Dentognathic remains of *Australopithecus afarensis* from Nefuraytu (Woranso-Mille, Ethiopia): Comparative description, geology, and paleoecological context

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Abstract

Australopithecus afarensis is the best-known and most dimorphic species in the early hominin fossil record. Here, we present a comparative description of new fossil specimens of *Au. afarensis* from Nefuraytu, a 3.330–3.207 million-years-old fossil collection area in the Woranso-Mille study area, central Afar, Ethiopia. These specimens include NFR-VP-1/29, one of the most complete mandibles assigned to the species thus far and among the largest mandibles attributed to *Au. afarensis*, likely representing a male individual. NFR-VP-1/29 retains almost all of the distinctive archaic features documented for *Au. afarensis*. These features include a posteriorly sloping symphysis, a low and rounded basally set inferior transverse torus, anterosuperiorly opening mental foramen, a lateral corpus hollow bound anteriorly by the C/P₃ jugae and posteriorly by the lateral prominence, and the ascending ramus arising high on the corpus. Dental morphology and metrics of the Nefuraytu specimens also falls within the range of *Au. afarensis*. The presence of this species at Woranso-Mille between 3.330–3.207 million years ago confirms the existence of this species in the area in close spatial and temporal proximity to other middle Pliocene hominin taxa such as the one represented by the Burtele foot (BRT-VP-2/73) and the recently named species *Au. deyiremeda*. This has important implications for our understanding of middle Pliocene hominin diversity.

Keywords: *Australopithecus afarensis*, hominin diversity, Nefuraytu, Woranso-Mille, Ethiopia

Introduction

Australopithecus afarensis is one of the best known hominin species in the Pliocene fossil record and hypothesized as the direct descendant of the 4.2–3.9 Ma *Australopithecus anamensis* (Leakey et al., 1995, 1998; Ward et al., 2001; White et al., 2006). Its remains have been recovered from sites in Ethiopia, Kenya, and Tanzania from deposits ranging in age from 3.7–2.9 million years ago (Ma) (Johanson and Taieb, 1976; Taieb et al., 1976; Johanson et al., 1978a,b, 1982a-c; Kimbel and White, 1988; Kimbel et al., 1985, 1994, 2004; White et al., 1993, 2000; Brown et al., 2001; Kimbel and Delezene, 2009; Harrison, 2011; Mbua et al., 2016). The best sample of the species comes from Hadar, in the Afar region of Ethiopia, where hundreds of specimens representing males and females of juvenile and adult individuals have been recovered since the early 1970s (Johanson and Taieb, 1976; Johanson et al., 1978a,b, 1982a-c; Kimbel et al., 1994, 2004). The large sample size and presence of *Au. afarensis* in a continuous stratigraphic succession at Hadar has been instrumental in addressing questions related to sexual dimorphism (Kimbel and White, 1988; Kimbel et al., 1994; Lockwood, et al. 1996) and temporal trends in morphological variation in the species (Lockwood et al., 2000).

Multidisciplinary investigations at the Woranso-Mille paleontological study area (Fig. 1), located north of Hadar (Taieb et al., 1976) and Ledi-Geraru (Dupont-Nivet et al., 2008), were initiated in 2004 (Haile-Selassie et al., 2007). Some of the areas within the Woranso-Mille study area were visited in the 1970s by members of the Rift Valley Research Mission in Ethiopia (RVRME), who collected fossil remains (mostly suids and cercopithecids) from various localities (Kalb, 2001). Since 2004, the Woranso-Mille project has thus far collected more than 9,000 vertebrate fossil specimens from more than 85 identified localities ranging in age from > 5.4 Ma to ca. 3 Ma. More than 65 mammalian taxa, including a number of species that are new

to science, have been identified as of the end of the 2015 field season. Of the total number of fossil specimens collected thus far, ca. 145 specimens belong to multiple early hominin taxa, most of which are dated to between 3.8 and 3.2 Ma (Deino et al., 2010; Haile-Selassie, 2010; Haile-Selassie et al., 2010a,b, 2012, 2015; Levin et al., 2015; Saylor et al., 2016a,b). These include cf. *Au. anamensis*, *Au. afarensis* and *Au. deyiremeda* (Haile-Selassie, 2010; Haile-Selassie et al., 2010a,b, 2015). In addition, the Burtele partial foot (BRT-VP-2/73), currently not assigned to a taxon (Haile-Selassie et al., 2012), may represent an already known early hominin from the Afar region other than *Au. afarensis* (i.e. *Ardipithecus ramidus*, *Au. anamensis* or *Au. deyiremeda*) or a species currently unknown from dentognathic remains (Haile-Selassie et al., 2015).

The 2005 discovery at Korsi Dora (Woranso-Mille) of the ca. 3.6 Ma partial skeleton assigned to *Au. afarensis* (KSD-VP-1/1; “Kadanuumuu”), a species well-represented at Hadar, extended the species’ geographic distribution by ca. 45 kilometers (km) north of Hadar. In addition to being the geochronologically oldest partial skeleton of an adult *Au. afarensis* and one of the largest individuals of the species, KSD-VP-1/1 also preserves the most complete adult scapula of the species. Together with the 3.3 Ma juvenile scapulae of DIK-1-1 (Alemseged et al., 2006; Green and Alemseged, 2012), the KSD-VP-1/1 scapula has helped us to further understand the shoulder girdle anatomy of the species (Melillo, 2011, 2016).

The new *Au. afarensis* dentognathic remains described here come from Nefuraytu (NFR-VP-1), a vertebrate locality in the north-central Woranso-Mille study area (Fig. 1). Nefuraytu was first surveyed in 2007, and 342 mammalian fossil remains, including six hominin specimens, have been cataloged to date. The hominin fossils described here (Fig. 2) derive from three fossiliferous horizons within a >40 m stratigraphic section. Magnetostratigraphic and radiometric

dating ($^{40}\text{Ar}/^{39}\text{Ar}$ on feldspar and U/Pb on zircon) indicate that the deposition of the NFR-VP-1 fossils occurred during the Mammoth paleomagnetic subchron (C2An.2r, with an astronomically calibrated age of 3.330–3.207 Ma; Lourens, et al. 2004; see discussions below).

Geological context and age

Lithology

A 44 m thick composite section was measured at Nefuraytu (Fig. 3). Three fossiliferous horizons at 18, 25 and 32 m above the base are associated with sandstones. The lithology of these sections consists of siltstone and claystone (including pedogenic carbonate) interstratified with fine-grained sandstones. Between 13-19 m a coarse detrital unit consists of coarse sandstone and gravel. The gravel, located 3 m below the lower fossiliferous bed, contains cobbles up to 15 cm in diameter.

Chronostratigraphy

The Nefuraytu sequence is isolated stratigraphically in that no direct connection to underlying or overlying strata can be observed. However, projection of the $\sim 1^\circ\text{E}$ dipping Nefuraytu strata, ~ 3 km westward towards Burtele (Haile-Selassie et al., 2015) indicates that the Nefuraytu strata are younger than the sequence at Burtele, in the absence of structural folds or flexures. Geochronological measurements and paleomagnetic stratigraphy (see below) support this inference and suggest that little if any strata are missing in the Burtele through Nefuraytu sequence.

Geochronology

Two thin (0-4 cm) reworked pumice tuff horizons are exposed in the lower third of the Nefuraytu section within a narrow (~ 20 – 30 cm) stratigraphic interval. Typically the pumice

clasts are < 1 cm, well-rounded, have a stretched bubble-wall texture, and are nearly aphyric but contain rare feldspar, zircon, biotite and apatite. An unusual feature of these tuffs is that the original volcanic glass is completely altered diagenetically to a white waxy clay or zeolite that dissolves immediately upon exposure to water. Shard pseudomorph textures are preserved, as observed microscopically. Attempts to extract enough feldspar of sufficient size for $^{40}\text{Ar}/^{39}\text{Ar}$ dating from the fine pumice were unsuccessful, so bulk-tuff extractions were processed and analyzed. A total of 151 single-crystal total-fusion $^{40}\text{Ar}/^{39}\text{Ar}$ analyses were acquired from two samples (WM07/N-1 from the lower tuff and WM07/N-2 from the upper). Procedures and methods are similar to those detailed in Deino et al. (2010). Sanidine from the Fish Canyon Tuff with a reference age of 28.198 ± 0.044 Ma was used (Kuiper et al., 2008), decay constants were those of Steiger and Jäger (1977), and atmospheric argon compositions were according to Lee et al. (2006).

