Hominin dental remains from the Pliocene localities at Lomekwi, Kenya (1982–2009)

Abstract

Increasing evidence for both taxonomic diversity and early stone manufacture during the Pliocene highlight the importance of the hominin fossil record from this epoch in eastern Africa. Here, we describe dental remains from Lomekwi (West Turkana, Kenya), which date from between 3.2 and 3.5 Ma. The sample was collected between 1982 and 2009 and includes five gnathic specimens and a total of 67 teeth (mostly isolated permanent postcanine teeth). Standard linear dimensions indicate that, while the Lomekwi teeth are relatively small, there is broad overlap in size with contemporary *Australopithecus afarensis* and *Australopithecus deyiremeda* specimens at most tooth positions. However, some dental characters differentiate this sample from these species including: a relatively large P_4 and M_3 compared with the M_1, a high incidence of well-developed protostylids and specific accessory molar cuspules. Due to a lack of well-preserved tooth crowns (and the complete absence of mandibular teeth) in the holotype and paratype of *Kenyanthropus platyops*, and limited comparable gnathic morphology in the new specimens, it cannot be determined whether these Lomekwi specimens should be attributed to this species. Attribution of these specimens is further complicated by a lack of certainty about position along the tooth row of many of the molar specimens. More comprehensive shape analyses of the external and internal morphology of these specimens, and additional fossil finds, would facilitate the taxonomic attribution of specimens in this taxonomically diverse period of human evolution.

Keywords: Dentition; *Kenyanthropus*; *Australopithecus*; Dental traits; Crown size

1. Introduction

Fossil discoveries over the last 25 years have resulted in a substantial increase in hominin species diversity during the Pliocene (Spoor, 2015; Haile-Selassie et al., 2016b; Spoor et al., 2016). In addition to *Ardipithecus ramidus* (4.8–4.3 Ma; Ethiopia),

Australopithecus afarensis (~3.8–3.0 Ma; Tanzania, Ethiopia) and *Australopithecus anamensis* (~4.2–3.8 Ma; Kenya, Ethiopia), which are well documented and previously thought to be the only hominin taxa during this time interval (Johanson et al., 1978; White et al., 1994; Leakey et al., 1995; Semaw et al., 2005; Kimbel et al., 2006; Kimbel and Delezene, 2009; Haile-Selassie et al., 2016), an additional three or four species have now been recognized, although not necessarily accepted universally. These are *Australopithecus bahrelghazali* Brunet et al., 1996 from Koro Toro, Chad and dated to ~3.5–3.0 Ma, *Kenyanthropus platyops* Leakey et al., 2001 from Lomekwi, Kenya and dated to ~3.5-3.3 Ma, *Australopithecus deyiremeda* Haile-Selassie et al., 2015 from Woranso-Mille and dated to ~3.5–3.3 Ma, Ethiopia, and *Australopithecus prometheus* from Sterkfontein Cave, South Africa and dated to ~3.7 Ma (Clarke and Kuman, 2019; Bruxelles et al., 2019;; but see Kramers and Dirks, 2017 for a younger age estimate).

Fieldwork exploring the Pliocene sediments at Lomekwi has not only led to the discovery of *K. platyops*, but also of the earliest known stone tools at ~3.3 Ma (Harmand et al., 2015). The latter occur in the same spatiotemporal range as hominin fossils such as the *K. platyops* paratype KNM-WT 38350, and this association has refocused attention on the nature and identity of all broadly contemporary hominin fossils found at Lomekwi. In this paper we describe and compare the dental specimens, including those discovered by the Koobi Fora Research Project between 1982 and 1999 (Brown et al., 2001; Leakey et al., 2001), as well as three previously unpublished specimens discovered in 2009 by a team from the National Museums of Kenya led by one of us (F.K.M.).

Four Pliocene hominin fossils from the lower Lomekwi and Kataboi Members at Lomekwi (3.2–3.5 Ma; Leakey et al, 2001) were found in the 1980s. Brown et al. (2001) attributed these to *A. afarensis* (partial mandibles KNM-WT 8556, 16006) or *A.* cf. *afarensis* (isolated molars KNM-WT 8557, 16003), noting that, at that time, this was the only contemporary hominin species known in the region and Africa in general. Subsequent finds were made in the late 1990s, including the cranium KNM-WT 40000 and isolated maxilla fragment KNM-WT 38350 that were designated the type specimens of *K. platyops* (Leakey

et al., 2001). Other specimens, mostly isolated teeth, were briefly listed and discussed by Leakey et al. (2001), but not attributed to *K. platyops* as no diagnostic link with the type or paratype could be made. The study did, however, note that the dental assemblage exhibited internally consistent characteristics, including lower molars with distinct protostylids and notably low-crowned I^2. In their review of the Omo-Turkana Basin hominins, Wood and Leakey (2011) noted that Leakey et al. (2001) reserved judgment about the taxonomy of these remains, but their inventory nevertheless list them as cf. *K. platyops*. Cerling et al. (2013) subsequently referred all specimens to *K. platyops* outright, making reference to Wood and Leakey (2011). The goals of this paper are to 1) provide basic anatomical descriptions and measurements of the dental specimens, and 2) evaluate their taxonomic affiliation within the context of other Pliocene eastern African hominin taxa.

2. Materials and methods

The Lomekwi specimens described here are listed in Table 1. They are housed in the National Museums of Kenya in Nairobi, catalogued using the accession code KNM-WT (full list of abbreviations given below). Some tooth class attributions differ from those given in Leakey et al. (2001: Table 1) or Wood and Leakey (2011: Appendix), and those in the present contribution should be considered the most up to date. Furthermore, two specimens, KNM-WT 38336 and KNM-WT 38348, were listed as hominins in Wood and Leakey (2011), but not included in Leakey et al. (2001) because it was not clear at the time if they were hominin or cercopithecoid. Here we include the I^1 KNM-WT 38336, but exclude KNM-WT 38348 because the unerupted right and left I_1 of this symphysis fragment have no enamel on their lingual surface, a characteristic of *Papio* and *Theropithecus*. We also include three new specimens found in 2009: two upper premolars (KNM-WT 66289, 66290) and a lower molar (KNM-WT 66291).

Information about the geological context and age of the Lomekwi specimens is given in Leakey et al. (2001), including reference to the palaeontology collection locality LO-5 where the 2009 specimens were found. The place of discovery of many of the 1980s and

1990s specimens was originally recorded on aerial photographs, and we used Google Earth v. 7.3.2.5776 (Google Inc.) to establish the associated latitude and longitude coordinates (Table 1). For the three specimens found in 2009 this information was collected directly using a GPS receiver.

Comparisons were made with teeth of *Ar. ramidus*, *A. anamensis*, *A. afarensis*, *A. deyiremeda*, *A. bahrelghazali*, and *Australopithecus africanus*, as well as hominins from the Kaiyumung Member at Lothagam, dated to around 3.5 Ma (Leakey and Walker, 2003), and from the Usno Formation in the Omo Valley (Howell, 1969), dated to 3.05 Ma (Feibel et al., 1989). Dental remains from South Turkwel, Kenya, dated to around 3.5 Ma, were considered, but there is little anatomical overlap with the fossils from Lomekwi, and they preserve almost no crown morphology due to wear and breakage (Ward et al, 1999). It is worth mentioning that these specimens from Lothagam, the Usno Formation and South Turkwel were all considered most similar to *A. afarensis* (Coppens, 1980; Leakey and Walker, 2003; Ward et al., 1999). However, as with the attribution of the Lomekwi hominins from the 1980s (Brown et al., 2001), this conclusion was based on *A. afarensis* being the only contemporary hominin species from eastern Africa known at the time, and the absence of particularly distinct morphology.

Accession codes and depositories of comparative specimens are: KNM-ER (northeastern side of Lake Turkana), KNM-KP (Kanapoi), KNM-LT (Lothagam) and KNM-WT (western side of Lake Turkana) at the National Museums of Kenya in Nairobi, Kenya; A.L.(Afar Locality), BRT-VP (Burtele Vertebrate Paleontology), WYT-VP (Waytaleyta Vertebrate Paleontology), B- (Brown Sands Locality) and W- (White Sands Locality) at the National Museum of Ethiopia in Addis Ababa, Ethiopia; LH (Laetoli Hominid) at the National Museum of Tanzania in Dar es Salaam, Tanzania; KT (Koro Toro) at the Centre National d'Appui à la Recherche in Ndjaména, Chad; and StW (Sterkfontein Witwatersrand) at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa.

Dental crown size and shape were analyzed using mesiodistal (MD) and buccolingual (BL)/labiolingual (LL) dimensions as defined in White (1977). We also report

crown measurements as defined in Tobias (1967) following Korenhof (1960: Fig. 3) and that widely used (e.g., Wood, 1991; Moggi-Cecchi et al., 2006), so that researchers can use either as required. For molars, the two measurement protocols primarily differ in whether a MD or BL crown diameter is taken along a single axis (White, 1977), or reflects the maximum distance between opposite crown faces, regardless of where these points fall (see discussion in Tobias, 1967). Measurements based on the two methods are most different for upper molar crowns that are rhomboid and skewed in shape, with values following White (1977) being consistently smaller. In the descriptions, right and left teeth are denoted by R and L, respectively.

The reported measurements follow Leakey et al. (2001), but the right M^2 of KNM-WT 40000 was remeasured using 2D and 3D images acquired with µCT (voxel size = 0.069 mm), providing improved information regarding crown morphology and preservation. As a consequence, the MD value following White (1977) increased by 0.5 mm because of a more accurate estimate of mesial interstitial wear, and the BL value increased by 0.2 mm to compensate for missing mesiolingual enamel. Of the measurements following Tobias (1967), reported in Spoor et al. (2010), only MD is increased by 0.9 mm because of an inaccurate measurement made in 2000 before the tooth was fully cleaned. All measurements, previously published and newly reported, were taken by F.S.

Comparative dental measurements were taken from the literature (Howells, 1969; White, 1977, 1980; White et al., 2000, 2006; Ward et al., 2001a, b, 2013, 2020; Leakey and Walker, 2003; Kimbel et al., 2004; Alemseged et al., 2005; Haile-Selassie, 2010; Haile-Selassie and Melillo, 2015; Haile-Selassie et al., 2015, 2016a), provided by W. Kimbel (*A. afarensis* from Hadar discovered after 2004; *A. africanus*), or taken by one of us (F.S.). Corrected P_4 measurements of KNM-KP 53160 were used here, as swapped MD and BL values were reported in Ward et al. (2020, Table 2) (J.M. Plavcan, pers. comm.). Statistical analyses were carried out in PAST v3 (Hammer et al., 2001).

