76 can be matched by small female chimpanzee canines, the shape and wear patterns are readily distinguishable between the two. The chimpanzee cervical cross-section is oval or teardrop-shaped with the major axis parallel to the post-canine tooth row axis. The ESC2 canine, although evincing significant amount of wear resulting in a substantial reduction in crown height, is not as tall as chimpanzees although comparable in cervical dimensions to the smallest female canines. The wear in ESC2/P76 is uniplanar, oblique to the occlusal plane, and has a distolingual orientation. In chimpanzees, the earliest stages of canine wear are on the distal portion of the lingual surface of the crown with a lingually oriented facet that maintains the sharp distal margin diagnostic of the sectorial canine complex. As wear progresses, the facet occasionally can become somewhat more distal facing without a significant loss of crown height. Only in extreme or unusual (due to tooth loss or malocclusion) does the wear facet become either more distal-facing or horizontal in chimpanzees.

A maxillary, perhaps female, lightly worn canine from *Nakalipithecus* is documented (KNM-NA 47594) and it presents a distinctive form by having a large projecting lingual basal tubercle and cingulum (Kunimatsu et al., 2007). It has a similar maximum (MD) length as that of the ESC2/P76 canine but it is somewhat LL broader. The canine has mesial and distal marginal 'shoulders' that are somewhat higher than extant African apes, but it still reflects the primitive condition of a tall robust crown. *Samburupithecus* and *Chororapithecus* maxillary canines are as yet undocumented.

Recent analyses of the *Ouranopithecus macedoniensis* dentitions (Koufos and de Bonis, 2006) have indicated that this species had a pattern of maxillary canine-P<sub>3</sub> wear that was unlike the extant apes. The maxillary canine apex is in occlusal contact with the mandibular canine distal cingulum producing apical wear on the maxillary tooth. There is apparently no occlusal contact between the maxillary canine and mandibular P<sub>3</sub>. 'The P<sub>3</sub> of *Ouranopithecus* lacks the mesial elongation of the protoconid which is in contact with the C<sup>5</sup>, providing the honing facet in most of the anthropoids (Koufos and de Bonis, 2006:233). In contrast, Haile-Selassie et al. (2010) identify a honing C/P<sub>3</sub> mechanism in *Ouranopithecus*. Although this species also exhibits enlarged molar and premolar crowns and thick occlusal enamel that may link it with the African ape clade (de Bonis and Mellentis, 1984; Begun and Kordos, 1997; Begun, 2005, 2009; Koufos, 2007), this is possibly a parallelism with the later hominins rather than as evidence of a phyletic link (Begun and Kordos, 1997; Haile-Selassie et al., 2004).

The ca. 6 Ma *Orrorin tugenensis* maxillary canine has a mesially located 'shallow, narrow vertical groove' (Senut et al., 2001:140) a character often found in extinct (e.g., *Ouranopithecus*) and extant apes (more often males than females), but not in other hominins. The similarly sized ESC2/P76 maxillary canine does have a small vertical furrow lingual to the mesial occlusal ridge yet is distinct

from the apes where the furrow is more mesially located. A similarly located, lingually positioned groove is present in the unworn *Ar. kadabba* canine (Haile-Selassie et al., 2004). The *Orrorin* canine has a triangular lingual profile due to the cervically located shoulders and a taller crown leading to the conclusion by Haile-Selassie et al. (2010) that the *Orrorin* canine is somewhat more primitive than the *Ar. kadabba* canine from the Middle Awash. Metrically, the basal crown dimensions of the *Orrorin* maxillary canine are quite similar to that of the ESC2/P76 specimen (*O. tugenensis* MD: 11.0 mm, BL: 9.3 mm; ESC2/P76 MD: 10.8 mm, BL: 9.3 mm) (Senut et al., 2001). The absence of the mesiolingual ridges and a more cervically positioned distal tubercle in *Orrorin* distinguishes it from the ESC2/P76 canine.

Compared with *Ar. ramidus* mandibular canines, the ESC2/P76 canine has a more pronounced distal marginal ridge and is not as LL wide as the *Ar. ramidus* teeth. The mesial shoulder in *Ar. ramidus* can be more angular (reflecting a less projecting cusp) and somewhat more cervically positioned mesial 'shoulder' (about 2.5 mm distant from the cervical margin [ESC2/P76] vs. 4.0 & 4.5 mm on the two As Duma *Ar. ramidus* maxillary canines (Simpson et al., in prep.)) with a lower relative height of the MMR. When shoulder height from the cervix is normalized by maximum cervical breadth, the magnitude of this difference becomes more obvious (ESC2/P76: 0.29; *Ar. ramidus*: 0.40, 0.49;  $N = 2$ ) indicating a lower positioned mesial 'shoulder'.

The root of the ESC2/P76 canine is more rectangular in cross-section at the cervix than in *Ar. ramidus* with mesial and distal faces nearly parallel to each other. This reflects a MD longer and more curved labial face of the ESC2/P76 canine than in *Ar. ramidus*. The Early Pliocene As Duma canines have a more reniform or mesially flattened oval radicular cross-section formed by a variably defined mesial radicular groove and a rounded distal margin. In occlusal plan, the ESC2/P76 canine has a greater labial projection that is less pronounced in the As Duma teeth. The angulation of the mesial occlusal crest relative to the root axis (when viewed either labially or lingually) is nearly the same in the two taxa.

