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Iron Age hunting and herding in coastal eastern Africa: ZooMS identification of domesticates and wild bovids at Panga ya Saidi, Kenya

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ABSTRACT

The morphological differentiation of African bovids in highly fragmented zooarchaeological assemblages is a major hindrance to reconstructing the nature and spread of pastoralism in sub-Saharan Africa. Here we employ collagen peptide mass fingerprinting, known as Zooarchaeology by Mass Spectrometry (ZooMS), coupled with recently published African ZooMS reference datasets, to identify domesticates and wild bovids in Iron Age assemblages at the cave site of Panga ya Saidi in southeast Kenya. Through ZooMS we have identified all three major African livestock—sheep (*Ovis aries*), goat (*Capra hircus*) and cattle (*Bos taurus*)—at the site for the first time. The results provide critical evidence for the use of domesticates by resident foraging populations during the Iron Age, the period associated with the arrival of food production in coastal Kenya. ZooMS results show that livestock at Panga ya Saidi form a minor component of the assemblage compared to wild bovids, demonstrating the persistence of hunting and the secondary role of acquiring livestock in hunter-gatherer foodways during the introduction of agro-pastoralism. This study sheds new light on the establishment of food production in coastal eastern Africa, particularly the role of interactions between hunter-gatherers and neighbouring agro-pastoral groups in what was a protracted regional transition to farming.

1. Introduction

The spread of food production in sub-Saharan Africa was a complex and multi-faceted process that transpired on regional scales at different times and likely involved a range of cultural and demographic processes including migration, diffusion, interaction and innovation (e.g., Marshall and Hildebrand, 2002; Kusimba and Kusimba, 2005; Boivin et al., 2013; Shipton et al., 2013; Gifford-Gonzalez, 2017; Crowther et al., 2018; M'Mbogori, 2018; Wang et al., 2020). Following the introductions of food production (herding and subsequently farming) into eastern and, later, southern Africa, archaeological and archaeogenetic evidence testify to the long-term coexistence of and interaction between food producers and local hunter-gatherer populations, with varying degrees of livestock use and/or adoption by the latter (Mutundu, 1999; Lane, 2004; Lane et al., 2007; Prendergast and Mutundu, 2009; Marshall et al., 2011; Prendergast, 2011; Lane, 2013b; Lane, 2015; Quintana Morales and Prendergast, 2017; Russell, 2017; Skoglund et al., 2017; Wang et al., 2020; Prendergast et al. 2019a). However, there is often a lack of clarity regarding the transition to farming and pastoralism, with strong regional variations in the patterning of this change. In eastern Africa, the spread of domestic animals across the region occurred in two main phases of demographic and/or cultural diffusion. The initial phase

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saw the spread of pastoralism throughout interior eastern Africa. This phase was relatively slow and piecemeal, with cattle (*Bos taurus*) and caprines (goat, *Capra hircus*, and sheep, *Ovis aries*) first appearing alongside new ceramic traditions in the Lake Turkana Basin ~5000 BP (Marshall et al., 1984; Hildebrand et al., 2018). After ~3300 BP, clear evidence for specialised pastoralism, with large numbers of livestock, appears further south in the Rift Valley and Victoria Basin (Marshall et al., 2011; Lane, 2013a).

The second major phase, which is the primary focus of this paper, occurred much later, and is associated initially with the spread of agro-pastoralists into the eastern African interior around Lake Victoria by ~2500 BP, and then to the Indian Ocean coast and hinterland of what is now Kenya and Tanzania by around ~2000 BP during the Iron Age. Although it is likely that domesticates arrived on the coast with the first agro-pastoral groups during the Early Iron Age (EIA, ~2000–1400 BP), this has yet to be demonstrated conclusively owing to poor faunal preservation in most EIA sites (Crowther et al., 2016a; Quintana Morales and Prendergast, 2017; Chami, 2009). Rather, the earliest unequivocal zooarchaeological evidence for domesticates reaching the Swahili Coast dates to the Middle Iron Age (MIA ~1400–1000 BP) (Prendergast et al., 2016; Prendergast et al., 2017a; Prendergast et al., 2017b; Quintana Morales and Prendergast, 2017; Crowther et al., 2018; Juma, 2004).

Archaeological evidence shows that occupation patterns on the eastern African coast changed dramatically during the Iron Age. The arrival of semi-sedentary agro-pastoralists is marked by the establishment of wattle and daub villages containing rich assemblages of pottery (Kwale Ware in the EIA, Tana or Triangular Incised Ware in the MIA), and evidence of iron production (Abungu and Mutoro, 1993; Horton and Middleton, 2000; Kusimba and Kusimba, 2005; LaViolette, 2008; Fleisher and Wynne-Jones, 2011; Chami, 2009). These settlements expanded rapidly down the Swahili Coast and onto the offshore islands, with the intensification of trading networks, leading to the emergence of major cosmopolitan ports such as Shanga and Manda in the Lamu Archipelago, Tumbe and Unguja Ukuu in the Zanzibar Archipelago, and Kilwa off the central coast of Tanzania in the mid-first millennium CE (e.g., Chittick, 1974; Chittick, 1984; Chami, 1994; Horton, 1996; Chami, 2004; Juma, 2004; Fleisher and LaViolette, 2013; Crowther et al., 2016a; Fitton and Wynne-Jones, 2017; Crowther et al., 2018).

Agro-pastoralists, however, did not enter an empty landscape; hunter-gatherer groups with Later Stone Age cultural traditions had occupied the region for tens of millennia, as evidenced by stone tool assemblages at a number of cave and rockshelter sites in the coastal uplands, littoral and offshore islands (e.g., Panga ya Saidi, Panga ya Mwandzumari and others in the Dzitsoni Uplands of southeast Kenya; Kuumbi Cave on Zanzibar) (Sinclair et al., 2006; Chami, 2009; Helm et al., 2012; Prendergast et al., 2016; Shipton et al., 2016; Crowther et al., 2018; Shipton et al., 2018). Contrary to earlier (often linguistic-based) models that envisaged the widespread and rapid assimilation or displacement of hunter-gatherer groups by agro-pastoral communities (e.g., Ehret, 1974; Philippson and Bahuchet, 1994; Ehret, 2002; Phillipson, 2002; Bellwood, 2005; Phillipson, 2005), recent archaeological and genetic evidence from the Swahili Coast suggests there was a long period of coexistence and interaction between the two groups (Kusimba and Kusimba, 2005; Helm et al., 2012; Shipton et al., 2013; Skoglund et al., 2017; Crowther et al., 2018). Foraging groups appear to have traded and acquired pottery, glass beads, and domestic crops from incoming farmers as part of complex relationships of interaction and exchange (Helm et al., 2012; Shipton et al., 2013; Crowther et al., 2018).

Unlike their agro-pastoral neighbours, who practiced mixed subsistence economies involving varying degrees of herding and agriculture alongside fishing and hunting (Prendergast et al., 2017b; Quintana Morales and Prendergast, 2017; Mudida and Horton in press), current evidence from sites with Later Stone Age lithic technology shows a continued reliance on hunting, even after the arrival of farming (Prendergast et al., 2016; Shipton et al., 2016; Crowther et al., 2018; Roberts et al., 2020). The extent to which coastal foragers adopted domesticates is presently unclear. Sites with mixed wild and domestic faunal assemblages may reflect foragers' acquisition of livestock from neighbouring herders through trade, theft, or gifts (Prendergast and Mutundu, 2009; Mutundu, 2010). Research further afield in southern Africa has suggested that, in some cases, small-scale livestock herding can be compatible with hunter-gather foodways, but fully fledged pastoralism is not (Fagan, 1967; Dusseldorp, 2016; Grody, 2016; Guillemard, 2020). Evaluating the social and ecological environments that facilitated the spread and/or adoption of domesticates on the eastern African coast depends upon secure identification of fauna in the archaeological record. However, such identifications are challenging due to the typically highly-fragmented nature of the archaeofaunal assemblages in the region and the presence of numerous species of morphologically similar wild bovids. To advance debates about domesticate adoption and use, the frequency of domesticates at a site needs to be understood, overcoming the limitations of zooarchaeological identification relying on morphological criteria alone (for debate on the reliability of morphological versus molecular identification of faunal remains in African contexts, see: Horsburgh and Moreno-Mayar, 2015; Horsburgh et al., 2016a; Horsburgh et al., 2016b; Horsburgh, 2018; Plug, 2018; Scott and Plug, 2019).