The $^{40}\text{Ar}/^{39}\text{Ar}$ results are presented as age probability-density spectra in Fig. 4 (see SOM A for complete data). Based on the inferred stratigraphic position of the Nefuraytu section from its proximity to the dated Burtele section as discussed above, and newly acquired magnetostratigraphy, we infer that the Nefuraytu section occupies the Mammoth reversed intervals in the Gauss chron, between 3.330–3.207 Ma (Lourens et al., 2004). However, virtually all of the $^{40}\text{Ar}/^{39}\text{Ar}$ results are older, and, given the reworked nature of the tuffs, likely reflect detrital contaminants. These xenocrystic components yield ages typical for the Woranso-Mille area, in particular reflecting early rift volcanism in the late Oligocene, and what are likely major proximal volcanic events at ~4.8 and ~7 Ma (Deino et al., 2010; Saylor et al., 2016b). Younger ages are present, but uncertainties in many cases are largely due to low K content and small grain size. Extracting just the analyses with an uncertainty of <1.5 Ma, and excluding likely detrital

material with an age of >4.5 Ma, yields the probability-density curves shown in the inset in Fig. 4. The youngest population from WM07/N-1 gives a weighted-mean age of 3.73 ± 0.05 Ma ($n = 7$), which is too old in reference to the known chronostratigraphy, but provides a maximum age. Sample WM07/N-1 gives a weighted-mean age of 3.41 ± 0.21 Ma ($n = 3$). While this result is probably nearly correct in magnitude, the uncertainty is large, as it is derived from just a few small plagioclase crystals ($\text{Ca/K} = 3.2\text{--}9.5$; lab numbers 25040-09, -13, and 25029-64, SOM A). However, U/Pb dating of the tuff yields a similar age (see below).

U-Pb dating

Sample WM12/N-1 (= WM07/N-1) is a tuff from the base of the Nefuraytu section. Magnetostratigraphic analyses suggest that it was deposited within a reversed interval (see section on Magnetostratigraphy). Small zircon crystals were separated from the tuff and subjected to single crystal ID-TIMS (isotope dilution-thermal ionization mass spectrometry) and a 3 dimensional total Pb/U isochron, constrained by 6 analyses, yields an age of 3.373 ± 0.047 Ma (here we report a 2 sigma uncertainty for consistency throughout the study), within uncertainty of an age of 3.330 Ma for the age of the base of subchron 2An.2r (=Mammoth) (Lourens et al., 2004) (Fig. 5; SOM B). Excess scatter in the zircon ages most likely results from protracted zircon crystallization at 10-20 ka level prior to eruption and deposition of the tuff, which is consistent with the finding that the isochron age of 3.369 Ma predates the age for the base of subchron 2An.2r, but eruption and deposition of the tuff occurred within and near the base of the latter (see SOM C for further details).

Magnetostratigraphy

Eight stratigraphic layers were sampled for polarity zonation at the Nefuraytu section (Fig. 3). The top sample (at 41 m) yielded normal polarity while the remainder of the section is

reversed. Five additional samples were collected at a shorter (25m), overlapping section located 2 km east, where all samples yielded reverse polarity. The nearby Burtele sequence is paleomagnetically normal, and is anchored in the next earlier chron by the precisely dated Burtele tuff at 3.469 ± 0.008 Ma (Haile-Selassie et al., 2012, 2015). These relationships suggest that the long (>35m) reverse polarity zone recorded by all but the uppermost strata at Nefuraytu belong within a younger reversal, most likely the Mammoth subchron (C2An.2r, 3.330-3.207 Ma; Lourens, et al. 2004). This chronological interpretation of the polarity sequence is based on: a) the apparent stratigraphic continuity to other sections; b) a general age limit of ~ 3.7 Ma [from $^{40}\text{Ar}/^{39}\text{Ar}$]; and c) an maximum age of 3.37 Ma [from U-Pb on zircons].

Associated fauna and paleoenvironment

Preservation of the fossils and taxonomic abundance in all three fossiliferous horizons at NFR are very similar. Partial skeletons of large mammals such as elephants, hippopotamuses, and rhinoceroses and complete crania of bovids are present, showing no sign of substantial carnivore ravaging or long distance transportation. All three horizons are associated with significant numbers of aquatic fauna such as fish and crocodiles. This indicates not only the presence of abundant water at all levels, but also homogeneity in depositional environments across all three horizons. Pending detailed taphonomic analyses, the high number of partial skeletons and lack of carnivore ravaging suggest that the animals were likely quickly buried after death in a low energy environment.

The faunal assemblage from NFR-VP-1 includes > 30 mammalian taxa and at least two aquatic avian species (Table 1). Terrestrial and aquatic reptiles are also common in addition to fish, gastropods, and bivalves. Papionines (particularly *Theropithecus oswaldi*) are the most abundant among the cercopithecids (14% of the total fauna and 90.1% of the cercopithecids),

while colobines are rare (1.5% of the total fauna and 9.9% of the cercopithecids). Among the specimens identified to a subfamily level, tragelaphins and aepycerotins (35.6% of the bovid assemblage) are abundant, each represented by at least two species. Only a single specimen of an alcelaphin has been recovered from the lower fossiliferous horizon and antilopins, neotragins, and reduncins are rare across all horizons (7.8% of the bovid assemblage identified to a subfamily level). The suid species *Notochoerus euilus* and *Kolpochoerus afarensis* are relatively abundant (24% of the total NFR faunal assemblage). Carnivores constitute 7% of the total NFR faunal assemblage. Among the carnivores, a large mustelid (*Enhydriodon* sp.) is present and the felids and hyaenids are represented by cf. *Dinofelis* sp. and cf. *Crocuta* sp., respectively. An unREFERRED canid is also known from two specimens.

Comparison of the NFR mammalian faunal assemblage with the fauna from the underlying sequence at Burtele, ca. 3 km to the west, shows significant taxonomic similarity, although the high relative abundance of alcelaphins and the presence of the suid *Nyanzachoerus kanamensis* at the Burtele localities (BRT-VP-1 and BRT-VP-2; see Haile-Selassie et al., 2012 for details) are noticeable differences. Some of the hominin specimens at BRT also represent a species distinct from *Au. afarensis*. Further comparisons with contemporaneous strata at Hadar (SH-4 and DD-1), ca. 45 km to the south, show that there are more mammalian taxa at NFR than at the contemporaneous Hadar SH-4 and DD-1 levels, although there are overlaps in some taxa (Table 1). Most of the tragelaphin, aepycerotin, and suid species present at NFR are also present at Hadar (Reed, 2008; Reed and Bibi, 2011). However, some bovid taxa that are present at Hadar are absent at NFR (e.g., *Ugandax*, *Parmularius*, *Damalops*). Generally, the bovid community at NFR appears to be slightly different from both the underlying BRT and contemporaneous levels

at Hadar. Understanding the causes for these apparent differences requires detailed analyses of these faunal assemblages in a paleoecological context.

Based on lithology and stratigraphy, we interpret the depositional environment at NFR as a distal fluvial plain, where episodic flooding deposited fine-grained overbank sediments that were exposed long enough for soil development to occur. The coarse sediments represent fluvial channel deposits. The presence of pedogenic carbonate in many of the soils that developed on these fluvial plains indicates seasonally dry environments at NFR.

Stable carbon isotope data from fossil teeth (Table 2) and pedogenic carbonates (Table 3) from NFR provide additional perspective on the environments in which the hominins and other mammals at NFR were deposited and lived. These data were initially reported in Levin et al. (2015) as part of a broader study on hominin and cercopithecoid dietary change at Woranso-Mille but here we highlight the results from samples collected at NFR. All carbon isotope data are reported in δ -notation where $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{VPDB}} - 1) \times 1000$ and per mil (‰) units, where R_{sample} and R_{VPDB} represent the ratio of ^{13}C and ^{12}C in the sample and standard Vienna Pee Dee Belemnite, respectively. The methods used for the stable isotope analysis of the pedogenic carbonates and fossil teeth from NFR are reported in Levin et al. (2015), where guidelines for interpreting the data are also provided. Pedogenic carbonates were sampled from four soil horizons at NFR (Fig. 3). However not all of the sampled horizons match intervals of pedogenic development on the composite section due to lateral variability in the lithology at NFR, typical of fluvial systems. The $\delta^{13}\text{C}$ values of pedogenic carbonates from NFR decrease upward from -2.5‰ at the base of the section to -11.5‰ at the top (Fig. 3), indicating a landscape dominated by C_4 vegetation prior to deposition of the lower fossil horizon and mixed C_3 - C_4 to C_3 -dominated landscapes in the middle and upper portions of the section.

Carbon isotope data from the teeth of hominins ($n = 1$), bovids ($n = 4$), giraffids ($n = 3$) and the suid *Not. euilus* ($n = 11$) from NFR indicate that grazers (*Not. euilus*), browsers (giraffids, unidentified bovid) and mixed feeders (tragelaphins) are represented in this sample. We do not have enough data to identify differences in the carbon isotope data from teeth sampled from the three fossiliferous horizons at NFR. The single hominin sampled from the lower fossiliferous horizon (NFR-VP-1/213; see Table 2) yields a $\delta^{13}\text{C}$ value of -9.1‰ , which indicates a diet dominated by C_3 foods. This may reflect a preference for C_3 resources by the hominins at NFR despite the availability of C_4 vegetation, which is indicated by both the carbon isotope data from other mammals and pedogenic carbonates. For comparison, the $\delta^{13}\text{C}$ value of the NFR hominin is within the range of the other mid-Pliocene hominins at Woranso-Mille which have a median value -7.5‰ (mean $-7.9 \pm 2.5\text{‰}$, range -11.8 to -3.8‰ , $n = 16$) and may represent multiple species (Levin et al., 2015). Overall, the $\delta^{13}\text{C}$ values from the Woranso-Mille hominins are significantly higher than those of *Au. anamensis* but they are indistinct from those from *Au. afarensis* and younger hominins (see Levin et al., 2015 and Cerling et al., 2013, for further details).

