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Fossil herbivore stable isotopes reveal Middle Pleistocene hominin palaeoenvironment in 'Green Arabia'

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Abstract:

Despite its largely hyper-arid and inhospitable climate today, the Arabian Peninsula is emerging as an important area for investigating Pleistocene hominin dispersals. Recently, a member of our own species was found in northern Arabia dating to *c*. 90 ka, while stone tools and fossil finds have hinted at an earlier, Middle Pleistocene, hominin presence. However, there remain few direct insights into Pleistocene environments, and associated hominin adaptations, that accompanied the movement of populations into this region. Here, we apply stable carbon and oxygen isotope analysis to fossil mammal tooth enamel (n=21) from the Middle Pleistocene locality of Ti's al Ghadah in Saudi Arabia associated with newly-discovered lithics and probable cutmarks. The results demonstrate productive grasslands in the interior of the Arabian Peninsula *c*. 300-500 ka, as well as aridity levels similar to those found in open savanna settings in eastern Africa today. The association between this palaeoenvironmental information and the earliest traces for hominin activity in this part of the world lead us to argue that Middle Pleistocene hominin dispersal into the interior of the Arabian Peninsula required no major novel adaptation.

Introduction

Studies of Pleistocene hominin dispersals beyond Africa are important for understanding the course of global human evolution and prehistory. In particular, analysis of the environmental context under which members of the genus *Homo* moved into Europe and Asia in the Early and Middle Pleistocene (2.6 Ma to 126 ka) relative to that of *Homo sapiens* populations expanding around the globe in the Late Pleistocene (126-12 ka) can provide insight into the potential ecologically unique nature of our species[1-3]. It has recently been highlighted that our species occupied and utilized a diversity of extreme environments, including deserts, tropical rainforests, palaearctic, and high-altitude settings, around the world during the Late Pleistocene[3]. By contrast, the dispersals of other earlier and contemporaneous *Homo* species into Europe and Asia appear to be best associated with generalized utilization of different forest and grassland mosaics proximate to riverine and lacustrine settings[2,4]. Yet, a paucity of associated palaeoenvironmental information has made it difficult to systematically test this distinction and many hold that non-*H. sapiens* members of the genus *Homo* demonstrate significant cultural[5-6] and ecologically adaptive[7-9] flexibility.

In spite of its crucial geographic position at the interface of Africa and Eurasia, the Arabian Peninsula has remained remarkably absent from adaptive models of Pleistocene hominin expansions until relatively recently, owing to a lack of well-constrained archaeological and palaeoecological data. Climate modeling[10], speleothem records[11], palaeontological findings[12-15], and geomorphological studies of palaeolake records[16-17] have been used to argue that at intervals in the past, notably during interglacials, the harsh, hyper-arid deserts that cover much of Arabia today were replaced by 'moister' and 'greener' conditions more hospitable to foraging occupation[18-19]. Furthermore, the find of a *H. sapiens* phalanx, in association with Middle Palaeolithic stone tools, at the site of Al Wusta dated to *c*. 90 ka provides definitive evidence for the early presence of our species in the interior of the Arabian Peninsula[20]. There have also been suggestions that stone tools in the Arabian interior are associated with an earlier period of Middle Pleistocene hominin dispersal[21-24]. However, despite the significance of climate and environmental change for hominin dispersal into the region, there has been no direct means of determining what 'wetter' represents in the context of regional ecology nor definitive identification of Middle Pleistocene hominin presence.

We undertook renewed archaeological and taphonomic analysis of fossil fauna found at the Middle Pleistocene (*c*. 500-300 ka) fossil locality of Ti's al Ghadah in the Nefud Desert of Saudi Arabia (Fig. 1; Supplementary Text 1 and 2; Supplementary Figures 1 and 2) and report, for the first time at the site, lithic artefacts in direct stratigraphic association with the fossil fauna. Ti's al Ghadah is one of the most important palaeontological sites in the region, representing the only dated faunal assemblage recovered from Middle Pleistocene Arabia[12-14]. Previous analyses have identified a suite of terrestrial and aquatic animals, including extinct elephants (*Palaeoloxodon* sp.), horses (*Equus hemionus*), and water birds (*Tachybaptus* sp. and *Anas* sp.)[12-14] (Supplementary Table 2), that have been used to argue the western Nefud Desert was significant less arid at times during the Middle Pleistocene than it is today. 'Middle Palaeolithic' artefacts of unknown age have also been recovered from the surface of the basin[24]. Yet, the lack of taphonomic analysis and scarcity of anthropogenic remains has made evaluating the relationship between hominins and fossil fauna difficult.

There has also been no way of analyzing, in detail, the vegetation and relative aridity associated with the Middle Pleistocene fossil assemblage, and potential hominin presence, at Ti's al Ghadah. Here, we performed stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope analysis

of 21 fossil fauna recovered from the site. $\delta^{13}C$ analysis of faunal tooth enamel is used to assess different types of biomass in animal diets[25-27]. Most terrestrial plants, including trees, herbs, shrubs, and shade-loving grasses follow the C_3 photosynthetic pathway[28]. C_4 photosynthesis is followed by most arid-adapted grasses and some sedges[29]. C_3 and C_4 plants have distinct and non-overlapping $\delta^{13}C$ values[30] that are passed into faunal consumers allowing reliance on tree and shrub versus grassland biomass to be determined in global ecosystems, including those of Arabia[12]. In faunal diets, prior to the impact of significant fossil fuel emission, average herbivore $\delta^{13}C$ values for C_3 and C_4 reliance are *c*. -12‰ and ~ 0‰, respectively[25-27](Fig. 3).