3. Results

3.1. Associated dentitions

KNM-WT 8556 This specimen is a partial mandible preserving the symphysis and right corpus to the level of the M_2 (Fig. 1). It includes the RP_3 to M_1 in their alveoli, as well as the isolated LP_3, partial RM_2, and partial RM_3. The LP_3 is mostly well preserved, but a small fragment of enamel has broken off the mesial ridge of the protoconid and a fine crack runs mesiodistally through the metaconid to the distal marginal ridge, with a branch running buccally through the distal fovea. Parts of the buccal and mesial root surfaces are missing, including the tip of the mesial root. The RP_3 also shows minor damage to the mesial ridge of its protoconid and all but cervical parts of the distal root are missing. The crown and roots of the RP_4 are fully preserved, but a large crack runs mesiodistally through the center of the crown. The crown of the RM_1 is missing a triangular fragment on the mesiolingual corner of the protoconid, associated with a crack that runs mesiodistally through the middle of the tooth crown. The full length of its roots is preserved but parts are missing at the level of the bifurcation. The crown of the RM_2 lacks mesial and distal portions, and most of the buccal face. The metaconid and entoconid are partially preserved, a small portion of the protoconid remains, and the hypoconid is almost complete. No roots are preserved. The occlusal surface of the RM_3 crown is relatively complete, but a small portion of the mesiolingual corner and all of the distal face are missing. Enamel is lost around the margin of the tooth towards the cervix except for small area below the mesial buccal groove. No roots are preserved.

LP_3 and RP_3: In occlusal view, the crown profile is buccolingually compressed on the mesial portion and asymmetric with a strong projection distolingually. The protoconid is larger than the metaconid, and the two cusps are separated by the central groove. The mesial fovea is deep and clearly defined, the mesial marginal ridge is thin and the distal fovea is large and lingually positioned. Both P_3s exhibit buccal ridges on the mesial and distal aspects of the protoconid, a small metaconulid and, although slightly worn, at least two accessory cuspules on the distal marginal ridge, The Tomes' root of the LP_3 is C-shaped in cross-section with a narrow mesial root and a plate-like distal root connected by a dentine

sheath buccally. Poor preservation of the RP_3 root makes it difficult to determine the degree of connection between the mesial and distal roots.

RP_4: The relatively large protoconid is positioned slightly distal to the smaller metaconid and a crest (possibly double) encloses a small mesial fovea. There is a small tubercle on the distal ridge of the protoconid and a large talonid basin is bordered distally by a clearly defined distal marginal ridge with four small accessory cuspules. The tip of the metaconid shows a small (~2 mm long) wear facet. There are two plate-like roots (mesial and distal), similar to those of molars.

RM_1: The moderately worn crown has an entoconid that is small relative to the hypoconulid, and no C6 or C7 is present. The occlusal surface, although worn, shows evidence of multiple secondary grooves in association with a Y-5 groove pattern. A very small and short protostylid crest runs mesiosuperiorly from the base of the mesiobuccal groove. The long, slit-like mesial fovea is incomplete because of missing portion of tooth. There is a lingually positioned small pit-like distal fovea.

RM_2: The preserved occlusal surface of the lightly worn M_2 exhibits a number of secondary grooves. There is no C7 and the presence of a C6 and protostylid cannot be assessed due to missing parts of the crown.

RM_3: There is an elongated slit-like mesial fovea and the occlusal surface is complex with numerous secondary grooves resulting in the development of small cuspules even inside the basin (e.g., between the hypoconid and entoconid). A deflecting wrinkle is present on the metaconid and a mesial trigonid crest originating from the tip of the protoconid that is interrupted by the longitudinal groove. Secondary grooves demarcate several small cuspules along the lingual margin including a small C7 (with a tiny cuspule mesially that could be considered a postmetaconulid). Two cuspules are present on the distal margin that could each be considered a C6 (the smaller one being closely associated with the entoconid). A small vertical groove on the protoconid is located mesial to the buccal groove. There is a hint of a small pit-like distal fovea but enamel lost from the crown in this area prevents certain interpretation.

KNM-WT 8556 is late juvenile or young adult in developmental age, based on the dental evidence that all preserved root apices of the P_3s, the RP_4 and the RM_1 are closed, but the RM_3 crown lacks any occlusal wear. It was first described in Brown et al. (2001) and attributed to *A. afarensis*. Aspects of it dental morphology were subsequently considered in Leakey et al. (2001), Delezene and Kimbel (2011) and Haile-Selassie and Melillo (2015). Brown et al. (2001) pointed out the similarity in P_3 morphology between KNM-WT 8556 and A.L. 333w-1a with respect to a large metaconid, but with a deeper mesial fovea. They also noted a more molarized P_4, similar or larger in size than comparative material from Hadar, and drew attention to particular Hadar molar specimens that are broadly similar in morphology to KNM-WT 8556.

Leakey et al. (2001) observed that, relative to its M_1, the P_4 and M_3 crowns of KNM-WT 8556 are larger than in most Plio-Pleistocene hominins, except *Paranthropus boisei*. Delezene and Kimbel (2011) provided a comprehensive analysis of P_3 crown morphology, including a principal components analysis (PCA) of 15 crown shape variables and concluded that variation within *A. afarensis* encompasses the KNM-WT 8556 P_3. They did note that the mesial fovea orientation, poorly-developed mesial marginal ridge and the presence of a distolingual cuspid differ from the typical *A. afarensis* P_3 condition. As no new P_3s have been discovered, there is nothing upon which to re-evaluate these conclusions. Haile-Selassie and Melillo (2015) agreed that the KNM-WT 8556 P_4 is more molarized than in *A. afarensis*, and resembles the P_4 of KT 12/H1, the holotype of *Australopithecus bahrelghazali* (Brunet et al., 1996).

KNM-WT 16006 This is a left hemimandible preserving the gonial angle and part of the corpus, the roots of the lower left M_1, except the mesiolingual portion, the roots and partial crown of the M_2, and mesial root and crown of the M_3 (Fig. 2).

LM_1: Mesial and distal plate-like roots are present, although the mesial root is missing a portion of the lingual radical. There is little that can be made in comparison to the other Lomekwi material whose molars consist primarily of crowns.

LM_2: Only a portion of the hypoconid and most of the hypoconulid are preserved on the distal portion of the tooth. Occlusal wear obscures any morphological detail.

LM_3: The lightly worn M_3 is complete except for a small vertically running sliver of enamel on the distal face. As is common for M_3, the crown base tapers distally from the protoconid/metaconid. The protoconid, metaconid and hypoconulid are large, while the entoconid and hypoconid are relatively small. The groove pattern is Y-5 and distally there is a hint of a C6. A well-delineated C7 is bordered mesially by a small postmetaconulid. There is a distinct protostylid crest extending from near the mesial marginal ridge to just distal to the mesiobuccal groove and a small tubercle intermediate between and at the base of the hypoconid and hypoconulid. Several vertical grooves traverse the buccal face of all three cusps (protoconid, hypoconid, hypoconulid). A shallow mesial fovea is demarcated distally by an interrupted trigonid crest running between the tips of the protoconid and metaconid. The distal fovea is a small but deep pit, lingual in position.

Brown et al. (2001) attributed this specimen to *A. afarensis* based on aspects of mandibular corpus morphology and similar tooth size to A.L. 145-35 and A.L. 266-1, although larger than A.L. 198-1. Brown et al. (2001) also noted that the large cingulum on the M_3 was not present in specimens from Hadar or Laetoli (LH 4 and LH 15).

KNM-WT 38343 KNM-WT 38343A is a fragment of right maxilla with I^2 root, partial C^1 crown with root, and three separate P^3 roots (Fig. 3). The bone is traversed with numerous tiny cracks. The canine crown preserves the distal half, with the distolingual quarter separated from the distolabial part by a 1.5 mm-wide crack. The canine is apically worn, and its completely preserved root is visible on the medial and superior aspect of the specimen. The cervix to apex length as preserved is 25 mm. The presence of at least one minor crack suggests that the original length was marginally shorter. The interalveolar distance suggests that a relatively large C^1–I^2 diastema was present, although this distance is enlarged by matrix-filled cracks.

KNW-WT 38343B is a mandibular fragment with M_1 roots and distal P_4 root. The side of the specimen is difficult to establish because what remains of the corpus is highly

fragmented and the shape of the roots is largely symmetrical. The distal P_4 root has a single root canal and is kidney-shaped in cross-section, with the concave surface mesially, suggesting that the P_4 was two-rooted. Wood and Leakey (2011) mistakenly listed this specimen as a maxilla fragment with M^1 or M^2 roots.

KNM-WT 38350 This specimen is a fragment of a left maxilla with the buccal roots of P^3, the buccal root and a portion of the lingual root of P^4 and the mesiobuccal root of M^1 (Fig. 4). Parts of the M^1 are preserved separately, including the lingual third of the crown and the lingual root with a small piece of maxillary bone which joins the larger fragment.

The partially worn M^1 crown preserves the hypocone and the distal half of the protocone with a deep lingual groove extending towards the cervix on the lingual face. This tooth must have had a MD crown dimension of between 10.0 and 11.0 mm (estimate 10.5 mm). This estimate is based on the preserved distal molar crown, a small sliver of enamel near the cervix on the mesial face, and the position of the alveolar septum between P^4 and M^1 (10.0 mm up to center of septum, 11.0 mm to mesial face of septum). The estimated BL crown dimension falls between 12.0 and 13.0 mm (mean 12.5 mm) based on the preserved lingual crown face and the position of the mesiobuccal root. The M^1 crown appears to have had a continuous crista obliqua, and a C5. The missing mesiolingual corner of the crown prevents assessment of Carabelli's cusp. The P^3 is three-rooted (2 buccal, 1 lingual) and the P^4 is two-rooted (1 buccal, 1 lingual), with the buccal root exhibiting grooves on the lingual and buccal sides (based on CT observation). Although the fragment looks particularly small, this is not the case when compared with other specimens. For example, both the P^4 and M^1 of LH 5 are similar in size at the cervix. Compared with KNM-WT 40000 both the premolar root sizes (which appear particularly thin in KNM-WT 38350) and the spreading distance between the P^3 buccal roots are very similar.