The Nefuraytu (NFR-VP-1) fossil hominins

Six hominin specimens were recovered from NFR-VP-1 between 2007 and 2011 (Fig. 2). Among these specimens is an almost complete mandible with most of the dentition (NFR-VP-1/29; Figs. 2A-D). The isolated teeth include two complete lower molar crowns (NFR-VP-1/2 and NFR-VP-1/58), an upper third molar (NFR-VP-1/213) (Figures 2E-G), and a lower canine fragment (NFR-VP-1/96). A small piece of the cranial vault (NFR-VP-1/214) has also been recovered. NFR-VP-1/96 and NFR-VP-1/214 are too fragmentary for detailed comparative analysis. These specimens, together with the two isolated teeth, cannot be assigned to any

specific species with confidence, largely due to the presence of more than one hominin species at Woranso-Mille at 3.5–3.3 Ma. Therefore, they are provisionally referred here to *Australopithecus* sp. Anatomical terminology used in the description of the NFR specimens follows Johanson et al. (1982) and abbreviations are provided in Table 4.

Comparative morphological description

NFR-VP-1/29: Mandible (left I₂, P₄-M₃; right P₄-M₃) (Figs. 2A-D)

Discovery and preservation The right half of the mandible was found on the surface. The lingual half of the M₁ and the complete M₂ were still attached to the mandible. The left half of the mandible was found after 12 days of surface scraping and sieving. None of the teeth was present on the corpus. All of the left mandibular teeth (I₂, P₄-M₃) and the right P₄ and M₃ were found by sieving. Anteriorly, the mandible was broken at the right I₂/c level. The roots of the right I₂-P₄ and M₃ are visible on the mandible. The ascending ramus is broken immediately behind the M₃. The root of the ascending ramus is flaked along its anterior edge. The canine socket lacks small bony surface around the alveolus. A thin crack runs from the alveolar region between the P₄ and M₁ infero-posteriorly toward the base of the lateral corpus. However, this crack has not altered the morphology of the lateral corpus. Anteriorly, a bony surface is missing around the right I₂ and the canine area obscuring the alveolar margin. The ascending ramus is also missing on this side. It is broken immediately behind the M₃ and the distal root of the M₃ and the root of the ascending ramus are also missing. All of the recovered postcanine crowns (except the right M₁ which is missing its buccal half) are preserved intact.

Occlusal aspect The dental arcade shape of *Au. afarensis* mandibles is highly variable (see Kimbel and Delezene, 2009 for details). NFR-VP-1/29 falls within the range of variation of *Au. afarensis* in this regard. It is slightly more open posteriorly than in A.L. 400-1a, MAK-VP-1/12,

and L.H.-4 but not as 'v-shaped' as in A.L. 288-1 (see Fig. 6). NFR-VP-1/29 has dimensions of ca. 18.5 mm between the canine alveoli and 42.3 mm at the M₃s most lingual points, compared to 21.2 mm and 34.8 mm in A.L. 400-1a, ca. 20.2 mm and ca. 38.0 mm in MAK-VP-1/12, and 22.3 mm and 39.0 mm in L.H.-4, respectively. In superior view, the incisor alveoli appear to be lined up in almost a straight line and do not form a well-defined arc as in most *Au. afarensis* mandibles. The postcanine tooth row is straight and the occlusal wear plane is heliocoidal as in most *Au. afarensis* mandibles even though the lingual tilt of the M₃s is particularly pronounced in the NFR mandible. Based on preserved roots, the incisors and canines appear to have been implanted vertically. The anterior symphysis to lateral corpus transition occurs at the canine level with a sharp bend and the P₃ root does not have a noticeable contribution in the transition. This is a condition also seen in L.H.-4, but is unlike most *Au. afarensis* mandibles where the transition is accomplished across an even curve in which both the canine and P₃ roots contribute (White et al., 2000). The superior and inferior transverse tori are well-developed particularly at the P₃ and P₄ levels. This discrete trait is also seen in some *Au. afarensis* mandibles (Kimbel et al., 2004), although most are nearly vertical in this region. When viewed occlusally, the P₄s of NFR-VP-1/29 are set distal to the postero-inferior edge of the symphysis as in A.L. 438-1g, A.L. 444-2b, whereas in most *Au. afarensis* mandibles the position of the P₄s is anterior to the postero-inferior edge of the symphysis. *Au. afarensis* specimens such as A.L. 207-13 and A.L. 266-1 show that the P₄s are set at the posterior-most margin of the symphysis. The extramolar sulcus (buccinator groove) of NFR-VP-1/29 cannot be accurately measured because the anterior edges of the ascending rami on both sides are broken, but it appears to be narrower than in most *Au. afarensis* mandibles (e.g., A.L. 438-1g, A.L. 444-2b, A.L. 128-23, and A.L. 266-1; White and Johanson, 1982; Kimbel et al., 2004).

Lateral aspect The corpus is deep anteriorly and narrows posteriorly due to the superior angulation of the corpus base. This is characteristic of most *Au. afarensis* mandibles (Kimbel et al., 2004). When viewed laterally, a weak Curve of Spee is noticeable along the postcanine tooth row (see Fig. 2C-D). The symphysis is angled postero-inferiorly for its superior half but rounded and bulbous at its base as in most *Au. afarensis* mandibles such as A.L. 400-1a (White and Johanson, 1982) but more receding than the geologically younger mandibles such as A.L. 288-1, A.L. 444-2b and A.L. 438-1g (Kimbel et al., 2004; see Figs. 7 and 8). It approaches L.H.-4 in its basal symphyseal morphology by the fact that its inferior torus extends more posteriorly than the superior torus. However, it is not as ‘cut away’ as in L.H.-4 (Fig. 8). The lateral prominence is not as robust as *Au. afarensis* specimens such as A.L. 444-2b and A.L. 438-1g, but it shows noticeable bilateral asymmetry. The expression of the prominence on the left side starts at the base of the origin of the ascending ramus and sweeps antero-inferiorly as a ridge-like structure terminating at the M₁ level. This expression is absent on the right side. The root of the ascending ramus begins at mid-M₂. Although the root of the ascending ramus is broken on both sides, it appears that it would have obscured most of the M₃. The lateral corpus hollow is bounded superiorly by the lateral prominence, antero-inferiorly by the P₃ jugum and a prominent ridge that runs postero-inferiorly from the base of the P₃ jugum to the corpus base ending at the M₁ level and postero-inferiorly by the well-defined oblique line that emanates from the lateral prominence and runs antero-inferiorly to terminate at the corpus base at M₁ level. This gives the lateral corpus contour hollow on the left side an inverted triangular shape. A small depression is present between the canine and the P₃ close to the alveolar margin. The extramolar sulcus is narrow (estimated to ca. 6-7 mm at the base of the ascending ramus between M₂ and M₃) relative to the corpus breadth at the base of the root of the ramus. The origin of the ascending ramus is

robust medio-laterally. Numerous platysmatic striae are present along the horizontal length of the corpus, particularly close to its base. These striae are mostly located below the main mental foramina and oriented postero-inferiorly. These striae have also been documented in *Au. afarensis* specimens such as A.L. 288-1, MAK-VP-1/2, and MAK-VP-1/12 (Johanson et al., 1982c; White et al., 2000).

There are multiple mental foramina on both sides of the mandible. The main mental foramen (2.5 mm x 2.5 mm) on the left side is situated at P₃/P₄ level slightly below mid-corpus height. This foramen opens antero-superiorly. A second, slightly smaller foramen (1.8 mm x 1.6 mm), is situated about two-thirds down the corpus height at mesial M₁ level. This foramen opens infero-posteriorly. At least three accessory foramina of variable size are visible on the left side. The main mental foramen on the right side (4.2 mm AP and 2.6 mm SI) is situated at P₄ level slightly below mid-corpus height and opens antero-superiorly. The exit of the foramen is deeply furrowed forming an antero-posteriorly oriented groove about 4.5 mm long. There are two accessory foramina: one close to the alveolar margin at P₃/P₄ and a second located 7 mm posterior to the main mental foramen.

Medial aspect The alveolar margin, where intact, such as on the right side between M₁ and M₃, is relatively sharp and less rounded. The alveolar prominence is strong particularly anteriorly below P₃-M₁. Corpus contour seems to have been interrupted by root jugum at the mesial M₁ root level on both sides. The anterior and posterior subalveolar fossae are clearly defined. The anterior subalveolar fossa is shallow, positioned at mid-corpus height, and sweeps antero-inferiorly from mesial M₁ to mid-M₂ level. The posterior alveolar fossa is deeper and wider and sweeps anteroinferiorly starting from the base at mid M₂ level to mid-corpus at distal M₃ level. The two fossae are separated by an anteroinferiorly sweeping ridge-like eminence. Posteriorly,

close to the broken gonial angle, a well-developed crest runs from the base of the corpus at distal M₂ level superiorly and then inferoposteriorly to the basally concave base of the corpus near the gonial angle. This crest probably marks the insertion for the anterior portion of the medial pterygoid muscle. The mylohyoid line is poorly defined. However, the mylohyoid groove is relatively deep and extends anteroinferiorly down to the posterior end of the lateral corpus at distal M₃. The base of the ascending ramus is clearly separated from the lateral corpus.