In this paper, we apply ZooMS using the new African bovid reference dataset (Janzen et al., in press) to re-examine faunal remains from the site of Panga ya Saidi (hereafter PYS), a large limestone cave in coastal Kenya. PYS is one of the few sites on the eastern African coast that provides a long-term record of hunter-gatherer occupation that continues after farming arrived during the Iron Age, with archaeological and genetic evidence showing that even after this arrival, the site continued to be occupied by people with hunter-gather related ancestry who generally practiced a hunter-gatherer lifestyle (Helm et al., 2012; Shipton et al., 2013; Skoglund et al., 2017; Shipton et al., 2018; Roberts et al., 2020). PYS thus presents a unique opportunity to examine the incorporation of livestock into coastal hunter-gatherer subsistence economies and foodways.

2. Background

2.1. Problems with differentiating domesticates in African zooarchaeology

The identification of domestic faunal remains based on osteological criteria has been a significant challenge for Africanist zooarchaeologists (e.g., Badenhorst, 2006; Gifford-Gonzalez and Hanotte, 2011; Horsburgh and Moreno-Mayar, 2015; Badenhorst, 2018; Prendergast et al., 2019). A major problem is not only the close morphological similarity of sheep and goat, but also the difficulty in distinguishing between other similarly sized wild bovids such as oribi (*Ourebia ourebi*) and Thomson's gazelle (*Eudorcas thomsonii*), particularly in fragmented assemblages (Balasse and Ambrose, 2005; Prendergast et al., 2019). Likewise, fragmentary remains of cattle can be difficult to differentiate from morphologically similar wild bovids such as African buffalo (*Syncerus caffer*) (Peters, 1988). As in many parts of Africa, the problem is exacerbated by poor faunal preservation, with bones often being heavily impacted by taphonomic factors including cultural processes such as breakage and cooking, carnivore or insect damage, and depositional or burial conditions including trampling, sediment compression, soil pH and humidity, leading to assemblages that are frequently highly fragmented (e.g., Lyman, 1994; Thompson, 2020). The combination of taphonomic damage and under-identification excludes important dietary and behavioural information from archaeological reconstructions, as domesticates were often selected at different times and places for different end uses.

2.2. ZooMS in Africa

New biomolecular techniques for species faunal identification, like collagen peptide fingerprinting, more commonly known as ZooMS (Zooarchaeology by Mass Spectrometry), can greatly improve reconstructions of the spread of pastoralism and the dynamics of herder-hunter interactions outside “core” centres of domestication. ZooMS is a minimally destructive biomolecular technique that extracts collagen by cleaving the proteins into peptides and measuring them using soft-ionisation mass spectrometry (Buckley et al., 2009).

The resulting collagen peptide sequence, or collagen fingerprint, has unique markers for identifying specimens to taxon. These taxonomic identifications are often coarse—to the level of family or sub-family—but in contexts of low taxonomic richness, ZooMS-based identifications may be narrowed to the genus and sometimes species levels. It is important to note that due to the absence of native cattle, sheep, or goat in sub-Saharan Africa, ZooMS identifications of *Bos*, *Ovis* or *Capra* in the region can be accepted as domestic. The innovation of ZooMS lies partly in its ability to identify morphologically ambiguous fragmented bones with small sample size requirements (<100 mg). It is also extremely cost effective and has much higher success rates compared to other biomolecular techniques such as ancient DNA (aDNA), which is generally poorly preserved at tropical latitudes (e.g., Campos, et al., 2012; Slatkin and Racimo, 2016); indeed, archaeogenetics has been shown to have limited applicability to faunal remains from the eastern African coast (Prendergast et al., 2017a). The application of ZooMS alongside proteomics has led to major global advances in our understanding of human evolution, enabling for example the identification of extinct hominins (e.g., Brown, et al., 2016; Chen et al., 2019; Lanigan et al., 2020) and understanding of deep time phylogenetic relationships (e.g., Buckley, 2015; Welker et al., 2017; Buckley et al., 2019; Cappellini et al., 2019), and providing insight into past human-animal interactions (e.g., Jaouen, et al., 2019; Sinet-Mathiot et al., 2019; Pothier Bouchard et al., 2020; Le Meillour et al., 2020). In Africa, ZooMS has been used in a small but growing number of studies that have examined faunal assemblages as well as bone and ivory tools (Coutu et al., 2016; Prendergast et al., 2017a; Desmond et al., 2018; Bradfield et al., 2019; Prendergast et al., 2019; Janzen et al., in press), highlighting its applicability in a range of African contexts and environments.

The utility of ZooMS for a particular study is strongly dependent on whether an appropriate collagen fingerprint reference library is available for relevant species in the geographic region of interest. In contrast to other regions where the method has been used successfully, such as southwestern Asia and Europe (e.g., Buckley and Kansa, 2011; Price et al., 2013; Pilaar Birch et al., 2018; Sinet-Mathiot et al., 2019), the use of ZooMS to identify domestic bovids has been relatively challenging in Africa, given the continent’s abundance of wild bovid species and the lack until recently of a comprehensive reference library for these species. Fortunately, a reference set of peptide markers for 20 modern wild African bovids has recently been produced (Janzen et al., in press), including all taxa known or expected to occur in archaeological assemblages in eastern Africa (see Supplementary Data 1 for reference library). Janzen et al. (in press) demonstrated that while all members of the family Bovidae share four common ZooMS markers (COL1α1 508–519 (P1), COL1α2 793–816 (D), COL1α2 454–483 (E) and COL1α2 292–309 (P2)), subfamilies (e.g., Bovinae and Hippotraginae), and in some cases narrower groupings such as tribe or genus, can be uniquely identified using the other five common ZooMS markers (COL1α2 978–990 (A/A′), COL1α2 484–498 (B), COL1α2 502–519 (C), COL1α1 586–618 (F/F′) and COL1α2 757–789 (G/G′)) as well as two novel markers (COL1α2 375 and α2 889) (see Brown et al., 2021 for ZooMS nomenclature system). Apart from the COL1α2 757–789 marker (m/z 3017/3033 for sheep and m/z 3077/3093 for goat) (Buckley et al., 2010), sheep and goat have identical peptide markers, however, the identification of a novel marker COL1α2 375 (m/z 1154, 2028 and 2044) (Janzen et al., in press) allows caprines to be separated from other wild bovids with identical markers. These reference data now permit us to explore questions of domesticate spread and adoption much more robustly at eastern African sites with poor morphological preservation of faunal remains.

2.3. Panga ya Saidi, southeastern Kenya

2.3.1. Ecological setting

PYS is a limestone cave complex located approximately 150 m above sea level on the Dzitsoni uplands of Kilifi District, southeastern Kenya (Fig. 1). The site is formed of three large inter-linked chambers and several smaller adjoining chambers. The Dzitsoni uplands are within the Zanzibar-Inhambane Regional Mosaic floristic region (White, 1983), with the primary vegetation represented by lowland moist forest and lowland dry forest remnants (Moomaw, 1960; Robertson, 1987; Robertson and Luke, 1993). The dominant plant communities in the vicinity of the site include lowland dry forest (*Manilkara-Diospyros*), Sokoke Forest (*Cynometra–Manilkara*), shale savanna (*Manilkara–Dalbergia*), lowland “Miombo” woodland (*Brachystegia–Afzelia*), lowland rainforest (*Sterculia–Chlorophora/Memecylon*) and lowland moist savanna (*Albizia–Anona/Panicum*) (Shipton et al., 2013). Today, human influence has significantly segregated the vegetation of this region, with much of the coastal forests now converted for growing crops, such as coconut and sisal, for both subsistence and commerce (Boxen et al., 1987). Similar to other contemporaneous faunal assemblages from coastal mosaic forests in eastern Africa (Helm, 2000a; Prendergast et al., 2016; Prendergast et al., 2017b), zooarchaeological evidence from PYS suggests that these environments supported small browsing bovids, primates and suids during the Holocene (Roberts et al., 2020), as is also true today (Burgess et al., 2000; Walsh, 2007; IUCN, 2016).