In *Ardipithecus kadabba* (Haile-Selassie et al., 2004) and *Ar. ramidus* (Suwa et al., 2009) canine wear can be distally directed with the initial stages of wear having a disto-lingual orientation in addition to apical wear. In the Middle Awash *Ar. kadabba*, it is recognized that there is an interlocking C/P<sub>3</sub> with the potential for honing (Haile-Selassie et al., 2009), a characteristic lost in *Ar. ramidus*. Suwa et al. (2009) showed that *Ar. ramidus* maxillary canines tend to wear flat with increasing age and unlike the distal facing oblique wear plane in the ESC2/P76 canine showing that *Ar. kadabba* and *Ar. ramidus* had slightly different C/P<sub>3</sub> occlusal relationships and wear histories. In *Australopithecus*, the distally-oriented wear plane is generally limited to the cusp apex and distal occlusal margin. There is a small wear facet on the mesial occlusal ridge as is seen in *Ar. ramidus*. The degree of occlusal attrition precludes assessment of this surface apically. Also, *Ar. ramidus* characteristically exhibits wear on the lingual ridge, wear that is not evident on the ESC2/P76 canine.

Overall, the ESC2/P76 canine, while retaining some primitive morphology (overall large size, lower 'shoulders') exhibits significant details indicating clearly its loss of the sectorial function (reduced height with wear, distal facing wear facet) and apomorphic morphology (lingual bulge, lingual facing mesial fissure) that allies it with the early hominins. More specifically, the presence of the mesio-lingual groove and the relative position of the mesial shoulder and distal tubercle ally this specimen with single specimen (ASK-VP-3/400) known for *Ar. kadabba* from Asa Koma, Middle Awash project area (Haile-Selassie et al., 2004). The absence of lingual ridges, presence of some 'lingual hollowing' (Haile-Selassie et al., 2004:1504) and lower 'shoulders' in the *Orrorin*

maxillary canine differs from *Ar. kadabba*. Although like *Orrorin*, there is a basal marginal ridge on the lingual surface of ESC2/P76, the evidence suggests allocation to *Ar. kadabba*.

### Mandibular P3

In the living and extinct African apes, the P<sub>3</sub> exhibits crown morphology reflecting its role in the sectorial complex (salient main cusp, mesio-buccal projecting margins). The transverse crest in the chimpanzee P<sub>3</sub> is obliquely oriented and is generally located in the distal half of the tooth due in large part to the expansion of the mesio-buccal portion of the crown as a functional part of the sectorial complex (Fig. 8). This includes a larger – although less circumscribed – anterior fovea with a large planar lingual face. The anterior fovea is larger than the posterior fovea in chimpanzees. Although a thin lingual rim (often incomplete) is common in chimpanzees, a defined anterior fovea is rare and phenetically distinguishable from hominins in that the mesio-lingual face of the fovea is a broad, more vertically oriented plane and by a thin marginal ridge that lacks an angular fovea. The lingual rim in chimpanzees is much thinner than the MMR of hominins. In the *Ardipithecus kadabba* and *Ar. ramidus* mandibular third premolars, thickening of this rim forms a mesial projection that appears as a mesial step along the mesial cuspal ridge when the tooth is viewed buccally. This step is absent in chimpanzees. Chimpanzees also have a more projecting and sloping mesio-buccal margin than in *Ardipithecus* resulting in a more asymmetric occlusal plan, a trait consistent with their sectorial complex. The ESC3/P50 crown also appears to have its major axis more oblique to the postcanine tooth row than do the African apes, with a reduction in size of and more vertically oriented mesio-buccal bulge. The DMR in chimpanzees is also thin unlike in ESC3/P50 where it is thickened and includes the formation of small tubercles.

Unlike *Ardipithecus*, the chimpanzee mandibular P<sub>3</sub> lacks the mesial and distal buccal ridges and the mesial tubercle that forms the ‘shoulder’ in the *Ardipithecus*. The enamel crown projects peripherally at the cervix forming a well-defined cervical neck in both chimpanzees and the ESC3/P50 tooth. *Ar. ramidus*, although sharing many similarities in overall crown form with the more ancient tooth, tends to lack this cervical ‘waisting’ (Simpson, pers. obs.).

While having similar minimal crown dimensions, the *Nakalipithecus* mandibular P3 is larger than the ESC3/P50 crown in the maximum dimension that corresponds to the disto-lingual – mesiobuccal axis and reflects a marked lingual projection which is a characteristic observed in the African apes.

The P<sub>3</sub> of *Ouranopithecus macedoniensis* is described (Koufos and de Bonis, 2006) as symmetrical (lacking the distolingual projection) with the transverse crest intersecting the distolingual margin. There is also an incipient anterior fovea and a mesio-buccal projection.

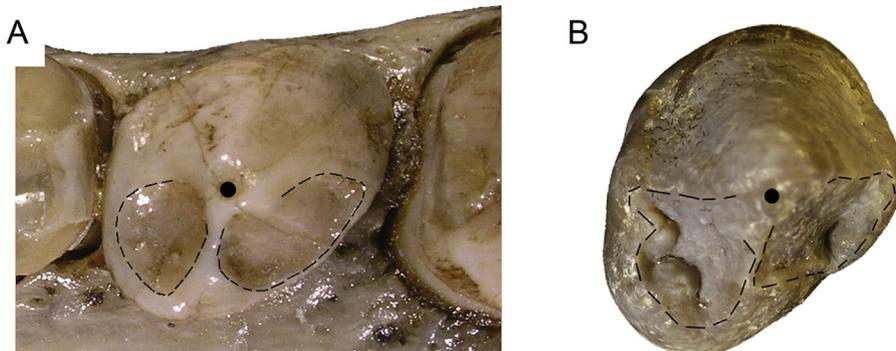
Even in specimens with advanced wear, no evidence of a honing facet is present and wear tends to lower the height of the crown. They note that the maxillary canine does not occlude with the P<sub>3</sub>.

The mandibular P3 is known for *Ar. kadabba* (ASK-VP-3/403 (Haile-Selassie et al. 2004, 2009)) and bears a strong resemblance to the ESC3/P50 premolar by having a similar asymmetric occlusal outline, incipient metaconid, occlusal salience, a reduced anterior fovea, and cervical waisting. While similar in overall size and shape with the later *Ar. ramidus* mandibular P3s, the relative proportions of the mesial and distal foveae (i.e., mesial < distal: *Ar. kadabba*; mesial > distal: *Ar. ramidus*) distinguish the two taxa.