Anterior symphyseal region In lateral view, the symphysis slope is comparable to most *Au. afarensis* specimens. However, the basal half slopes more, comparable to L.H.-4. Incisal incisura are present immediately below the I₂ alveolar margins. These incisura allow the formation of two vertical ridges (juga) starting from midline level and going all the way to the alveolar margin between the first incisors. There is a palpable eminence at the position of the symphyseal tuber. In superior view, the shape of the symphysis tends to be flat rather than a gentle curve. The canine jugum, partially preserved on the right side, is strong and visible anteriorly.

Posterior symphyseal region The postincisive planum is posteriorly concave both transversely and superoinferiorly. However, it is both transversely and superoinferiorly narrower than *Au. afarensis* specimens such as A.L. 400-1a, and MAK-VP-1/12. The planum is short and less steep superoinferiorly. The transverse narrowness is largely due to the strong transverse torus/alveolar prominence at the P₃-M₁ level. Otherwise, NFR is bilaterally wider at C/P₃ level than most *Au. afarensis* specimens. A well-developed superior transverse torus marks the superior border of the deep digastric fossa. The inferior transverse torus at midline is as thick as its superior counterpart and extends more posteriorly than the superior transverse torus. This gives the basal half of the symphysis a more receding appearance. This is in some ways similar

to L.H.-4 although it is not as “cut-away” as the latter. The fossa is larger than in A.L. 400-1a. It is divided into two chambers by a rounded bony septum. The supraspinous foramen is situated at midline at the end of the bony septum dividing the two digastric fossae chambers. There is no visible mental spine here.

Basal aspect The corpus base is almost evenly thick starting from the posterior end of the digastric fossae (Fig. 2B). The basal margin is rounded for the most part and slightly everted posteriorly. The digastric fossae are shallow but well defined. Immediately posterior to the digastric fossae, there are strong crests (prominent on the left side) along the base of the corpus marking the insertion for the anterior part of the mylohyoid muscles. These crests continue posteriorly all the way to the level of the third molar. They sweep superiorly and then inferiorly at the level of M₂ and M₃. Anterior to the broken gonial angle on the left side, there are well-developed tubercles on both the medial and lateral sides.

Symphyseal cross-section The shape and inclination of the NFR-VP-1/29 symphysis is comparable to *Au. afarensis* specimens such as MAK-VP-1/12, A.L. 400-1a, and A.L. 333w-60 (White et al., 2000; Kimbel et al., 2004) (Figs. 7 and 8). It is more receding than almost all of the *Au. afarensis* mandibles from the upper part of the Kada Hadar Member (e.g., A.L. 417-1a, A.L. 437-1, A.L. 437-2, 438-1g, and A.L. 444-2; see Figs. 7 and 8).

Mandibular cross section at M₁ A coronal section of NFR-VP-1/29 at the M₁ level shows that it is most similar to A.L. 333w-60 and to some degree to MAK-VP-1/12, in terms of having a well-developed superior transverse torus compared to the inferior transverse torus. However, the lateral wall of NFR-VP-1/29 is more vertical than those of these two specimens, and more like A.L. 198-1 (see Figure 5.31 in Kimbel et al., 2004 and Fig. 9 here). The mandibular corpus shape index ((breadth/height) *100) of NFR-VP-1/29 is 58.4% on the right side and 61.2% on the left

side with an average of 59.8% (see Table 5 for measurements). The average index is identical to A.L. 438-1, whereas the index on the right side is similar to specimens such as A.L. 333w-32+60, MAK-VP-1/12, and L.H.-4 (Kimbel et al., 2004). In general, the average index is slightly larger than the mean for *Au. afarensis* but within 1 standard deviation of all known *Au. afarensis* mandibles (see Kimbel et al., 2004 for further discussions).

Internal corpus anatomy The cortex is thickest at the corpus base and evenly thick on the lateral wall and at the inferior transverse torus. It is also relatively thick along the alveolar margin. However, cortical thickness at the superior transverse torus is extremely thin. This is also the case in *Au. afarensis* mandibles such as A.L. 277-1 (White and Johanson, 1982). The central part of the corpus is mostly filled with trabecular bone, and in some areas hollow, but gets denser in the peripheral areas. Coronal section between the P₄ and M₁ shows that the corpus on the right side is filled with trabeculae more than the left side although the significance or reason for the bilateral asymmetry requires further investigation.

Dentition The crowns of the anterior teeth (I₁-P₃) of NFR-VP-1/29, except for the left I₂ crown, which was found isolated, are missing, with only their roots preserved on both sides. The P₄-M₃ row on the left side is preserved intact. The same is true for the right side except for the buccal half of the M₁, which is broken off. All preserved teeth show no sign of surface weathering or other biotic and/or abiotic alterations although wear in some of the teeth has minimally obliterated occlusal morphology. Measurements are provided in Table 6.

The left I₂ crown was recovered isolated from the jaw. The crown is intact, with a clean break at the CEJ. The mesial half of the incisal edge is slightly more worn than the distal half. It has dentine exposed across the entire occlusal surface with a slight tilt lingually. Its overall shape and morphology is similar to *Au. afarensis* I₂s (Kimbel et al., 2004). The MD of the crown flares

from the cervix (4.2 mm) up to the occlusal surface (6.6 mm). The MD is close to the mean of *Au. afarensis* (6.3 mm; $n=7$). The LaL dimension at its base close to the CEJ is 8.4 mm, slightly above the mean for *Au. afarensis* (8.0 mm). The labial face is SI flat but slightly convex labially. The lingual face is concave above the basal swelling and lacks any sign of vertical mesial and distal grooves, unlike *Au. afarensis* specimens such as A.L. 400-1a. However, its occlusal wear is almost identical with A.L. 400-1a, particularly in the distal half of the incisal edge being more worn than the medial half. The mesial IPF measures 2.6 mm SI and 2.5 mm LaL. The distal IPF is slight larger, measuring 2.8 mm SI and 2.6 mm LaL.

The P₄ crowns on both left and right sides are preserved intact. The right side is slightly more worn than the left side. However, they appear to be identical in their occlusal morphology. The description here is based on the less worn left side. The Med is placed more mesially than the Prd. The Prd occupies almost the entire buccal half of the crown, is worn flat, and has a small dentine exposure measuring 1.4 mm by 1.0 mm (1.6 mm by 1.0 mm on the right side). The Fa is obliterated by wear and only a small pit (small slit-like groove on the right side) is visible as a remnant of the Fa. However, the Mmr appears to have been thick. The Fp is positioned slightly lower (closer to the root) and more lingually than the Fa. When viewed mesially or distally, the buccal face slightly slopes occlusally, whereas the lingual face is vertical. In lateral view, it has a shallow vertical groove on its distobuccal corner that gets wider from its base toward the occlusal surface. In mesial view, the IPF is set high, close to the occlusal rim and measures 4.5 BL and 2.7 SI. Summary statistics of dental crown size and shape for early *Australopithecus* taxa and NFR are provided in Table 7.

In terms of premolar root morphology, the P₃s of NFR-VP-1/29 have a mesiobuccally positioned circular root with a single root canal and a plate-like distal root with two root canals

that converge distally (Fig. 10). The P₄s have two BL elongated plate-like roots for most of the root length below the crown base and each root has two root canals. The distal root is positioned more lingually than the mesial counterpart and it is also slightly larger. Each root has two root canals and the distal root bifurcates close to the tip of the root.

The M₁ crown is intact on the left side, whereas the buccal half is missing on the right side. Therefore, the description is based on the left side. The crown is a MD long rectangle with rounded corners. Both of the lingual and buccal faces are mildly bilobate. The Prd, Med, and Hyd are of comparable size. The End is smaller and almost the same size as the Hld. The Fa, Fc, and Fp are obliterated by wear. The Prd and Hyd are worn flat and have centrally positioned rounded dentine pits. The pit on the Prd has a diameter of 1.9 mm. The one on the Hyd measures 1.2 mm. The Med and End tips are polished by wear but with no dentine exposure. These two cusps are separated by a transverse groove that extended to the lingual wall, also dividing them half way on the lingual side. The Hld is worn flat but with no dentine exposure. It is separated from the Hyd by a small groove located on the disto-buccal corner closer to the occlusal rim.

Both left and right M₂ crowns are preserved intact. The occlusal outline is a mesio-distally elongated rectangle with rounded corners. All of the five major cusps are bounded by visible transverse and longitudinal grooves. The Prd is the largest cusp followed by (from largest to smallest) the Med, Hyd, End, and Hld. The Dmr is expressed more like C6 on the distolingual corner of the crown. The Fa is obliterated by wear and a deep longitudinal groove separates the Prd from the Med. The Prd and Hyd are separated by a deep transverse groove that extends all the way from the occlusal surface to the buccal wall of the crown. The Fc is deep and positioned more lingually. The small slit-like Fp is also positioned more lingually. A short shallow groove

separates the Hyd from the Hld on the occlusal surface. The Med and End are higher than the other cusps. Their tips are worn flat but with no dentine exposure.