The Dzitsoni coastal uplands were an important region in eastern Africa for early forager and agro-pastoral communities due to access to multiple ecozones to maximise resource availability, including the low coastal plain and the interior plateau (Fig. 1) (Abungu and Mutoro, 1993; Kusimba, 1999; Helm, 2000a; Shipton et al., 2013; Shipton et al., 2018; Roberts et al., 2020). Although the site was in close proximity to the coastline throughout the Pleistocene and Holocene (currently 15 km away), evidence suggests that marine resources were not exploited in significant quantities until the Holocene (Shipton et al., 2018). Overall, the environmental diversity of this region, coupled with the changes happening throughout broader eastern Africa, such as the aridification of the sub-Saharan interior, facilitated the long-term persistence of hunter-gatherer occupation at the site, which appears to have been a refugium throughout its 78,000 year occupation history (Shipton et al., 2018).

2.3.2. Archaeological background

Excavations at PYS have been ongoing since 2010 by an international team from the Max Planck Institute for the Science of Human History (formerly based at the University of Oxford) and the National Museums of Kenya. These excavations have revealed a long sequence of human occupation, including in each of the last five marine isotope stages (Helm et al., 2012; Shipton et al., 2013; Shipton et al., 2018). The main depositional sequences at PYS comprises 19 stratigraphic layers, with dense concentrations of lithic artefacts as well as associated archaeobotanical remains, tetrapod and marine fauna, and cultural material such as shell and glass beads, ochre, engraved bone and shell, and pottery (Helm et al., 2012; Crowther et al., 2016b; D’Errico et al., 2020; Roberts et al., 2020). Radiocarbon and optically stimulated luminescence dating revealed the site was occupied from at least 78,000 BP to around 320 BP. Artefact density suggests that occupation of the site increased in intensity from c. 67,000 BP onwards, but was comparatively less intensive during the most recent phase of the last ~500 years (Layer 1) (Shipton et al., 2018; Roberts et al., 2020). Late Holocene or Iron Age deposits are represented by Layers 2–3 (1180–960 cal BP, MIA) and Layer 1 (500–320 cal BP, Late Iron Age/LIA), together comprising the ~top 30 cm of the deposit. These phases are characterised by a continuation of Later Stone Age lithic technologies such as blades and backed artefacts (Shipton et al., 2018), as well as the addition of new

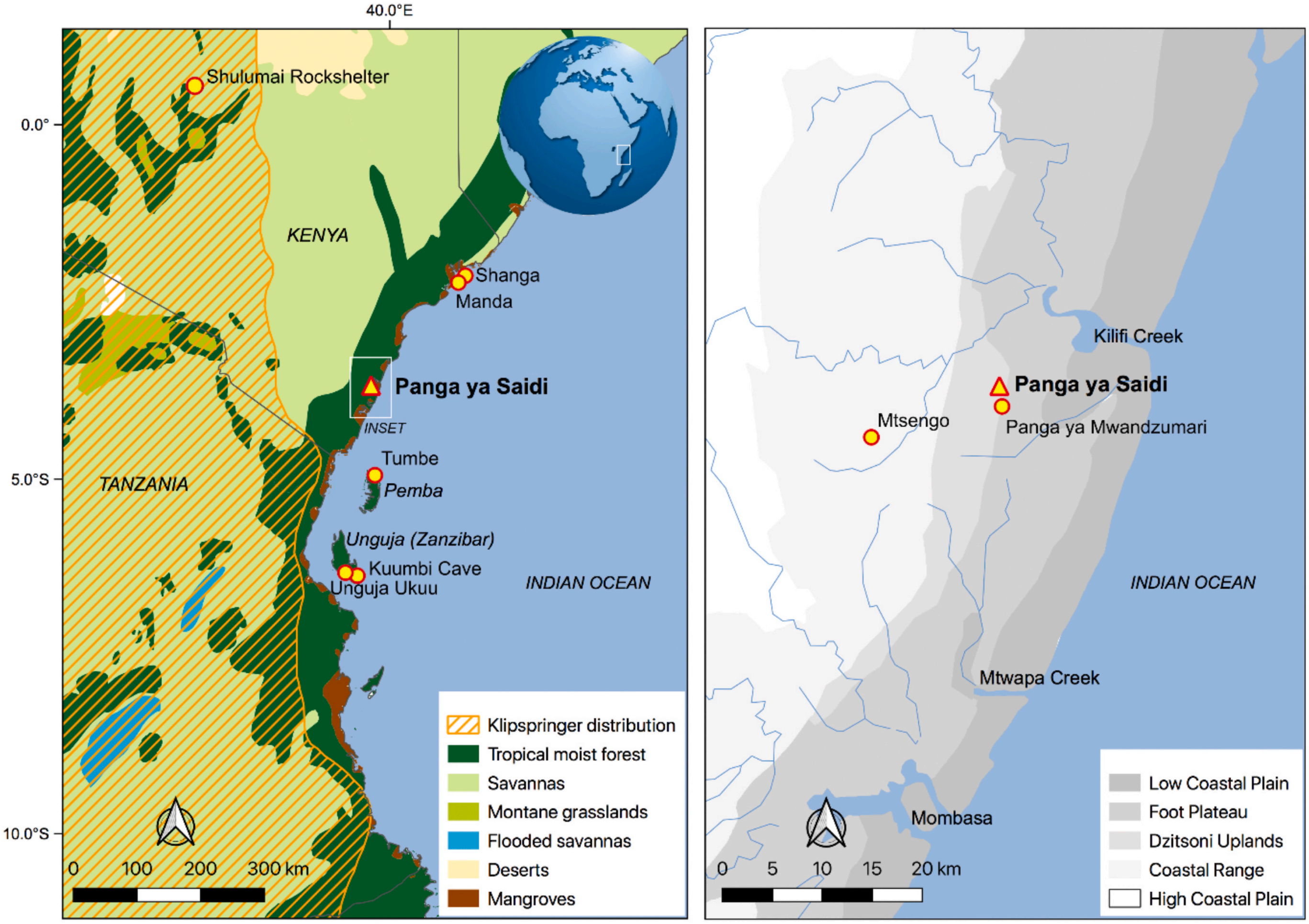

Fig. 1. Map of coastal eastern African showing the location of Panga ya Saidi in south-eastern Kenya in relation to modern vegetation zones and distribution of klipspringer (data from IUCN 2016,left), main physiographic regions (right), and other sites mentioned in text.

cultural elements such as local Tana Tradition pottery (Helm et al., 2012), glass beads acquired, probably indirectly, through long-distance Indian Ocean trade (Boivin et al., 2013), and crops such as sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*) and finger millet (*Eleusine coracana*) (Crowther et al., 2016b; Crowther et al., 2018), indicating growing interactions between food producing groups and hunter-gatherers. Notably, there is no stratified Early Iron Age Kwale pottery at the site, suggesting there may have been a delayed interaction between farming and foraging groups in the coast region (Crowther et al., 2018), a scenario supported by genetic analyses (Skoglund et al., 2017).