$\delta^{18}O$ data from fossil herbivore tooth enamel reflect precipitation source, humidity, temperature, and also plant water. These multiple influences can often make faunal enamel $\delta^{18}O$ difficult to interpret as a past environmental signal. This is particularly the case in areas like the Arabian Peninsula where the source water, and therefore $\delta^{18}O$, for precipitation may have changed over time[10]. Evaporation exerts a positive effect on $\delta^{18}O$, particularly in arid desert regions such as the centre of the Arabian Peninsula, so that continental water bodies and soils in areas with a water deficit are ^{18}O-enriched. This effect is even stronger in plants due to the process of evapo-transpiration[32-33]. The difference between the $\delta^{18}O$ from tooth enamel of obligate drinkers such as equids (that must drink from open water sources) and non-obligate drinkers such as *Oryx* spp. (that can meet their water requirements through the consumption of plants) will be strongly influenced by palaeoaridity[34-35] at a given locale, and will not be effected by changes in the precipitation or source water baseline (Supplementary Text 2). Finally, due to the fact that tooth enamel forms incrementally, sequential $\delta^{13}C$ and $\delta^{18}O$ analysis of animal tooth enamel can be used to look at temporal changes in vegetation and water source during the period of tooth enamel formation[36]. The preservation of all samples was also checked using FTIR as per[31] (Supplementary Text 3).

Results

The fossil faunal remains and newly-discovered stone tools analysed in this study were recovered from a sandy horizon ('Unit 5') directly beneath a palaeolake deposit in the Ti's al Ghadah basin[14] (Fig. 2). The lithic artefacts, coupled with new taphonomic evidence suggestive of anthropogenic accumulation of bones on-site, confirm a hominin presence in association with the faunal remains analysed here (Fig. 2; see also Supplementary Text 4). These findings represent the oldest radiometrically dated hominin presence in the Arabian Peninsula, as well as the first anthropogenically modified faunal assemblage from the Pleistocene. In total, six unretouched flakes and one retouched flake were recovered from Unit 5. A further six chunks were recovered with the artefacts and likely represent highly fragmented debitage. The lithics and debitage fragments are made on a brown coloured lacustrine chert, and this material is known from lakebeds across the Nefud[18-20]. At the MIS 5 site of Al Wusta, 3km from Ti's al Ghaddah, similar lacustrine chert was the main raw material used by hominins[20]. Despite difficulties in knapping such material, the artefacts are finely made and similar to one another in terms of technology (Fig. 2A). The lithics consist of small flakes struck from prepared cores and a side-retouched flake ('side scraper').

In addition, associated faunal material includes two medium-sized ungulate rib fragments that bear tentatively assigned cut marks (TAG13/133 and TAG13/900; Fig. 2D and E). These markings are V-shaped in cross-section and run parallel to each other and either perpendicular or obliquely to the long axis of the bone. Shoulder effect and shoulder flaking

is apparent, the latter in the form of Hertzian cones. No internal microstriations were observed, although fine-scale features, such as microstriations, are quickly removed during chemical alteration[37]. The direction and location of the markings is consistent with cut marks produced during filleting of meat from around the rib[38]. Notches with a broad arcuate planform and conchoidal medullary flake scar, reminiscent of notches produced during hammerstone percussion, were also identified and suggest hominins may have broken open long bones to exploit marrow (Suppelementary Text 4; Figs 2B and Suppelementary Figure 12). Together with the evidence of the newly-identified associated lithics, this makes Ti's al Ghadah the first, at least partially anthropogenic faunal assemblage from the Arabian Peninsula in the Pleistocene.

The $\delta^{13}C$ data from all of the sampled fossil mammals (elephants, *Oryx* sp., hartebeest, equids, and unidentified bovids) associated with this hominin presence show an unequivocal dominance of C_4 vegetation in the diets of herbivores ($\delta^{13}C$ range = -0.8 to 3.3‰), (Fig. 3) (Supplementary Table 5), and suggests that rainfall occurred during the warm season. The $\delta^{13}C$ evidence also fits with climate simulations suggesting that the periodic amelioration of Arabian environments reflects the incursion of the African monsoon system[10]. The uniformity of C_4 consumption by all animals suggests the presence of extensive, productive C_4 grasslands in the vicinity of the palaeolake. The $\delta^{18}O$ range of fauna from Ti's al Ghadah is high ($\delta^{18}O$ range = -5.6 to 6.2‰) – though not higher than Pliocene, Pleistocene, and contemporary African ecosystems[34-35,39-40]. Differences in $\delta^{18}O$ between obligate drinking equids, hartebeest, and elephants and non-obligate drinking *Oryx* sp. allow more detailed estimations of relative environmental aridity to be made (Suppelementary Text 2).

The $\delta^{18}O$ difference (non-obligate drinker median = 0.0‰, obligate drinker median = 1.7‰, difference = 1.7‰) between these taxa is 6.0‰ lower than that found between modern equids/camels (median = 0.7‰) and Arabian oryx (8.4‰) in central Arabia today (difference = 7.7 ‰), demonstrating that conditions were considerably wetter in the region's past. This difference is compared to $\delta^{18}O$ datasets of obligate drinking and non-obligate drinking mammals in present day East Africa (where sample size for each group exceeds n=5) [35] (Fig. 4) (Supplementary Text 2; Supplementary Table 9). While caution is warranted given that taxon-specific habits could vary through time, when the difference between obligate and non-obligate drinker $\delta^{18}O$ from Ti's al Ghadah is compared to that of modern day Tsavo (1.7‰) and Laikipia (1.3‰), Middle Pleistocene ecological conditions in the interior of Arabia appear to approximate that of a relatively humid African savanna today (Fig. 4) (Supplementary Text 2). Such a reconstruction is supported by the results of a mixed ANOVA performed to compare the difference between obligate drinkers and non-obligate drinkers at each site (Supplementary Tables 10 and 11). While Tsavo and Laikipia show no significant difference between these 'drinker' groups, there is a significant difference found between these groups at Ti's al Ghadah.