Both left and right M₃ crowns are preserved intact. Although both crowns are almost identical in terms of their occlusal morphology, description is based on the left side for consistency. The occlusal outline is an MD elongate rectangle that tapers distally and ends in a rounded distal rim. All of the major cusps are bounded by well-developed grooves. The Prd is the largest in terms of its surface area, followed from largest to smallest by the Med, End, Hyd and Hld. The C6 is well developed and only slightly smaller than the Hld. The occlusal surface of the buccal cusps is polished by wear but with no dentine exposure. The apex of C6 also shows polishing on its tip. The Med and End are relatively high and show some polishing. The Fa is represented by two small dots on the lingual and buccal sides of the longitudinal groove that bounds the Prd and Med and ends at the mesial edge of the Fc. Two deep transverse grooves that extend to the buccal surface separate the Med, Hyd, and Hld from each other. Three grooves that separate the three distal cusps and the C6 from each other terminate in the centrally positioned relatively deep Fp. The lingual and buccal walls are trilobate and the buccal wall slightly tapers occlusally compared to the vertical lingual wall.

NFR-VP-1/2: RM₁ (Fig. 2E)

This specimen is a surface discovery and consists of a complete but unerupted crown. It is broken at the CEJ and it has no sign of wear on any of the cusps. Some enamel is chipped at the mesio-buccal corner close to the CEJ. Its occlusal outline is a MD elongate rectangle, slightly tapering distally with rounded angles. The Med is the largest. All of the other cusps, except the Hld, are subequal. A small C6 is present. The two lingual cusps are much higher than their buccal counterparts. All five major cusps are bounded by grooves. The Med and Prd are

separated by a short longitudinal groove that emanates from the Fa. The Fa is a slit-like structure bound mesially by a well-defined Mmr. The grooves that separate all other cusps emanate from the slightly buccally positioned Fc and extend as deep grooves onto the lingual and buccal walls, extending all the way to the CEJ. The buccal and lingual walls are therefore trilobate and bilobate, respectively. A small inverted V-shaped Fp is bounded by the Hld, End and a C6.

NFR-VP-1/58: RM₂ or RM₃ (Fig. 2F)

This specimen is a surface discovery and consists of a complete crown. It is broken at the CEJ. The buccal cusps are polished indicating that the crown was in occlusion, but it has no sign of dentine exposure. The Med is the largest cusp followed by the subequal Prd and Hyd. The Hld is the smallest. There is a small C6 distal to the End. All major cusps are separated by transverse and longitudinal grooves. The transverse groove separating the Prd from the Hyd and the Med from the End extend further into the buccal and lingual walls of the crown, making these walls bilobate. A number of secondary fissures run down from the Med and Prd toward the Mlg. The slit-like Fa is centrally positioned and mesially bounded by a well-defined Mmr (1.3 mm). The Fc is positioned more lingually and manifested as the junction point for all the grooves that separate the major cusps. A tiny Fp that is positioned more lingually is present and bound by the End, Hld, and a tiny C6. The mesial IPF is concave mesially and measures 4.0 mm MD and 2.5 mm SI. There is no sign of a distal IPF and the distal wall is rounded. However, its dimensions best fit into the second molar distribution of *Au. afarensis* (see discussion below).

NFR-VP-1/96: L/C fragment (not figured)

This is an extremely worn lingual half of a lower canine. The entire preserved lengths of the crown and the root are 6.9 mm and 17.5 mm, respectively. The crown is worn all the way to the level of the distal tubercle and none of its parts is preserved enough for detailed description.

NFR-VP-1/213: RM³ (Fig. 2G)

This is a complete M³ crown with a small part of its root (6.5 mm long below the protocone) preserved. A hairline crack runs longitudinally across the protocone and hypocone close to the lingual edge of the cusps. However, the occlusal morphology is not affected by the crack. It has premortem enamel chipping on the buccal wall of the paracone close to the occlusal rim. The occlusal outline is trapezoidal, tapering distally. All major cusps are polished by wear although no dentine is exposed on any of them. The paracone is slightly pointy compared to all other cusps. The protocone is the largest cusp followed by the paracone. The hypocone and metacone are smaller and subequal. A number of short lingual grooves are present on the protocone. The groove separating the protocone from the hypocone runs all the way down to the CEJ across the lingual wall. The Fa is obliterated by wear. A slit-like Fc runs from the lingual rim as a continuation of the central lingual groove and terminates between the paracone and the metacone. A small Fp is centrally positioned bounded by the small metacone and the Dmr. The IPF is 4.4 mm MD and 1.4 mm BL. The crown is 12.2 mm MD (12.7 mm corrected for IPF) and 13.8 BL.

NFR-VP-1/214: Frontal fragment (not figured)

This is a small frontal fragment with dimensions of 22.5 mm by 22.2 mm. Its fragmentary nature does not allow detailed description.

Metric comparisons

Metric analysis reinforces the assignment of the Nefuraytu mandible to *Au. afarensis*. The specimen shows postcanine megadontia and other heavy-mastication features that typify this species. Dentognathic dimensions fall within or very close to the range of variation documented by specimens from Hadar, Laetoli and Dikika (Fig. 11, Tables 5 and 6; see SOM D for the list of

Au. anamensis and *Au. afarensis* specimens included in the comparative analysis). The large overall size of NFR-VP-1/29 suggests that it represents a male individual.

The NFR-VP-1/29 P₄ crowns are most similar in size to large *Au. afarensis* specimens such as A.L. 582-11 and L.H.-3, and larger than any *Au. anamensis* P₄s known to date. They are further *Au. afarensis*-like in crown shape (Fig. 11A, Table 7), showing the distinct MD expansion that is absent in *Au. anamensis* (Ward, 2014). The NFR-VP-1/29 P₄ crowns are not as large or MD-expanded as the KNM-WT 8556 P₄.

Au. afarensis tends to have larger M₁ crowns than *Au. anamensis* ($t = -2.6, p < 0.05$). The NFR-VP-1/29 M₁ crown is among the largest known for *Au. afarensis* (second only to DIK-2-1) and it falls near the *Au. afarensis* mean for crown shape (Fig. 11B, Table 7). The isolated NFR-VP-1/2 M₁ crown falls at the *Au. afarensis* mean with regard to size, but is narrower than any other specimen in the comparative sample.

Other dental dimensions preserved in the Nefuraytu specimens do not differentiate species, but they fall within or very close to the known *Au. afarensis* range of variation (Fig. 11, Table 6). The I₂ has MD and BL dimensions of 6.6 mm and 8.5 mm, respectively. It is slightly above the mean for *Au. afarensis* (MD = 6.2 mm [$n = 5$]; BL = 8.0 mm [$n = 7$]). Its BL is closer to that of A.L. 444-2 (8.8 mm), the specimen that so far represents the upper limit for this dimension in the species (Kimbel et al., 2004). NFR-VP-1/29 M₂s are large, similar to A.L. 188-1 and KNM-KP 30500 in crown size and shape. The isolated M₂ NFR-VP-1/58 also falls close to the mean values of the *Au. afarensis* crown size and shape. NFR-VP-1/29 M₃s are large and similar to A.L. 620-1 and KNM-KP 47953 in crown size and shape. NFR-VP-1/213 (M³) falls within the range of both *Au. anamensis* and *Au. afarensis* in terms of its MD and BL dimensions. It is almost identical to the *Au. anamensis* specimen (ARA-VP- 14/1) from the Middle Awash in

both its MD and BL dimensions. It is also similar to the *Au. afarensis* specimen (A.L. 770-1a) from Hadar in its MD dimension although the Hadar specimen is much wider in its BL dimension. However, the shape of NFR-VP-1/213 falls outside the 95% confidence interval of *Au. anamensis* and falls at the lower end of *Au. afarensis* (Table 7).

The NFR-VP-1/29 mandibular corpus is large, most similar to geologically younger *Au. afarensis* specimens from the upper part of the Denen Dora Member (A.L. 333w-32+60) and the Kada Hadar Member (A.L. 437-1, A.L. 437-2, A.L. 438-1, and A.L. 444-2) (Fig. 11E-F). All of these Hadar mandibles are younger than 3.22 Ma (Kimbel et al., 2004; Campisano et al., 2007). It is also similar in size to the Dikika mandible (DIK-2-1), which was recovered from the Basal Member of the Hadar Formation below the 3.42 Ma Sidi Hakoma Tuff (Alemseged et al., 2005). The corpus shape ratio $(= (\text{breadth/height}) * 100)$ of NFR-VP-1/29 at the M_1 level is 59.8, almost identical to the mean of 23 *Au. afarensis* mandibles (58.2), and distinct from the broad corpora of the *Au. deyiremeda* mandibles. KNM-WT 8556 was described as robust and assigned to *Au. afarensis* (Brown et al., 2001). However, the corpus of this mandible is fairly similar to the NFR mandible in terms of corpus dimensions, but distinct from the broad mandibles of *Au. deyiremeda*. The corpus dimensions of the two mandibles assigned to *Au. bahrelghazali* (KT-12 and KT-40; Brunet et al. 1996; Guy et al. 2008) are unknown although the size of the P_4 of KT 12 falls within the range of *Au. afarensis* (see Figure 11A).

