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RESEARCH ARTICLE

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Human burials at the Kisese II rockshelter, Tanzania

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Abstract

Objectives: The Late Pleistocene and early Holocene in eastern Africa are associated with complex evolutionary and demographic processes that contributed to the population variability observed in the region today. However, there are relatively few human skeletal remains from this time period. Here we describe six individuals from the Kisese II rockshelter in Tanzania that were excavated in 1956, present a radiocarbon date for one of the individuals, and compare craniodental morphological diversity among eastern African populations.

Materials and Methods: This study used standard biometric analyses to assess the age, sex, and stature of the Kisese II individuals. Eastern African craniodental morphological variation was assessed using measures of dental size and a subset of Howells' cranial measurements for the Kisese II individuals as well as early Holocene, early pastoralist, Pastoral Neolithic, and modern African individuals.

Results: Our results suggest a minimum of six individuals from the Kisese II collections with two adults and four juveniles. While the dating for most of the burials is uncertain, one individual is directly radiocarbon dated to ~7.1 ka indicating that at least one burial is early Holocene in age. Craniodental metric comparisons indicate that the Kisese II individuals extend the amount of human morphological diversity among Holocene eastern Africans.

Conclusions: Our findings contribute to a growing body of evidence that Late Pleistocene and early Holocene eastern Africans exhibited relatively high amounts of morphological diversity. However, the Kisese II individuals suggest morphological similarity at localized sites potentially supporting increased regionalization during the early Holocene.

KEYWORDS
early Holocene, eastern Africa, morphological variation

1 | INTRODUCTION

Human (and more broadly, hominin) skeletal remains from eastern Africa play a central role in discussions about human origins, the evolution of morphological diversity within *Homo sapiens*, and population dispersals and interactions associated with the spread of animal and plant domesticates. Yet despite their importance, little is known about human morphological variation from the region. This is because (1) there are relatively few sites with human remains, (2) bones (when preserved) tend to be fragmentary, (3) there are persistent issues with chronological dating, and (4) archeological research in the region has a history of being underfunded and under-published (Grine, 2016; Lahr, 2016; Prendergast & Sawchuk, 2018; Rightmire, 1975). Additionally, only a small proportion of sites preserve multiple individuals to permit assessment of intra-population variability. This is especially true of Late Pleistocene and early Holocene skeletons associated with Later Stone Age (LSA) foragers that antedate demographic shifts related to the spreads of pastoralism, iron-working, and farming over the past 5000 thousand years (5 ka) as suggested by genetic, skeletal, linguistic, and archeological evidence (Marshall & Hildebrand, 2002; Prendergast et al., 2019; Tishkoff et al., 2009; Wang et al., 2020). Given this paucity of data, new samples from LSA archeological contexts are potentially transformative for understanding patterns of morphology, biology, and population history among ancient eastern Africans.

Eastern African LSA archeological sites with well-described and published human remains are limited to fishing localities around Lake Turkana in northern Kenya (Angel et al., 1980; Barthelme, 1985; Lahr et al., 2016; Phillipson, 1977), Lukenya Hill in Central Kenya (Gramly, 1976; Gramly & Rightmire, 1973; Tryon et al., 2015), Mumba Rockshelter in northern Tanzania (Bräuer, 1980; Mehlman, 1989), and Mlambalasi Rockshelter in southern Tanzania (Biittner et al., 2017; Sawchuk & Willoughby, 2015). Within the Horn of Africa, LSA burials are known from Gogoshiis Qabe in Somalia (Brandt, 1988) and Mota in Ethiopia (Arthur et al., 2019; Gallego Llorente et al., 2015). Other LSA burials are found in shell middens around Lake Victoria and are attributed to Kansyore fisher-foragers, some of whom may have interacted with herders (Dale & Ashley, 2010; Leakey, 1935; Robertshaw et al., 1983). Depending on one's perception of "eastern" Africa (e.g., Shea, 2020), this sample could be extended to include individuals from Ishango in the Democratic Republic of the Congo (Crevecoeur et al., 2016), Gwisho Springs in Zambia (Fagen, 1971), and Hora, Fingira and Chencherere II in Malawi (summarized in Skoglund et al., 2017). Larger archeological skeletal collections from eastern Africa are associated with later time periods: early herders living around Lake Turkana ~5–4 ka (Hildebrand et al., 2018; Sawchuk et al., 2019) and Pastoral Neolithic (PN) herders in southern Kenya and northern Tanzania ~4–1.5 ka (Ambrose, 2001; Bower, 1991; Sawchuk et al., 2018).

Previous research on Late Pleistocene LSA individuals indicates at least some populations exhibit patterns of morphological diversity distinct from recent sub-Saharan Africans (Crevecoeur et al., 2009; Crevecoeur et al., 2016; Grine et al., 2007; Mounier et al., 2018; Reiner et al., 2017; Stojanowski, 2014; Tryon et al., 2015). This could reflect phenotypic variation since lost to genetic drift and other demographic processes (Lahr, 2016; Lahr & Foley, 1998; Manica et al., 2007). However, research has been stymied by very small sample sizes with poor geographic and temporal coverage, and few samples from LSA archeological sites have sufficiently large samples to robustly assess intra-regional population variability.

Here we add Kisese II rockshelter in Tanzania to the list of eastern Africa sites with LSA skeletal remains. The site preserves a relatively continuous sequence spanning portions of at least the last 47 ka that contains faunal remains, stone tools, ochre, and ostrich eggshell beads (described in Ranhorn et al., n.d. [in review]; Tryon et al., 2018). We provide here the first descriptions of six human burials from the site that were excavated in 1956 by Raymond R. Inskeep and present a direct radiocarbon date for one individual confirming an early Holocene age and therefore an LSA archeological context. Our objective is to provide the first formal documentation and comparison of these individuals, and in doing so contribute to understanding of human morphological variation among past eastern African populations.

2 | MATERIALS AND METHODS

2.1 | Historical and chronological context

The site of Kisese II is one of several hundred painted rock shelters in the Kondoa region of north-central Tanzania (4°29′30.47″S, 35°48′43.31″E; Figure 1), an area with one of the largest concentrations of rock art in Africa (Mabulla & Gidna, 2014) and recognized by UNESCO as the Kondoa Rock Art Sites World Heritage Site. Nearly all of the art at the site is of the naturalistic tradition described by Bwasiri and Smith (2015), red in color with human figures and wild animals as dominant representations. Initial investigation of the rock art in 1935 by L.S.B. and M.D. Leakey led to trial excavations by them at Kisese II in 1951 (Leakey, 1935, 1983; Leakey & Leakey, 1950). Kisese II was targeted because, unusual for the area, it preserved a