Excavations at PYS produced a large, but highly fragmented faunal assemblage. For this study we focused on the assemblages recovered during the 2011 (Trench 3) and 2013 (Trench 4; an extension of Trench 3, total area 6 m^2) excavations, which together produced a total of 21.1 kg of tetrapod bones (mammals, birds, and reptiles). During the initial zooarchaeological analysis, careful attention was paid to dental morphology to distinguish among bovids, however, due to fragmentation, identification to tribe or lower taxonomic level was frequently impossible. In total, 5239 specimens (number of identified specimens, NISP) were identified across all phases of occupation, many of them only to body size class (Brain, 1981) and broad taxonomic categories such as “bovid” (16% total NISP) or “mammal” (37% total NISP) (Roberts et al., 2020). The zooarchaeological analysis demonstrated that small bovids were abundant throughout the sequence, especially in the earliest and latest phases of occupation. The latter phase comprised 80–100% small browsing taxa such as the bovid tribe Cephalophini (duiker) and Neotragini (e.g., dik-dik, suni). Medium-sized browsers in the tribe Tragelaphini (e.g., bushbuck) were also shown to be present in the latest phase alongside unidentified larger bovid remains (Roberts et al., 2020). The zooarchaeological results showed a dominance of fauna adapted to mostly semi-closed and closed environments, with grazing bovids such as Alcelaphini, Bovini, and Reduncini not being identifiable among the fragmented large bovid remains in the latest phase. Overall, the initial zooarchaeological analysis at PYS was able to demonstrate a long record of wild resource exploitation. Domesticated animals were not identified in the large assemblage, with the exception of four tentatively assigned cf. caprine remains (minimum number of individuals, MNI=1) in the Middle to Late Iron Age phase (Roberts et al., 2020).

3. Materials and methods

3.1. Sample Selection

From PYS Trenches 3 and 4, a total of 622 identified macromammal specimens (NISP) were recorded in the Iron Age deposits (micromammals, reptiles, and birds totalled a further 1608 NISP). These included a NISP of 35 bovids with compatible body sizes to caprines (e.g., Bovid Size 1–2 or Bovid Size 2), which were the primary target of this study and thus optimal for ZooMS sampling. 105 specimens were selected for ZooMS analysis, representing nine contexts spanning the Iron Age (Layers 1–3) occupation of the site (Table 1). Of these, 57 specimens were previously identified as indeterminate bovids using morphological criteria (e.g., Bovid Size 1, Size 1–2, etc.), a total of 45

Table 1
Samples from PYS selected for ZooMS per chronological phase and context according to broad morphological identification groups.

Layer[a]	Context	cf. Caprine[b]	Bovid Indet.[c]	Mammal Indet.[d]	Total
1	301			2	**2**
	401		5	(9)	**14**
	402		2	2 (11)	**15**
2	305	1	4	15	**20**
	405		6	1 (3)	**10**
	406		1		**1**
	407		11	2	**13**
3	307	2	24		**26**
	408		4		**4**
Total		**3**	**57**	**45**	**105**

[a] Layer and context equivalents based on Shipton et al. (2018).
[b] Identified as Bovid Size 1–2 cf. caprine.
[c] Includes Bovid Size Classes 1, 1–2, 2, 2 (caprine sized), and 2–3.
[d] Includes Mammal Size Classes 1, 1–2, 2, 2 (caprine sized), 2–3, 3 and 3–4. Numbers in parentheses indicate the number of these remains that were originally classified as “not identified”.

were identified only as indeterminate mammals (e.g., Mammal Size 1, Size 2, etc.), 22 as part of the original morphological analysis, and 23 from originally unidentified fragments that were assigned to Mammal Size classes for the purposes of this study. Of the four specimens originally identified as Bovid Size 1–2 cf. caprine, three were re-located and sampled for this study.

3.2. *ZooMS protocol*

Between ~10 and 80 mg of bone was removed per specimen for ZooMS analysis. Samples were removed either by drilling while avoiding diagnostic features (e.g., the diaphysis of a phalanx) to remove small chunks of bone (26 samples) or more commonly by carefully breaking off small pieces from already-broken ends (79 samples). Sampling was carried out at the National Museums of Kenya (NMK) in Nairobi where the PYS collections are stored, and samples were exported to Germany for pre-treatment and analysis. Laboratory work for this study was conducted at the Max Planck Institute for the Science of Human History in Jena, Germany using dedicated ZooMS facilities.

The samples were separated into two groups for processing, the first were those analysed solely using ZooMS (n=75), while the second were analysed using both ZooMS and stable isotope analysis (the latter results not reported here) (n=30) and thus required a different digestion protocol. For the 30 bones that were also analysed for stable isotopes, ZooMS was carried out using the resulting lyophilised collagen from stable isotopes preparation protocol (Coutu et al., 2016). 100 μL of AmBic was added to 0.1 mg of collagen and incubated for 1 h at 65°C. The resulting supernatant was treated with trypsin at 37°C for 18 h.

Given the generally poor collagen preservation reported elsewhere for many African samples (e.g., (Janzen et al.,), bones that were not included in the stable isotope study were analysed using two established ZooMS protocols. The first accesses collagen through gelatinisation of the bone (Buckley et al., 2009; Welker et al., 2015) and the second utilises collagen which solubilises during acid demineralisation (van der Sluis et al., 2014). This allowed us to follow both protocols on the same bone sample and select the best resulting spectra from either protocol for taxonomic identification (external link: https://doi.org/10.5281/zenodo.3960967).

For the acid insoluble protocol, bone samples were first demineralised in 0.6 M hydrochloric acid (HCl) for at least 18 h, after which the HCl supernatant containing the acid soluble fraction was removed (Welker et al., 2015; Brown et al., 2020b). The demineralised bone comprising the acid insoluble fraction was rinsed three times with 50 mM ammonium bicarbonate (AmBic), incubated at 70°C in 100 μL of 50 mM AmBic and 50 μl of the resulting supernatant was treated with trypsin (Pierce ™ Trypsin Protease, Thermo Scientific) at 37°C for 18 h.

Next, the supernatant containing the acid soluble fraction was transferred into 30kDA molecular weight cut-off (MWCO) ultrafilters and centrifuged at 3700 rpm (van der Sluis et al., 2014; Brown et al., 2020a). The remaining residue was then rinsed twice with 500 μL of 50 mM AmBic and centrifuged again at 3700 rpm. The remaining residue was resuspended with 200 μL of 50 mM AmBic, half of which was removed and stored at −20 °C as a backup. The remaining 100 μL was then treated with trypsin (Pierce™ Trypsin Protease, Thermo Scientific) and incubated at 37°C for 18 h.

Following collagen extraction and digestion for all three protocols, the samples were subjected to C18 clean-up mixed with a matrix solution of α-cyano-4-hydroxycinnamic of 10 mg/mL in 50% ACN/0.1% TFA and allowed to co-crystallise. All samples were spotted in triplicate and analysed using an Autoflex MALDI-ToF (Bruker Daltonics, Bremen). Samples were analysed alongside multiple blanks to monitor intra-laboratory contamination, all of which returned negative results and were determined to be empty of collagen.

The resulting mass spectra were screened for diagnostic markers using the FlexAnalysis (Bruker Daltonics, Bremen) and mMass software (Strohalm et al., 2008). High quality collagen sequences (with good signal and noise levels) were peakpicked with a minimum signal noise ratio of S/N=6 to identify the spectra to the lowest taxonomic level and then compared against a reference library for species identification (Supplementary Data 1) (Buckley et al., 2010; Welker et al., 2015; Janzen et al., in press).

4. Results

The overall success rate for ZooMS analysis of the PYS faunal samples was high; of the 105 samples analysed, 86 (82%) yielded collagen, while 27 (26%) yielded a full set of markers, 40 (38%) had fewer than four missing markers, and a further 19 yielded collagen but had four or more missing markers (18%); only 19 (18%) samples yielded no collagen (Fig. 2). This success rate compares very favourably with previous ZooMS analyses at PYS (Prendergast et al., 2017a), which analysed 137 Muridae specimens, all from Iron Age contexts, of which 89 (65%) succeeded in producing readable collagen sequences. It is also much higher than that achieved in a recent study of 201 samples from six open-air Zambian sites by the AfriZooMS project, where only 60% (121) of faunal samples tested yielded collagen spectra (Janzen et al., in press). The higher success rate in our study may be related to local preservation conditions and the nature of the faunal material under analysis, though inter-taxonomic differences in collagen preservation are not fully yet understood. Together, these results underline the generally excellent collagen preservation conditions afforded by PYS, at least for the upper layers, despite the humid tropical climate.