KNM-WT 38358 This set of associated teeth consists of an incisor, fragmentary crowns of molars and unidentified tooth crown fragments. Their association is based on their discovery in close proximity during screening and their developmental and anatomical compatibility (Fig. 5).

KNM-WT 38358A is a RI^2 preserving a lightly worn crown and most of the root. Enamel is lost at the cervix on the mesiolabial and lingual faces (Fig. 5a). The tooth is relatively low-crowned (the height to the very lightly worn occlusal surface is 9.1 mm). The MD length of 7.5 mm and the LL width of ~7.6 mm are almost equal. There is a distinct oval wear facet on the distal corner of the occlusal surface, and a second facet along the incisal margin has exposed a thin sliver of dentine along the mesial half of the occlusal surface. The lingual surface is distinctly cupped and bordered by clear mesial and distal marginal ridges converging on the gingival eminence, which is broken at the cervix. The mesial and distal incisal angles lie at approximately the same level. There is an elongated interstitial wear facet on the mesial face for the RI^1 and a small interstitial wear facet for the RC^1 on the labial portion of the distal face close to the cervix and to the distal incisal angle. The low position of this facet indicates that it may have been made by the erupting canine. Although the enamel surface is polished, light bands of perikymata are visible on the labial surface. The root is mesiodistally compressed and appears to have been broken close to the tip. If this is the case it is relatively short, 11.7 mm from the distal incisal angle to the break. Vertical grooves occur on both mesial and distal faces of the root. This tooth is unlike any known for *A. afarensis* due to the low crown and very cupped lingual face.

KNM-WT 38358B is a distobuccal fragment of a RM^2 preserving the metacone and parts of the protocone, paracone, and hypocone (Fig. 5b). The occlusal surface is less worn than in KNM-WT 38358E, making it likely that, if these teeth belong to the same individual, KNM-WT 38358B should be an M^2. Perikymata are visible on the lingual face and are close together at the cervix (cf. *A. anamensis* but not *P. boisei*; C. Dean pers. comm.).

KNM-WT 38358C is a LM_3 preserving a very lightly worn crown but missing the distolingual quarter (Fig. 5c). Its identification as an M_3 is based on the marked distal tapering of the crown that is visible on the buccal margin (and on the association with KNM-WT 38358D). The groove pattern appears to be Y-5, but the missing entoconid makes this difficult to determine with certainty. The missing distolingual portion of the crown prevents assessment of a C6 or C7. There is a distinct protostylid running along the buccal face from

the buccal groove to the base of the protoconid. There is a moderately long but shallow mesial fovea with a small pit at each end. The mesial half of this tooth is wide buccolingually with the two mesial cusps in close proximity compared to the breadth at the cervix. The buccal face is distinctly sloping.

KNM-WT 38358D is a buccal half of a LM_1 crown preserving most of the protoconid and hypoconid (Fig. 5d). Preserved cusps are moderately worn but without dentine exposure. There is evidence of a crest-like protostylid on the buccal face of the protoconid, although its original size cannot be determined due to weathering on of the enamel surface.

KNM-WT 38358E is an indeterminate moderately worn crown fragment. Preserved grooves suggest it could be the distolingual corner of a LM^1 (Fig. 5e). The identification as a M^1 would be consistent with the presence and degree of wear of the LM^2 (KNM-WT 38358B) and the RM^3 (KNM-WT 38358F).

KNM-WT 38358F is a mesiolingual corner of a RM^3 preserving most of the protocone and part of the paracone (Fig. 5f). There is little evidence of wear and a trace of a Carabelli's cusp on the mesial face.

KNM-WT 38358G–I are three small Indeterminate tooth fragments (Fig. 5g–i).

KNM-WT 38359 This is a set of molars found in close proximity, which along with their morphological and developmental compatibility, is the basis for their association (Fig. 6).

KNM-WT 38359A is a RM_1 with a complete, very slightly worn crown and partial distal root (Fig. 6a). The occlusal surface is moderately complex with secondary grooves traversing the slopes of the cusps and they are particularly marked on the metaconid. There is no C6, or C7, but there is an incipient postmetaconulid in the form of a clear ridge running from the lingual border into the occlusal basin. The primary cusps form a +5 groove pattern and the hypoconulid is relatively large. A large, crest-like protostylid passes from the mesiobuccal corner and across the mesiobuccal groove. A distinct mesial fovea, formed buccally by a mesial crest on the protoconid, is bisected by the longitudinal groove. The distal fovea is small and pit-like, and primarily associated with the entoconid.

KNM-WT 38359B is a RM_2 with a complete unworn crown but lacking roots (Fig. 6b). As in KNM-WT 38359A, there is a prominent postmetaconulid ridge, no C6 and no C7. The hypoconulid is large and the primary cusps form a Y-5 pattern. A large, crest-like protostylid passes from a point just distal to the mesiobuccal corner and across the mesiobuccal groove. A wide and deep mesial fovea and large distal fovea are bisected by the longitudinal groove. The occlusal surface is relatively simple and lacks secondary grooves.

KNM-WT 38361 This is a set of tooth germs (many fragmentary) was recovered mostly through screening over a large area. Their general proximity and similar developmental stage is the basis for their association (Fig. 7).

KNM-WT 38361A is a LI^1 germ missing the mesial third of the crown (Fig. 7a). The tooth is broken close to the cervix and at the incisal angle a small portion of the root is preserved, and the unworn occlusal surface is crenulated by many small mammelons. The lingual face is dished and the preserved marginal ridge is not exceptionally developed. Perikymata are visible on the labial face. The crown is low, having a preserved height of 11.4 mm on the labial face relative to a preserved labiolingual width of 6.8 mm, and as the gingival eminence is lost the tooth would have been several millimeters wider than this (the preserved mesiodistal width is 7.7 mm and the actual width is unlikely to have been less than 9 mm). This tooth contrasts with the higher crowned, less cupped I^1 of *A. afarensis* and *A. anamensis*.

KNM-WT 38361B is a LI^2 germ with a complete crown (Fig. 7b). The lingual face is smooth and dished and the labial face preserves perikymata. The lingual marginal ridges are somewhat lightly developed (and less so than in KNM-WT 38358A). There are distinct but small mammelons along the incisal ridge. This tooth is similar in morphology to KNM-WT 38358 in being low-crowned (8.3 mm in height relative to a labiolingual width >5.8 mm and a mesiodistal width of 7.6 mm), and in having a cupped lingual face. It is also very similar in anterior crown profile to KNM-WT 38358A, with a relatively vertical mesial face and a pronounced bulge on the distal face.

KNM-WT 38361D is a RC^{1} germ that has an incomplete crown, and lacks enamel at the basal eminence and close to the cervix at the mesial and distal margins (Fig. 7c). The distinct central ridge is broken close to the cusp tip but as the crown is incompletely formed little can be said of the morphology.

KNM-WT 38361E is a partial (split from the apex towards the cervix) and incompletely formed canine crown (Fig. 7d). Its identification as maxillary or mandibular is hampered by a lack of preserved diagnostic morphology. There is a distinct fossa bordered by a marginal ridge and a second vertical ridge.

KNM-WT 38361F is a $RP^{4?}$ germ (antimere of KNM-WT 38361G). Only the buccal half of the crown is preserved (Fig. 7e). Mesial to the distinct marginal ridge is a second parallel ridge, which borders a deep groove running parallel to the deep distal fovea. The cusp surface is complicated by many secondary grooves and enamel ridges. The remaining buccal portion of the mesial fovea is small and indistinct compared to the distal fovea.

KNM-WT 38361G is a $LP^{4?}$ germ (antimere of KNM-WT 38361F). The buccal cusp only is preserved (Fig. 7f). Distinct secondary grooves and grooves traverse the lingual face of the cusp. The enamel was not fully mineralized, as evidenced by numerous small cracks, indicating it is a developing tooth germ.

KNM-WT 38361H is a $LP^{3?}$ germ (antimere of KNM-WT 38361I). Similar to KNM-WT 38361G, the weathered crown was not fully mineralized and indicates it is a developing tooth germ (Fig. 7g). The buccal cusp is larger and slightly higher than the lingual. The mesial fovea is deep and bordered mesially by the marginal ridge and distally by a second clearly defined ridge. The distal fovea is indistinctly defined with the central groove terminating close to the marginal ridge. Secondary grooves and grooves run from each of the cusps to the central groove.

KNM-WT 38361I is a partial and developing $RP^{3?}$ germ (antimere of KNM-WT 38361H), preserving the lingual cusp (Fig. 7h).

KNM-WT 38362 Two maxillary molars whose association as antimeres is based on their discovery in close proximity and their shared morphology (Fig. 8). They were recovered

during screening with specimens attributed above to KNM-WT 38361. If they are M^1, then they could be from the same individual, but if they are M^2 then they would be developmentally incompatible with KNM-WT 38361.

KNM-WT 38362A is a RM^1 or RM^2 crown that is lightly worn and lacks roots (Fig. 8a). The occlusal surface has numerous secondary grooves. A Carabelli's cusp is present as a notched shelf on the mesial face of the protocone and the crista obliqua is bisected by the longitudinal groove. The mesial fovea extends far buccally and less so lingually from the most mesial point of the longitudinal groove. A triangular island of enamel (puffy ridge) is defined by the mesial fovea and a secondary groove of the paracone that leaves the longitudinal groove close to the mesial fovea. There is a small pit-like distal fovea, truncated lingually by a distinct distal cuspule. The distolingual groove extends along two thirds of the lingual face and is deep and clearly defined.

KNM-WT 38362B is a LM^1 or LM^2 that is the antimere of 38362A based on similar size and matching occlusal morphology (including the mesial fovea, crista obliqua and groove patterning). A Carabelli's cusp is present as a notched shelf (although not as pronounced as in KNM-WT 38362A) on the mesial face of the protocone (Fig. 8b). The crown is broken longitudinally through the two buccal cusps and lacks the distal margin and much of the enamel towards the cervix on the distolingual margin.