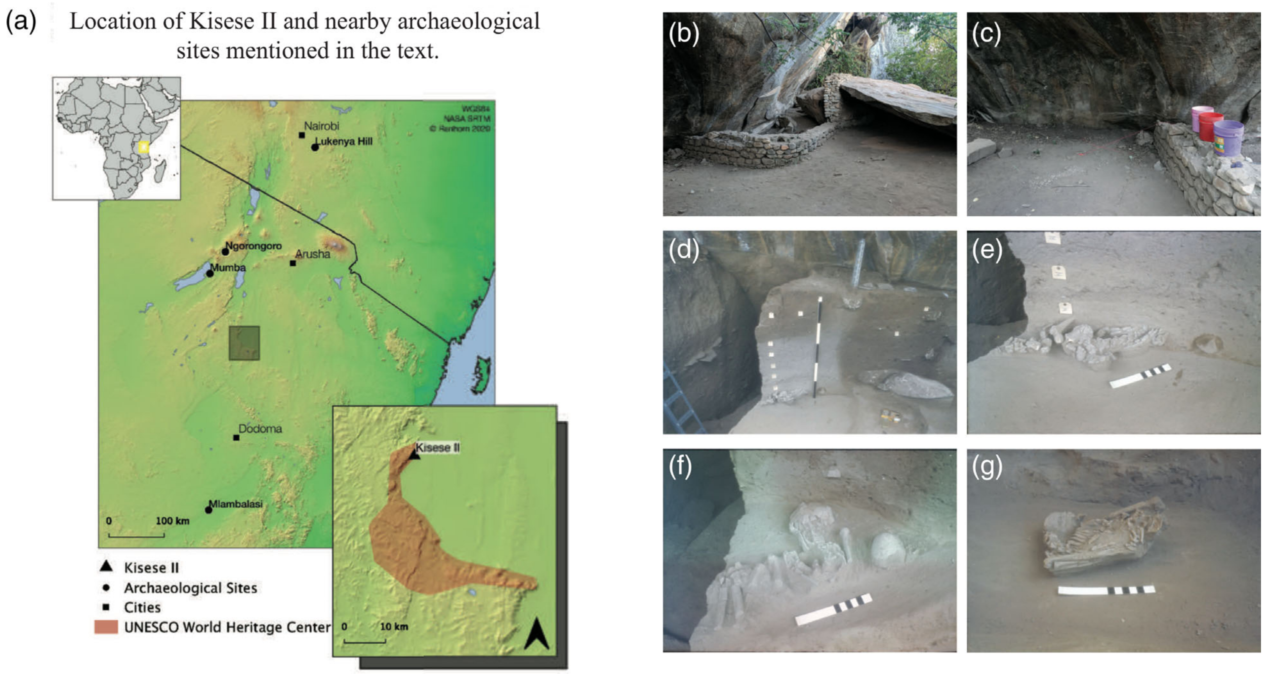

FIGURE 1 Map and Inskeep photos (a) a map of eastern Africa with the location of Kisese II. (b) Kisese II in 2018, and (c) the area approximately corresponding with the area shown in (d–g); photos by Samantha Porter. Photos (d–f) are of Inskeep's excavation of "burial III/IV" and show at least two individuals in spit VII. Ostrich eggshell C^{14} dates obtained from spit VII suggest two calibrated age ranges that provide minimum age estimates: 12.87–12.15 and 42.79–41.73 ka. The cranium on the right shows fracture patterns and partially-healed cranial trauma that matches juvenile KNM-KX 9 (Figure S3). Notes associated with the skeletal material suggest KNM-KX 1 is also shown in the burial III/IV photo, although the fracture patterns on the ossa coxae visible in the photographs do not precisely match KNM-KX 1. (g) Inskeep's photos show one other burial labeled "burial 2" that contains an older juvenile or adult buried on their side

deep (>6-m-thick) stratigraphic sequence that was rich in artifacts and fossils. Because of this, L.S.B. Leakey hired R.R. Inskeep to conduct more extensive excavations there in 1956.

Inskeep is best known for his long and prolific career as an archeologist working in South Africa; Kisese II was his first project as a field director, and uncharacteristically, is one of the few sites that he excavated without fully publishing (Tryon et al., 2019). Neither the Leakeys nor Inskeep ever published more than a passing reference or brief reports on their work at Kisese II, and the presence of burials is not mentioned in any of these publications (Inskeep, 1962; Leakey, 1935, 1983; Leakey & Leakey, 1950). The only published reference of the burials is a brief mention by Ambrose (1986), who unsuccessfully sampled two of the individuals in the 1980s for isotopic analysis. Material from the 1956 excavations was dispersed among multiple institutions (detailed in Tryon et al., 2019). Inskeep notes in an undated draft of a report on Kisese II shared with us by his wife Adi (now deceased) that "…the fauna and human remains…were carried by Louis Leakey from Kisese to Nairobi for study and safe keeping."

The human remains were accessioned by the National Museums of Kenya (NMK) and remain in Nairobi to this day, although the artifacts and fauna from the 1951 and 1956 excavations were returned to the National Museums of Tanzania (NMT) in Dar es Salaam in 2012 under the aegis of A. Kwekason. The collections in Nairobi are from burials assigned Roman or Arabic numerals. Isolated human remains in Dar es Salaam were found during subsequent detailed study of the fauna and have only stratigraphic information (excavation level) associated with them. Renewed excavations by Ranhorn at Kisese II in 2017–2019 did not encounter additional burials.

2.2 | Kisese II biometric analyses

The ages, and in some cases, even stratigraphic contexts of the skeletal material are largely unknown. Our investigation of the Kisese II material began in 2011 and includes analyses of archival material from the Leakey and Inskeep excavations. Archival notes found with the specimens suggest Inskeep's spit numbers for some of the burials can be matched with ^{14}C dates obtained from ostrich eggshell beads with known stratigraphic context (Tryon et al., 2018). Given that the burials are intrusive and initiated in overlying strata, these dates for the excavation spits provide maximum ages only. The right petrous portions of two individuals (KNM KX 4/5/6 and 7/8) were sampled for ancient DNA analysis in 2017; one sample has produced a direct date which we report below.

As all the burials lack provenience information, individuals were anatomically associated. Age, sex, and metric analyses for all remains were organized by the individual, and the metric comparisons were focused on the crania and dentition (Tables S1–S6). Skeletal fragments from the NMT have not been matched to an individual (Table S7). Dental wear was scored for the adults using the Scott (1979) system that assessed dentine exposure on each molar cusp. Dental wear scores were summed to calculate a wear score for each individual (Table S8). Age was determined for all skeletal material using a combination of dental eruption, suture fusion, and closure of skeletal growth plates (Buikstra & Ubelaker, 1994; Cunningham et al., 2016; Ubelaker, 1989; Table S9). Sex was determined for the adult material on the ossa coxae using the Phenice (1969) scoring of the ventral arc, subpubic concavity, and ischiopubic ramus ridge, as well as differences in the greater sciatic notch and preauricular sulcus (Buikstra & Ubelaker, 1994). Sex differences in adult skull morphology were determined by scoring the nuchal crest, mastoid process, supraorbital margin, glabella, and mental eminence (Acsadi & Nemeskeri, 1970; Table S10). Sex was not determined for the juvenile remains. Stature estimations for the adults were recorded using measurements from the calcaneus and talus (Holland, 1995; Table S11).