Of the 86 PYS specimens that yielded collagen, five (5.6%) were identified by ZooMS as domesticates including one sheep, two goat, and two cattle specimens (MNI=3). The three specimens identified morphologically as Bovid Size 1–2 cf. caprine all yielded good ZooMS spectra but were identified as wild bovids. Instead, two were identified as klipspringer (*Oreotragus oreotragus*), while the other did not yield all markers necessary for a more specific identification beyond Tragelaphini or *Oreotragus* because these two groups have similar peptide profiles (Janzen et al., in pres) (Table 2). Due to the size difference between *Oreotragus* and members of Tragelaphini, based on the original osteological identification, this identification is most likely to be *Oreotragus*. The two specimens identified as goat using ZooMS had been identified morphologically as Bovid Size 1 and Mammal Size 2 (in the latter case, with a note that it was caprine-sized), the sheep was identified as Bovid Size 2, while the two cattle remains were previously identified as Bovid Size 1 and 2 (Table 2).

A suite of other wild fauna as well as a human bone were also identified by ZooMS (Table 2). The wild fauna included an array of wild bovids (including four taxa that could be identified to the species level), which comprised 70% of the successful ZooMS identifications, as well as

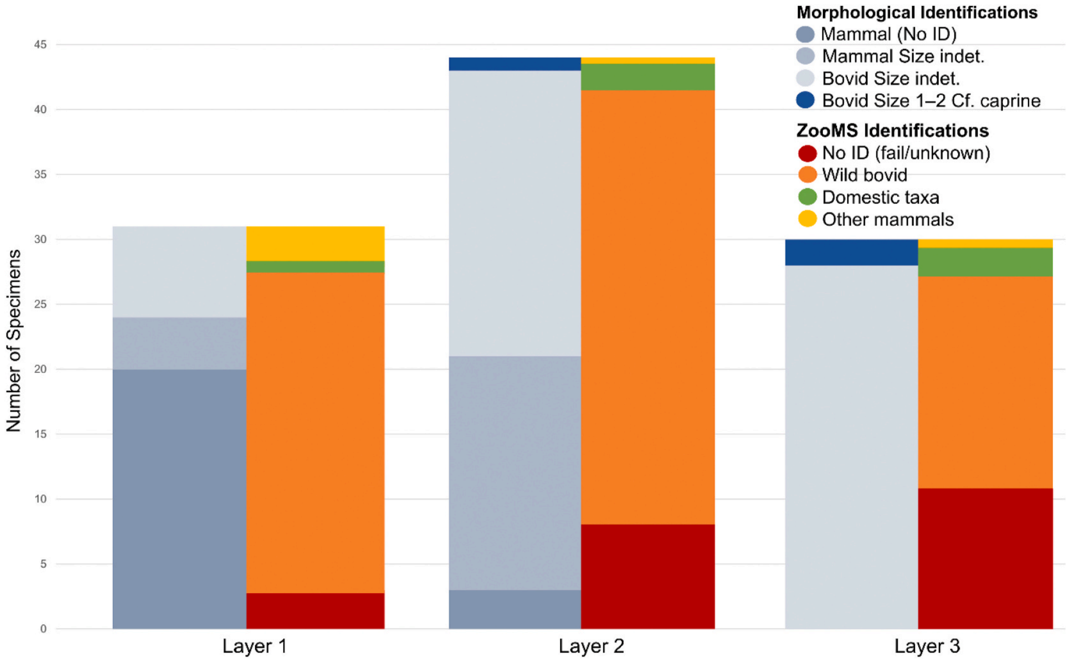

Fig. 2. Comparison of morphological and ZooMS identifications by chronological layer.

a suid and three cercopithecid monkeys (Table 2). The three monkeys identified with ZooMS were identified morphologically as Mammal Size 1, 2, and 3, while the suid was identified previously as Mammal Size 1. The human bone originated from context 402, which was unsurprising as this context was a grave fill containing a complete adult human skeleton that also yielded aDNA (Skoglund et al., 2017; Shipton et al., 2018). The human bone fragment was originally amongst the unidentified remains, which were then classed as Mammal Size 2. The differences between the zooarchaeological size class classifications and ZooMS identifications reflect the highly fragmented faunal assemblage making positive identifications challenging. 83% (87/105) of the ZooMS identifications confirmed the original size class identifications, underlining how useful ZooMS is alongside morphological identification methods.

The identification of wild bovids with ZooMS was in many cases (n=16) restricted to broader identifications owing to the absence of between two and six diagnostic markers from the collagen sequence. For wild bovid identification, the presence of peptide markers COL1α2 978–990 („A" at m/z 1150/1166, 1180/1196, or 1192/1208), COL1α2 502–519 („C″ at m/z 1550 or 1580), COL1α1 585–617 („F″ at m/z 2853 or 2883), and COL1α2 757–789 („G" at m/z 3033 or 3059) are essential for differentiating between taxa. Fourteen of the 16 specimens were identified to either Tragelaphini or *Oreotragus oreotragus* (in most cases based on the presence of all diagnostic markers except G and G′ which are necessary to separate them). Notably, 34 of the 86 successful specimens were identified with ZooMS as klipspringers and while the tribe Neotragini (to which klipspringers belong) was frequently identified at the site, this particular species was assumed to be not present due to its current geographical range (discussed below). Morphological analysis thus relied on comparative skeletons of other neotragines common to the area today, especially suni (*Neotragus moschatus*), steenbok (*Raphicerus campestris*), and dik-dik (*Madoqua* sp.), and identifications were reported at the tribe level (Roberts et al., 2020). Klipspringers can be uniquely identified using ZooMS by the COL1α2 757–789 (G') marker (at m/z 3033), which distinguishes it from like-sized bovids including duikers (most likely including the blue duiker, *Philantomba monticola*) and the novel marker COL1α2 375 at m/z 2028/2044, which distinguishes it from suni (Janzen et al., in press) (Fig. 3). However, not all members of the Neotragini or Cephalophinae have been analysed, and more proteomic work is needed to determine whether more bovid taxa can be uniquely identified.

5. Discussion

5.1. *The impact of domestic livestock on hunting economies at PYS*

Where previously there were no definitive identifications of domesticates at PYS, despite zooarchaeological analysis of 5239 specimens from the site, ZooMS has now confirmed the presence at PYS of all three major domestic bovids introduced to eastern Africa in prehistory: sheep, goat, and cattle. These species occupy a quantitatively minor proportion of the overall assemblage compared to wild bovids (5.6% vs 70% respectively based on the ZooMS results of the sample of 105 specimens). Based on associated radiocarbon dates (Crowther et al., 2018; Shipton et al., 2018), the specimens identified as goat and cattle appear together, as early as 1180–960 cal BP (Layers 2 and 3), while sheep are only present much later, around 500–300 cal BP (Layer 1). This suggests the occupants of PYS began exploiting domesticates at least as early as they appear at neighbouring agro-pastoral sites (Helm, 2000a; Helm et al., 2012; Prendergast et al., 2016; Prendergast et al., 2017b; Quintana Morales and Prendergast, 2017). Their frequency at PYS suggests that domesticates may have been acquired only infrequently, possibly through exchange and other interactions rather than adopted as components of a part-time herding economy alongside long-established hunting lifeways.

The ZooMS results thus support previous zooarchaeological and isotopic evidence indicating that even in the Iron Age, there remained a heavy reliance on wild species at PYS (Shipton et al., 2018; Roberts et al., 2020). The Iron Age occupation phase of the site was dominated by woodland and forest adapted species such as small browsing bovids (Cephalophinae and Neotragini), suids, and primates, which were all confirmed by ZooMS. These data fit with a longer-term pattern of hunting behaviour that spans the Pleistocene and Holocene, continuing long after livestock appeared in the region. Stable isotope analysis of faunal remains has shown that through time, PYS was dominated by a relatively stable mixture of closed forest and open woodland, with sporadic appearances of open grassland during the Late Pleistocene (Roberts et al., 2020). The long-term occupation of PYS is likely due in

Table 2
Distribution of wild and domesticated species identified with ZooMS compared with morphological identifications. Identifications marked with an asterisk (*) indicate the specimen was classified as "not identified" prior to this study. Samples that failed (n=19) or were unidentifiable against our reference library (n=3) were excluded. Bovid indet. means that a specific identification was not possible due to missing markers, see Supplementary Data Table 1. Caprine size (CS) was given as an additional size estimation for some specimens. Results are listed in order of context depth. All contexts date to the Late Holocene/Iron Age.