There is no correlation between the $\delta^{13}C$ and $\delta^{18}O$ values in the Ti's al Ghadah fossil dataset (Multiple R-squared=0.04, $p<0.01$, adjusted R-squared=-0.01, $p<0.01$), indicating that access to vegetation was independent of factors affecting faunal $\delta^{18}O$. This is also borne out in sequential $\delta^{13}C$ and $\delta^{18}O$ analyses of selected fossil teeth that enables the identification of potential environmental seasonality or mobility. The sequential $\delta^{13}C$ data, from all taxa, document a homogeneous source of lush C_4 vegetation, likely in the form of grasses, at Ti's al Ghadah (Figs. 5-6, Supplementary Tables 5 and 7). This could either be linked to the persistence of C_4 vegetation in the western Nefud Desert or animal movements tracking seasonal availability of C_4 resources. Sequential $\delta^{18}O$ provided more insights in this regard and *Oryx* sp. $\delta^{18}O$ documents clear, sigmoidal fluctuations usually associated with seasonal

variations in regional environmental conditions rather than use of different water sources[36,40] – in this case seasonal variation in the evaporative stresses placed on plants consumed (Fig. 5). Similar, although dampened, sigmoidal curves can also be seen in the equid individuals sampled, suggesting seasonal changes in the level of evaporation affecting the drinking water imbibed by these individuals (Fig. 6). These results are consistent with environmental seasonality in ranges covered by the two taxa sampled. Furthermore, the difference in the degree of acuteness of these seasonal changes between the *Oryx* sp. and equids further highlights the validity of using the relative magnitude $\delta^{18}O$ distinctions between non-obligate and obligate drinking taxa as a palaeoaridity indicator.

The two *Palaeoloxodon recki* specimens demonstrate very little variation in either $\delta^{13}C$ or $\delta^{18}O$ through the formation of the tooth, suggesting reliable access to stable water bodies and C_4 grasses (Fig. 6). Given documentation of seasonal patterns in $\delta^{18}O$ in *Oryx* sp. and equids with more limited ranges, the fact that *Palaeoloxodon recki* documents limited changes suggests that these animals were migrating over much larger distances, perhaps following lake and river systems with relatively similar $\delta^{18}O$ values. Furthermore, geomorphological insights have also suggested that the T'is al Ghadah palaeolake would have been relatively shallow (Supplementary Text 1), further suggesting that *Palaeoloxodon recki* had to range to obtain enough water throughout the year. The potential undertaking of significant, long-distance migrations in search of water and vegetation would fit with the behaviours documented among African elephants today[41]. Furthermore, such results are also compatible with suggestions based on palaeolake and palaeoriver modeling, using Geographical Information Systems, that indicate that Ti's al Ghadah was not an isolated oasis, but rather part of a broader, often interconnected, chain of palaeolakes during wet intervals[19].

Discussion

The recovery of unambiguous hominin-produced lithic material, in association with evidence from the fossil record suggestive of hominin butchery activities, reported here and dated to *c*. 500-300 ka, represents the oldest dated hominin occupation in Arabia. While the small sample size makes detailed descriptions of the assemblage's lithic technology and cultural attributions currently difficult, they demonstrate a Middle Pleistocene hominin presence in Arabia. It is considerably older than the previously oldest site of Jebel Qattar-1 at *c*. 210 ka[23] and, alongside recent research[42], highlights the benefits of systematic, detailed taphonomic study of fossil material when exploring hominin arrival in different parts of the world. In addition to recent finds of *H. sapiens* in the Arabian interior *c*. 90 ka[20], the Ti's al Ghadah evidence highlights that focus on Pleistocene *Homo* expansions should not solely be limited to Eurasia, Africa, and the Levant. The identification of Afro-tropical, Saharao-Arabian, and Palearctic fauna[12-15] in association with hominin presence also highlights the possibility of Middle, and perhaps also Early, Pleistocene hominin migrations into the Arabian Peninsula from Africa and Eurasia. Future systematic survey and excavation will help to further constrain the chronology and nature of hominin dispersal into this part of the world.

The stable isotope data from fauna directly associated with these traces of hominin activity at Ti's al Ghadah provide detailed insights into palaeoaridity and palaeovegetation in this part of Arabia during periods of hominin migration. A substantial corpus of environmental data exists for the Late Pleistocene (from MIS7 onwards) documenting recurrent humid episodes[17,19,43-44] (Supplementary Text 5), although generally deficient knowledge of evapotranspiration and insufficient on-the-ground testing of the results of climate change models has led to limited understanding as to what 'wetter' represents in the context of regional vegetation and biomass. Meanwhile, modern Arabian landscapes, to which we might

look for analogues, have been heavily modified by Holocene anthropogenic activity. The situation is even worse for the Middle Pleistocene (pre-MIS6 on the MIS stage of the date mean). As Supplementary Table 13 shows (Supplementary Text 5), the majority of these three proxies from from three locales (the Hoti and Al Mukalla caves in Oman and Yemen, and the alluvial fan complexes of the Hajar mountains. Only a few exist for northern Arabia, demonstrating the importance of the Ti's al Ghadah assemblage for studying environmental conditions associated with hominin incurrences