KNM-WT 39954 This is a set of two mandibular premolars whose association is based on the consistent degree of development and preservation and their discovery in close proximity (Fig. 9). Wood and Leakey (2011) listed these specimens as part of KNM-WT 38362, but the association with the upper molars cannot be demonstrated.

KNM-WT 39954A is a LP_3 partial crown preserving the metaconid and lingual half of the distal fovea (Fig. 9a). The preserved morphology is similar to that of KNM-WT 8556.

KNM-WT 39954B is a RP_4 partial crown preserving distobuccal portion of the protoconid, the distolingual portion of the metaconid, a tubercle distal to the metaconid, and the mesial half of the distal marginal ridge (Fig. 9b). The preserved morphology is similar to that of KNM-WT 8556.

KNM-WT 40000 The upper dentition that is preserved in the holotype cranium of *K. platyops* is described in detail elsewhere (Leakey et al., 2001; Spoor et al., 2010). In addition to the roots of the left I^1 to M^2 and the right C^1 to M^3 parts of molar crowns remain, but only the RM^2 morphology is sufficiently preserved to estimate crown dimensions (Fig. 11k). Heavily worn enamel covers the paracone, metacone and lingual margin, with dentine exposed in the area in between. All premolars are three-rooted (Leakey et al., 2001).

3.2. Unassociated mandibular teeth

KNM-WT 8557 A LM_1 or LM_2 with a very lightly worn crown with roots, lacking the mesial portion of the tooth and the root tips (Fig. 10a). A triangular portion of the mesiobuccal quadrant of the tooth is separated from the rest of the crown by a large obliquely running crack. The hypoconulid and entoconid are roughly equal in size and height. The groove pattern is Y-5, and there are numerous secondary grooves present within the occlusal basin. There is a large distal fovea but no C6. On the lingual side there is a small C7 and a postmetaconulid. There is a protostylid crest that originates at the buccal groove and terminates at the fractured protostylid surface. Wood and Leakey (2011) interpreted the specimen as an M_3, perhaps because of the absence of a distal interstitial facet and the apparent distal tapering of the crown outline. However, the near-absence of occlusal wear suggests that the molar may not have erupted fully, and the crown appearance is the consequence of the dislocated buccal fragment. Moreover, the distal root is plate-like and buccolingually wide, as is typical for M_1 and M_2, but unlike the consistently more columnar, triangular shape of M_3 (Brown et al., 2001).

KNM-WT 38333 A LM_1 (or M_2), with inferred molar position based foremost on size (Fig. 10b). The enamel surface is pitted by weathering, but the unworn crown exhibits five main cusps with a Y-5 pattern. There is no C6, and two small secondary grooves running parallel to the lingual groove towards the lingual margin delimit a small C7. The hypoconulid is distinct but much smaller than both the hypoconid and entoconid. Numerous secondary grooves result in a complex occlusal surface. While no protostylid crest is associated with

the buccal groove, a slight notch runs vertically on the mesiobuccal corner of the protoconid. The prominent mesial fovea is long and deep, and the distal fovea is defined by a deep pit at the distal end of the longitudinal groove.

KNM-WT 38334 A LM_1 (or M_2) with a well preserved crown that is lightly worn and roots that are broken at their tips (Fig. 10c). There are five main cusps with a Y-5 pattern and no evidence of a C6, C7 or protostylid. Secondary grooves run into the occlusal basin from each cusp. Mesial and distal foveae are deep, pit-like, with the mesial being larger.

KNM-WT 38335 This is a fragment of a lightly worn right mandibular molar with a partial protoconid, almost complete hypoconid, and partial hypoconulid, entoconid, and metaconid preserved (Fig. 10d). There are no strong morphological grounds to favor one molar position over another.

KNM-WT 38339 A LM_2 (or M_1), with inferred molar position based on a relatively wide crown (Fig. 10e). The crown is moderately worn with no dentine exposure and little trace of secondary grooves in the occlusal basin. Enamel is lost at the cervix around much of the crown. The groove pattern is Y-5, with the entoconid being relatively small compared to the other cusps. There is no C6 or C7, but a large protostylid crest runs from the mesiobuccal corner near the mesial marginal ridge to the mesiobuccal groove. The crown is buccolingually wide mesially and with a sloping buccal surface. The two mesial cusps are in close proximity compared to the breadth at the cervix. There is a slit-like mesial fovea that extends more lingually than buccally, and a short, lingually positioned distal fovea.

KNM-WT 38341 The crown of this lower molar is weathered and cracked with enamel lost on most parts except for a mesiolingual patch on the occlusal surface and a small sliver on the mesial surface (Fig. 10f). The mesial and distal roots are plate-like and their apices are missing. The preserved occlusal surface is heavily worn with two areas of dentine showing large pits. A large matrix-filled crack runs obliquely through the crown bisecting the protoconid and the entoconid. Both the crown and the roots are traversed by many smaller cracks. The position of this molar is uncertain but it is inferred to be either an LM_2 or LM_3 based on crown size and the presence of a relatively narrow trigonid.

KNM-WT 38342 A LM_1 (or M_2), with inferred molar position based on a relatively small crown size (Fig. 10g). The crown is very lightly worn and the enamel is fractured off much of the mesial face and towards the cervix on part of the mesial, mesiolingual and distobuccal faces. The roots are not preserved. The five main cusps display a Y-5 configuration and there is no C6. There are two minor crests running into the occlusal basin on the distal ridge of the metaconid that could be interpreted as an incipient C7 and postmetaconulid, respectively. A short, slit-like mesial fovea and a longer, slit-like distal fovea, are both bisected by a longitudinal groove. The hypoconulid is relatively large and a faint protostylid crest extends from the mesiobuccal corner of the protoconid but does not reach the mesiobuccal groove.

KNM-WT 38344 A RM_1 or M_2, with no strong evidence to favor one molar position over the other (Fig. 10h). The crown is very lightly worn and the roots and mesiolingual portion of the metaconid are lost. The groove pattern is +5, there is no C6, and a small C7 is bordered mesially by a larger postmetaconulid. Only a small portion of the mesial fovea is preserved and there is a deep pit-like distal fovea. The hypoconulid is roughly equal in size to the entoconid and there are many secondary grooves within the occlusal basin, particularly on the lingual cusps. A prominent protostylid extends from the mesial face of the protoconid to the mesiobuccal groove.

KNM-WT 38347 This is a diminutive left mandibular molar (Fig. 10i). Based on small crown size, Leakey et al. (2001) listed this specimen as a LdP_4. However, putting aside the small crown size the mesiodistally elongated crown, presence of a large C6, relatively short dentine horns on the talonid (not shown) lead us to identify this tooth as an M_3 (or M_2), even acknowledging that its small size is extremely aberrant within the sample (see Section 3.3). It is possible that it is an M_4 or distomolar (which occurs infrequently in various extant and extinct hominids); however, accessory molars tend to be small in size and/or with reduced crown complexity (see plates in Schwartz, 1984). The five primary cusps form a Y-pattern and there is no C7. A short but deep mesial fovea extends preferentially onto the metaconid and there is no distal fovea. The mesiobuccal and distobuccal grooves are both deep.

KNM-WT 38349 An unworn RM_1 or M_2, which does not preserve roots (Fig. 10j). There is no strong evidence to favor one molar position over the other. A moderately sized C6 is present on the lingual half of the distal crown. A prominent postmetaconulid ridge is present, but there is no evidence of a C7. The hypoconulid is relatively small compared to the hypoconid and there is a deep pit on the distobuccal corner. The five main cusps are in a Y-5 configuration and numerous deep secondary grooves are present on the occlusal surface. A thin protostylid crest runs from the mesial face of the protoconid to the buccal groove. There is a short and deep mesial fovea and no distal fovea. Wood and Leakey (2011) listed this specimen as a $RM_{2?}$.

KNM-WT 38352 A RM_1 (or M_2), with molar position inferred from the lack of distal tapering of the crown (Fig. 10k). The unworn crown does not preserve roots and is likely at or near crown completion. The outer enamel surface is very weathered with patches of enamel missing particularly on the buccal face of the protoconid. Enamel fragments and some dentine are also lost from around the circumference of the crown base. The occlusal surface is complex, with many secondary grooves traversing the metaconid and entoconid. The hypoconulid is large, there is no evidence of a C6, but there is some suggestion of a postmetaconulid ridge. The groove pattern is +5; however, there is a distinct lingual crest from the protoconid that crosses the middle of the occlusal basin (matched also on the hypoconid). There is a crest-like protostylid that reaches the buccal groove but is missing mesially. A short, shallow mesial fovea is somewhat interrupted by a central groove. The distal fovea contains a single mesially positioned distinct pit.

KNM-WT 38357 A RM_1 (or M_2), with molar position inferred from relatively small crown size (Fig. 10l). The roots lack tips, and have some mandibular bone attached. The crown is complete, but worn to expose a deep continuous dentine pit on the buccal half, bordered by continuous enamel along the buccal margin; no dentine is exposed on the lingual cusps. No C7 is present, and the presence of a C6 is difficult to confirm; however, there is evidence of small cusp, delineated by grooves, distal to the entoconid. A small, groove-like depression

and small pit on the worn mesiobuccal margin suggests there may have been a distinct crest-like protostylid prior to its removal by occlusal wear.

KNM-WT 39949 A LP_4 with a weathered crown and enamel lost on the lingual and much of distal face, and at the cervix around the entire margin of the tooth (Fig. 10m). The occlusal surface has many secondary grooves still visible in spite of the weathering. The talonid basin is large and asymmetric and the two main cusps appear to have been of approximately equal in height. The talonid is asymmetric. There are prominent distobuccal, distal and distolingual cuspules. Wood and Leakey (2011) listed this specimen as part of KNM-WT 38362, but the association with the upper molars cannot be demonstrated.

KNM-WT 39950 A RM_3 (or M_2), with inferred molar position based on overall crown size and the apparent tapering of the distal half of the crown (Fig. 10n)—although there are not as many secondary grooves present on the occlusal surface as one might expect for an M_3. The crown is lightly worn, with a triangular piece lost distally and enamel lost at the cervix around much of the tooth crown. Apart from the upper portion of the buccal part of the mesial root, the roots are missing. The primary cusps form a Y5 pattern. The presence of a C6 cannot be determined and there is no C7. There is a deep, but buccolingually narrow slit-like mesial fovea and a large, crest-like protostylid that extends from the buccal face of the protoconid to beyond the buccal groove. Wood and Leakey (2011) listed this specimen as part of KNM-WT 38362, but the association with the upper molars cannot be demonstrated.