Given its size, the ESC3/P50 tooth's protoconid is salient with more vertical cusp margins than in early *Australopithecus*. The ESC3/P50 mandibular third premolar is somewhat more asymmetric in occlusal plan and has a relatively smaller posterior fovea than in early *Australopithecus*. Both taxa may share a very small anterior fovea, but in *Australopithecus* the posterior fovea is clearly enlarged forming a basin. Two morphological correlates of this are that the transverse crest and cusp apex is more centrally positioned in the *Ardipithecus* rather than more anteriorly located as in *Australopithecus*. In the ESC3/P50 specimen, the transverse crest nearly divides the crown into equal length mesial and distal segments. This seems to be a characteristic of the *Ardipithecus* in general differing from early *Australopithecus* that have a more mesially positioned transverse crest and PRD cusp tip. The lingual face of the anterior fovea is planar and mesiodistally extensive in both the latest Miocene and As Duma mandibular P3s. *Australopithecus afarensis* (e.g., A.L. 288-1, A.L. 400-1, etc.) premolars have relatively smaller anterior foveae (Johanson et al., 1982).

There appear to be separate mesiobuccal and distal roots in the *Ar. kadabba* mandibular P3 with a plate-like distal root. In chimpanzees, root form is variable ranging from a fused ‘Tome's root’ with multiple pulp chambers and a prominent mesiolingual radicular groove to double roots usually having a plate-like distal root (Wood et al. 1988). The 6–7 Ma *Sahelanthropus* P3 also has two distinct roots (Brunet et al., 2002, 2005). In *Ar. ramidus*, the limited data indicate that the mandibular third premolar commonly has a fused single root with two pulp chambers although two separate roots are known (Simpson et al., in prep.). Variability in root number and morphology in the early hominins including *Au. anamensis* (Ward et al., 2001a,b) and *Au. afarensis* (Ward et al., 1982) may be a consequence of premolar enlargement and ‘molarization’ rather than a plesiomorphic retention.

In the unworn ESC3/P50 P<sub>3</sub>, it is not possible to evaluate its occlusal wear pattern. However, the reduction of mesiobuccal projection indicate that even if this tooth retained elements of sectorial wear with the maxillary canine, it was clearly no longer optimally shaped to perform this function. A small wear facet is present on the buccal face of the Middle Awash *Ar. kadabba*



**Figure 8.** Mandibular third premolar. A. *Pan troglodytes*. B. ESC3/P50. The mesial and distal fossae are outlined. Note the difference in the relative size of the mesial and distal fossae and the thickness and continuity of the mesial and distal marginal ridges. Chimpanzee specimen from Hamann-Todd osteological collection, CMNH.

mandibular P3 (Haile-Selassie et al., 2004) indicating there was overlapping wear in that individual.

#### Mandibular P4

The Gona mandibular fourth premolar is readily distinguishable from chimpanzees by the presence of defined mesial and distal buccal ridges that coalesce forming a cervical bulge or rounded cingulum. The chimpanzee premolars tend to be more rectangular in outline and differ from the latest Miocene ABD1/P1 premolar that presents a more obliquely oriented oval or parallelogram occlusal plan with an asymmetric projection of the distolingual corner. Also, chimpanzees have very projecting trigonid (especially the PRD) relative to their talonid basin. As in the mandibular P3, the MMR is thinner in *Pan* and it does not form a step along the pre-protocristid as it does in *Ardipithecus*. Plus, the chimpanzee P4 has thinner enamel and sharper occlusal crests.

As in chimpanzees (although not to the same degree), the ABD1/P1 P4 crown has a pronounced cusp projection in unworn teeth and retains a trigonid/distal fovea step with wear. The mesio-distal step is retained even with marked wear as in the Early Pliocene As Duma *Ardipithecus* whereas in *Au. afarensis*, increased occlusal wear tends to flatten the entire occlusal plane. The chimpanzee dentition has thinner enamel and well-defined occlusal crests than does ABD1/P1.

The *Nakalipithecus* mandibular P4 is substantially larger and relatively BL broader (BL/MD = 1.35) than the ABD1/P1 (BL/MD = 1.19) crown. Like the ABD1/P1 crown, it has a projecting distolingual corner and has a distal fovea larger than the mesial fovea.

A number of mandibular P4s are known for *Ouranopithecus* (Koufos and de Bonis, 2006). While the specimens identified as females (RPI-79, -84, -88) (Koufos and de Bonis, 2006) have similar MD lengths (8.1–8.6 mm) as the Gona P4, they are somewhat BL broader (10.1–10.5 mm).

*Sahelanthropus tchadensis*, *O. tugenensis*, and *Ar. kadabba* samples include mandibular P4s although none is complete. What limited data are available show a similarity in overall size of these teeth (*S. tchadensis* MD: 8.0 mm, BL: nd; *O. tugenensis* MD: (8.0) mm, BL: (9.0) mm; *Ar. kadabba* MD: (8.1) mm, BL: 10.0 mm; ABD1/P1 MD: 8.3 mm, BL: 9.9 mm (Brunet et al., 2002; Haile-Selassie, 2001a,b) (Table 2). The talonid in the ardiipiths is not as enlarged as in the more recent hominin teeth – especially *Australopithecus* – and the anterior fovea has a greater relative contribution to the occlusal plan. Overall, the transverse crest is slightly more distally located in the Late Miocene and Early Pliocene *Ardipithecus* teeth. The Middle Awash mandibular P4 (ALA-VP-2/10) has a fused Tomes' root with three separate root canals.

The *S. tchadensis* mandibular P4s (TM 266-02-154-1; TM 247-01-02, TM 292-02-01) have two distinct plate-like roots with evidence of three pulp canals, and large talonid and buccal grooves (Brunet et al., 2002, 2005). Although evidence for root number is ambiguous in the ABD1/P1 premolar, they too have three pulp chamber apices, an enlarged talonid, and buccal ridging. The ABD1/P1 crown is slightly larger in MD length than the Toros-Menalla crown plus it appears to have a larger anterior fovea.