The data presented here highlight the presence of abundant C_4 grasslands and aridity levels somewhat similar to those found in East Africa today. The comparison of obligate and non-obligate drinker stable oxygen isotopes has been little-developed beyond Africa, yet we hope to have shown here that this methodology could and should be applied to other parts of Asia, such as the Thar Desert, central Asia, and eastern Asia in order to develop more detailed understandings of hominin adaptations to semi-arid and arid environments in these parts of the world. The data reported here also fits with palaeoecological reconstructions based on the fossil taxa identified at T'is al Ghadah[12-15](Supplementary Table 2). The presence of various grassland taxa (*Palaeoloxodon* and an alcelaphine), fish and birds with strong affinities toward water (e.g. *Anas* and *Tachybaptus*) imply the presence of expansive grasses and large perennial water sources[12-15] (Supplementary Figure 3; Supplementary Table 2). The presence of a large felid (*Panthera gombaszoegensis*) and hyena indicate that the western Nefud Desert was also host to a substantial prey-biomass[13-14]. Alongside evidence from sequential isotopic analysis of the wide-ranging *Palaeoloxodom recki* reported here, attainment of lake sequences should also help to clarify wider, regional environmental trends during the earliest arrival of hominins into Arabia. Overall, however, Early and Middle Pleistocene hominin populations would seemingly have been able to extend not only into the Levant, but also deep into the Arabian Peninsula, potentially making use of access to a combination of African and Eurasian medium and large sized mammals, as well as similar grassland habitats[4,15,45].

The identification of Late Pleistocene *H. sapiens* and Middle Pleistocene hominins in the interior of the Arabian Peninsula opens up the possibility of exploring the adaptive capacities of different hominin taxa in what is, today, an extreme environment. The proto-global distribution of non-*H. sapiens* Middle Pleistocene *Homo*, as well as growing evidence for its cultural capacity[5-6], have been argued to represent a potential adaptive threshold, demonstrating the exploitation of new environments (e.g.[7,46]). In line with previous suggestions[4-15], we demonstrate that Middle Pleistocene hominin expansions into this region would not necessarily have required new innovations or adaptations to harsh desertic aridity and imply a range expansion similar to other large and medium sized mammal populations moving between Africa, the Levant, and Eurasia[15]. By contrast, although our own species was also reliant on periods of increased precipitation to access the Arabian Peninsula[20], it appears to have had a wide geographic spread[20-21,47], penetrating further into the dunefields and living under conditions that were perhaps harsher than their Middle Pleistocene predecessors[16,48]. Recent research in the Kalahari and Namib Deserts of southern Africa has also highlighted that our species was potentially uniquely able to occupy arid regions during periods of limited surface water in the Late Pleistocene[49-50]. Future work, and the application of palaeoenvironmental methodologies akin to that developed here, should enable further testing as to whether our species is ecologically unique within the genus *Homo*.

Methods

Lithic and faunal analysis

Lithic artefacts were recovered from Unit 5 of trench 6. The lithic material and debitage was measured, recorded, and drawn following previously published protocols[51].

Fossil identification and analysis was conducted at the Australian National University (ANU) and the University of New South Wales (UNSW), Australia, and facilitated by comparative osteological material. Each specimen was examined by eye and hand-lens (10-20x) and at different angles to identify fine-scale surface modifications that only become apparent at certain angles of light exposure. Bone surface modifications, such as tooth and percussion marks, were analyzed and recorded following standard methodologies for taphonomic analysis of fossil faunal assemblages (e.g. [52-53]). Cut marks are defined as V-shaped grooves and are often accompanied with features such as shoulder effect, flaking and microstriations[54], and were considered when analyzing modifications in this study. Markings suspected of being cut marks were further inspected by Scanning Electron Microscopy (SEM) (Supplementary Text 4). Notches were defined as circular to semi-circular breaks in the edge of midshaft fragments and are typically produced by both hominins and large carnivores when exploiting within bone nutrients (i.e. marrow)[52]. Dynamic loading forces associated with hammerstone percussion tend to produce notches that are wider and shallower than those generated by carnivores, allowing notches to be quantitatively differentiated. Notch morphology was determined following the protocol described in Capaldo and Blumenschine[52] and notches were compared to those generated by carnivores, un-modified hammerstones, and modified hammerstones under experimental settings[52,55](Supplementary Figure 13) (Supplementary Text 4).

Stable isotope analysis

Tooth enamel samples were selected from the available fauna from deposits at Ti's al Ghadah dated to *c*. 300-500 k*a* (Supplementary Texts 1 and 2, Supplementary Table 3). Fossil equids, extinct elephants, and hartebeest were targeted for stable oxygen isotope measurement as abundant obligate drinkers, while *Oryx* sp. comprise the non-obligate drinker sample from the site (Supplementary Text 2). To provide a modern baseline estimate of aridity in Saudi Arabia for these taxa, $\delta^{18}O$ measurements were made on modern equids (*Equus caballus*) (n=4) and camels (*Camelus dromedarius*) (n=2) reliant on oasis water and compared to the $\delta^{18}O$ of modern samples of Arabian oryx (*Oryx leucoryx*) (n=7) from the same region (Supplementary Text 2; Supplementary Table 4). Sequential $\delta^{13}C$ and $\delta^{18}O$ was also measured on two extinct elephant molars, three equids, and five *Oryx* sp. fossil teeth (Supplementary Texts 1 and 2). Fourier Transform Infrared Spectroscopy (FTIR) was used to assess enamel preservation (Supplementary Text 3).