Temporal trends

The NFR-VP-1/213 M^3 , assigned here to *Australopithecus* sp., falls very close to the size expected for *Au. afarensis* specimens dated to 3.3-3.2 Ma, corroborating the trend reported for this element (Lockwood et al., 2000). However, the dimensions of the NFR-VP-1/29 mandibular corpus are considerably larger than would be expected for its geological age, and a similar

observation has been made for DIK-2-1 (Alemseged et al., 2005). The addition of these more recent specimens to the *Au. afarensis* hypodigm slightly alters the support for the temporal trend hypothesis, as concerns the mandibular corpus. Lockwood et al. (2000) reported a significant increase in mandible size over time for metrics considered (geometric mean of corpus height and breadth, corpus height independently and breadth independently). Using the methodology described by Lockwood et al. (2000), in which the Spearman rank correlation coefficient (r_s) is reported but the significance of the correlation is judged using a permutation test of the gamma statistic (p_Γ), and an expanded sample that includes the Maka mandibles (MAK-VP-1/12, MAK-VP-1/2; White et al., 2000), the Dikika mandible (DIK-2-1; Alemseged et al., 2005) and NFR-VP-1/29, we found that the temporal trend in corpus size (as represented by the geometric mean of height and breadth) at the M_1 level remains significant ($r_s = 0.43$, $p_\Gamma < 0.05$), as does the trend in corpus height ($r_s = 0.39$, $p_\Gamma < 0.05$). In contrast, the trend in corpus breadth drops below the level of significance (breadth $r_s = 0.28$, $p_\Gamma = 0.09$).

***Au. afarensis* and *Au. deyiremeda* at Woranso-Mille**

Most of the differences that distinguish NFR-VP-1/29 from *Au. deyiremeda* are also differences that distinguish the latter from *Au. afarensis* (Fig. 12; see Haile-Selassie et al., 2015, for details). For example, *Au. deyiremeda* mandibles (BRT-VP-3/14 and WYT-VP-2/10) are especially broad for their overall small size (Fig. 11E-F). The ramus root is positioned more anteriorly than is typical for *Au. afarensis*, giving the *Au. deyiremeda* corpus cross section a more inflated appearance (Fig. 9). In contrast, NFR-VP-1/29 is a very large mandible but not especially broad—its corpus dimensions at all positions along the tooth row are representative of *Au. afarensis*. It also exhibits a typical *Au. afarensis*-like corpus cross-section (Fig. 9).

Discussion

NFR-VP-1/29 is a large mandible, overlapping in its size with the geologically younger specimens of *Au. afarensis* from the Kada Hadar Member (e.g., A.L. 417-1, A.L. 437-1, A.L. 437-2, A.L. 438-1g, and A.L. 444-2). Morphologically, however, its symphysis is more sloping than these specimens and more similar to the geologically older specimens such as A.L. 330-5, A.L. 400-1a and MAK-VP-1/12 (White et al., 2000; Kimbel et al., 2004), while its corpus cross-section at M₁ can easily be subsumed within the range of variation seen in *Au. afarensis* (Fig. 9). The development of the superior transverse torus of NFR-VP-1/29 is also best matched by A.L. 333w-32+60. Overall, NFR-VP-1/29 retains almost all of the distinctive archaic features documented for *Au. afarensis* (Kimbel et al., 2004). These features include a posteriorly sloping symphysis, a low and rounded basally set inferior transverse torus, antero-superiorly opening mental foramen, a lateral corpus hollow bound anteriorly by the C/P₃ jugae and posteriorly by the lateral prominence, and ascending ramus arising posterior and high on the corpus (Johanson and White, 1979; White et al., 1981, 2000; Johanson et al., 1982c; Kimbel et al., 2004; Kimbel and Delezenne, 2009). Its dentition also falls within the size range of *Au. afarensis* (see Table 6).

In addition to being one of the few well preserved mandibles of *Au. afarensis*, NFR-VP-1/29 is also important in testing the hypothesis related to the temporal trend in *Au. afarensis* mandibular corpus size increase (Lockwood et al., 2000). Given its geological age and size, NFR-VP-1/29 might appear to counter the hypothesized temporal trend (Lockwood et al., 2000), in a similar way as DIK-2-1 (Alemseged et al., 2005). However, given the extensive size variation in *Au. afarensis* mandibles, NFR-VP-1/29 could yet be another large mandible from a horizon that is older than 3.2 Ma. As Alemseged et al. (2006) clearly noted, there are, for example, large and small *Au. afarensis* mandibles from a single horizon at Maka in the Middle

Awash (White et al., 2000), which are dated to ca. 3.4 Ma and contemporaneous with DIK-2-1. Therefore, the presence of few large mandibles in older horizons does not necessarily falsify the observed trend that is inferred from a larger sample size (Lockwood et al., 2000).

Given the overall size of NFR-VP-1/29, which is comparable to specimens such as A.L. 333w-60 from the Denen Dora Member (>3.2 Ma), it is possible to argue that mandibular corpus size increase in *Au. afarensis* might have started earlier than the Kada Hadar Member. Other mandibles from the Denen Dora Member, such as A.L. 487-1 and A.L. 620-1, are also relatively larger than the average-sized *Au. afarensis* mandibles. Dimensions of the isolated teeth from Nefuraytu are also above the average for the species in terms of their MD and BL dimensions even though they fall within the documented range of variation for the species.

NFR-VP-1/29 is contemporaneous with WYT-VP-2/10, one of the paratypes of *Au. deyiremeda* (Haile-Selassie et al., 2015). However, in addition to the metric differences described above, NFR-VP-1/29 is further distinguished from *Au. deyiremeda* in overall mandibular configuration. For example, *Au. deyiremeda* mandibles are distinguished from NFR-VP-1/29 and other *Au. afarensis* mandibles by their more anteriorly positioned origin of the ascending ramus, relatively smaller teeth compared to corpus size, wide extramolar sulcus, BL inflated corpus at the level of the molars, and poorly developed lateral corpus hollow (Haile-Selassie et al., 2015; See Fig. 12). Thus, despite its temporal and spatial proximity to *Au. deyiremeda*, NFR-VP-1/29 does not belong to the latter species and further confirms that there were at least two contemporaneous hominin species in the Woranso-Mille region during the middle Pliocene.

Conclusion

Hominin fossils from the Nefuraytu locality of the Woranso-Mille paleontological study area are chronologically placed between 3.330 Ma and 3.207 Ma. The hominin fossils from this locality include isolated teeth and a complete mandible with dentition (NFR-VP-1/29). Comparative analyses of these specimens show that they are metrically and morphologically indistinguishable from the well-known and contemporaneous species *Au. afarensis*. NFR-VP-1/29 is most similar to specimens such as the 3.2 Ma A.L. 333w-60 from Hadar and 3.4 Ma MAK-VP-1/12 from the Middle Awash and retains most of the primitive dentognathic features described for *Au. afarensis*. NFR-VP-1/29 is metrically and morphologically different from *Au. deyiremeda* and within the range of morphological and metric variation observed in *Au. afarensis*. Thus, although it was found in close temporal and spatial proximity with *Au. deyiremeda*, the morphological and metric evidence supports assignment of the Nefuraytu hominins to *Au. afarensis*. This is significant for two major reasons. First, the NFR specimens assigned to *Au. afarensis* and the KSD-VP-1/1 partial skeleton (Haile-Selassie et al., 2010b) sample the northernmost occurrence of the species thus far known in the fossil record of eastern Africa. Second, they clearly indicate that *Au. afarensis* at Woranso-Mille was living in close proximity with other related hominin taxa, such as the species represented by the Burtele foot (BRT-VP-2/73; Haile-Selassie et al., 2012) and *Au. deyiremeda* (Haile-Selassie et al., 2015).

The Woranso-Mille study area has yielded a number of middle Pliocene fossil hominin remains ranging in age from ca. 3.0 Ma to >3.8 Ma. The fossil remains from the study area appear to represent multiple hominin taxa, sometimes overlapping not only in time but also in space. The presence of cf. *Au. anamensis* at >3.7 Ma (Haile-Selassie, 2010), *Au. afarensis* at 3.6 Ma (Haile-Selassie et al., 2010b) and 3.3–3.2 Ma, the Burtele foot at 3.4–3.3 Ma (Haile-Selassie et al., 2012), and the recently named 3.5–3.3 Ma *Au. deyiremeda* (Haile-Selassie et al., 2015) at

Woranso-Mille are all clear evidence that there were multiple contemporaneous hominin species in eastern Africa during the middle Pliocene. Analyses of associated faunal assemblages, stable carbon isotope data from fossil teeth and pedogenic carbonates indicate that these hominins were living in mixed C₃-C₄ to C₃-dominated landscapes at Woranso-Mille.