The mandibular P4 is also known for *O. tugenensis* (BAR 1390'00) although missing a significant portion of its enamel, it is known to be a two rooted tooth with an ovoid occlusal plan and projecting cusp apices (Senut et al., 2001). Again, the ABD1/P1 premolar is slightly larger in MD length than the known *O. tugenensis* tooth and somewhat larger in the BL dimension. It differs from the *Orrorin* P4 by having equally salient PRD and MED cusps (although wear has perhaps contributed to this degree of projection) and a less ovoid occlusal plan. Additional comparative analyses need to be conducted to clarify the morphological similarities and differences in anatomical detail between the three Late Miocene taxa.

*Ardipithecus ramidus* mandibular fourth premolars from both Aramis (Middle Awash) and As Duma characteristically have a single root with, where visible in the As Duma collections, a single pulp chamber with an oval cervical cross-section although the Early Pliocene mandible fragment from Tabarin (KNM-TH 13150) which may also be assignable to *Ar. ramidus*, appears to have a double rooted P4 (Ward and Hill, 1987; Hill and Ward, 1988). In addition, the *Ar. ramidus* mandibular P4s have a more oval occlusal plan.

Although the roots are missing from the ABD1 premolar, the triangular cervical cross-section is somewhat suggestive of a multi-root system. Additional more complete fossils are necessary to clarify this issue. Like the *Ar. kadabba* mandibular fourth premolar from the Middle Awash (ALA-VP-2/10) (Fig. 9), the ABD1/P1 premolar crown, although broken at the cervix is suggestive of a more complex radicular morphology than seen in the single-rooted *Ar. ramidus* teeth. In addition, the ALA-VP-2/10 crown, while sharing a similar occlusal plan with a projecting disto-lingual corner, lacks the sloping buccal face and has a reduced 'step' down to the talonid – characters that distinguish the two teeth. As both *Sahelanthropus* (TM 266-02-154-1) and *Orrorin* mandibular P4 (BAR 1390'00) have two distinct offset roots in their mandibular fourth premolars, this appears to be a reasonably reliable means of distinguishing the latest Miocene teeth from both *Ar. kadabba* (which lacks offset roots) and the single-rooted *Ar. ramidus*.

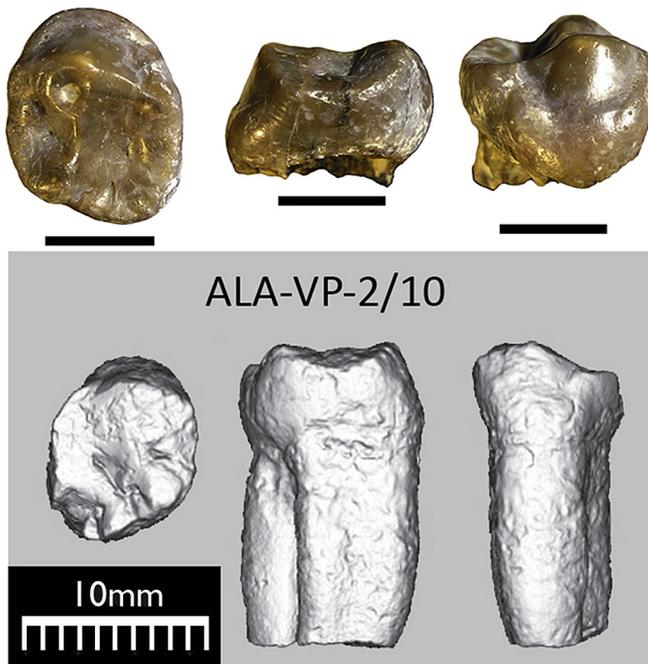
Overall, the Gona premolar is distinguishable from the Late Miocene non-hominin teeth by smaller crown size with a relatively narrower BL breadth. The ca. 6.3 Ma ABD1/P1 P4 crown is similar in

**Table 2**

Dental metrics from latest Miocene, earliest Pliocene hominins, and common chimpanzees.

Position		Gona Miocene	<i>Ar. kadabba</i>	<i>S. tchadensis</i>	<i>O. tugenensis</i>	<i>Ar. ramidus</i>	<i>Pan troglodytes schweini</i>	<i>Pan troglodytes troglodytes</i>
Maxillary C	MD	10.8 (a)	nd	nd	11.0	9.9–12.2 (a)	13.3 ± 2.26 (a)	13.5 ± 2.23 (a)
	BL	9.3 (b)	>10.1	10.2	9.3			
Maxillary M1 or	MD	10.6	(10.3)–(10.6)	(10.9)–(11.5)	11.4	9.8–11.1	10.7 ± 0.59	10.5 ± 0.63
	BL	12.5	11.6–12.1	nd	10.6	11.2–13.0	11.2 ± 0.56	11.4 ± 0.66
Maxillary M2	MD	10.6	nd	13.0	nd	11.0–12.8	10.6 ± 0.65	10.6 ± 0.66
	BL	12.5	nd	(12.8)	nd	13.3–15.3	11.40 ± 0.68	11.9 ± 0.79
Maxillary M3	MD	(10.4)	10.9	10.7–10.8	10.2–10.3	10.2–12.1	9.7 ± 0.85	9.7 ± 0.71
	BL	(11.6)	12.2	12.7–14.9	12.9–13.1	12.3–15.3	10.6 ± 0.64	11.3 ± 0.78
Mandibular P3	(a)	9.2	nd	nd	nd	9.2–11.5 (a)	11.0 ± 0.67	11.3 ± 0.84
	(b)	8.3	nd	nd	nd	7.0–8.2 (b)	7.5 ± 0.56	7.8 ± 0.63
Mandibular P4	MD	8.3	(8.3)	8.0	(8.0)	7.3–8.9	8.0 ± 0.69	7.9 ± 0.49
	BL	9.9	10.0–(10.4)	nd	(9.0)	9.0–10.2	8.8 ± 0.61	8.7 ± 0.68