21 samples were selected for stable carbon and oxygen isotope analysis of tooth enamel from the available fossil material from Unit 5 at Ti's al Ghadah. All teeth that could be confidently identified from excavations by the Palaeodeserts team between 2013 and 2014, as well as excavations by the Saudi Arabian Geological Survey in 2011 (Supplementary Table 3), were sampled. We selected 5 *Oryx* sp., 3 *Equid* sp. and 2 *Palaeoloxodon recki* teeth for additional, sequential analysis based on their completeness and robustness to endure additional sampling (Supplementary Table 3, Supplementary Tables 5-7). The 5 fossil *Oryx* sp. were, in turn, compared to 1 modern *Oryx* sp. (Supplementary Tables 4 and 8) in order to provide a modern baseline for seasonal changes in $\delta^{18}O$ in this non-obligate drinker.

All teeth or teeth fragments were cleaned using air-abrasion to remove any adhering external material. Enamel powder for bulk analysis was obtained using gentle abrasion with a

diamond-tipped drill along the full length of the buccal surface in order to ensure a representative measurement for the entire period of enamel formation. For sequential samples, each sample was a 1–2 mm-wide groove perpendicular to the tooth growth axis, through the thickness of the enamel layer. The distance of the base of each sample groove from the enamel/root junction from the furthest sample margin was recorded.

All enamel powder was pretreated to remove organic or secondary carbonate contaminates. This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified H_2O and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified H_2O (as per.[56-57]). Following reaction with 100% phosphoric acid, gases evolved from the samples were analyzed to stable carbon and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for the Science of Human History. Carbon and oxygen isotope values were compared against international standards (NBS 19, MERCK) registered by the International Atomic Energy Agency. Replicate analysis of OES standards suggests that machine measurement error is *c.* ± 0.1‰ for $\delta^{13}C$ and ± 0.2‰ for $\delta^{18}O$. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard (n=20, ± 0.2‰ for $\delta^{13}C$ and ± 0.3‰).

The relationship between $\delta^{18}O$ and Site and Group (obligate and non-obligate drinkers) was determined using a mixed Site*Group ANOVA comparative test, followed by post-hoc Tukey pair-wise comparisons. Statistical regression analyses were undertaken to discern the statistical correlation between $\delta^{13}C$ and $\delta^{18}O$ at Ti's al Ghadah. All statistical analyses were conducted using the free program R software[58].

Data availability

All data generated or analysed during this study are included in the published article and its supplementary information files.

Acknowledgments

The authors declare no conflict of interest.

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Author contributions:
PR, MS, and MP, planned the project. PR, MS, NA, PB, HSG, EMLS, JLT, JL, JZ, and ISZ performed the experiments. PR, MS, NA, PB, HSG, EMLS, JLT, JL, JZ, and ISZ performed data analysis. All authors interpreted the data. All authors wrote and provided comment on the paper.

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List of Figures:

Figure 1. Maps showing A) the position of the Ti's al Ghadah fossil site and the Mahazat as-Sayd Protected Area in the context of Saudi Arabia and B) A view of the Ti's al Ghadah basin showing in blue the extent of the lacustrine deposit overlying the main fossil faunal deposit.

Figure 2. A) chert flakes with dihedral striking platforms (i, iii and iv) and a side retouched flake (ii). B) medium-sized bovid proximal metacarpal (TAG14/121) in cortical (i) and medullary (ii and iii) view. In the inset a wide striae field (white box) is visible adjacent the flake scar (dashed line). A adhering bone flake (arrow) and conchoidal flake scar (dashed line) are visible from the medullary. The refitted piece (iii) exhibits a smooth, oblique fracture pattern indicating the bone was broken while fresh. C) a tibia shaft fragment (TAG14/9235) in cortical (i) and medullary (ii) view. An indeterminate narrow, V-shaped groove with a forked end (arrows) runs parallel to the long axis of the bone. A conchoidal flake scar is present on the medullary surface (dashed line). D) dorsal view (i) of a medium-sized mammalian rib fragment (TAG13/900) with two probable cut marks that run obliquely to the long axis of the rib. Shoulder effect (arrows) is clearly visible in the SEM image (ii). E) a medium-sized mammalian rib fragment (TAG13/133) with multiple parallel grooves running perpendicular to the long axis of the bone and shoulder effect in the form of Hertzian cones (triangles) that are clearly visible in the SEM image (ii). F) a medium-sized bovid metapodial shaft fragment (TAG14/9257) in cortical (ii) and medullary (ii) view with multiple opposing notches and conchoidal flake scars (dashed lines), and numerous carnivore tooth scores (arrows), suggesting the bone was broken open by a large carnivore. G) medium-size mammalian shaft bone flake (TAG13/9134) in medullary (i) and cortical (ii) view. Smooth and oblique fracture pattern indicates the bone was broken while fresh and likely by a dynamic force. The surface exhibits pitting (arrows) and the bone flake has tentatively been attributed to be the result of hammerstone percussion. Solid scale bar = 20 mm. Dashed scale bar = 0.5 mm.