Layer	Context	ZooMS Sample No.	Element	Morphological Identification	ZooMS Identification
Domesticates					
1	401	PYS81	Phalanx 1	Bovid Size 2	*Ovis aries* (Sheep)
2	305	PYS45	Limb bone	Mammal Size 2 (CS)	*Capra hircus* (Goat)
	407	PYS26	Indeterminate	Bovid Size 2	*Bos taurus* (Cattle)
3	307	PYS56	Limb bone	Bovid Size 1	*Capra hircus* (Goat)
	307	PYS58	Limb bone	Bovid Size 1	*Bos taurus* (Cattle)
Wild Bovids					
1	301	PYS49	Rib	Mammal Size 1	*Sylvicapra grimmia* (Bush duiker)
	301	PYS50	Metapodial	Mammal Size 1	*Oreotragus oreotragus* (Klipspringer)
	401	PYS79	Sacrum	Bovid Size 1	*Sylvicapra grimmia* (Bush duiker)
	401	PYS82	Metatarsal	Bovid Size 1–2	*Sylvicapra grimmia* (Bush duiker)
	401	PYS84	Limb bone	Mammal Size 2*	*Sylvicapra grimmia* (Bush duiker)
	401	PYS86	Limb bone	Mammal Size 1–2*	*Sylvicapra grimmia* (Bush duiker)
	401	PYS80	Metapodial	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	401	PYS85	Limb bone	Mammal Size 2*	*Oreotragus oreotragus* (Klipspringer)
	401	PYS89	Limb bone	Mammal Size 2*	*Oreotragus oreotragus* (Klipspringer)
	401	PYS90	Lumbar vert.	Mammal Size 2*	*Oreotragus oreotragus* (Klipspringer)
	401	PYS91	Indeterminate	Mammal Size 3–4*	*Oreotragus oreotragus* (Klipspringer)
	401	PYS83	Indeterminate	Mammal Size 3–4*	*Oreotragus oreotragus* (Klipspringer)
	401	PYS77	Mandible	Bovid Size 2–3	Tragelaphini or *Oreotragus oreotragus*
	402	PYS92	Radius	Bovid Size 1	*Sylvicapra grimmia* (Bush duiker)
	402	PYS103	Limb bone	Mammal Size 2*	*Sylvicapra grimmia* (Bush duiker)
	402	PYS97	Limb bone	Mammal Size 2–3*	*Oreotragus oreotragus* (Klipspringer)
	402	PYS102	Limb bone	Mammal Size 2*	*Oreotragus oreotragus* (Klipspringer)
	402	PYS108	Limb bone	Mammal Size 2*	*Oreotragus oreotragus* (Klipspringer)
	402	PYS109	Limb bone	Mammal Size 2*	*Oreotragus oreotragus* (Klipspringer)
	402	PYS06	Tibia	Mammal Size 2	*Oreotragus oreotragus* (Klipspringer)
	402	PYS99	Limb bone	Mammal Size 2*	Tragelaphini (e.g., bushbuck)
	402	PYS110	Scapula	Mammal Size 1*	Tragelaphini (e.g., bushbuck)
	402	PYS104	Rib	Mammal Size 2*	Tragelaphini or *Oreotragus oreotragus*
	402	PYS107	Limb bone	Mammal Size 2*	Tragelaphini or *Oreotragus oreotragus*
2	305	PYS28	Lumbar vert.	Bovid Size 2 (CS)	*Sylvicapra grimmia* (Bush duiker)
	305	PYS33	Vertebra	Mammal Size 1–2	*Sylvicapra grimmia* (Bush duiker)
	305	PYS35	Limb bone	Mammal Size 2 (CS)	*Sylvicapra grimmia* (Bush duiker)
	305	PYS38	Limb bone	Mammal Size 2 (CS)	*Sylvicapra grimmia* (Bush duiker)
	305	PYS42	Limb bone	Mammal Size 2 (CS)	Bovid indet.
	305	PYS30	Upper molar	Bovid 1–2 cf. caprine	*Oreotragus oreotragus* (Klipspringer)
	305	PYS31	Orbit	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	305	PYS32	Orbit	Bovid Size 1–2	*Oreotragus oreotragus* (Klipspringer)
	305	PYS34	Cranial bone	Mammal Size 1–2	*Oreotragus oreotragus* (Klipspringer)
	305	PYS36	Limb bone	Mammal Size 2 (CS)	*Oreotragus oreotragus* (Klipspringer)
	305	PYS41	Limb bone	Mammal Size 2 (CS)	*Oreotragus oreotragus* (Klipspringer)
	305	PYS43	Thoracic vert.	Mammal Size 2 (CS)	*Oreotragus oreotragus* (Klipspringer)
	305	PYS44	Limb bone	Mammal Size 2 (CS)	*Oreotragus oreotragus* (Klipspringer)
	305	PYS46	Rib	Mammal Size 2 (CS)	*Oreotragus oreotragus* (Klipspringer)
	305	PYS37	Limb bone	Mammal Size 2 (CS)	*Oreotragus oreotragus* (Klipspringer)
	305	PYS39	Limb bone	Mammal Size 2 (CS)	Tragelaphini or *Oreotragus oreotragus*
	405	PYS10	Axial indet.	Bovid Size 2	*Madoqua* sp. (Dik-dik)
	405	PYS09	Indeterminate	Bovid Size 2	*Sylvicapra grimmia* (Bush duiker)
	405	PYS114	Limb bone	Mammal Size 1	*Sylvicapra grimmia* (Bush duiker)
	405	PYS11	Limb bone	Bovid Size 2	Tragelaphini or *Oreotragus oreotragus*
	405	PYS112	Limb bone	Mammal Size 2*	Tragelaphini or *Oreotragus oreotragus*
	405	PYS111	Indeterminate	Mammal Size 3	*Oreotragus oreotragus* (Klipspringer)
	405	PYS12	Limb bone	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	405	PYS13	Limb bone	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	406	PYS14	Metacarpal	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	407	PYS22	Limb bone	Bovid Size 2	*Madoqua* sp. (Dik-dik)
	407	PYS15	Thoracic vert.	Mammal Size 1	*Sylvicapra grimmia* (Bush duiker)
	407	PYS17	Phalanx 2	Mammal Size 1	Tragelaphini *or Oreotragus oreotragus*
	407	PYS24	Limb bone	Bovid Size 2	Tragelaphini or *Oreotragus oreotragus*
	407	PYS25	Indeterminate	Bovid Size 2	Tragelaphini or *Oreotragus oreotragus*
	407	PYS16	Metacarpal	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	407	PYS18	Phalanx 2	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	407	PYS23	Limb bone	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
3	307	PYS51	Phalanx 1	Bovid Size 1–2 cf. caprine	*Oreotragus oreotragus* (Klipspringer)
	307	PYS60	Limb bone	Bovid Size 1	*Oreotragus oreotragus* (Klipspringer)
	307	PYS59	Metapodial	Bovid Size 1	*Oreotragus oreotragus*(Klipspringer)
	307	PYS74	Limb bone	Bovid Size 1	*Oreotragus oreotragus* (Klipspringer)
	307	PYS53	Radius	Bovid Size 1	*Sylvicapra grimmia* (Bush duiker)
	307	PYS62	Humerus	Bovid Size 1	*Sylvicapra grimmia* (Bush duiker)
	307	PYS65	Limb bone	Bovid Size 1	*Sylvicapra grimmia* (Bush duiker)

(*continued on next page*)

Table 2 (*continued*)