2.3 | Comparative populations

Cranial metrics from KNM-KX 2, the only complete undistorted skull, were compared to published data from 476 adults from five recent African populations: the San (*n* = 82) and Zulu (*n* = 101) from southern Africa, the Taita (*n* = 83) from Kenya, a sample from Egypt (*n* = 111), and the Dogon (*n* = 99) from Mali (Howells, 1973, 1989, 1995; https://web.utk.edu/~auerbach/HOWL.htm). The individuals from Howells' dataset were also compared to a sample of 48 African Holocene adults divided into early Holocene LSA (~10.0–4.0 ka; *n* = 7) and Pastoral Neolithic (~3.5–2.0 ka; *n* = 41) groups (Angel et al., 1980; Bräuer, 1983; Gabel, 1965; Leakey, 1935, 1942, 1950; Merrick & Monaghan, 1984; Prendergast et al., 2014; Tables S12 and S13). The early Holocene/LSA individuals are geographically, temporally, and culturally diverse but are all associated with hunting-fishing-gathering lifeways, including ceramic-using Kansyore foragers who may have interacted with food producers (Dale & Ashley, 2010). The Pastoral Neolithic individuals represent specialized pastoralists found throughout the Central Rift of Kenya and Tanzania who are divided based on material culture among other factors into at least two cultural traditions, the Elmenteitan and Savanna Pastoral Neolithic, but are genetically closely related (Prendergast et al., 2019). All measurements for the African Holocene comparative sample were collected from the literature. Early pastoralist (~5.0–4.0 ka) comparative samples were too fragmented for inclusion in the cranial analyses. Cranial measurements were also recorded from the KNM-KX 1 skull but excluded from the analyses because of asymmetry (detailed below; Table S14).

Dental metric analyses were undertaken using a sample of 158 African Holocene adults divided into early Holocene/LSA (~10.0–4.0 ka; *n* = 37), early pastoralist (~5.0–4.0 ka; *n* = 32), and Pastoral Neolithic (~3.5–2.0 ka; *n* = 89) groups (Ambrose, 1986; Angel et al., 1980; Barthelme, 1985; Biittner et al., 2017; Brown, 1966; Coon, 1971; Hildebrand & Grillo, 2012; Hildebrand et al., 2018; Ikeda and Hayama, 1982; Leakey, 1935, 1966; Leakey et al., 1943; Leakey & Leakey, 1950; Merrick & Monaghan, 1984; Nelson, 1995; Phillipson, 1977; Prendergast et al., 2019; Rightmire, 1975; Robertshaw et al., 1983, 1991; Sassoon, 1968; Sawchuk, 2017; Sawchuk & Willoughby, 2015; Sawchuk et al., 2019; Schepartz, 1987; Siiriäinen, 1977; Stiles & Munro-Hay, 1981; Wandibba, 1983; Wang et al., 2020; Table S12). The dental comparative dataset includes an early pastoralist group representing the first herders in eastern Africa who lived around Lake Turkana, northern Kenya and pursued a mixed economy of fishing and herding and possessed novel lithic, ceramic, and mortuary traditions (Hildebrand et al., 2018; Sawchuk et al., 2019). Dental metric data were recorded by one author (Sawchuk) at the National Museums of Kenya and Turkana Basin Institute (Turkwel facility) in Kenya, the National Museum and House of Culture in Tanzania, Harvard University's Peabody Museum of Archaeology and Ethnology and the National Museum of Natural History in the United States, and the Duckworth Laboratory at the University of Cambridge in England. The adult dentition from KNM-KX 1, KNM-KX 2, and KNM-KX 4/5/6 were included in the dental comparative analyses (Table S15).

2.4 | Kisese II craniodental metric analyses

A series of 49 measures were recorded from the KNM-KX 1 and KNM-KX 2 crania, most following Howells (1973, 1989, 1995). Given the fragmentary nature of the Holocene sample, the comparative analyses focused on nine of the Howells measurements: basion-nasion length (BNL), biauricular breadth (AUB), bizygomatic breadth (ZYB), glabello-occipital length-(GOL), maximum cranial breadth (XCB), minimum cranial breadth (WCB), nasal breadth (NLB), nasal height (NLH), and orbit height (OBH; Table S14). Unilateral measurements were recorded on the left side, but the right side was substituted if measurements on the left side were not possible. Males and females were analyzed together to increase the Holocene sample size and because sex determination for KNM-KX 1 and KNM-KX 2 is not definitive. Some measures for the comparative sample were approximated due to preservation (as described in Angel et al., 1980; Bräuer, 1983; Leakey, 1935).

Maximum mesiodistal and buccolingual measures were recorded from all teeth using standard sliding calipers. Third molars were excluded from the analyses due to high variability. Measurements were not recorded for worn teeth (wear ≥ stage 4, per Smith, 1984) or when affected by calculus, debris, or consolidant. Marginally chipped, broken, and reconstructed teeth were recorded when the damage did not affect the specific measurement taken. Analyses were performed on left teeth, with right antimeres substituted in for missing data wherever possible, and males and females were analyzed together. Dental nonmetric analyses that include the Kisese II dentition are reported elsewhere (Sawchuk, 2017), and adult postcranial measurements are not analyzed (except for stature) but provided in Table S16.

All analyses were performed in R (R core team, 2017). Group variance and normality were tested for the cranial and dental metric data using Bartlett's and Shapiro–Wilk's tests. While all measures passed