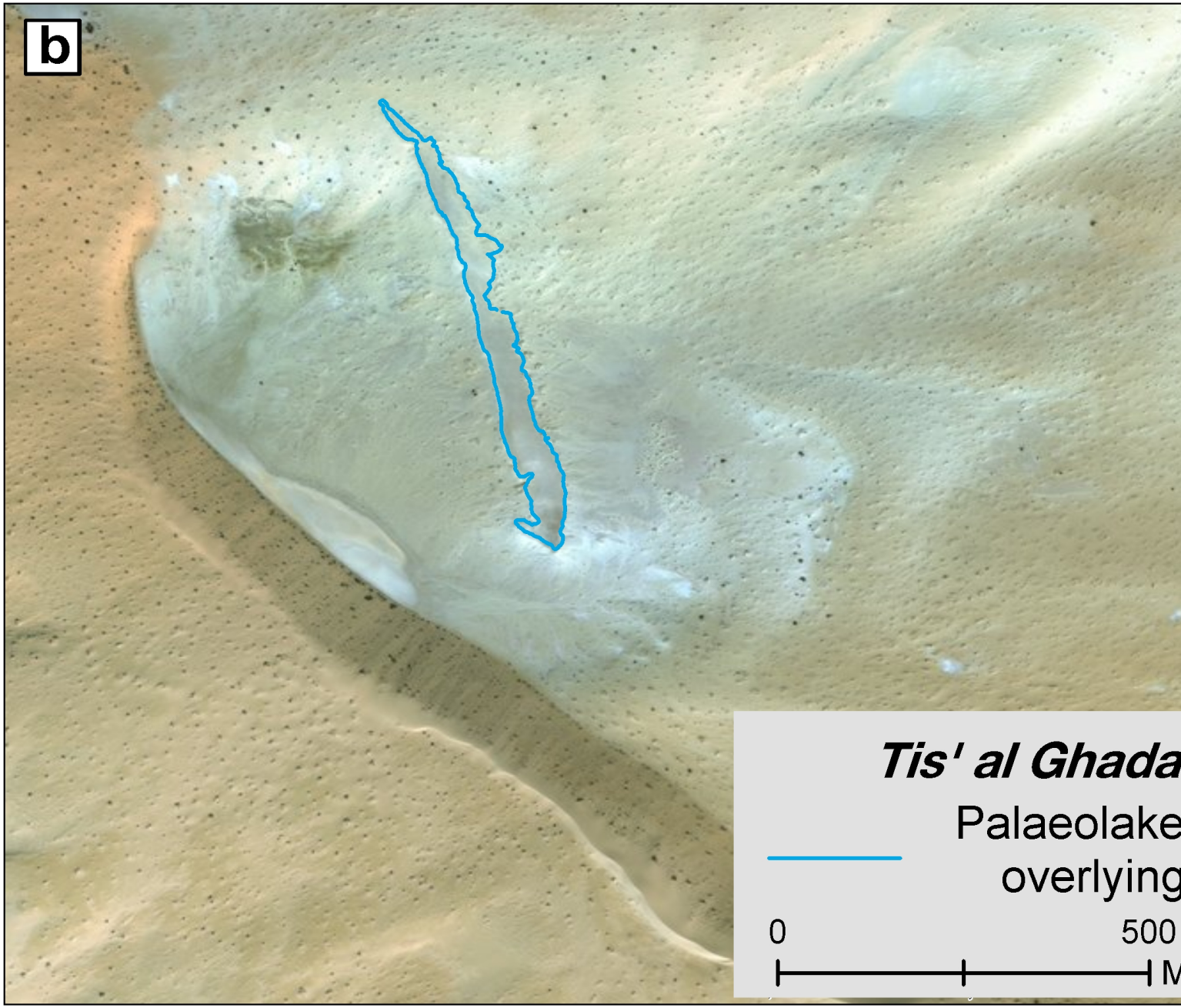
Figure 3. $\delta^{13}C$ and $\delta^{18}O$ measurements from the tooth enamel of fossil fauna from Ti's al Ghadah, Saudi Arabia analyzed in this study. VPDB, Vienna PeeDee Belemnite.