Gona specimens: maxillary canine: ESC3/P76; Maxillary M1 or Maxillary M2: ESC8/P1; Maxillary M3: ESC2/P430; Mandibular P3: ESC3/P50; Mandibular P4: ABD1/P1. *Ar. kadabba* data from Haile-Selassie 2001a,b and Haile-Selassie et al., 2004; 2009. *S. tchadensis* data from Brunet et al., 2002, 2005. *O. tugenensis* data from Senut et al., 2001. *Ar. ramidus* and *Pan* (*P. t. schweinfurthi*, *P. t. troglodytes*) data from Suwa et al., 2009. Chimpanzee data are sex combined sample (sample size ranges from 30 to 77 by species and position) means, all other entries are ranges. Data for both maxillary M1 and maxillary M2 dimensions are presented to address uncertainty in the identification of the ESC8/P1 molar. MD = mesiodistal. BL = buccolingual. a = maximal dimension. b = dimension perpendicular to maximum dimension.



**Figure 9.** Comparison of ABD1/P1 and *Ardipithecus kadabba* (ALA-VP-2/10) mandibular premolars. Top: ABD1/P1 (right mandibular P4) – occlusal, medial, and buccal views. Bottom: ALA-VP-2/10 (left mandibular P4) – occlusal, medial, and buccal views. The ALA-VP-2/10 image is reconstructed from microCT examination. Image provided and used by permission of Y. Haile-Selassie.

size and proportions with the other early hominins. The ABD/P1 crown is distinguishable from those known for the Ethiopian *Ardipithecus ramidus* which have a single root. While this tooth possibly could be assigned to any of the three terminal Miocene hominin groups given the currently known materials, it appears most similar to *Ardipithecus kadabba* and we allocate this mandibular P4 to cf. *Ardipithecus kadabba* with the recognition that additional similarly aged fossils are needed to test this hypothesis.

#### Maxillary first/second molar

The ESC8/P1 molar is BL broader (12.5 mm), although similar in MD length (10.6 mm), to the M<sup>1</sup> in chimpanzees ( $\delta$ MD:  $10.3 \pm 0.56$ ;  $\delta$ BLmes:  $11.7 \pm 0.70$ ;  $\text{♀}$ MD:  $10.1 \pm 0.72$ ;  $\text{♀}$ BLmes:  $10.9 \pm 1.01$  (Swindler, 2002); sexes and subspecies combined MD: 10.5–10.7; sexes and subspecies combined BL: 11.2–11.4 (Suwa et al., 2009)) (Table 2). In addition, *P. troglodytes* tend to have more peripheralized cusp apices, more salient buccal cusps, and thinner enamel than does the Gona tooth.

The 9.5 Ma *S. kiptalami* (Ishida and Pickford, 1997; Pickford and Ishida, 1998) molars have the same generalized, low cusped morphology with an increase in enamel thickness as the ESC8 crown, yet they are larger in size and retain portions of a cingulum, which distinguishes it from the Gona molar.

The molars of *Ouranopithecus macedoniensis* bear some morphological similarity with ESC8/P1 although those teeth are markedly larger (ESC8/P1: MD: 10.6 mm; BL: 12.5 mm; *Ouranopithecus* M1: MD: 12.6–14.4,  $n = 5$ ; 13.9–15.1,  $n = 5$  (Koufos and de Bonis, 2006)).

Maxillary molars are also known from a small sample for *Sahelanthropus* (Brunet et al., 2002; 2005). The two known *Sahelanthropus* maxillary first molars are MD longer than the ESC8/P1 crown, while the BL breadths are unknown in these fractured teeth. The second molar is the largest crown of the maxillary molars in *Sahelanthropus* and the third molar has a similar MD dimension as the first molar.

The maxillary first molar, but not the maxillary second molar, is known from the Middle Awash Late Miocene *Ar. kadabba* collections. The crown dimensions (ASK-VP-3/401: MD = 10.4 mm, BL = 11.7 mm; ASK-VP-3/402: MD = 10.3 mm, BL = 11.6 mm; STD-VP-2/63: MD = (10.6 mm), BL = 12.1 mm) (Haile-Selassie, 2001a) (Table 2) of these three teeth are similar in size to the ESC8/P1 molar (MD = 10.6 mm; BL = 12.5 mm) although the ESC8/P1 tooth is somewhat broader in the BL axis.

The Gona Late Miocene molar bear the common hominoid cusp pattern. They are distinguishable from extant African apes by their more bunodont crown and thicker enamel. While similar in general conformation, the Gona maxillary molar is substantially smaller in size than are those known for the Late Miocene apes, yet similar in size and shape to the other early hominins.