Layer	Context	ZooMS Sample No.	Element	Morphological Identification	ZooMS Identification
	307	PYS69	Limb bone	Bovid Size 1	*Sylvicapra grimmia* (Bush duiker)
	307	PYS55	Radius	Bovid Size 1	Tragelaphini or *Oreotragus oreotragus*
	307	PYS52	Navi-cuboid	Bovid Size 1–2 cf. caprine	Tragelaphini or *Oreotragus oreotragus*
	307	PYS57	Metapodial	Bovid Size 1	Tragelaphini or *Oreotragus oreotragus*
	307	PYS61	Rib	Bovid Size 1	Tragelaphini or *Oreotragus oreotragus*
	307	PYS70	Metapodial	Bovid Size 1	Wild Bovid indet.
	408	PYS03	Upper limb	Bovid Size 2	*Oreotragus oreotragus* (Klipspringer)
	408	PYS04	Upper limb	Bovid Size 2	*Sylvicapra grimmia* (Bush duiker)
	408	PYS01	Femur	Bovid Size 2	Tragelaphini or *Oreotragus oreotragus*
Other					
1	402	PYS95	Rib	Mammal Size 2*	*Homo sapiens* (Human)
	401	PYS88	Rib	Mammal Size 3*	Cercopithecidae (Monkey)
	402	PYS05	Caudal vert.	Mammal Size 2	Cercopithecidae (Monkey)
2	405	PYS113	Limb bone	Mammal Size 1*	Cercopithecidae (Monkey)
3	307	PYS73	Limb bone	Bovid Size 1	Suidae

part to its location, which afforded ready access to different ecological zones, such as forest and coastline, which were integral to the occupants' subsistence lifeways. The persistence of hunting into the Iron Age is not unique to the coastal region of Kenya, but is also documented throughout the Rift Valley and nearby Laikipia plateau where distinct forager groups also lived alongside herders and agro-pastoralists during the Iron Age (Ambrose et al., 1984; Causey, 2010; Lane, 2011). The presence of goat at PYS is also consistent more broadly with evidence from sites across the Swahili coast, where goats are typically much more common than sheep in Iron Age assemblages (Quintana Morales and Prendergast, 2017). As mixed feeders, goats would have been highly suited to the coastal forest mosaic landscape of the region compared to sheep and cattle, which prefer open grassland. The identification of sheep and cattle at PYS is therefore interesting and raises questions about the subsistence behaviour and choices made by local communities, and their possible interaction with neighbouring food producers, given that these livestock are less well-adapted to woodland environments.

5.2. Livestock trading or herding?

To address the question of whether the occupants of PYS acquired domesticates for immediate consumption or engaged in small-scale stock-keeping, some consideration of the differences implied by these two scenarios in terms of lifeways and subsistence behaviours, as well as their respective archaeological signatures is required. While agro-pastoralism implies that a community is partially or completely sedentary and mostly relies on domesticated livestock and crops for subsistence (Hodgson, 2000), other types of herding are also possible. Furthermore, distinct categories such as “pastoralist” and “hunter-gatherer”, particularly when defined by the frequency of domestic versus wild fauna remains at a site, can be problematic for archaeological interpretations of past subsistence behaviours (Kusimba and Kusimba, 2005). Such definitional frameworks have limited utility for understanding regional complexities including potential trading behaviours and overlook the possibility that domesticated animals present at a site may not have been herded by its occupants. Based on simple wild-to-domestic ratios, it is therefore difficult to distinguish archaeologically whether livestock present at a site were acquired for immediate consumption or were under long-term management (Prendergast and Mutundu, 2009). Herding itself, in contrast to highly specialised pastoralism, should be viewed as a sliding scale of dependency on livestock, and in an archaeological setting, a direct relationship between the number of domesticated faunal remains and a community's degree of reliance on livestock should not be assumed.

At PYS, the quantitative evidence seems to suggest that livestock were either kept in small numbers or acquired from neighbouring agro-pastoralist groups. A broadly parallel case is that of Shulumai Rockshelter in the Mukogodo Hills of north-central Kenya (Fig. 1), an area historically occupied by Mukogodo foragers who had regular contact with neighbouring pastoralists, eventually becoming integrated into the pastoralist community (Mutundu, 1999; Cronk, 2004). In the historic deposits, the proportion of domestic fauna was low (6% NISP), suggesting that the occupants were acquiring livestock through occasional exchanges; however, ethnohistoric (written and oral) records clearly show that the Mukogodo had access to domestic stock for long-term stock keeping (Prendergast and Mutundu, 2009). Similarly, ethnohistorical records show that during the twentieth century, Waata groups in Kenya exchanged forest products, such as honey, for domesticated crops/animals with the Oromo people (Kassam and Bashuna, 2004). Without contemporaneous historical accounts for PYS, it is difficult to suggest whether the occupants were acquiring domestic stock for immediate consumption or on a more long-term basis. Regardless of what the livestock were used for and how they were kept, the presence of domesticates at PYS highlights the distinct but inter-connected nature of resource use between hunter-gatherers and neighbouring farming communities.

5.3. The role of domesticates in forager-farmer interactions

The results of this study support established evidence from PYS and more broadly throughout the coastal and upland region, showing an intensification of trade and interactions between local hunter-gatherers and early agro-pastoralist communities throughout the Middle to Late Iron Age. These exchanges also included material culture, such as imported glass beads and ceramics, as well as domesticated crops (Kusimba and Kusimba, 2005; Helm et al., 2012; Shipton et al., 2013; Crowther et al., 2018). This fluid interaction among co-existing groups was also commonly seen throughout the more distant central Rift Valley until very recently (Ambrose, 1984; Mutundu, 1999). In eastern Africa, social connections between herding and foraging groups are seen as a resource safety net, with hunter-gatherer groups seeking out food production in times of resource depletion or environmental change, and pastoralists joining hunter-gatherer communities during times of stock loss, for example (Sobania, 1988; Spear and Waller, 1993; Marshall, 1994; Mutundu, 1999; Marshall and Hildebrand, 2002; Dusseldorp, 2016; Prendergast, 2020).

PYS also contrasts with agro-pastoral sites on the eastern Africa coast, which were typically first occupied by food producing communities that migrated to the region during the Iron Age. At nearby Mtsengo, for example, which was occupied in the fourteenth and fifteenth century CE (contemporaneous with Layer 1 at PYS), faunal evidence indicates a much heavier reliance on domesticated livestock (cattle 47% and caprine 23%) over wild species, suggesting the larger-scale incorporation of domesticates into subsistence systems (Helm, 2000b). Other sites such as Shanga, Manda and Tumbe however, which were occupied during the MIA (contemporaneous with Layer 2–3 at PYS), do show a more mixed herding-hunting regime, with a high