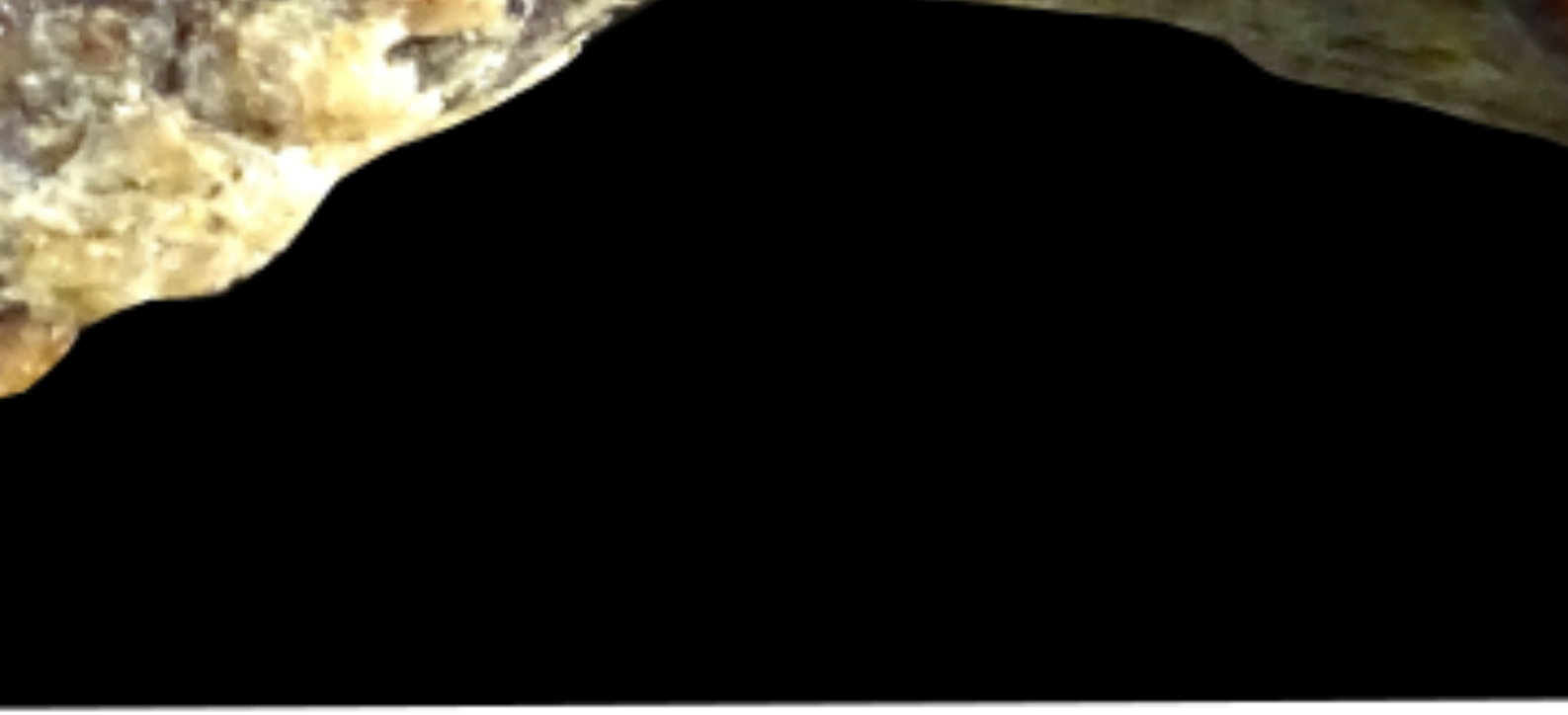
Figure 4. $\delta^{18}O$ values for non-obligate and obligate drinking taxa at the East African localities of Laikipia (Kenya) and Tsavo (Kenya) reported by Blumenthal et al.[35], for modern Saudi Arabia, and for the Middle Pleistocene Ti's al Ghadah (TAG) (Saudi Arabia) assemblage. Boxes show the median and the lower (25%) and upper (75%) quartiles; whiskers encompass all data points within 1.5 × the interquartile range of the box. VPDB, Vienna PeeDee Belemnite.

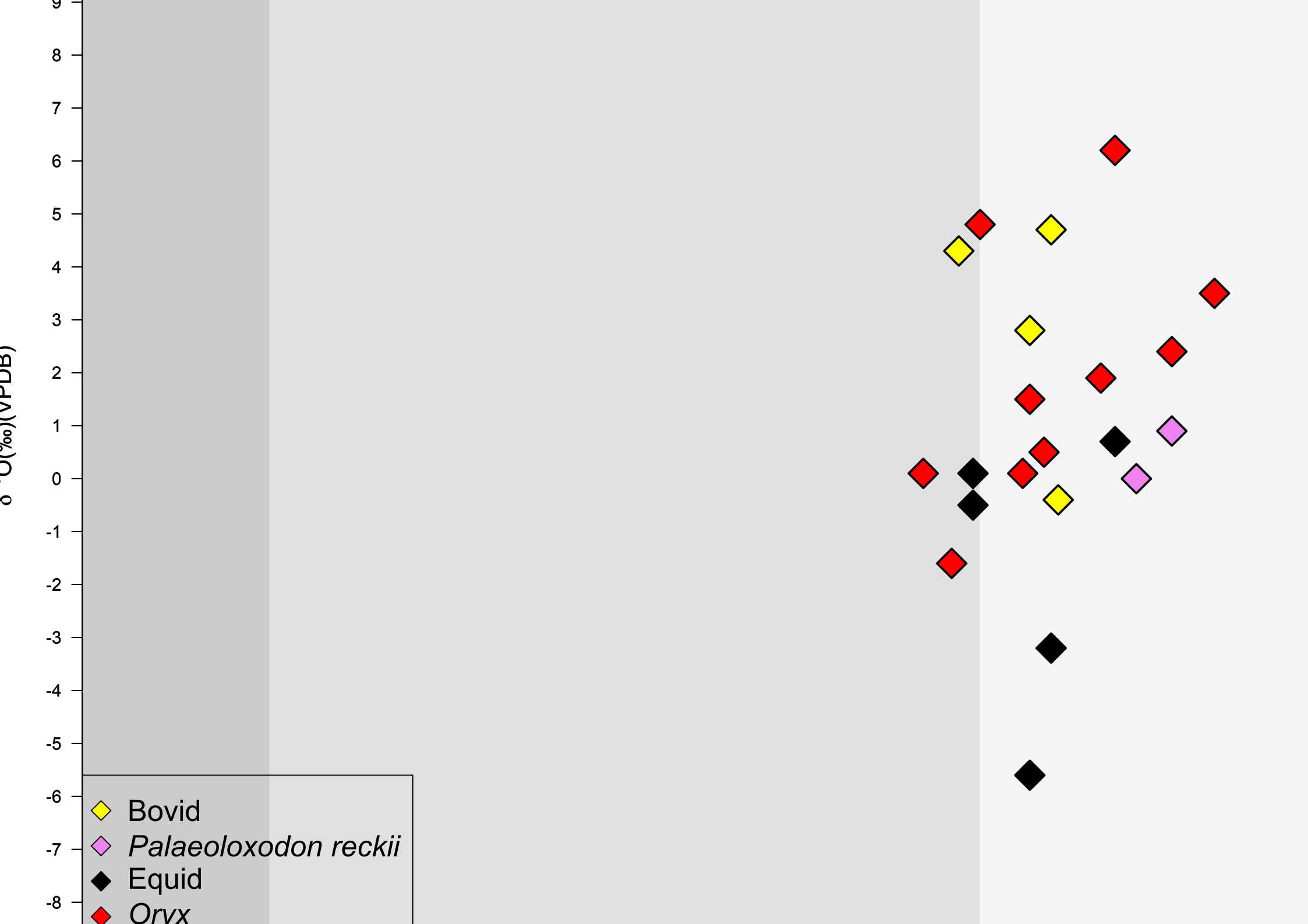
Figure 5. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements for *Oryx* sp. samples TAG 1551, TAG 1541, TAG 149, TAG 942, and TAG 944 from the Middle Pleistocene levels of T'is al Ghadah and one modern Oryx sp. sample from the Mahazat as-Sayd Protected Area. VPDB, Vienna PeeDee Belemnite.