#### Maxillary third molar

Like the first/second molar discussed above, the ESC2/P430 tooth lacks the derived conditions of later hominins including crown enlargement and enamel thickening. *P. troglodytes* M<sup>3</sup> crown dimensions are somewhat dimorphic (Swindler, 2002; Suwa et al., 2009). The ESC2/P430 M<sup>3</sup> is not statistically different from *P. t. troglodytes* male mean (Swindler, 2002; Suwa et al., 2009) although it would be a large female. *Pan t. schweinfurthi* crowns have a similar MD length but are less BL broad (Suwa et al., 2009) having a similar BL/MD ratio as the ESC2 crown. *Pan paniscus* (Swindler, 2002; Suwa et al., 2009) has even smaller crowns than common chimpanzees or the ESC2 third molar. *Sahelanthropus tchadensis* M<sup>3</sup>s are slightly larger mesio-distally, but are markedly buccolingually broader (TM266-10-060-1: MD: 10.8 mm; BL: 14.9 mm; BL/MD: 1.38; TM 266-01-447: MD: 10.7 mm; BL: 12.7 mm; BL/MD: 1.19) (Brunet et al., 2002) than the ESC2 specimen (BL/MD: 1.12). The *Orrorin tugenensis* maxillary third molars have similar MD dimensions as the ESC2 crown but, like the *S. tchadensis* teeth, they are relatively BL broad (BAR 1426'00: MD: 10.2 mm; BL: 13.1 mm; BL/MD: 1.28; BAR 1900'00: MD: 10.3 mm; BL: 12.9 mm; BL/MD: 1.25) (Senut et al., 2001). The *Ardipithecus kadabba* slightly worn M3 (STD-VP-2/62) from the Middle Awash area (Haile-Selassie, 2001a,b) is somewhat larger (MD: 10.9 mm; BL: 12.2 mm; BL/MD: 1.12) but has a near identical breadth/length ratio as the ESC2/P430 crown. However, it does differ slightly in morphological detail since the ESC2 third molar appears to have a more pronounced distal tapering (perhaps exaggerated by loss of marginal enamel), a more cusply complex talon, and a larger distal fovea but to a degree well within the normal range of intraspecific variation.

Compared with the known specimens of *Ar. ramidus* (White et al., 1994; Semaw et al., 2005; Suwa et al., 2009), the ESC2/P430 tooth is at the smallest end of the size range, especially in BL breadth, from both the Aramis ( $n = 4$ ) and Gona collections. The subsequent *Australopithecus anamensis* and *Au. afarensis* species increase the M<sup>3</sup> in crown size dimensions and enamel thickness indicating punctuated change in dental form and probably diet.

#### Discussion

If the current *Pan-hominin* speciation dates of 6–8 Ma are reasonable, the latest Miocene fossils from the Gona and Middle Awash project areas in Ethiopia, Tugen Hills and Lothagam in Kenya, and Toros Menalla, Chad very closely postdate the chimpanzee-human divergence. As expected, there are a number of morphological characters shown by these teeth that reflect their temporal proximity to the last common ancestor (LCA) (e.g., more cervically positioned 'shoulders' on the canine, asymmetric premolar crowns, smaller molar crown dimensions, and thinner occlusal enamel) yet share a number of derived traits with *Australopithecus* (canine size

reduction, reduced sectorial wear, general conformation of molar crowns) (Ward et al., 2013) supporting hominin attribution of the ca. 5.4 Ma ESC2, ESC3, and ESC8 teeth.

Alternatively, if a more recent *Pan-Homo* separation date of 3–5 Ma is used (Sarmiento, 2010), then these Late Miocene fossils bear no special relationship with either later hominins or African apes. While that position is not advocated here, it would suggest that the origins of canine reduction and bipedality are not hominin apomorphies but adaptive options adopted independently by a diverse array of apes that subsequently went extinct. The morphotype of the extant apes (committed quadrupeds, dimorphic sectorial canines) is likely a retention with modifications of the ancestral African ape form (White et al., 2010) rather than a reversion to a more primitive form as advocated by Sarmiento (2010). In addition, removing all fossil hominins older than 4 Ma from our ancestry would raise the possibility that *Australopithecus* arose without any obvious antecedents despite a number of detailed phenetic similarities between *Ar. ramidus* and *Au. anamensis* (White et al., 1996, 2006; Leakey et al., 1998). Fortunately, the richness of the fossil record allows a resolution of the problem by providing a series of fossils with demonstrable elements of phyletic continuity, lacking evidence of evolutionary reversals, and that are functionally explicable.

The anatomy of the Gona latest Miocene teeth differ from the fossil and extant African ape morphology in the same ways as more recent hominins. Dental morphology exhibited by the Gona teeth that distinguish them from the fossil and extant apes include loss or reduction of the sectorial or honing mechanism between the maxillary canine and mandibular P3 and reduced canine height. The mandibular third premolar is distinguishable from those apes with a C/P<sub>3</sub> honing complex by its elaboration of the mesial marginal ridge, less bulbous mesio-buccal surface, and increased length in the distal marginal ridge. The sectorial complex is a widespread, hence plesiomorphic, condition in apes with strong implications for intrasexual and intersexual social behavior of these primates as it is intimately associated with reproductive fitness. The loss of this character reflects a profound change in inter-individual relations that is uniquely found in humans and our ancestors (Darwin, 1871). This does not mean that the earliest hominin social structure has no parallels in the higher primates, only that the means by which the relations were mediated had shifted fundamentally.

Haile-Selassie et al. (2004) provided a diagnosis and justification for elevating the subspecies *Ar. ramidus kadabba* (Haile-Selassie, 2001b) to the level of species named *Ar. kadabba*. The distinguishing features were the more primitive characteristics of the C/P3 occlusion pattern (changes in size, shape, and wear of the maxillary canine and mandibular third premolar) – some features shared by the Gona Project latest Miocene hominins. Based on preliminary comparisons with the 4.3–4.6 Ma As Duma (Semaw et al., 2005; Simpson et al., in prep.) and Middle Awash (Suwa et al., 2009) collections of *Ar. ramidus* the ca. 5.4 Ma teeth from the ESC sites are phenetically similar (i.e., size and occlusal shape of the mandibular third premolar, and maxillary first molar crowns) linking the two samples into a single clade. For example, the As Duma *Ar. ramidus* mandibular third premolars have, like ESC3/P50, similar crown dimensions and length of the mesial and distal PRD ridges, asymmetric occlusal plans, enclosed anterior fovea, distally oriented transverse ridges, and a mesial buccal ridge. However, *Ar. kadabba* and *Ar. ramidus* are distinguishable based on the degree of cervical waisting, size and shape differences in the mesial fovea, and probably the shape of the roots (lack of a blade-like distal root in *Ar. ramidus*). Additional differences between these taxa can be found in the morphology of the maxillary canine with the older tooth having a relatively lower distal shoulder. The Early Pliocene canines from As Duma and Aramis are approximately the same size (Aramis maxillary canine maximum dimension: 11.3 ± 0.65 mm, *n* = 4 (Suwa et al.,