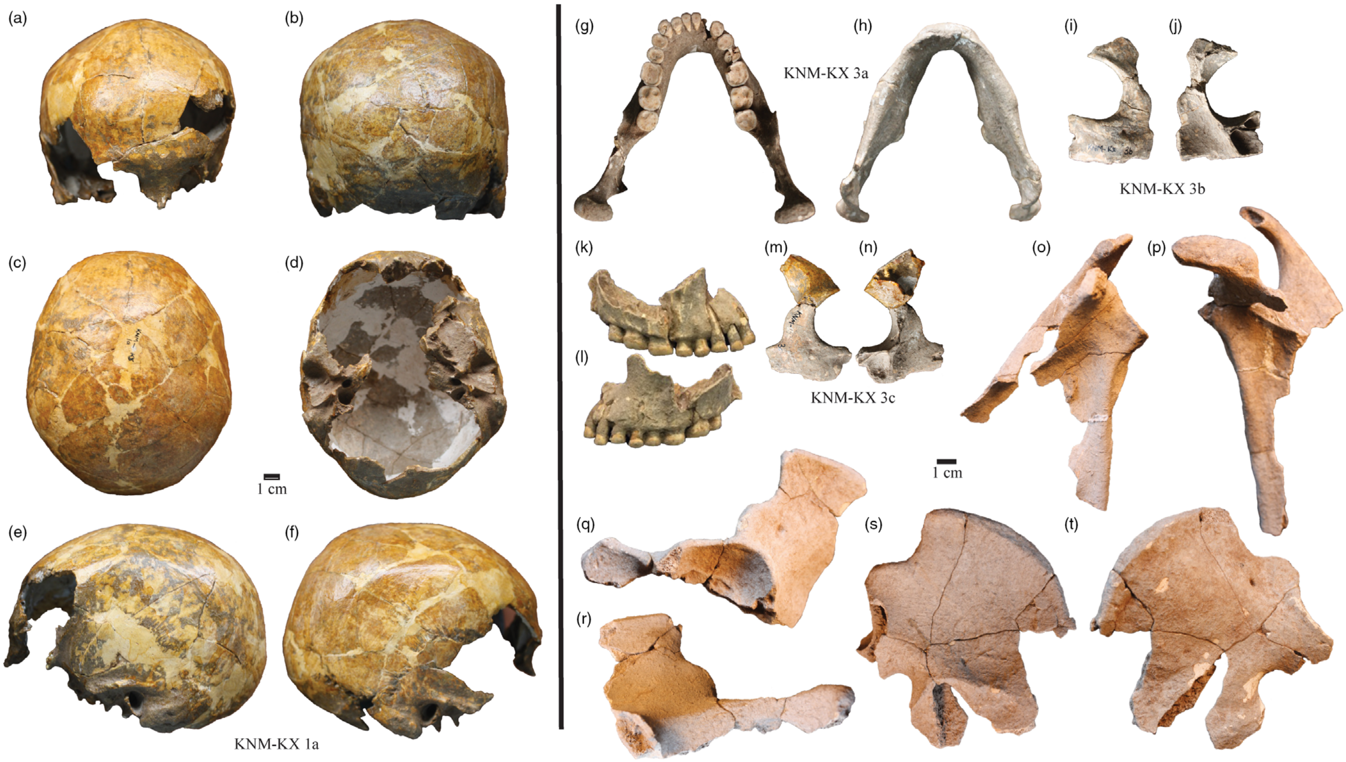

FIGURE 2 Cranial remains of KNM-KX 1. The cranium is shown in (a) anterior, (b) posterior, (c) superior, (d) inferior, (e) left lateral, and (f) right lateral views. The mandible is shown in (g) superior and (h) inferior views. Left (i and j) and right (m and n) zygomatic fragments, with some frontal and maxilla, are shown in anterior and posterior views. Right (k) and left (l) maxillary fragments are shown in lateral view. Right (o) and left (p) scapulae are shown in posterior view. The left (q and r) and right (s and t) ossa coxae are shown in medial and laterial views. The maxillae, scapula, and ossa coxae are not numbered

Bartlett's tests (all $p > 0.05$), some measures were not normally distributed and groups' sample sizes were not equal. We used non-parametric Kruskal-Wallis tests to determine whether dental and cranial measurements differed between groups. Pairwise comparisons between groups were performed using post hoc Dunn tests with a Bonferroni correction for multiple comparisons in the R package "dunn.test" (Dinno & Dinno, 2017). Significance for all analyses was set at 0.05.

3 | RESULTS

Analyses of the Kisese II rockshelter burials suggest a minimum number of six individuals (Tables S1–S6). The KNM Kisese II collections were commingled, and individuals were sorted anatomically. None of the individuals were mineralized, and the physical condition of the specimens were similar to that of the fossil fauna found throughout the stratigraphic sequence. None of the individuals had anatomical features that fell outside the range of modern African diversity.

3.1 | Preservation

KNM-KX 1 consists of a partial skull and postcranial elements (Figure 2; Table S1). Fragments of cranium KNM-KX 1a had been previously reconstructed using plaster and consolidant resulting in artificial cranial deformation and asymmetry. For example, the right zygomatic/frontal fragment KNM-KX 3c can be rearticulated at the frontal, but the inferior border of the zygomatic touches the petrous portion of the temporal. This suggests the cranium has been compressed anteroposteriorly. The mediolateral reconstruction appears to be more accurate in that the right and left parietal bosses and changes in the temporal lines occur approximately in the same coronal planes. Mandible KNM-KX 3a is well preserved with full adult dentition missing only the coronoid processes, a small portion of the right gonial angle, the right second incisor and alveolus, and the crown of the right fourth premolar. The mandibular rami have been fragmented and reconstructed. The mandible occludes with the two maxillary fragments preserving full adult dentition. Both the mandibular and maxillary dentition have similar wear with high dentin exposure (Table S8). Several postcranial elements with similar preservation and coloration are associated with KNM-KX 1.

KNM-KX 2 is well preserved with a complete skull missing only a few teeth (Figure 3; Table S2). The teeth have a lower degree of dental wear compared to KNM-KX 1 (Table S8). The postcrania are also well preserved although missing elements. The distal left second rib of KNM-KX 2 is enlarged due to osteomyelitis and includes a cloaca (5.82 mm in diameter). A lower right rib also shows pathological changes associated with osteomyelitis. The shape of the rib deviates

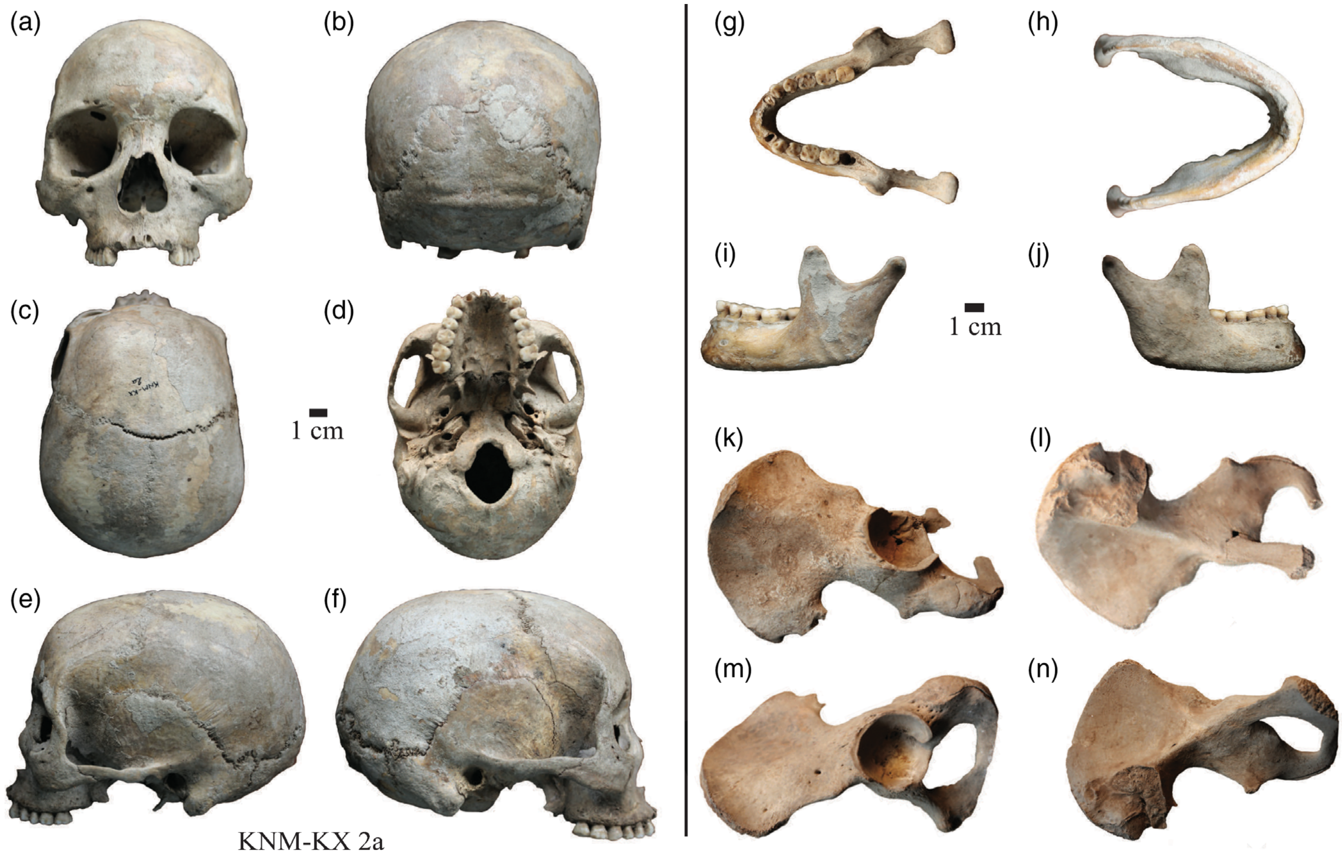

FIGURE 3 Cranial remains associated with KNM-KX 2. The cranium is shown in (a) anterior, (b) posterior, (c) superior, (d) inferior, (e) left lateral, and (f) right lateral views. The mandible is shown in (g) superior, (h) inferior, (i) left lateral, and (j) right lateral views. The right and left ossa coxae are shown in (k and m) medial and (l and n) lateral views. The mandible and ossa coxae are not numbered

to arch medially and the pleural surface of the rib is uneven. Bone around this area is smooth indicating that the changes occurred prior to death. This rib also exhibits a series of broad shallow parallel marks that differ in coloration from the rest of the bone and likely occurred postmortem.