KNM-WT 39951 A RM_2 or M_3, with no strong evidence to favor one molar position over the other (Fig. 10o). It preserves the buccal half of a lightly worn crown, extending from a partially preserved protoconid to the hypoconulid. There are multiple grooves on the occlusal surface and a distinct and prominent protostylid crest (with cuspule) is present. Wood and Leakey (2011) listed this specimen as part of KNM-WT 38362, but the association with the upper molars cannot be demonstrated.

KNM-WT 39952 A left mandibular molar with little grounds to indicate a particular molar position (Fig. 10p). It comprises a partial crown with weathered enamel, although some secondary grooves can be discerned. Only the buccal half of the crown is preserved and

includes the protoconid and hypoconid. There is a distinct protostylid crest extending from the buccal face of the protoconid to beyond the mesiobuccal groove. Wood and Leakey (2011) listed this specimen as part of KNM-WT 38362, but the association with the upper molars cannot be demonstrated.

KNM-WT 39953 This is a buccal fragment of a left mandibular molar with little grounds to indicate a particular molar position (Fig. 10q). The distal half of the protoconid, most of the hypoconid, a mesial portion of the hypoconulid and a buccal portion of the entoconid are preserved. The remnants of a protostylid are present on the weathered buccal face. Wood and Leakey (2011) listed this specimen as part of KNM-WT 38362, but the association with the upper molars cannot be demonstrated.

KNM-WT 39955 A LC_1 preserving the distal portion of the lingual face (Fig. 10r). The distal lingual groove is clearly defined by the distinct distal marginal ridge and the central ridge. These converge at the basal eminence, which is flat rather than bulbous. There is a small cuspule at the base of the distal ridge. The preserved crown height is 12.9 mm (measured on the lingual face). This specimen is possibly associated with KNM-WT 38361.

KNM-WT 66291 A LM_2 (or M_3), with inferred molar position based on its relatively large size but lack of tapering on the distal half of the crown (Fig. 10s). The crown is unworn and complete, as there is a small amount of root formation below the cervix. The occlusal basin is complex and covered with numerous secondary grooves. There is an incipient postmetaconulid, a C7, and three secondary cuspules on the distal marginal ridge forming the distal border of a deep distal fovea. The mesial fovea is deep and wide extending well towards the metaconid cusp tip. There is a well-developed protostylid running from the mesial face of the protoconid to past the buccal groove.

3.3 Unassociated maxillary teeth

KNM-WT 16003 This is an almost unworn RM^3 with molar position inferred from the marked tapering of the distal half of the crown (Fig. 11a). The mesial and buccal roots lack tips and the distobuccal root is lost. Enamel is lost close to the cervical margin at the mesiobuccal

corner and part of the buccal margin. There are numerous secondary grooves on the occlusal surface that form puffy ridges on all the cusps. There is a distinct slit-like mesial fovea, largely confined to the buccal half of the tooth. As for all other upper molars described here, a secondary groove on the paracone that runs parallel to the mesial fovea delineates a distinct puffy ridge of enamel. The distal fovea is small and indistinct. A C5 occurs on the distal margin buccal to the longitudinal groove. The lingual groove extends onto the lingual face as far as the cervix. The enamel tip of the metacone is indented and poorly developed. An additional deep groove leaves the lingual groove mesiolingually and runs obliquely almost to the tip of the protocone. Several vertically running grooves lightly indent the mesial faces of the protocone and hypocone. These are most marked on the protocone where they can be considered as a manifestation of Carabelli's cusp.

KNM-WT 38332 A LM^3 (or M^2) with molar position inferred based on tapering of the distal half of the crown and the relatively small metacone and hypocone (Fig. 11b). The unworn occlusal surface suggests this could be a germ. The mesial face is missing and much of the enamel on the distal face is lost. The enamel surface is pitted and damaged through weathering, but numerous secondary grooves are still visible on the occlusal surface. The presence of Carabelli's cusp cannot be assessed due to missing fragments of the crown. There is no crista obliqua. The morphology of the mesial fovea is not clear due to the missing mesial part of the tooth, but there is a small part of a puffy island of enamel preserved close to the mesial break. A secondary groove dividing the hypocone appears to delineate a small C5. The distal fovea takes the form of a distinct slit-like groove running distal to the metacone cusp tip. Wood and Leakey (2011) listed this specimen as a RM^2.

KNM-WT 38336 This moderately worn LI^1 preserves a complete root (Fig. 11c). It was not reported in Leakey et al. (2001) because attribution to *Theropithecus* could not be excluded at the time. Wood and Leakey (2011) listed the specimen as hominin, and this attribution is indeed supported by its straight root, flat labial crown surface that is only slightly angled lingually, and an enamel cervix that only gently curves up mesially and distally. Enamel

thickness of 0.65 mm on the labial surface appears thin, but not dissimilar to that of the KNM-WT 38361 I^1, measured at an equivalent crown location (0.76 mm).

KNM-WT 38337 A RM^1 (or M^2) with molar position based on relatively small crown size and rectangular crown shape (Fig. 11d). The crown is slightly worn with no dentine exposure and the roots are missing their apices. Weathering obscures much of the occlusal detail. Carabelli's cusp is expressed as a small pit on the mesiolingual corner of the crown. The crista obliqua is shallowly bisected by the longitudinal groove. The mesial portion of the paracone is cut by a secondary groove that runs parallel to the mesial fovea and defines an elongated puffy ridge. The mesial fovea, like that of KNM-WT 38338 (see below), is confined to the buccal portion of the crown. The distal fovea is a broad deep slit-like groove close to the distal margin. There is no C5. Wood and Leakey (2011) listed this specimen as a RM^1. On the other hand, Cerrito and Bailey (2019) questioned the identification as a permanent tooth, stating that KNM-WT 38337 is more likely a dP^4, based on the crown size and morphology shown by *A. afarensis*. To assess this interpretation we examined the six available dP^4s of the latter species (A.L. 333-86; A.L. 333-105; DIK-1-1A; LH 3a; LH 6d; LH 21), and found that their crown morphology does indeed differ consistently from that of permanent molars. The crown height is notably lower relative to the BL diameter, and the lingual crown face has a more sloping orientation. In occlusal view the distal face forms a gentle curve projecting furthest distally at mid-crown. In light of these differences KNM-WT 38337 is far more likely to be a M^1 than a dP^4; it has a high crown, steep lingual face and a relatively straight distal margin projecting furthest at the hypocone (Fig. 11d). The roots of KNM-WT 38337, as seen in mesiodistal view, are splayed but straight, and unlike the curved shape in dP^4s that is associated with the presence of the P^4 crypt underneath.

KNM-WT 38338 A RM^1 or RM^2 with no strong evidence to favor one molar position over the other (Fig. 11e). This is a triangular fragment that is broken across an oblique line running from the mesiolingual corner to the distobuccal corner. The paracone, most of metacone and the partial protocone are preserved. There is little occlusal wear, and no mesial interstitial facet. Secondary grooves run towards the cusp tips of the paracone and the metacone. The

mesial fovea is continuous with the longitudinal groove but is only expressed buccally, appearing as a shallow groove passing towards the buccal margin. A deep secondary groove on the paracone runs parallel to the mesial fovea delineating an elongated puffy ridge. The buccal groove deeply cuts the lower third of the buccal face. Wood and Leakey (2011) listed this specimen as a RM^2.

KNM-WT 38346 A LdP^4 based on small crown size, root splay and thin enamel (Fig. 11f). It was originally listed as a RM^1 or RM^2 by Leakey et al. (2001). Preserved are the worn lingual half of the crown and the almost complete lingual root. A pinhead-sized dentine pit is exposed on the protocone and a larger area of dentine is partially preserved on the hypocone. Wear obscures the occlusal detail of this fragment. The fragmentary nature and moderate degree of wear prevent meaningful metrical comparisons of this specimen.

KNM-WT 38355 A RM^2 or RM^3 based on the small metacone and distally tapering crown, but with no strong evidence to favor one molar position over the other (Fig. 11g). While the preserved crown is weathered, the tips of the paracone, metacone and hypocone appear to be unworn, and the lingual half of the protocone is missing. Much of the mesiolingual portion and mesial and distal faces are missing. There is no crista obliqua and there is a small distal cuspule immediately lingual to a quite diminutive metacone. Wood and Leakey (2011) listed this specimen as a $RM^{2?}$.

KNM-WT 38356 A RM^1 or RM^2 based on a lack of distal tapering, but with no strong evidence to favor one molar position over the other (Fig. 11h). A chip is missing from the mesiobuccal corner, and much of the protocone is not preserved. The occlusal surface is slightly worn but there is no dentine exposure. A distinct crista obliqua connects the protocone and metacone. The mesial fovea is a continuation of the longitudinal groove and takes the form of a small shallow groove passing towards the buccal face parallel to the mesial margin. A secondary groove traversing the paracone delimits a triangular puffy ridge of enamel. There is no distal cuspule and the distal fovea is deep and forms an open 'V'.

KNM-WT 66289 A RP^3 or RP^4 with no strong evidence to favor one position over the other (Fig. 11i). The moderately worn crown exhibits a large dentine pit over the lingual cusp, and

little relief left of the buccal cusp. Enamel is missing from the buccal and distal face. Buccal root(s) broken off directly above the buccolingual bifurcation, showing 8-shaped cross-section with two root canals. This indicates that the tooth was either three-rooted or had a strongly grooved, near-divided buccal root. The lingual root is broken off at approximately halfway.

KNM-WT 66290 A LP^3 or LP^4 with no strong evidence to favor one premolar position over the other (Fig. 11j). The crown preserves the lingual cusp and half of the buccal cusp and the roots are missing. There is little or no wear visible, but enamel substantially weathered. The lingual cusp is placed mesially and the median longitudinal groove is deep, with ridges coming from buccal and lingual cusps, mesial and distal from each other respectively (i.e., there is no continuous ridge between both cusps).