2009); Gona maximum dimension: 11.1 mm, *n* = 1 (Semaw et al., 2005)) (Table 2) as the ESC2/P76 tooth, but the *Ar. ramidus* canine has a less convex projecting labial face, a less robust root and a slightly taller mesial shoulder. An additional distinguishing feature between the two *Ardipithecus* species may be the morphology of the mandibular fourth premolar roots with the ABD1/P11 crown possibly having a more complex radicular pattern than the single rooted Early Pliocene teeth. The form of the roots in the mandibular fourth premolar distinguishes between *Ar. kadabba* ('Tomes root') and *Ar. ramidus* (single root) although it has been observed that the Tabarin mandible had a two-rooted P4 (Ward and Hill, 1987).

The Gona maxillary canine and the mandibular P3 share unique anatomical traits with the Late Miocene Middle Awash homologues, thus, these teeth are allocated to *Ar. kadabba*. The maxillary molar (ESC8/P1) is also assigned to *Ar. kadabba* due to overall similarities in size and shape. The older crown (ABD1/P1) is more difficult to assign due in large part to the lack of similarly aged comparative specimens. The mandibular P4 retains enough significant anatomy that identifies it as a hominin and perhaps with links to later taxa such as *Ar. kadabba*. Here, our proposed allocation of the P4 to cf. *Ardipithecus kadabba* is reasonable while some may prefer the more conservative assignment of the ABD1/P1 P4 crown to Hominina, *gen. et sp. indet.* In either case, the recovery of additional fossils is essential to address this issue.

While the ca. 5.4 Ma teeth are here assigned to *Ar. kadabba* based on several unique characters (as well as spatial and temporal proximity), there is the lingering issue of whether *Ar. kadabba* is assignable to the genus *Ardipithecus* rather than assignment to other named genera (e.g., *Sahelanthropus* or *Orrorin*) or a new genus. We follow existing nomenclature by assigning '*kadabba*' to *Ardipithecus* (Haile-Selassie, 2001a,b; Haile-Selassie et al., 2004, 2009) although Haile-Selassie (2001a,b) also suggested that *Orrorin* and early *Ardipithecus* may be conspecific, a proposition that requires additional analyses and fossil evidence. Can the genus *Ardipithecus* accommodate both '*kadabba*' and '*ramidus*'? Classification is a practical means of dealing with the organization of the diversity of biological organisms that are hypotheses based on existing data. Clearly phenetic differences exist between *kadabba* and *ramidus*, which are separated in time by up to 1.4 million years, however the scope of these differences are well within the ranges of variation found within early *Australopithecus* (e.g., *Au. anamensis* and *Au. afarensis*), an apparently anagenetic lineage that spans about 1.3 million years (Kimbel et al., 2006; Haile-Selassie et al., 2010; Ward, 2014). The character and nature of differences between the '*kadabba*' and '*ramidus*' samples (e.g., canine size and form, foveal proportions on the mandibular P3, lower P4 root number) are reasonably accommodated within a single genus that spans over a million years. However, this allocation of *kadabba* to *Ardipithecus* is an hypothesis that will be tested when addition fossils – beyond the limited samples now known – are recovered.

Phyletically, *Ardipithecus* is part of the hominin clade as demonstrated by their apomorphic loss of the sectorial shearing complex. This alone removes them from the chimpanzee clade and suggestions that they were uniquely ancestral to extant chimpanzees (Senut et al., 2001; Sarmiento, 2010) are untenable. This position has become even more apparent by the analysis of the *Ar. ramidus* fossils (White et al., 2009; Suwa et al., 2009; Lovejoy et al., 2009a,b,c) that puts into sharper focus the historical polarities for a variety of dental, cranial, and postcranial anatomies between the chimpanzees and the hominins. It is reasonable to accept that latest Miocene and Early Pliocene Gona samples belong to a single evolving taxon (genus *Ardipithecus*) although distinguishable in significant ways allowing assignment to distinct, but probably time-successive, species (*Ar. kadabba* and *Ar. ramidus*). Phenetically, the *Ardipithecus* dental anatomy is a reasonable ancestor to that of

the subsequent australopithecids (Leakey et al., 1995; White et al., 1996, 2006). While the ca. 4.2 Ma *Ardipithecus-Australopithecus* transition involved a series of significant anatomical changes, notably in the dentition (increase in size of post canine teeth, increase in enamel thickness, change in morphology of the canines and deciduous molars), since this occurred in similar habitats (White et al., 2006) suggests that this was most likely an elaboration of an established adaptive pattern.

These newly discovered latest Miocene teeth contribute to our understanding of the morphology and context of our earliest ancestors. No apomorphic trait links these teeth with the extant apes, and therefore, suggestions that *Ardipithecus* is a chimpanzee ancestor or preserve a chimpanzee-like phenotype (Wood and Harrison, 2011) are not borne out by the data. These teeth are clearly derived in the direction of later hominins, most notably by the reduced or absent sectorial C/P3 wear pattern. These few remains highlight the need for additional fossils that can lead to more robust comparisons between the existing samples as well as further elaborate hominin paleobiology in the crucial period between 10 and 6 Ma.