KNM-KX 4/5/6 had dark brown/orange staining around the lambdoidal suture and on most of the occipital. Importantly, there are two associated basiocciputs of similar developmental age indicating that there are at least two individuals associated with KNM-KX 4/5/6 (Table S3). Both basiocciputs lack fusion of the lateral portions (partes lateralis), and the pars lateralis (shown in Figure S1E and S1F) has been glued to the pars basilaris. It is possible one of the basiocciputs associated with KNM-KX 4/5/6 belongs to KNM-KX 10, as this individual is also dentally less than 5 years of age (Table 1). Dental wear was scored for the adult dentition (Table S8).

KNM-KX 7/8 has not undergone reconstruction and some elements, for example KNM-KX 8a, indicate post-depositional deformation (Table S4). A gray matrix is adhering to the posterior aspects of the mandible, and a nodule of this matrix is present on the lingual aspect of the mandibular ramus. The mandible was fractured at the symphysis, and the halves have been glued.

KNM-KX 9 consists of a partial cranial vault and separate right and left petrous portions of the temporal bones (Table S5). A dark brown matrix is present on the cranium and petrous bones and the cranium has white etching on the left and right parietals. The left frontal bone of KNM-KX 9 exhibits partially healed cranial trauma 4.17 mm in diameter (Figure S3C).

KNM-KX 10 consists only of maxillae and a mandible preserving some of the dentition (Table S6). The mandible has been fractured in two locations and refit. Individuals KNM-KX 9 and KNM-KX 10 do not preserve any overlapping elements, and it is possible these elements belong to the same individual. However, the cranium of KNM-KX 9 is larger than KNM-KX 4/5/6, which has a similar age estimate as KNM-KX 10 (Table 1).

3.2 | Chronological dates of the specimens

Most of Inskeep's notes associated with the site have been lost, and thus our reconstructions of the age, depth, and archeological associations of the human remains are incomplete. We know the following: (1) The site was excavated to a depth of ~6 m without reaching bedrock. (2) Excavation was done in arbitrary "spits" or levels that were assigned Roman numerals from the top downward. These horizontal spits were ~15 cm thick, except for the uppermost spits, with spit I ~59 cm thick and spit II ~0.21 cm thick. (3) A series of 29 radiocarbon

TABLE 1 Summary of aging methods and estimates for the Kisese II individuals

	Dental aging[a]	Epiphyseal fusion[b]	Cranial suture closure[c]	Pubic symphysis[d]	Auricular surface[e]	Pubic symphysis[f]	Composite age
KNM KX 1/3	21+		35–43	Phase 4/5: 25–30	Phase 3/4: 30–39	Phase 3 male-ventral rampart completing, smooth symphysis face, no lipping on margin, and gap on the ventral surface.	25–43
KNM KX 2	21+	Sphenoccipital synchondrosis: 19–25; Ischial tuberosities: 17–19	<18	Phase 1:18–19	Phase 2: Age 25–29.	Phase 1-female-billowy surface composed of ridges. The upper and lower extremities are not defined.	18–25
KNM-KX 4/5/6	5y – +16mo	Basiocciput: <5; Left and right humerus: <11 (male)					3–5
KNM-KX 7/8	2y – +8mo	Basiocciput: <5; Humerus: <10; Scapula: <14					2y ± 8mo
KNM-KX 9			<20				<20
KNM-KX 10	3y – +12mo						3y ± 12mo

[a]Ubelaker (1989).
[b]Buikstra and Ubelaker (1994).
[c]Meindl and Lovejoy (1985).
[d]Todd (1921a, 1921b).
[e]Lovejoy et al., 1985; Meindl and Lovejoy, 1985; Bedford et al., 1989.
[f]Brooks and Suchey (1990).

dates spanning ~4–47 ka on ostrich eggshell fragments from the site provides a basic chronological framework for the upper 3 m of the sequence (Tryon et al., 2018). (4) The lower part of the archeological sequence can be broadly attributed to the Middle Stone Age, with a shift to technologies typical of LSA foragers occurring in spits XVII–XI dated to ~40–34 ka. While understudied at present, the youngest spits I and II include a range of ceramic types, diminutive backed microliths of non-local obsidian, and evidence for iron production. Material culture is consistent with occupation of the site by populations of foragers who used ceramics (perhaps with Kansyore affinities), pastoralists (broadly attributed to the Pastoral Neolithic), and iron-equipped agricultural groups beginning in the mid-to-late Holocene, broadly within the last 5 ka (Inskeep, 1962; Leakey, 1983; Tryon et al., 2018). The age of the youngest radiocarbon-dated ostrich eggshell fragment at ~4 ka almost certainly does not record the age of the last use of the shelter. (5) Ochre that may have been used in painting the rock walls is found throughout the excavation, but clear evidence for the age of the rock art at the site is found only at the interface of spits I–II, where a buried painted slab that could be fitted back onto the wall of the shelter was recovered (Inskeep, 1962).

For the burials, Inskeep was inconsistent in his use of Roman or Arabic numerals. It is reasonable to assume that they were numbered as they were found, and it may be that burial number correlates with depth, although this is unconfirmed. Handwritten notes in the NMK (presumably from Inskeep) suggest that burial 5 is KNM-KX 10. Photographs and stratigraphic profiles from Inskeep's archives allow us to confidently reconstruct the depth and location only for burial III/IV (found in spit VII). These photographs depict the remains of at least three individuals, of which two were buried on their side in a flexed position (Figure 1). These photographs suggest Inskeep's burial III/IV corresponds with KNM-KX 9 and possibly KNM-KX 1. Inskeep's photos show skeletal elements (such as a humerus and femur) that were not present in the KNM and NMT Kisese II collections at the time of study (2014 and 2015). As with much of the non-human fossil fauna (Ranhorn et al., n.d. [in review]; Tryon et al., 2019), substantial portions of the collection recovered in 1956 are no longer available for study. The finds recovered during faunal analysis that are now in Dar es Salaam do have stratigraphic levels associated with them, and these suggest that human remains at the site are found as deep as spit XIV, some 1.8 m below the 1956 surface of the site. As noted above, we assume that all of the burials are intrusive from upper layers, and the depths where they were found do not correspond with age, but rather provide a maximum age for the time of the burial.