3.4. Qualitative comparisons

Lower molars When unworn or lightly worn, the occlusal surface of the lower molars is traversed by numerous secondary grooves (e.g., KNM-WT 8556 LM_3, 16006 RM_3, 38344, 38349, 66291), which are particularly evident on the two lingual cusps. The buccal face slopes gently towards the occlusal surface giving a broad puffy appearance, whereas the lingual face is close to vertical. The groove pattern is usually a Y5, but three specimens (KNM-WT 38344, 38352 and 38359A) have a +5 pattern. C6 is generally absent but is present on five molars (KNM-WT 8556 M_1 and M_3, 16006 M_3, 38347 and 38349). A few specimens show a small C7, positioned in the lingual groove and delineated on the occlusal and lingual surface (KNM-WT 8557, 38333, 38344, 66291 and M_3 of KNM-WT 8556 and 16006). Most of these specimens (not KNM-WT 38333) also exhibit a postmetaconulid with either a free cusp or marked ridge. A postmetaconulid ridge (with no cusp) is found in the absence of a C7 in KNM-WT 38359A, B, 38349 and 38352. A C7 can be found in *A. afarensis* (e.g., A.L. 400-1 and 145-35), but a postmetaconulid with the same expression as seen in the Lomekwi sample is rare in this species (and in the *A. deyiremeda* and *Australopithecus* sp. material from Woranso-Mille), the LM_2 of A.L. 333w-1 perhaps being

most similar (a tooth which also has a small C7). A C7 and/or a postmetaconulid is rarely found in *A. anamensis*. A prominent 'shoulder' on the distal ridge of the metaconid is present in some specimens, such as KNM-KP 31728, and KNM-ER 20422 and 30201, although it is not clear whether this is a postmetaconulid and it is not similar to the ridge/cusp present in the Lomekwi specimens (see Skinner et al., 2015: Supplementary Fig. 2). A similar 'shouldering' is also seen in *A. africanus* (e.g., StW 586 M_3), as is a marked postmetaconulid ridge (e.g., StW 537 M2) and a C7 (e.g., StW 537 M_3); however there are no specimens of this species that clearly resemble the Lomekwi pattern (Skinner et al., 2015: Supplementary Figs. 6 and 7). A well-developed protostylid is generally present and is very consistent in its expression as a prominent crest that runs from the buccal groove to below the mesiobuccal face of the protoconid (e.g., KNM-WT 16006, 38339, 38344, 38349, 38359A, B, 39950, 39951, 39952, and 66291; and similar but less prominent in KNM-WT 38358C, D). This form of protostylid is most similar to types 5 and 6 described by Hlusko (2004) and its marked expression in the Lomekwi molars would align most with frequency distributions reported for *A. anamensis* and *A. africanus*. Additionally, it does not resemble the protostylid expression present in the large *A. afarensis* sample which has a low overall frequency of protostylid and few examples of prominent crest-like expression as seen in the Lomekwi sample. The only specimen with protostylid expression approaching the prominent crest often seen in the Lomekwi sample is A.L. 330-5, although it is not as marked and restricted to the distal half of the protoconid buccal face.

Lower premolars The P_3 of KNM-WT 8556 has a prominent metaconid (a form likely matched by the partial P_3 of KNM-WT 39954); however, this is not particularly distinctive compared to samples of *A. afarensis* and *A. africanus*. The small P_4 sample of Lomekwi is consistently molarized, with an expanded talonid and the presence of multiple tubercles along the distal talonid ridge. Haile-Selassie and Melillo (2015) noted similar talonid expansion of P_4 crown morphology with the *Australopithecus* sp. material from Woranso-Mille, but also some differences (including overall size and mesiodistal elongation). The P_3

and P_4 morphology differ from *A. deyiremeda* (BRT-VP-3/14), which expresses an almost unicuspid P_3 and lacks molarization of the P_4 (Haile-Selassie et al., 2015).

Upper molars The maxillary molar sample presents a consistent gross morphology with regard to crown shape, discrete trait expression and groove pattern. First molars tend to be approximately rectangular, with crown shape in more distal molars being more rounded and with a prominent distal projection of the hypocone. The mesial fovea tends to be expressed only on the buccal portion of the tooth as an elongated groove. A C5 is present on KNM-WT 16003, 38332, and possibly 38350. Otherwise there tends to be a prominent distal subtriangular region demarcated by a deep groove on the distal border of the metacone (KNM-WT 38337, 38355, 38356, 38358B, 38362A). Only a few maxillary molars preserve the mesiolingual corner of the protocone, but those that do exhibit minor expressions of Carabelli's cusp. These range from a small pit or furrow (KNM-WT 38358F and 38337), or a cingulum-like crest restricted to the mesial face (KNM-WT 38362A, B). The crista obliqua is weakly expressed and usually bisected by the longitudinal transverse groove. On all preserved upper molars there is a characteristic island of enamel that is expressed as a puffy ridge defined by the mesial fovea (which is normally a groove) and a secondary groove that runs from the longitudinal groove towards the paracone cusp tip. In *A. afarensis* this feature is similarly expressed in A.L. 486-1 (RM^2), and less so in A.L. 200-1 (both M^2), but otherwise not commonly found. Unworn specimens (KNM-WT 16003) suggest a tendency towards numerous secondary grooves on the occlusal surface; however the overall frequency of this is difficult to assess due to moderate wear on most maxillary molars.

Upper premolars The maxillary premolar crown sample is represented by right and left P^3 and P^4 in KNM-WT 38361 and two isolated maxillary premolars (KNM-WT 66289 and 66290) of uncertain position. The lingual cusp of the P^3 is mesially positioned (also in KNM-WT 66290) and there is a mesial crest on the lingual face of the paracone that demarcates a mesial fovea. This mesial crest is even more prominent in the P^4 of KNM-WT 38361F, in which it crosses the mesial portion of the crown, meets the buccal marginal ridge, and strongly demarcates a mesial fovea. Due to the fragmented nature of the crown, the mesial

cusp position on the P^4 is uncertain. Maxillary premolars are mostly three-rooted, as seen in KNM-WT 38343, 38350, 40000 and 66289. The P^4 of KNM-WT 38350 has a deeply grooved buccal root that can be seen as being morphologically close to a double buccal root, although it contains only a single oval root canal inside. Three-rooted P^3 are variably seen in *Australopithecus* species, including in *A. afarensis* specimens A.L. 199-1 (right side), A.L. 417-1d, A.L. 427-1a (left side), A.L. 442-1 (right side), A.L. 444-2 (right side) and A.L. 822-1. A three-rooted P^4 is found in some *A. africanus* specimens, and in the *A. deyiremeda* maxilla (Haile-Selassie et al., 2015), but in *A. afarensis* it is only known from the Garusi 1 maxilla and the right side of A.L. 822-1. The combination seen in KNM-WT 38350, a three-rooted P^3 and a two-rooted P^4 with a buccal root that is buccally and lingually grooved and has a single root canal, is only seen in A.L. 822-1 (left side).

3.5. Metrical comparisons

Lower molars Figure 12 presents bivariate plots of buccolingual and mesiodistal dimensions for M_1, M_2 and M_3. Comparison of tooth size between mandibular molars from Lomekwi and samples of *Australopithecus* and *Ardipithecus* is complicated by the fact that molar position is uncertain for many Lomekwi specimens. Thus, Lomekwi molars that could be M_1 or M_2 are included in both plots for comparison (and similarly for molars that could be M_2 or M_3). The M_1 plot reveals a large overlap between the comparative taxa with the majority of Lomekwi molars falling close to the *A. anamensis* sample and within the *A. afarensis* sample (the *A. africanus* sample is the most variable and contains specimens that are wider buccolingually. The M_2s of *Australopithecus* sp. from Woranso-Mille exceed variation at Lomekwi, and the *A. deyiremeda* M_2 (BRT-VP-3/14) is similar to KNM-WT 38339 in size. There are two Lomekwi M_1s (KNM-WT 8556 and KNM-WT 38359) whose crown dimensions locate them at the upper and lower margins of the Lomekwi molars whose position along the molar row is uncertain (with the exception of KNM-WT 38334). This would support the interpretation that many, if not all of these, are M_1 (but see below). Omo M_1s either fall on the margin of the distribution of the Lomekwi molars (W-508) or exhibit slight mesiodistal elongation (W-572).

The M_2 sample distributions exhibit less overlap among the hominin taxa than is evident in either the M_1 or M_3 samples. A number of *A. afarensis* molars fall on the smaller half of the graph and *A. anamensis* molars fall in the region of overlap between *A. afarensis* and *A. africanus*. M_2s of *Australopithecus* sp. from Woranso-Mille are variable in size, with two falling within the *A. afarensis* cluster and one being similar in size and proportions to the largest *A. africanus* M_2. The single *A. deyiremeda* M_2 and that from Lothagam (KNM-WT 23183) fall in the overlapping region. In this plot, a number of Lomekwi molars fall in the half of the *A. afarensis* plot representing the smallest M_2; however, this may be because they are actually M_1 (although some are in proximity to the Lomekwi M_2 KNM-WT 38359). Based on crown shape, cusp patterning and dentine horn morphology KNM-WT 38347 is identified here as an M_2 or M_3, rather than a dP_4 as originally suggested (Leakey et al., 2001). However, it is diminutive for these molar classes, as can be seen in the bivariate plots. KNM-WT 39950 may be identified as an M_3, but could possibly be an M_2, and it is much larger than KNM-WT 38359 and plots with the largest M_2 of the comparative taxa and among the middle range of M_3 (supporting its current interpretation as most likely an M_3). The position of W-752 in this plot could suggest that it is an M_2 and would thus fall in with most comparative samples in terms of size.

The M_3 comparisons exhibit almost complete overlap of the comparative taxa, but with *A. africanus* presenting a number of molars that are relatively expanded buccolingually. Two *Australopithecus* sp. M_3 from Woranso-Mille are relatively small compared to those from Lomekwi (ignoring KNM-WT 38347), but a third M_3 is relatively large. The molar of *A. deyiremeda* falls in the middle of the Lomekwi sample. The M_3 from Lothagam (KNM-LT 23182) falls within or adjacent to the convex hulls of the three comparative taxa and sits in close proximity to two of the M_3 from Lomekwi (KNM-WT 16006 and 38358C). The M_3 of KNM-WT 8556 is relatively long and falls near the top end of *A. afarensis* M_3. As in the M_2 plot, KNM-WT 38347 remains exceedingly small in comparison to the M_3 samples of all taxa.