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### Appendix 1. Details of Gona Project Adu-Asa Formation chronometric control

Sample	Unit	Location	Lab #	Irradiation #	Material	n	MSWD	Mean age	Age(Ma) ± 2s
ESCASH-13*	Ogote Ash-fall	West of rhyolite dome	55440	NM-186K	Plagioclase	8	0.43		<b>5.57 ± 0.15</b>
GON05-216b*	Kobo'o Tuff	near ESC sites	55993	NM-192K	Sanidine & Plagioclase	10	0.92		<b>5.44 ± 0.06</b>
GON05-265c*	Belewa Tuff	in Belewa drainage	55994	NM-192K	Sanidine	14	2.09		5.49 ± 0.03
								Plateau Age	
Sample	Unit	Location	Lab #	Irradiation #	Material	% <sup>39</sup> Ar	n	MSWD	Age(Ma) ± 2s
ESCASH-7†	porphyritic basalt	caps N ESC sites	55388-01	NM-186B	Ground-mass	84.6	6	18.8	<b>6.48 ± 0.42</b>
ESCASH-8†	porphyritic basalt	caps N ESC sites	55389-01	NM-186B	Ground-mass	82.5	7	4.3	<b>6.13 ± 0.56</b>
ESCASH-18†	porphyritic basalt	caps N ESC sites	57133-01	NM-208C	Ground-mass	86.2	7	2.1	6.37 ± 0.32
GON05-213†	porphyritic basalt	above ESC 8	57178-01	NM-208K	Ground-mass	89.7	8	2.3	6.07 ± 0.17
GON05-230†	Bodele B Tuff	below BDL sites	55975-01	NM-192H	Plagioclase	73.3	7	5.7	<b>6.48 ± 0.22</b>
GON05-246†	Bodele B Tuff	South Gona	55976-01	NM-192H	Plagioclase	51.0	6	2.1	<b>6.24 ± 0.19</b>
WMASH-57†	basalt flow	caps Adu-Asa Form.	57139-01	NM-208D	Ground-mass	65.0	3	3.3	<b>5.18 ± 0.33</b>
WMASH-58†	basalt flow	caps Adu-Asa Form.	57137-01	NM-208C	Ground-mass	73.5	6	3.3	<b>5.55 ± 0.16</b>
WMASH-66†	basalt flow	caps Adu-Asa Form.	57136-02	NM-208C	Ground-mass	83.3	7	1.3	<b>5.66 ± 0.11</b>
Sample	n	MSWD	<sup>40</sup> Ar/ <sup>36</sup> Ar ± 2s	Age(Ma) ± 2s	Comments				
ESCASH-13*	8	0.52	300 ± 200	5.57 ± 0.18	good				
GON05-216b*	10	1.00	294 ± 4	5.45 ± 0.06	very good				
GON05-265c*	14	0.38	309 ± 17	<b>5.47 ± 0.04</b>	very good				
Sample	n	MSWD	<sup>40</sup> Ar/ <sup>36</sup> Ar ± 2s	Age(Ma) ± 2s	Comments				
ESCASH-7†	6	20.3	338.6 ± 122.7	6.12 ± 1.06	usable				
ESCASH-8†	7	5.1	295.6 ± 12.4	6.13 ± 1.30	usable				
ESCASH-18†	7	1.5	299.7 ± 4.1	<b>6.04 ± 0.43</b>	good (isochron age)				
GON05-213†	8	2.4	299.6 ± 8.3	<b>5.89 ± 0.41</b>	good (isochron age)				
GON05-230†	7	4.2	322.0 ± 28.0	6.18 ± 0.35	fair				
GON05-246†	6	2.8	294.1 ± 23.6	6.26 ± 0.30	fair				
WMASH-57†	3	0.5	311.9 ± 14.0	4.60 ± 0.52	fair				
WMASH-58†	6	0.8	284.7 ± 5.7	5.76 ± 0.13	good				
WMASH-66†	7	1.0	293.1 ± 2.8	5.76 ± 0.15	very good				

\*Single Crystal Analyses.

† Step-heated Analyses.

Ages are calculated relative to FC-2 Fish Canyon Tuff sanidine interlaboratory standard (28.02 Ma, Renne et al., 1999).

Analyses were performed at New Mexico Geochronology Research Laboratory using an MAP 215-50 mass spectrometer on line with automated all-metal extraction system. All errors are reported at ±2σ, unless otherwise noted.

Details of irradiation, analytical procedures, calculation methods, analytical data, and locations of samples are from Kleinsasser et al., 2008.

Analyses in italics indicate low-radiogenic yield analyses with poor precision and questionable accuracy.

Bold denotes preferred ages. High MSWD values are outlined.

## Appendix 2. Preliminary faunal list from the Gona Project Late Miocene

### ○ Mammalia

#### ■ Bovidae

- Zephyreduncinus oundagaisus
- Reduncini, gen. et sp. indet. (cf. *Kobus* sp.)
- Reduncini, gen. et sp. indet. (cf. *Redunca* sp.)
- Boselaphini, cf. *Tragoportax*
- *Tragelaphus* sp.
- Aepycerotini, gen. et sp. indet.
- *Ugandax* sp.

#### ■ Suidae

- *Nyanzachoerus* sp.
- cf. *Nyanzachoerus kuseralensis*

#### ■ Hippopotamidae, gen. et sp. indet. A.

#### ■ Hippopotamidae, gen. et sp. indet. B.

#### ■ Giraffidae, gen. et sp. indet.

#### ■ Perissodactyla

- *Eurygnathohippus* cf. *feibeli*
- Dicerotini, *Diceros* sp.

#### ■ Proboscidea

- *Anancus kenyensis*
- Elephantidae gen. et sp. indet.

#### ■ Rodentia

- cf. *Tachyoryctes*
- cf. *Thryonomys*
- Hystrichidae, gen. et sp. indet.

#### ■ Primates

- *Ardipithecus kadabba*
- Hominina, gen. et sp. indet.
- cf. *Kuseracolobus aramisi*
- Colobinae gen. et sp. indet.
- Papionini gen. et sp. indet.
- cf. *Pliopapio alemui*

#### ■ Carnivora

- *Machairodus* sp.
- Mustelidae gen. et sp. indet.
- ?Viverridae
- *Bonisiacyon aakir*

### ○ Reptilia

- Geochelonia
- *Varanus* sp.
- Crocodylia gen. et sp. indet.

### ○ Pisces

- cf. Ciconiidae gen. et sp. indet.

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