Burials III/IV and 7 were each associated with ostrich eggshell beads in the NMK. Ostrich eggshell bead size decreases with time at Kisese II (Tryon et al., 2018), providing a potential relative dating tool for these individuals. The beads from burial III/IV are smaller than those from burial 7 as expected given the higher stratigraphic position of burial III/IV. Comparison of bead size suggests that beads with both burials are larger than those above spit VII (Ranhorn et al., n.d.

[in review]). However, as we cannot rule out the possibility that these beads were simply fill from the surrounding sediment rather than grave goods associated with the actual burial, a Pleistocene age remains an unconfirmed possibility.

Given all these uncertainties, direct dates on the Kisese II individuals are paramount for determining the antiquity of human remains at the site. Due to the delicacy of the collection, only pilot destructive sampling was allowed. The petrous portion associated with KNM-KX 4/5/6 produced a date of 6210 ± 30 radiocarbon years before present (PSUAMS-4718). Following the recommendations of Hogg et al. (2020) and using the method reported by Tryon et al. (2018) for sub-equatorial tropical regions, we calibrated the radiocarbon date using a mixed model that incorporated data from both the northern and southern hemispheres, using OxCal 4.4 software (Ramsey, 2009) and the IntCal20 calibration curves (Hogg et al., 2020; Reimer et al., 2020). The resultant estimated age range for the KNM-KX 4/5/6 individual is 7239–6985 cal yr BP at the 95% confidence interval. This is the first radiocarbon date on human remains from the site and establishes an early Holocene/LSA antiquity for at least one of the burials and potentially others.

3.3 | Age

KNM-KX 1: The mandible and maxilla preserve fully erupted adult dentition. Age was assessed using the closure and fusion of cranial sutures indicating an age range of 35–43 years (Buikstra & Ubelaker, 1994; Meindl & Lovejoy, 1985). The pubic symphysis corresponded with Phase 4/5 and an age range of 25–30 years. Similarly, the auricular surface was estimated to be Phase 3/4 and an age range of 30–39. KNM-KX 1 has an estimated age range of 25–43 years.

KNM-KX 2: Cranial and postcranial remains of KNM-KX 2 are well preserved. Adult mandibular and maxillary dentition are fully erupted with occlusal wear. The spheno-occipital synchondrosis is partially fused indicating an age of 18–24 or potentially younger (Cunningham et al., 2016). Age was also assessed using cranial suture closure (following Buikstra & Ubelaker, 1994; Meindl & Lovejoy, 1985), and KNM-KX 2a was assessed to have no suture closure corresponding with an age of less than 18 (Table S9). Age was assessed from right os coxae using three methods. Secondary ossification centers on the iliac crest and the ischial tuberosity are partially fused indicating an age range from 14 to 22 years (Buikstra & Ubelaker, 1994). An age range of 18–19 was estimated from the pubic symphysis of the left os coxae (Table 1; Brooks & Suchey, 1990; Katz & Suchey, 1986; Todd, 1921a, 1921b). The auricular surface corresponded with Phase 1–2 and an age estimate ranging from 20 to 29 years (Bedford et al., 1989; Lovejoy et al., 1985). Collectively, age estimates for KNM-KX 2 range from 18 to 29 years but a younger range of 18–25 is more likely based on the lack of fusion of the spheno-occipital synchondrosis.

KNM-KX 4/5/6: The mandible (KNM-KX 6a/6b) preserves the fully occluded and worn deciduous first and second molars as well as the crown of the adult right canine, the adult left first incisor, and a crypt for the left adult second molar (Figure S1). Based on the available dentition, this eruption pattern is most similar to individuals aged 5 years ±16 months (Ubelaker, 1989). There are two basiocciputs associated with this individual, but they both lack fusion of the lateral portions (partes lateralis) suggesting an age of less than five (Cunningham et al., 2016). No postcranial elements have any epiphyseal fusion. Of the available elements, Buikstra and Ubelaker (1994) indicates that humeral distal epiphyseal fusion in males occurs first indicating that KNM-KX 4/5/6 is less than age 11. Taken together, the cranial and postcranial evidence suggests KNM-KX 4/5/6 is between three and 5 years of age.

KNM-KX 7/8: All deciduous teeth were erupted except for the canines and second deciduous molars that were partially erupted (Figure S2). First adult molar crown was forming in the crypt. This pattern of dental eruption most closely aligned with individuals aged 2 years ± 8 months (Ubelaker, 1989). The basiocciput (pars basilaris) associated with this individual was unfused from the lateral portions (partes lateralis) suggesting an age of less than five (Cunningham et al., 2016). The two postcranial elements, a partial right humerus and a left scapula, show no epiphyseal fusion suggesting ages of less than 10 and 14, respectively. Individual KNM-KX 7/8 is likely aged 2 years ± 8 months.

KNM-KX 9: Age was not easily assessed for KNM-KX 9 because of the relative paucity of materials (Figure S3). The coronal suture does not show any age-related closure suggesting the individual was 20 years old or younger (Meindl & Lovejoy, 1985). Specimen KNM-KX 9a/8c preserves the left portion of the sagittal suture posterior to bregma but the degree of closure cannot be assessed. Age was not estimated from the petrous fragments.

KNM-KX 10: All visible deciduous mandibular and maxillary dentition were fully erupted and the crown of the first adult molars are visible in their crypts (Figure S4). Using Ubelaker (1989), age of KNM-KX 10 was estimated as 3 years ±12 months.

3.4 | Sex

Sex was determined for the two adult individuals, KNM-KX 1 and KNM-KX 2, from the skull and os coxae (Table 2). We did not assess sex for the juvenile individuals.

KNM-KX 1: Sex was estimated from the skull using scoring detailed in Acsadi and Nemeskeri (1970). Scoring of the nuchal crest and glabella was ambiguous, and the mastoid process and mental eminence were possibly female. The supraorbital margin was not scored. Sex for the skull was indeterminate. On the os coxae, the ventral arc, subpubic concavity and medial ridge were not preserved. The greater sciatic notch was scored on the right os coxae fragment as narrow indicating male, and a preauricular sulcus was absent suggesting the individual is male (Karsten, 2018). Individual KNM-KX 1 is possibly male.

KNM-KX 2: Sex determination from the skull followed Acsadi and Nemeskeri (1970). The nuchal crest, supraorbital margin, and mental eminence were ambiguous, but the left mastoid process and glabella trended toward female. Sex from the skull is possibly female. The ventral arc, subpubic concavity and the medial ridge were scored on the left os coxae as possibly males (Table 2). The greater sciatic notch was

TABLE 2 Summary of methods and estimates of sex for the Kisese II individuals

	Skull morphology[a]	Subpubic region[b]	Greater sciatic notch[c]	Preauricular sulcus[d]	Sex determination
KNM KX 1/3	Indeterminate	-	Narrow notch: 5; M	Absent: 0, M	Possibly male
KNM KX 2	F?	Ventral arc: 2; Subpubic concavity: 3; Ischiopubic ramus: 3; M?	Wide notch: 2; F?	Wide sulcus: 2	Possibly female

[a]Acsadi and Nemeskeri (1970).
[b]Phenice (1969).
[c]Walker (2005).
[d]Karsten (2018).

wide indicating female, and a wide preauricular sulcus was present. Individual KNM-KX 2 is possibly female.