Finally, whereas the recovery of more fossils representing the newly named middle Pliocene hominin taxa from eastern and central Africa (Brunet et al., 1996; Leakey et al., 2001; Haile-Selassie et al., 2015), and a better understanding of their paleobiology is of paramount importance to test the hypothesis that multiple related hominin taxa lived contemporaneously, and at times in close proximity, instant predilections for subsuming some or all of the named middle Pliocene hominin species to *Au. afarensis* without credible evidence is clearly unwarranted. Only the recovery of more complete fossils will clarify these issues.

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Figure Captions

Figure 1. A geological map showing the location and lithology of the Burtele-Nefuraytu (BRT-NFR) localities within the Woranso-Mille study area. The image below shows a panoramic view of the fossiliferous sediments at Nefuraytu.

Figure 2. Nefuraytu (NFR) hominins. Occlusal (A), basal (B), right lateral (C), and left lateral (D) views of NFR-VP-1/29; Occlusal views of NFR-VP-1/2 (E), NFR-VP-1/58 (F), NFR-VP-1/213 (G).

Figure 3: Stratigraphic correlation between Nefuraytu and Burtele areas showing the inferred position of the Nefuraytu strata above those at Burtele (located 4 km to the west). The figure shows the stratigraphic position of a dated tuff at Burtele (Haile-Selassie et al., 2012, 2015), paleomagnetic and soil carbonate samples from Nefuraytu (Levin et al., 2015), and sandstones beds with in-situ vertebrate fossils. Black bars and white bars adjacent to sections indicate normal (N) and reversed (R) polarity, respectively. A composite N-R-N polarity sequence is tentatively correlated with the Astronomically tuned Neogene Time Scale (ATNTS) from Lourens et al. (2004). The stratigraphic position, paleomagnetic directions and available $^{40}\text{Ar}/^{39}\text{Ar}$ and U/Pb age constrain the age of the Nefuraytu fossils to between 3.330 and 3.207 Ma. All geographic coordinates are listed using the WGS-84 Datum. The stereoplot shows the primary paleomagnetic directions for the Nefuraytu stratigraphic succession after AF and thermal demagnetization. Reverse polarity is shown for most samples with a mean direction of $176^\circ\text{-}20^\circ$. Only one sample located 3m below the top of the section shows evidence for normal polarity, the inclination of this sample is still negative probably because the secondary magnetization has not been completely removed. Stereographic projection

referenced to magnetic north (declination 2° E), with solid symbols on lower hemisphere (+ inclination) and open symbols on upper hemisphere (- inclination).

Figure 4: Age probability-density spectra of single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating results for pumice tuff samples WM07/N-1 and WM07/N-2 (bottom-most plot), above which are plotted several corresponding derived parameters (ranked age, moles ^{39}Ar , Ca/K ratio, and % $^{40}\text{Ar}^*$, the percent radiogenic ^{40}Ar). The inset graph shows a subset of the analyses inferred to best define or constrain the emplacement age of the tuffs, with weighted-mean ages. All errors are shown at 1σ .

Figure 5. Three-dimensional total Pb/U isochron diagram (Ludwig, 2009) of six zircon analyses from sample WM12/N-1. The $^{204}\text{Pb}/^{206}\text{Pb}$ axis, which is not shown, lies perpendicular to the plane of the plot.

Figure 6. Occlusal views of *Au. afarensis* mandibles. A) A.L. 288-1n; B) MAK-VP-1/12 (Image courtesy of Tim White); C) A.L. 400-1a; D) NFR-VP-1/29. Scale bar is 2 cm.

Figure 7. Outline of symphyseal cross section of some *Au. afarensis* mandibles from Hadar, Middle Awash, and Laetoli (top and middle row) compared to *Au. afarensis* (NFR-VP-1/29) and *Au. deyiremeda* (BRT-VP-3/14 and WYT-VP-2/10) mandibles from the Woranso-Mille (bottom row). Note that NFR-VP-1/29 is most similar to MAK-VP-1/12 while the Mandibles of *Au. deyiremeda* appear to be different from those of *Au. afarensis* in variable ways. The cross sections of *Au. afarensis* mandibles are modified from Kimbel et al.'s (2004) Figure 5.29 which was compiled from cross sections published in White et al., 2000; Brunet et al., 1996; and Ward et al., 2001. All outlines are not to scale.

Figure 8. Right lateral views of *Au. afarensis* mandibles. A) A.L. 288-1n; B) A.L. 444-2b; C) MAK-VP-1/12 (Image courtesy of Tim White); D) NFR-VP-1/29; E) A.L. 400-1a; F) L.H.-4 (cast). Scale bar is 2 cm.

Figure 9. Outline of mandibular corpus cross section at M_1 of some *Au. afarensis* mandibles from Hadar, Middle Awash, and Laetoli (top and middle row) compared to NFR-VP-1/29 and *Au. deyiremeda* (BRT-VP-3/14 and WYT-VP-2/10) mandibles from the Woranso-Mille (bottom row). Note that NFR-VP-1/29 is most similar to A.L. 333w-60 and to some degree MAK-VP-1/12, in terms of having a well-developed superior transverse torus compared to the inferior transverse torus. However, the mandibles of *Au. deyiremeda* appear to be different from those of *Au. afarensis* in having an extremely broad corpus. The cross sections of *Au. afarensis* mandibles are modified from Kimbel et al.'s (2004) Figure 5.31 which was compiled from cross sections published in White et al., 2000; Brunet et al., 1996; and Ward et al., 2001. All outlines are not to scale.

Figure 10. Premolar root morphology of NFR-VP-1/29. A) Immediately below crown base; B) at mid-root level. Note that the mesial root of the P_3 is rounded and mesiobuccally positioned, whereas the distal root is plate-like and has two root canals. The mesial and distal roots of the P_4 are both plate-like and have two root canals each. The distal root bifurcates into two roots toward its tip.

Figure 11. Bivariate plots of mandibular dental and corpus dimensions in early-mid Pliocene hominins. The NFR-VP-1/29 dentition and corpus are large, but fall within or border the documented *Au. afarensis* range. Filled black circles: NFR-VP-1/29. Open circles: isolated mandibular teeth from NFR-VP-1. Red squares: *Au. afarensis*. Blue triangles:

Au. anamensis. Green diamonds: *Au. deyiremeda*. Gray crosses: specimens from Lomekwi. MD = mesiodistal; BL = buccolingual; HT = height; BR = breadth.

Figure 12. Comparison of NFR-VP-1/29 (*Au. afarensis*) and BRT-VP-3/14 (paratype of *Au. deyiremeda*). The black arrows show the differences between the two mandibles in terms of the origin of the ascending ramus (1), the size of the extramolar sulcus (2), and corpus inflation at the level of the molars. Scale bar is 2 cm.

Table 1

Table 1. NFR-VP-1 faunal list based on 342 catalogued specimens.

Aves	Canidae
Gen. et sp. indet (large)	Gen et sp. indet.
Gen. et sp. indet (small)	Rhinocerotidae
Bovidae	<i>Ceratotherium efficax</i>
<i>Aepyceros</i> cf. <i>A. datoadeni</i>	<i>Diceros</i> sp.
<i>Aepyceros</i> sp.	Soricidae
Antilopini gen. et sp. indet.	Gen et sp. indet.
Neotragini gen. et sp. indet.	Equidae
Reduncini gen. et sp. indet.	<i>Eurygnathohippus hasumense</i>
<i>Tragelaphus kyaloi</i>	Cercopithecidae
<i>Tragelaphus</i> cf. <i>T. lockwoodi</i>	Papionini gen et sp. indet.
<i>Oryx</i> sp.	<i>Theropithecus oswaldi</i> aff. spp.
Giraffidae	Colobinae gen et sp. indet.
<i>Giraffa</i> sp.	Hominidae
<i>Sivatherium maurusium</i>	<i>Australopithecus afarensis</i>
Hippopotamidae	Hystriidae
<i>Hexaprotodon</i> cf. <i>H. corydoni</i>	<i>Hystrix</i> sp.
Tayassuidae	Thryonomyidae
cf. <i>Cainochoerus</i> sp.	<i>Thryonomys</i> sp.
Suidae	Orycteropodidae
<i>Kolpochoerus afarensis</i>	<i>Orycteropus</i> sp.
<i>Notochoerus euilus</i>	Elephantidae
Mustelidae	<i>Elephas recki</i>
<i>Enhydriodon</i> sp.	Squamata
Felidae	Teleost
cf. <i>Dinofelis</i> sp.	Chelonia
Hyaenidae	Crocodylidae
cf. <i>Crocota</i> sp.	

Table 2

Table 2. Stable carbon and oxygen isotope data of fossil teeth from Nefuraytu.