Upper molars Figure 13 presents bivariate plots of buccolingual and mesiodistal dimensions for M^1, M^2 and M^3. As with the mandibular molar metrical comparisons above, comparison of

tooth size between maxillary molars is complicated by uncertain molar positions for a number of Lomekwi specimens. A bivariate plot of the M^1 reveals overlap in molar dimensions between *A. afarensis* and *A. africanus,* with *A. anamensis* tending to exhibit relatively small M^1. The position of B2-23b and W-753 in the plot suggests they are likely M^1s and in proximity to Lomekwi specimens such as WT 38350 and WT 38337, respectively.

Unlike in the M^1 sample, *A. anamensis* and *A. afarensis* share extensive size overlap in the M^2 sample, with *A. africanus* being more variable and with a number of relatively large molars. Three *Australopithecus* sp. M^2 from Woranso-Mille are quite variable in size and the single *A. deyiremeda* molar is relatively small. The M^1 or M^2 KNM-WT 38337 is also relatively small, most notably if it is interpreted as an M^2, in which case it would be similar to the M^2 of KNM-WT 40000. Conversely, KNM-WT 38362A falls in the large end of M^1 but in the middle range of *A. afarensis* and *A. anamensis* M^2, suggesting it could be a second molar. The position of W-749 in the M^1 and M^2 plots might indicate that it is an M^2 (where it is in close proximity to WT 38362A).

The plot of M^3 resembles that of the M^2, with broad overlap between *A. anamensis* and *A. afarensis*. The two *Australopithecus* sp. specimens from Woranso-Mille fall on the borders of the *A. afarensis* convex hull and within the *A. africanus* sample. The single Lomekwi M^3 falls towards the larger end of the *A. afarensis* and *A. anamensis* samples.

Cerrito and Bailey (2019) reported that their estimates of the M^2 crown dimensions of KNM-WT 40000 are larger than those published in Leakey et al. (2001). However, (a) they took their measurements from Spoor et al. (2010: Fig. 2e), which is not suitable for this purpose, (b) their MD and BL measurement definitions follow Tobias (1967) whereas those in Leakey et al. (2001) follow White (1977), and (c) matrix-filled cracks in the crown of up to 1.2 mm were not considered (S. Bailey, pers. comm.).

Lower premolars A bivariate plot of the maximum oblique and maximum perpendicular dimension of the P_3 and the mesiodistal and buccolingual dimensions of the P_4 (Fig. 14) shows general overlap in the comparative sample (in this case we have split the Hadar, Laetoli, and Dikika samples of *A. afarensis*, given the marked degree of variation). The

premolars of *A. deyiremeda* are obliquely (P_3) or mesiodistally (P_4) compressed relative to those of the other taxa, while the *Australopithecus* sp. P_3 from Woranso-Mille has a maximum crown diameter that is particularly small. The only measureable P_3 from Lomekwi are the left and right specimens of KNM-WT 8556, which plot with the *A. afarensis* (Hadar) and *A. africanus* samples, being relatively wide in perpendicular dimension relative to most of *A. anamensis*. They are also similar in size to the P_3 of *A. bahrelghazali*. W-978 is situated at the lower margin of the *A. afarensis* convex hull and not close to KNM-WT 8556.For the P_4 sample there is broad overlap between the taxa included, as with most other tooth positions, and in this case the large sample of *Australopithecus* sp. P_4 from Woranso-Mille overlaps with those of *A. anamensis*, *A. afarensis* and *A. africanus*. The specimens of *A. deyiremeda* are relatively small, while those of *A. bahrelghazali* fall in the mid to upper range of *A. afarensis* and *A. africanus*. The only measureable P_4 from Lomekwi, KNM-WT8556, is mesiodistally and buccolingually large and falls at the outer limits of the *A. afarensis* and *A. africanus* samples. W-23 sits in the middle of the *A. afarensis* and *A. africanus* clusters, being both buccolingually and mesiodistally smaller than WT 8556.

Upper premolars As the position of the two most complete maxillary premolars is uncertain, their mesiodistal and buccolingual dimensions are plotted against P^3 and P^4 of the comparative sample in Figure 15. In the P^3 plot, the two Lomekwi specimens fall at the upper range of *A. afarensis* and close to *A. anamensis* and *A. africanus*. B7-39a is smaller than both Lomekwi specimens. In the P^4 plot, KNM-WT 66289 falls within the *A. anamensis* convex hull while KNM-WT 38361H falls within the *A. afarensis* convex hull. Unfortunately, linear dimensions offer little evidence to the likely premolar position of these specimens.

Anterior teeth A bivariate plot of crown height and mesiodistal width (Fig. 16) of the I^2 shows considerable variation in *A. africanus*, and *A. afarensis* tending to have relatively wide incisors for their height. Both Lomekwi specimens, KNM-WT 38358a and 38361b exhibit particularly low crowns for their width. This, coupled with the distinct ‘cupped’ lingual surface differentiates the Lomekwi incisors from the comparative sample of *Australopithecus*. The

fragmentary canines of KNM-WT 38361 are germs and preserve little in the way of diagnostic morphology.

Relative tooth size of KNM-WT 8556 Following initial observations by Leakey et al. (2001), the relative tooth size of KNM-WT 8556 can now be analyzed based on substantially larger comparative samples. Results confirm that the specimen stands out by having the largest P_4 crown area relative to M_1 crown area in the sample (Fig. 17). Leakey et al. (2001) noted that M_3 crown area is large relative to M_1 crown area as well, and plots show that KNM-WT 8556 is more specifically characterized by its great mesiodistal M_3 length relative to M_1 length (Fig. 17).

4. Discussion

The hominin sample from the middle Pliocene at Lomekwi includes mostly isolated teeth, as well as a few cranial and mandibular specimens, but no postcranial elements. Comparative analyses have thus far focused on the cranium KNM-WT 40000 (holotype) and partial maxilla KNM-WT 38350 (paratype) of *K. platyops* (Leakey et al., 2001; Spoor et al., 2010, 2016). Small molar crown size and root morphology of premolars and incisors are part of the species description, but other aspects cannot be compared with the isolated Lomekwi teeth because the tooth crowns of these two type specimens are poorly preserved. Our new comparative analyses of crown size demonstrate that the M^2 and M^1 of KNM-WT 40000 and KNM-WT 38350, respectively, are indeed among the smallest in the early hominin sample. One isolated M^1 or M^2 (KNM-WT 38337) is similar in size to the M^2 of KNM-WT 40000, but another one (KNM-WT 38362) is clearly larger, although within levels of hominin intraspecific variation. The three-rooted or near three-rooted morphology of the upper premolars in KNM-WT 40000 and KNM-WT 38350 is also found in the other upper premolars from Lomekwi. The I^1 and I^2 roots of KNM-WT 40000 appear to be more similar in size than seen in other hominin species (Leakey et al., 2001), an unexpected observation that in the Lomekwi sample can only be compared indirectly with the partial I^1 germ and a I^2 germ of KNM-WT

38361, which both lack root development. Detailed analysis of the KNM-WT 40000 roots using µCT will need to be the first step to confirm the preliminary observations.

The specimen in the Lomekwi sample that provides the most comprehensive record of dental morphology is the partial mandible KNM-WT 8556. The current study re-examined its dental crown proportions as highlighted by Leakey et al. (2001). It is confirmed that the P_4 crown area is particularly large, relative to M_1 area, and the M_3 is found to be strikingly long mesiodistally compared with the length of the M_1. Both features place KNM-WT 8556 outside the known variation of *Australopithecus* (Leakey et al., 2001; Kimbel and Delezene, 2009; Haile-Selassie and Melillo, 2015), as does the symphyseal morphology with a distinctly horizontal postincisive plane, a superoinferiorly thick (deep) lower torus and a superiorly placed genioglossal pit (Brown et al., 2001; Leakey et al., 2001).

Apparent similarities between the holotype maxillae of *K. platyops* and *A. deyiremeda* were pointed out by Spoor (2015), but subsequently shown to be based on different underlying morphological patterns (Spoor et al., 2016). Likewise, KNM-WT 8556 and the *A. deyiremeda* mandible BRT-VP-3/14 can be seen to share a relatively long M_3 crown and an anteriorly positioned origin of the ramus, but the latter specimen has a more robust corpus, a less developed P_3 metaconid and a less molarized P_4 (Haile-Selassie et al., 2015).

KNM-WT 8556 being distinct from *Australopithecus* raises the question whether this specimen should be attributed to *K. platyops*, noting that it comes from the same locality (LO-5) and has approximately the same age (3.3 Ma) as the paratype KNM-WT 38350 of that species (Leakey et al., 2001). Although such an attribution seems plausible, it would be prudent to await the outcome of research comparing the mandibular dental arcade shape of KNM-WT 8556 and the typical maxillary shape of *K. platyops*, using methods previously developed to compare early *Homo* specimens (Spoor et al., 2015, 2016),

The middle Pliocene dental sample from Lomekwi appears to show a consistent morphological pattern, despite representing a time period of about 300 kyr (3.5–3.2 Ma). Tooth crown size and shape as well as occlusal morphology do not appear to exceed intraspecific variation shown by early hominin species considered here, acknowledging that

at many tooth positions the sample size is too low to make meaningful inferences. One exception to this, however, is KNM-WT 38347. It is the smallest mandibular molar in the entire comparative hominin sample (Fig. 12), assuming this specimen is indeed a permanent molar rather than a dP_4. That the narrow crown shape and cusp patterning suggest that it is an M_2 or M_3 rather than M_1 further emphasizes the small crown size of this specimen, and increases the variation of the combined Lomekwi sample beyond that shown by various hominin species. Additionally, while the overall crown size of KNM-WT 38333 is consistent with other molars in the sample, the very small hypoconulid and relatively small hypoconid result in a crown configuration that is not found in either the Lomekwi or other comparative samples. More detailed analyses of cusp proportions and/or groove patterning in a broader comparative sample might clarify how unique this pattern is among Pliocene hominins.