3.5 | Stature

Despite their presence in photos from the excavation, no adult long bones were found in the Kisese II collections at NMK or NMT. Stature estimates for the adults were based on measurements of the calcaneus and talus for African-American females and males (Holland, 1995). These measures suggest an average stature of 167.86 (±5.38) cm, a minimum stature of 154.45 cm, and a maximum stature of 172.28 cm for the individual labeled KNM-KX 1 (Table S11). The burial labeled KNM-KX 2 had an average stature of 167.79 (±5.57), a minimum stature of 154.00 cm, and a maximum of 173.22 cm (Table S11).

3.6 | Comparative cranial metric analyses

Cranial measurements from KNM-KX 2 were compared to early Holocene/LSA (~10.0–4.0 ka), Pastoral Neolithic (~3.5–2.0 ka), and modern African groups (Figure 4). The nine cranial measurements included in the comparative sample varied significantly across the population groups (Kruskal-Wallis: χ^2 = 51.96–202.27, $df = 7$, $p < 0.01$). Pairwise tests were not used for the cranial metric analyses because the Kisese II sample only consisted of one individual. The Taita, Early Holocene/LSA, Pastoral Neolithic, and KNM-KX 2 all had a similar ratio of maximum cranial breadth and length compared to the other modern African populations. Dimensions of the nasal aperture for KNM-KX 2 were smaller than most of the modern African populations but overlapped with Egyptian individuals. Kruskal-Wallis tests for all cranial measurements across individual sites within the early Holocene/LSA and Pastoral Neolithic samples were not significant (all $p > 0.05$).

3.7 | Comparative dental metric analyses

Although there was overlap between groups, most mesiodistal and buccolingual measures varied chronologically such that the early Holocene/LSA (~10.0–4.0 ka) individuals had the largest teeth followed by early pastoralists. The smallest teeth are found in the Pastoral Neolithic (~3.5–2.0 ka) sample (Figure 4). With the exception of the mesiodistal length of the upper canine and lower second incisor, there were no significant differences in measurements for the incisors and canines. Dental measures varied significantly for upper third and fourth premolar mesiodistal length and the upper fourth premolar buccolingual width (Kruskal-Wallis: χ^2 = 16.00–9.52, $df = 3$, $p < 0.02$). Only buccolingual width of the lower third premolar varied significantly in the lower premolars ($\chi^2 = 10.00$, $df = 3$, $p = 0.02$). However, pairwise group comparisons for the premolars indicated the Kisese II samples did not significantly differ from the other groups (all $p > 0.05$).

Buccolingual and mesiodistal measures from the upper and lower first and second molars significantly differed across groups (χ^2 = 11.52–24.48, $df = 3$, $p < 0.01$), with the exception of mesiodistal length of the upper first molar ($\chi^2 = 1.37$, $df = 3$, $p = 0.71$). The Kisese II upper first molar buccolingual width was significantly smaller than the early Holocene/LSA ($p = 0.02$) and early pastoralist ($p = 0.01$) samples but did not differ from the Pastoral Neolithic group ($p = 0.42$). Pairwise comparisons suggest the Kisese II dentitions did not differ from the other groups for the upper second molar buccolingual and mesiodistal measurements (both $p > 0.05$). Pairwise comparisons indicate the Kisese II buccolingual measurements for the first and second lower molars were significantly smaller than the early Holocene/LSA group (LM1 $p = 0.05$; LM2 $p = 0.03$).

4 | DISCUSSION AND CONCLUSIONS

Kisese II rockshelter has yielded artifacts and faunal remains that span much of the Late Pleistocene and Holocene and document a number of archeological transitions in eastern Africa (Ranhorn et al., n.d. [in review]; Tryon et al., 2018). Here we provide the first descriptions of the human remains found at the site, which represent at least six individuals encompassing both sexes and ranging in age from young children to middle-aged adults. It is important to stress that we have adopted as an initial approach one that emphasizes morphology and comparison at the population level rather than one that seeks to understand the lived experiences of those buried at Kisese II. Given the history and nature of this legacy skeletal collection, our first goal