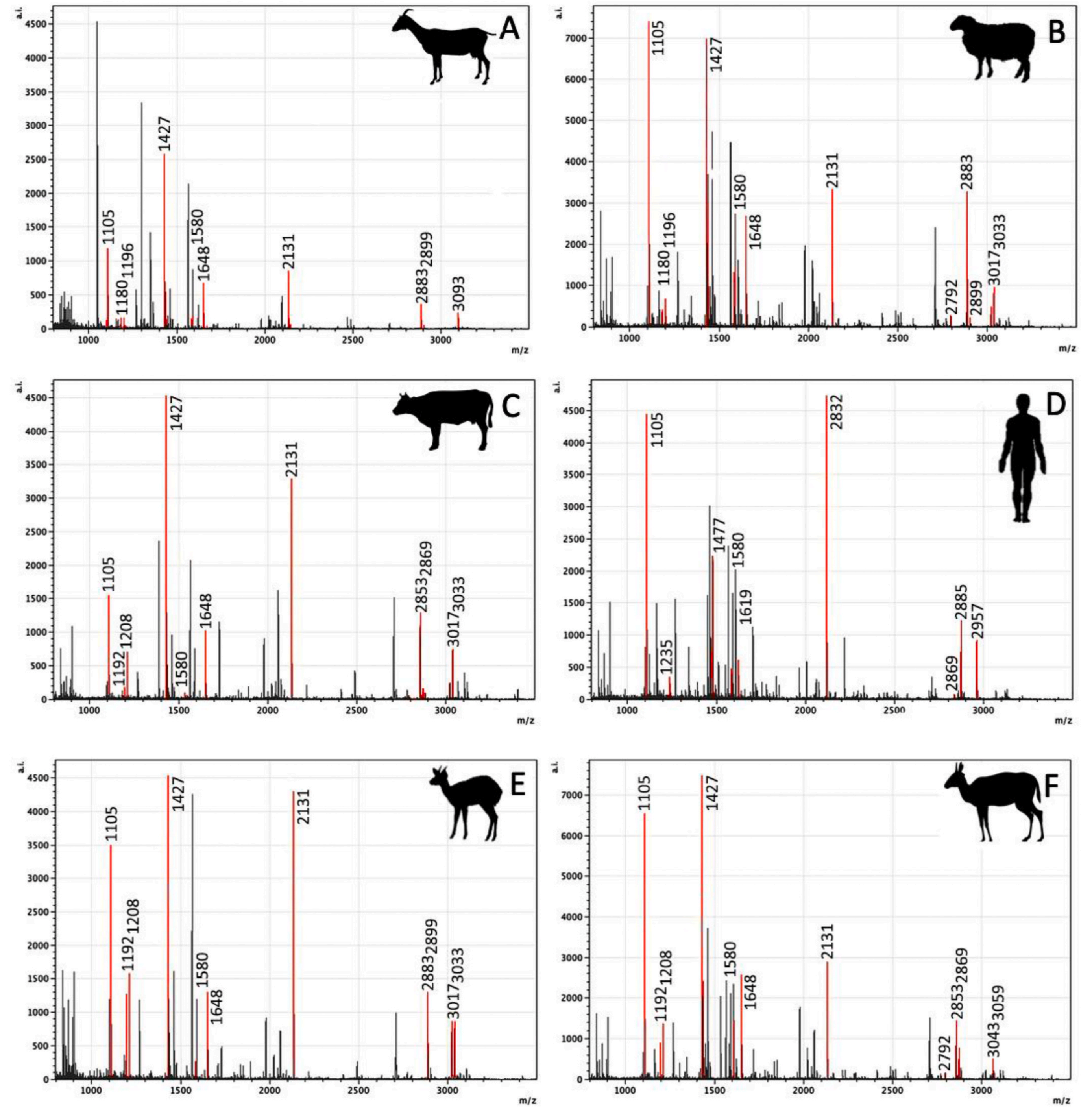

Fig. 3. Selection of ZooMS spectra from the study. A) Goat, *Capra hircus* (PYS45), B) Sheep, *Ovis aries* (PYS81), C) Cattle, *Bos taurus* (PYS26), D) Human, *Homo sapiens* (PYS95), E) Klipspringer, *Oreotragus oreotragus* (PYS03), F) Bush Duiker, *Sylvicapra grimmia* (PYS82). Red lines indicate diagnostic peaks for each taxon (see Supplementary Data 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

number of domestic fauna while still relying on marine resources and hunting (Quintana Morales and Prendergast, 2017). Altogether, this may indicate a need for more predictable access to resources at neighbouring agro-pastoral sites compared to PYS, particularly for those located on the dry coastal plain that would be more suited for specialised agro-pastoralism compared to broad scale hunting and gathering.

The presence, albeit limited, of marine fish and shellfish species, as well as Indian Ocean glass beads in the Iron Age deposits at PYS also suggest travel or exchange for products from the coast roughly 15 km away (Shipton et al., 2013), indicating trading relationships with coastal lowland agro-pastoralists. Such an interpretation is supported by ethnographic accounts documenting the importance of resource trading between agro-pastoralists and foraging groups. These relationships were based on reciprocal needs for wild and domestic resources such as milk or meat, as well as social exchanges such as marriage, with livestock traded in order to fortify political, economic and social ties between groups (Lokuruka, 2006; Russell and Lander, 2015; Russell, 2017). What is increasingly demonstrated by new research is the emergence of a subsistence mosaic in coastal eastern Africa, where different hunter-gatherer groups interacted with agro-pastoralists in different ways (Crowther et al., 2018).

5.4. *Behavioural and ecological implications of klipspringers at PYS*

An important outcome of the PYS ZooMS analysis was the identification throughout the Late Holocene sequence of klipspringers, which had not been identified at PYS before. Thirty-four klipspringer specimens were identified via ZooMS in contexts from Layers 1–3, showing their sustained presence at the site from at least 1180–300 cal BP according to associated radiocarbon dates (Shipton et al., 2018). PYS is not within the historic range of klipspringers, and the closest part of their current range is approximately 80 km away (IUCN 2016) (Fig. 1); as a result, this species was not considered likely to have been present at the site and therefore was undetected prior to the ZooMS study. Klipspringers belong to the tribe Neotragini, a "catch-all" group of small bovids that includes dik-dik, steenbok, and suni, all of which inhabit the coastal forest mosaic today. Neotragini were frequently identified at PYS, based on both dental and postcranial remains. In the Trench 3 and 4 Iron Age levels, 12 of the 33 bovid remains morphologically identifiable to tribe were reported as Neotragini (Roberts et al., 2020). While these were not identified to genus, they were assumed to be taxa common to the area around PYS today, such as dik-dik or suni. Based on the ZooMS results, we now consider it possible that many of these identified Neotragini may be klipspringer.

Several scenarios can be invoked to explain why klipspringer was present archaeologically at PYS, despite the fact that it is not found in the region today (see Fig. 1 for their contemporary distribution). One possibility is that klipspringers were regionally extirpated in the recent past as a result of environmental change, though this does not seem likely given that stable isotope studies indicate the local environment has remained relatively stable over the course of the Holocene (Roberts et al., 2020). Additional isotopic studies at the site, focused on the Iron Age levels, may help address questions regarding recent environmental shifts, particularly in the last 1000 years. More recent disruptions to habitat from increased occupation of the coast by agro-pastoralists, as well as urban development over the last 500 years may have been a factor, particularly given that klipspringer appear to inhabit similar tropical moist forests further to the south in Tanzania and Mozambique. Alternatively, people occupying PYS may have travelled to hunt and trap klipspringers, which if true, opens up further questions about hunting regimes and possible trade and exchange behaviours. The small size of klipspringers would have made them easily transportable from different occupation areas. At this stage, it is fair to assume that any of these options are possible in explaining the presence of a species that is absent from the surrounding region today. A final possibility considered here is that this finding reflects limitations with the ZooMS reference dataset, although, the likelihood of this is slim, given that markers for members of all African bovid tribes have been established (Janzen et al., in press). Future ZooMS analysis on faunal assemblages from earlier layers at PYS as well as neighbouring Iron Age sites may help to shed light on this question.

6. Conclusion

This study has demonstrated the significant impact that biomolecular techniques such as ZooMS can have on our understanding of early interactions between hunter-gatherer and agro-pastoralists in eastern Africa, by identifying for the first time domesticated fauna at a site previously associated only with hunting. These results have demonstrated the relatively minor presence of domesticates compared to wild fauna at the site, which contributes to the story of a gradual integration of livestock into foraging communities either through exchange or low-level herding behaviours. The abundance of wild bovids compared to the minor presence of domesticated fauna is consistent with previous zooarchaeological results based on morphological analyses, and provides us with a better understanding of how hunter-forager subsistence behaviours were transformed by the arrival of food producers in their local territories. The evidence from PYS shows that foraging groups at the site coexisted with agro-pastoralist groups long after farming arrived on the coast, while apparently not fundamentally changing their subsistence behaviours. It is clear that we need more refined regional studies, involving multi-proxy analyses to help build higher-resolution subsistence models throughout eastern Africa. The larger scale application of ZooMS at more sites has enormous potential to shed light on the relative importance of domesticates and wild taxa, across time and space, allowing us to clarify local patterns in the spread of farming and the persistence of foraging populations that have been challenging to reconstruct from fragmentary and taphonomically impacted assemblages.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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