Contemporary hominin-bearing sites geographically closest to Lomekwi are at Lothagam (~3.5 Ma) and South Turkwel (~3.6–3.2 Ma). The M_2 (KNM-LT 23183) and M_3 (KNM-LT 23182) from Lothagam are broadly similar in size and shape to the Lomekwi mandibular molar sample. The protostylid morphology on KNM-LT 21283 is very similar to Lomekwi (e.g., KNM-WT 38359B), as is the shape and size of the mesial fovea. The crown shape and C7 of KNM-LT 23183 are similar to the M_3 in KNM-WT 16006. As it stands, there is no evidence to suggest these samples could not be conspecific. Unfortunately, the associated dentition from South Turkwel (Ward et al., 1999), which is also roughly equivalent in geological age to Lomewki, is highly worn and fragmentary and there is no diagnostic morphology upon which to make a meaningful comparison with the Lomekwi dental sample described here. Samples from the Usno Formation at Omo are very limited in number and in our quantitative analysis are equivocal with respect to their similarities to Lomekwi. It is worth noting that the protostylid expression of W-508 from Omo is also similar to Lomekwi in expressing a marked crest that traverses the whole buccal face of the protoconid.

For all tooth positions, the isolated Lomekwi teeth show considerable size overlap with the comparative hominin taxa used in this study, and linear dimensions do not allow us to refine their taxonomic attribution. Our analysis of the molar dimensions was complicated

by uncertainty in molar position for a number of specimens and the possibility that the sample represents more than one species. What can be concluded from the metric analyses of the Lomekwi molars is that they are most similar in size to *A. afarensis* and *A. anamensis*, but often overlap with the range of *A. africanus*, *A. deyiremeda* and *Australopithecus* sp. from Woranso-Mille. Of the only known mandibular premolars, those of KNM-WT 8556, the P_4 is most similar in size to the largest *A. afarensis* and *A. africanus* specimens, and larger than premolars of *A. anamensis*, *A. deyiremeda* and *Australopithecus* sp. from Woranso-Mille. However, it is its large crown size compared to the M_1 that stands out. The P_3 is more similar in size to most *Australopithecus* species, except *A. deyiremeda* and *Australopithecus* sp. from Woranso-Mille. The maxillary premolars overlap with *A. afarensis*, *A. africanus*, *A. anamensis*, but are larger than *A. deyiremeda*. The two I^2s appear to be lower crowned than seen in *A. afarensis and A. africanus*, but few unworn specimens are available for comparison. The frequent occurrence of dental traits like prominent, shelf-like protostylids sets the sample apart from *A. afarensis*. Future analyses could incorporate more aspects of crown morphology using either 2D or 3D geometric morphometrics of the crown surface (Haile-Selassie et al., 2015), enamel dentine junction morphology (Skinner et al., 2008), and enamel thickness (Skinner et al., 2015).

Recent archaeological discoveries at Lomekwi have caused a paradigm shift in our understanding of *Australopithecus* grade material culture and subsistence and highlight the importance of clarifying hominin systematics in the period from 3–4 Ma in eastern Africa (Harmand et al., 2015). Leakey et al. (2001) decided not to attribute all Pliocene hominin specimens found at Lomekwi to *K. platyops*, because most cannot be associated morphologically with KNM-WT 40000 (holotype) and KNM-WT 38350 (paratype). The findings of the current study seem largely compatible with interpreting the Lomekwi and Lothagam samples as a single species, except for the small KNM-WT 38347 molar (and possibly KNM-WT 38333). We nevertheless feel that a conservative approach is preferable and that attribution to cf. *K. platyops* or *K. platyops* should not be done by default and is unwarranted based on current knowledge (contra Wood and Leakey, 2011; Cerling et al.,

2013; Levin et al., 2015). Instead, the association between cranium KNM-WT 40000 and mandibles KNM-WT 8556 and 16006 can be explored further as a starting point to confirm or reject the conspecificity of the Lomekwi sample. Additional fossil hominin finds in the region, attributable to *K. platyops* or otherwise, will help to integrate the dental, cranial and mandibular evidence.

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Figure captions

Figure 1. KNM-WT 8556, hemimandible: a) occlusal; b) lateral; c) medial views.

Figure 2. KNM-WT 16006, hemimandble: a) medial; b) lateral; c) occlusal views.

Figure 3. a–c) KNM-WT 38343A, partial maxilla: a) lateral; b) medial; c) occlusal views. d–f) KNM-WT 38343B, mandibular corpus: d) lateral; e) medial; f) occlusal views. Abbreviations: A = anterior; P = posterior; L = lateral, M = medial; S = superior; I = Inferior.

Figure 4. KNM-WT 38350, partial maxilla of *Kenyanthropus platyops* (paratype): a) lateral; b) superior; c) occlusal; d) posterior.

Figure 5. Associated dentition KNM-WT 38358: a) KNM-WT 38358A, RI^2 in labial (left) and lingual (right) views; b) KNM-WT 38358B, RM^2; c) KNM-WT 38358C, LM_3; d) KNM-WT 38358D, LM_1; e) KNM-WT 38358E, LM^1; f) KNM-WT 38358F, RM^3; g) KNM-WT 38358G, crown fragment; h) KNM-WT 38358H, crown fragment; i) KNM-WT 38358I, crown fragment. Abbreviations: B = buccal; L = lingual; M = mesial; D = distal. Orientations not provided for h, g, and i as they are fragments. View is occlusal unless otherwise indicated.

Figure 6. Associated dentition KNM-WT 38359, in occlusal view: a) KNM-WT 38359A, RM_1; b) KNM-WT 38359B, RM_2. Abbreviations: B = buccal, L = lingual; M = mesial; D = distal.

Figure 7. Associated dentition KNM-WT 38361: a) KNM-WT 38361A, LI^1 in lingual (left) and labial (right) views; b) KNM-WT 38361B, LI^2 in lingual (left) and labial (right) views; c) KNM-WT 38361D, RC^1 in distal view; d) KNM-WT 38361E, $C^1/_1$ in either mesial or distal view (as tooth type is uncertain); e) KNM-WT 38361F, $RP^{4?}$; f) KNM-WT 38361G, $LP^{4?}$; g) KNM-WT 38361H, $LP^{3?}$; h) KNM-WT 38361I, $RP^{3?}$. Abbreviations: B = buccal; L = lingual; D = Distal; M = mesial; La = labial. View is occlusal unless otherwise indicated.

Figure 8. Associated dentition KNM-WT 38362, in occlusal view: a) KNM-WT 38362A, $RM^{1\ or\ 2}$; b) KNM-WT 38362B, $LM^{1\ or\ 2}$. Abbreviations: B = buccal; L = lingual; M = mesial; D = distal.

Figure 9. Associated dentition KNM-WT 39954, in occlusal view: a) KNM-WT 39954A, LP_3; b) KNM-WT 39954B, RP_4. Abbreviations: B = buccal; L = lingual; M = mesial; D = distal.

Figure 10. Isolated mandibular teeth: a) KNM-WT 8557, LM_1 (or M_2); b) KNM-WT 38333, LM_1 (or M_2); c) KNM-WT 38334, LM_1 (or M_2); d) KNM-WT 38335, RM_1 or M_2 or M_3; e) KNM-WT 38339, LM_2 (or M_1); f) KNM-WT 38341, LM_2 or M_3; g) KNM-WT 38342, LM_1 (or M_2); h) KNM-WT 38344, RM_1 or M_2; i) KNM-WT 38347, LM_2 or M_3; j) KNM-WT 38349, RM_1 or M_2; k) KNM-WT 38352, RM_1 (or M_2); l) KNM-WT 38357, RM_1 (or M_2); m) KNM-WT 39949, LP_4; n) KNM-WT 39950, RM_3 (or M_2); o) KNM-WT 39951, RM_2 or M_3; p) KNM-WT 39952, LM_1 or M_2

or M_3; q) KNM-WT 39953, LM_1 or M_2 or M_3; r) KNM-WT 39955, LC_1 in lingual view; s) KNM-WT 66291, LM_2 (or M_3). View is occlusal unless otherwise indicated. Tooth type identifications in brackets are possible but less likely based on qualitative and quantitative assessment. Mesial at top except for KNM-WT 39955. Abbreviations: B = buccal; L = lingual; M = mesial; D = distal.

Figure 11. Isolated maxillary teeth: a) KNM-WT 16003, RM^3; b) KNM-WT 38332, LM^3 (or M^2); c) KNM-WT 38336, LI^1 in labial view; d) KNM-WT 38337, RM^1 (or M^2); e) KNM-WT 38338, RM^1 or M^2; f) KNM-WT 38346, LdP^4; g) KNM-WT 38355, RM^2 or M^3; h) KNM-WT 38356, RM^1 or M^2; i) KNM-WT 66289, RP^3 or P^4 in occlusal (top) and apical (bottom) view; j) KNM-WT 66290, LP^3 or P^4; k) KNM-WT 40000, RM^2. View is occlusal unless otherwise indicated. Tooth type identifications in brackets are possible but less likely based on qualitative and quantitative assessment. Mesial at top except for KNM-WT 38336 and the inferior view of KNM-WT 66289. Abbreviations: B = buccal; L = lingual; M = mesial; D = distal.

Figure 12. Bivariate plots of mesiodistal and buccolingual dimensions of M_1 (top), M_2 (middle), and M_3 (bottom). Lomekwi specimens are identified individually by catalogue number and when tooth position is uncertain specimens are included in multiple plots and the most likely positions are noted in brackets.

Figure 13. Bivariate plots of mesiodistal and buccolingual dimensions of M^1 (top), M^2 (middle), and M^3 (bottom). Lomekwi specimens are identified individually by catalogue number and when tooth position is uncertain specimens are included in multiple plots and the most likely positions are noted in brackets.

Figure 14. Bivariate plots of mesiodistal and buccolingual dimensions of the P_3 (top) and P_4 (bottom). Lomekwi specimens are identified individually by catalogue number.

Figure 15. Bivariate plots of mesiodistal and buccolingual dimensions of the P^3 (top) and P^4 (bottom). Lomekwi specimens are identified individually by catalogue number and when tooth position is uncertain specimens are included in multiple plots.

Figure 16. Bivariate plot of mesiodistal length and crown height of the I^2. For specimens showing occlusal wear or incomplete crown development, an arrow indicates that the preserved values are minima. The length of the arrow is arbitrary and does not represent the estimated difference to full crown height. Lomekwi specimens are identified individually by catalogue number.

Figure 17. Relative tooth size in KNM-WT 8556: M_1 vs. P_4 area (top); M_1 vs. M_3 area(middle); M_1 mesiodistal length vs. M_3 mesiodistal length (bottom).