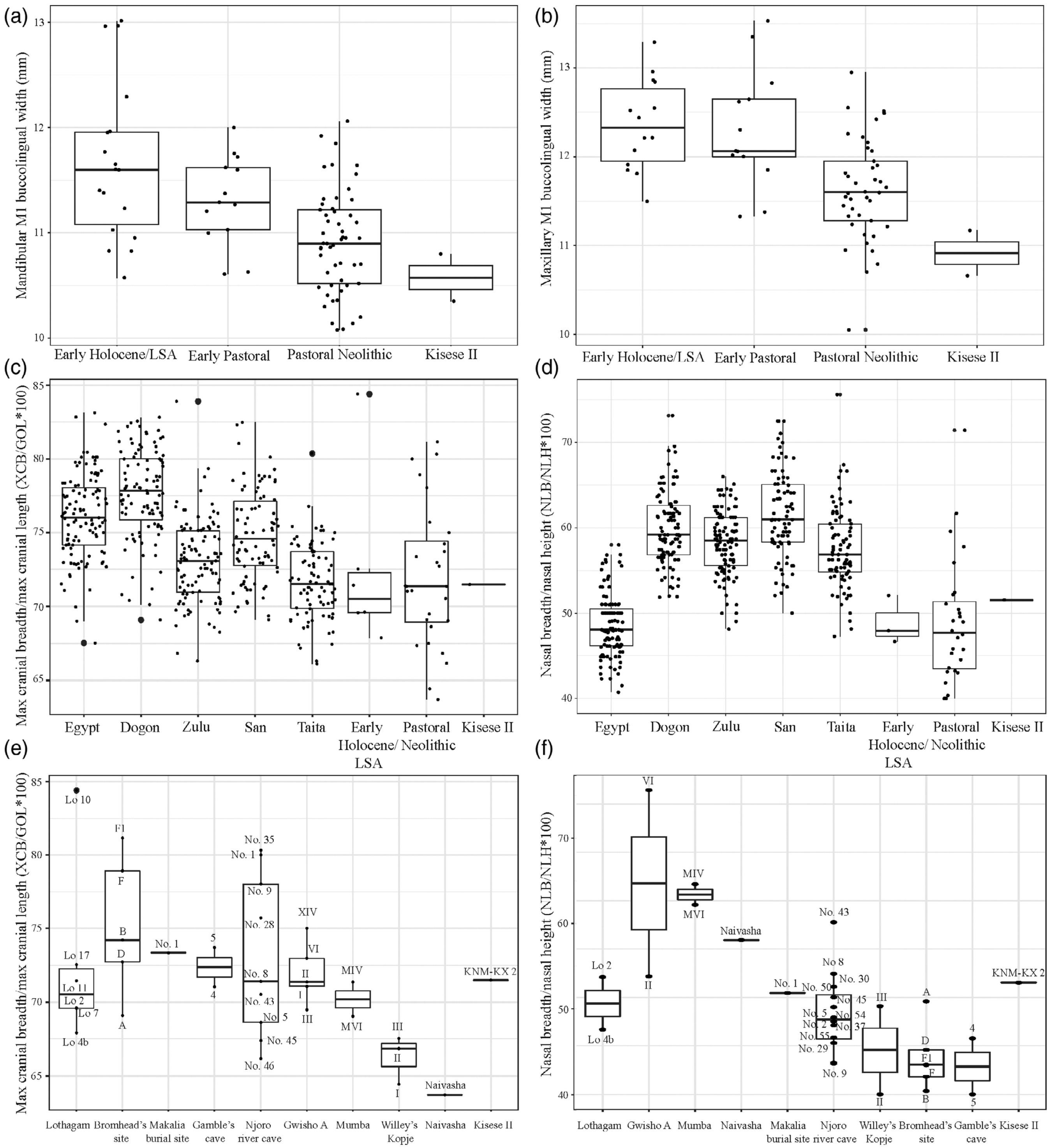

FIGURE 4 Cranial and dental metric comparisons. Boxplots showing mandibular (a) and maxillary (b) buccolingual widths. Boxplots of the ratio of maximum cranial breadth to length (c) and nasal breadth to length (d). Boxplots showing the ratios maximum cranial breadth to length (e) and nasal breadth to length (f) in the early Holocene later stone age (LSA) and pastoral Neolithic samples. For all plots, the upper and lower bound of the boxes corresponds with the 25th and 75th percentiles and the whiskers extend 1.5 times the interquartile range in either direction. The median is represented by a horizontal line inside the boxes

is to describe individuals excavated more than 50 years ago who have largely been forgotten since. Future archival work, stratigraphic and contextual information from renewed excavations at Kisese II, and other approaches (e.g., isotopic analyses and/or studies of dental calculus and ancient DNA) may well provide a more nuanced understanding of these early occupants of the Kondoa region.

Our results indicate that individuals buried at Kisese II significantly expand the range of morphological variation of eastern African human populations during the Holocene and perhaps Late Pleistocene. Our interpretations are necessarily tempered by two limitations: (1) With the exception of KNM-KX 4/5/6 at ~7.1 ka, the Kisese II individuals as yet lack firm relative or chronometric dates and cannot be demonstrably associated with particular artifact types. (2) Photos from Inskeep's excavations show that adult long bones were present at the time of excavation, but these elements have been subsequently lost. The collection available for study is therefore only a portion of what was recovered in 1956. This is, unfortunately, a pattern characteristic of much of the Kisese II assemblage as a whole (detailed in Tryon et al., 2019).

These same archival photographs do, however, indicate that at least two individuals were buried on their side in a flexed position. Flexed burial postures date to ~15 ka in Tanzania with the oldest evidence from Mlambalasi in the Iringa region ~350 km to the south (Sawchuk & Willoughby, 2015), and are noted at the closer (~80 km) site of Mumba (Bräuer, 1980). Ostrich eggshell beads were also present in levels associated with the burials at all three sites (Biittner et al., 2017; Bushozi, 2020; Mehlman, 1979; Tryon et al., 2018). Evidence from Kisese II may reflect a shared mortuary behavior in the region.

Craniodental comparisons highlight similarities between the Kisese II sample and eastern African Pastoral Neolithic groups. The Kisese II deposits suggest discontinuous human occupation over at least the last 47 ka, occupied by populations using stone, ceramic, and iron technologies that hunted but who used domestic stock (e.g., sheep or goat) at least occasionally (Tryon, 2019). We cannot associate individual burials with particular technologies or archeological entities, but comparison of the date of ~7.1 ka for KNM-KX 4/5/6 with established regional chronologies firmly indicates that this individual antedates the introduction of either domestic stock or iron into the region, and can instead be associated with either aceramic or potentially ceramic (cf. Kansyore) LSA foragers (reviewed in Mehlman, 1979; Prendergast et al., 2014). With a date of ~7.1 ka, dental measurements of KNM-KX 4/5/6 are expected to be most similar to the early Holocene comparative sample. However, buccolingual and mesiodistal dental measures of KNM-KX 4/5/6, as well as KNM-KX 1 and KNM-KX 2, were closest to the Pastoral Neolithic sample, broadly dated from 4–1.5 ka (Figure 4). This suggests the individuals from Kisese II had relatively smaller dentitions than early Holocene foragers, but similar to those of early pastoralist and Pastoral Neolithic eastern Africans. If KNM-KX 1 and KNM-KX 2 are substantially younger than KNM-KX 4/5/6, the Kisese II samples would imply the relative persistence of small teeth at the site across the Holocene.

Our findings contribute to a growing body of evidence that suggests that human skeletal remains from the Late Pleistocene and early Holocene in eastern Africa exhibit relatively high amounts of morphological diversity (Crevecoeur et al., 2009; Crevecoeur et al., 2016; Grine et al., 2007; Mounier et al., 2018; Stojanowski, 2014). Compared to other eastern Africans, KNM-KX 2 had a similar cranial breadth and length, but relatively small dentition, and a relatively large nasal aperture. While our analyses of cranial metrics were limited by the presence of only one comparable adult cranium, KNM-KX 2 was within the range of variation of modern Africans and overlapped with the early Holocene and Pastoral Neolithic comparative samples. Of note, KNM-KX 2 differed from the burials at the nearby site of Mumba, particularly in nasal dimensions. These results suggest that KNM-KX 2 differs morphologically from chronologically and geographicallysimilar sites. These analyses highlight variation in Late Pleistocene-early Holocene humans and may indicate that LSA eastern African foragers possibly exhibited greater morphological variation relative to contemporary Africans. These results mirror high levels of material cultural variation observed among LSA sites and potentially support interpretations of increasing regionalization seen in the archeological record (for discussion, see Tryon & Faith, 2013; Tryon & Ranhorn, 2020; Wilshaw, 2016).

Individuals buried at Kisese II provide an opportunity to explore human regional variation during the Holocene and potentially the Late Pleistocene. Collectively, our metric analyses suggest (1) substantial variation in craniodental morphology among Holocene and possibly Late Pleistocene eastern African populations, but also (2) morphological similarity at localized sites like Kisese II during the Holocene. Continued exploration of Kisese II's archival and excavated materials will improve not only our understanding of the burials' archeological context at the site, but also regional variation in human morphology and behavior in eastern Africa among LSA sites. Future research that combines morphological data with other lines of evidence, such as regional differences in how stone or ceramic artifacts were made and used (Ashley & Grillo, 2015; Seitsonen et al., 2013; Wilshaw, 2016), patterns of long distance raw material exchange (e.g., Frahm & Tryon, 2018; Mehlman, 1989; Prendergast et al., 2013), burial practices, and aDNA recovery (Prendergast et al., 2019; Wang et al., 2020), has immense potential for reconstructing complex social interactions during this time in the African past.

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AUTHOR CONTRIBUTIONS

Myra F. Laird: Conceptualization; data curation; formal analysis; investigation; methodology; writing-original draft; writing-review & editing. **Elizabeth Sawchuk:** Data curation; funding acquisition; investigation; resources; writing-original draft; writing-review & editing. **Amandus Kwekason:** Project administration; resources; writing-review & editing. **Audax Mabulla:** Project administration; resources; writing-review & editing. **Emmanuel Ndiema:** Resources; writing-review & editing. **Christian Tryon:** Conceptualization; funding acquisition; investigation; project administration; resources; writing-original draft; writing-review & editing. **Jason Lewis:** Conceptualization; funding acquisition; project administration; resources; writing-review & editing. **Kathryn Ranhorn:** Project administration; writing-review & editing; resources; funding acquisition.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dental comparative data in this study are available from the corresponding author upon reasonable request. All other data to support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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