Specimen	Taxon	Element	$\delta^{13}\text{C}$ avg*	$\delta^{13}\text{C}$ stdv	$\delta^{18}\text{O}$ avg	$\delta^{18}\text{O}$ stdv	n	Strat position**
NFR-VP-1/213	Hominini gen. sp. inde	LM3	-9.1	--	1.1	--	1	Lower
NFR-VP-1/125	Bovidae gen. sp. Indet	molar	-10.1	--	2.3	--	1	Upper
NFR-VP-1/146	<i>Tragelaphus</i> sp.	molar	-5.8	--	-1.5	--	1	Lower
NFR-VP-1/152	<i>Tragelaphus</i> sp.	molar	-8.4	--	6.3	--	1	Lower
NFR-VP-1/154	<i>Tragelaphus</i> sp.	molar	-8.7	0.4	4.8	0.0	2	Lower
NFR-VP-1/42	<i>Sivatherium</i> sp.	molar	-9.7	--	3.6	--	1	Upper
NFR-VP-1/133	<i>Sivatherium</i> sp.	molar frag.	-9.1	--	2.6	--	1	Upper
NFR-VP-1/134	<i>Giraffa</i> sp.	molar	-10.5	--	4.5	--	1	Upper
NFR-VP-1/1	<i>Notochoerus euilus</i>	M3	-1.8	--	-1.1	--	1	Lower
NFR-VP-1/7A	<i>Notochoerus euilus</i>	M3	-0.7	--	-0.4	--	1	Lower
NFR-VP-1/14	<i>Notochoerus euilus</i>	(M3?) frag.	-0.6	--	0.7	--	1	Lower
NFR-VP-1/16	<i>Notochoerus euilus</i>	M3	-0.6	0.1	2.2	0.0	2	Lower
NFR-VP-1/20	<i>Notochoerus euilus</i>	M3	0.1	--	3.5	--	1	Lower
NFR-VP-1/24	<i>Notochoerus euilus</i>	M3	-0.2	0.0	1.0	0.2	2	Lower
NFR-VP-1/34	<i>Notochoerus euilus</i>	M3	-0.7	--	-1.2	--	1	Lower
NFR-VP-1/50	<i>Notochoerus euilus</i>	M3	-2.4	--	-4.9	--	1	Lower
NFR-VP-1/190	<i>Notochoerus euilus</i>	M3	-1.6	--	1.5	--	1	Lower
NFR-VP-1/197	<i>Notochoerus euilus</i>	M3	-3.6	--	-2.3	--	1	Lower
NFR-VP-1/227	<i>Notochoerus euilus</i>	M3	-0.4	--	-2.1	--	1	Upper

All data were originally published in Levin et al. (2015).

* $\delta^{13}\text{C}$ values are reported in ‰ units relative to VPDB. Mean $\delta^{13}\text{C}$ values are reported if the powder tooth enamel was measured multiple times.

**Strat position refers to whether the specimen was found associated with the upper or lower fossiliferous horizon at Nefuraytu.

Table 3

Table 3. Stable carbon and oxygen isotope data from pedogenic carbonates at Nefuraytu.

Sample ID	$\delta^{13}\text{C}$ avg	$\delta^{13}\text{C}$ stdv	$\delta^{18}\text{O}$ avg	$\delta^{18}\text{O}$ stdv	n	Latitude	Longitude
WM11-NFR-154	-2.5	0.9	-8.2	0.2	3	11.47341	40.58930
WM11-NFR-155	-7.4	0.3	-3.3	0.6	2	11.47226	40.58846
WM11-NFR-156	-11.6	--	-1.5	--	1	11.47072	40.58766
WM11-NFR-158	-11.5	0.3	-5.2	0.0	2	11.47088	40.58801

Mean values are reported if multiple carbonate nodules from a single paleosol were sampled. Latitude and longitude are reported relative to the WGS84 datum. All data were initially reported in Levin et al. (2015). Note that some coordinates have been updated from what is reported in Levin et al. (2015); the coordinates reported here are correct.

Table 4. Abbreviations of dental and directional terminology used in the comparative description (adopted from Johanson and White, 1982).

Pa= paracone	Fa = anterior fovea
Pr= protocone	Fp = posterior fovea
Me= metacone	Fc = central fovea
Hy= hypocone	Mmr = mesial marginal ridge
Prd = protoconid	Dmr = distal marginal ridge
Med = metaconid	MD = mesiodistal(ly)
Hyd = hypoconid	BL = buccolingual(ly)
Hld = hypoconulid	LaL = labiolingual(ly)
End = entoconid	AP = anteroposterior(ly)
C6 = tuberculum sextum	SI = superoinferior(ly)
IPF = interproximal facet	ML = mediolateral(ly)
Mlg = median longitudinal groove	L = Left
CEJ = cervicoenamel junction	R = Right

Table 5

Table 5. Mandibular dimensions of NFR-VP-1/29. Values in parentheses are best estimates. All measurements are in mm.

At crowns			C	P ₃	P ₄	M ₁	M ₂	M ₃
Between crowns	I ₁ /I ₁	I ₁ /I ₂	I ₂ /C	C/P ₃	P ₃ /P ₄	P ₄ /M ₁	M ₁ /M ₂	M ₂ /M ₃
Perpendicular corpus height								
Midline	43.7							
Right at crowns					39.7	37.7	33	-
Right between crowns		(44.5)	(42.4)	40.8	41.6	39.1	35.1	32
Left at crowns					39.4	38.1	34.9	32.9
Left between crowns				41.2	41	39.6	36.6	33.7
Minimum corpus breadth								
Midline	23.5							
Right at crowns		-	25.1	23.5	21.5	22	24.9	26.6
Right between crowns		24.1	24.8	23.5	22.9	21.9	22.6	26
Left at crowns		23.1	-	24.5	23.4	23.3	24.8	28.3
Left between crowns		-	-	24.9	23.2	22.8	25.7	27.8
			C	P ₃	P ₄	M ₁	M ₂	M ₃
Bi-internal alveolar margin breadth			(18.3)	28.1	33.4	34.7	37.3	44.2
Bi-crown center breadth			-	(39.5)	42.8	47.1	48.5	52.3

Table 6

Table 6. Dental measurements of NFR-VP-1/29 and summary statistics of *Au. anamensis* and *Au. afarensis*.

Specimen/ Taxon	I ₂		P ₄		M ₁		M ₂		M ₃	
	MD	LaL	MD	BL	MD	BL	MD	BL	MD	BL
NFR-VP-1/29										
R	-	-	10.8	12.3	14.5	-	15.7	14.9	17.1	15.2
L	6.6	8.5	10.5	12.5	14.3	13.8	15.6	15	17.3	14.7
Average	-	-	10.65	12.4	14.4	-	15.65	14.95	17.2	14.95
<i>Au. anamensis</i>										
<i>n</i>	2	3	8	8	10	10	7	7	7	7
Average	8.5	8.3	9.09	11.34	12.56	11.72	14.71	13.4	15.41	13.54
Range	(8.4 - 8.6)	(7.7 - 8.7)	(7.3 - 10.1)	(9.5 - 13.2)	(11.6 - 13.8)	(10.4 - 13.5)	(13.8 - 16.1)	(12.2 - 14.9)	(13.9 - 17.2)	(12.1 - 15.1)
Stdv	-	0.53	0.95	1.33	0.89	0.91	0.94	0.93	1.28	0.88
<i>Au. afarensis</i>										
<i>n</i>	5	5	19	19	22	22	28	28	21	21
Average	6.2	8.2	9.78	11.06	13.18	12.63	14.27	13.42	15.2	13.37
Range	(5.0 - 7.2)	(6.7 - 8.8)	(7.7 - 11.4)	(9.8 - 12.8)	(11.2 - 14.8)	(11.0 - 14.0)	(12.4 - 16.2)	(11.1 - 15.2)	(13.4 - 18.1)	(11.3 - 15.3)
Stdv	0.85	0.86	1.06	0.81	0.77	0.81	1.15	0.96	1.27	0.94

Measurements were compiled from White (1977, 1980), Johanson and White (1982), Ward et al. (2001), Kimbel et al. (2004), White et al. (2006), and Ward (2014). R = right; L = left; AVG = average; Stdv = standard deviation. All measurements are in mm.

Table 7

Table 7. Crown shape index ($= (BL/MD) \cdot 100$) and crown size ($= \sqrt{(MD \cdot BL)}$) in early-middle Pliocene hominins.

Boldface indicates a significant difference between *Au. anamensis* and *Au. afarensis* ($p < 0.05$) using a t-test.

<i>Au. anamensis</i>			<i>Au. afarensis</i>			NFR-VP-				KNM-WT	
						1/29	1/2	1/58	1/213	<i>Au. deyiremeda</i>	8556 16006
	<i>n</i>	$\bar{x}$	σ	<i>n</i>	$\bar{x}$	σ					
I ₂	1			4							
shape		98.8	--		126.9	31.5	128.8				
size		8.5	--		7.0	0.6	7.5				
P ₄	8			19							
shape		125.0	10.0		113.8	10.1	116.5			129.3	111.6
size		10.1	1.0		10.4	0.9	11.5			9.3	11.8
M ₁	10			22							
shape		93.4	4.4		95.9	3.7	96.5	85.6		100	93.6
size		12.1	0.9		12.9	0.8	14.1	12.9		10.6	13.5
M ₂	7			28							
shape		91.1	3.3		94.2	5.4	95.5	89.3		98.6	
size		14.0	0.9		13.8	1.0	15.3	14.1		13.9	
M ₃	7			21							
shape		88.2	6.5		88.4	5.1	86.9			98.7	86.4
size		14.4	0.9		14.2	7.2	16.0			15.3	14.3
M ³	10			13							
shape		119.5	7.8		115.7	5.5			108.7		
size		13.0	1.0		13.3	1.2			13.2		

Figureg

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12