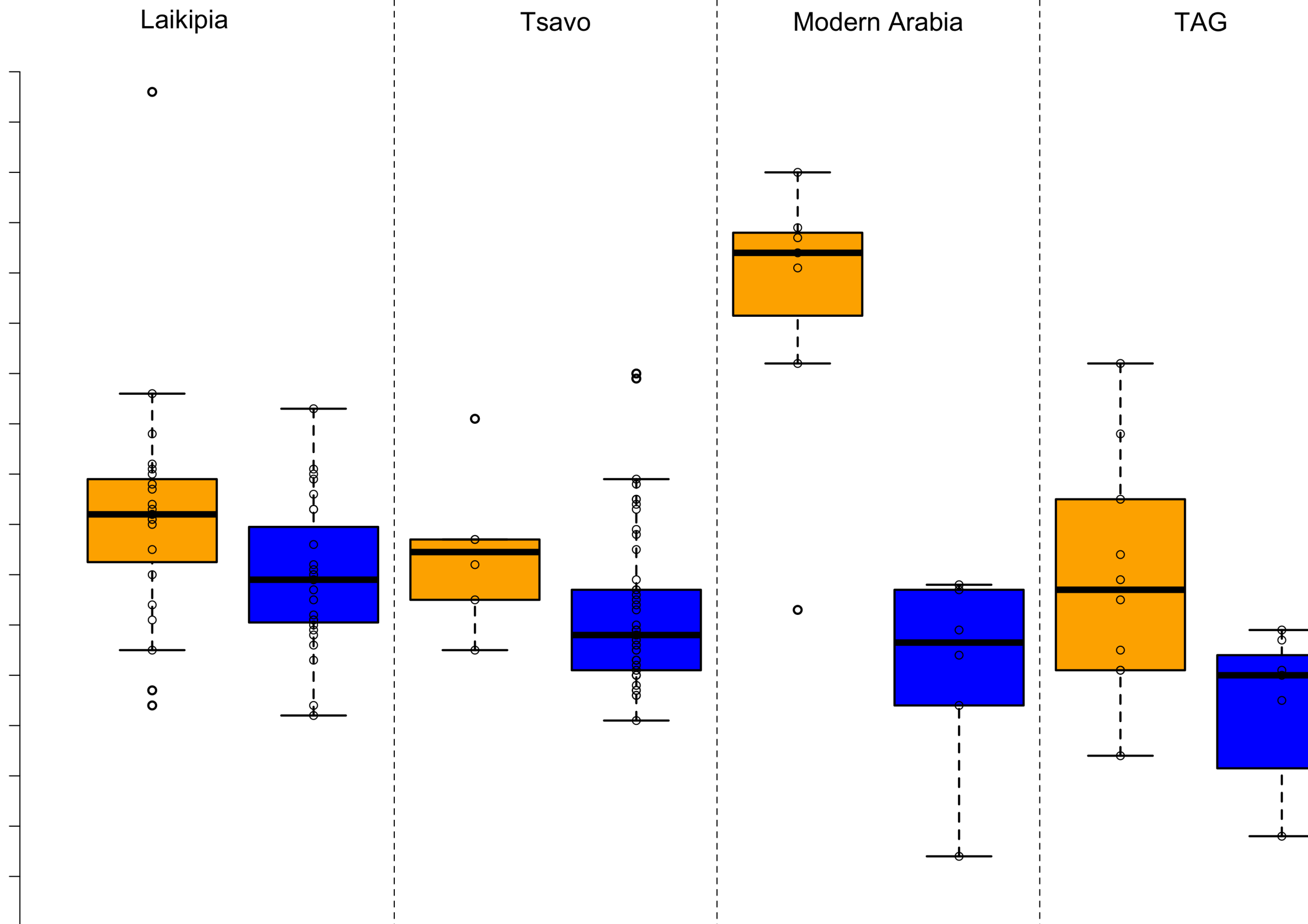
Figure 6. Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements for equid samples SGS180, SGS57 and SGS1094 and *Palaeoloxodon reckii* samples TAG14 301 and TAG14 129 from the Middle Pleistocene levels of T'is al Ghadah. VPDB, Vienna PeeDee Belemnite.

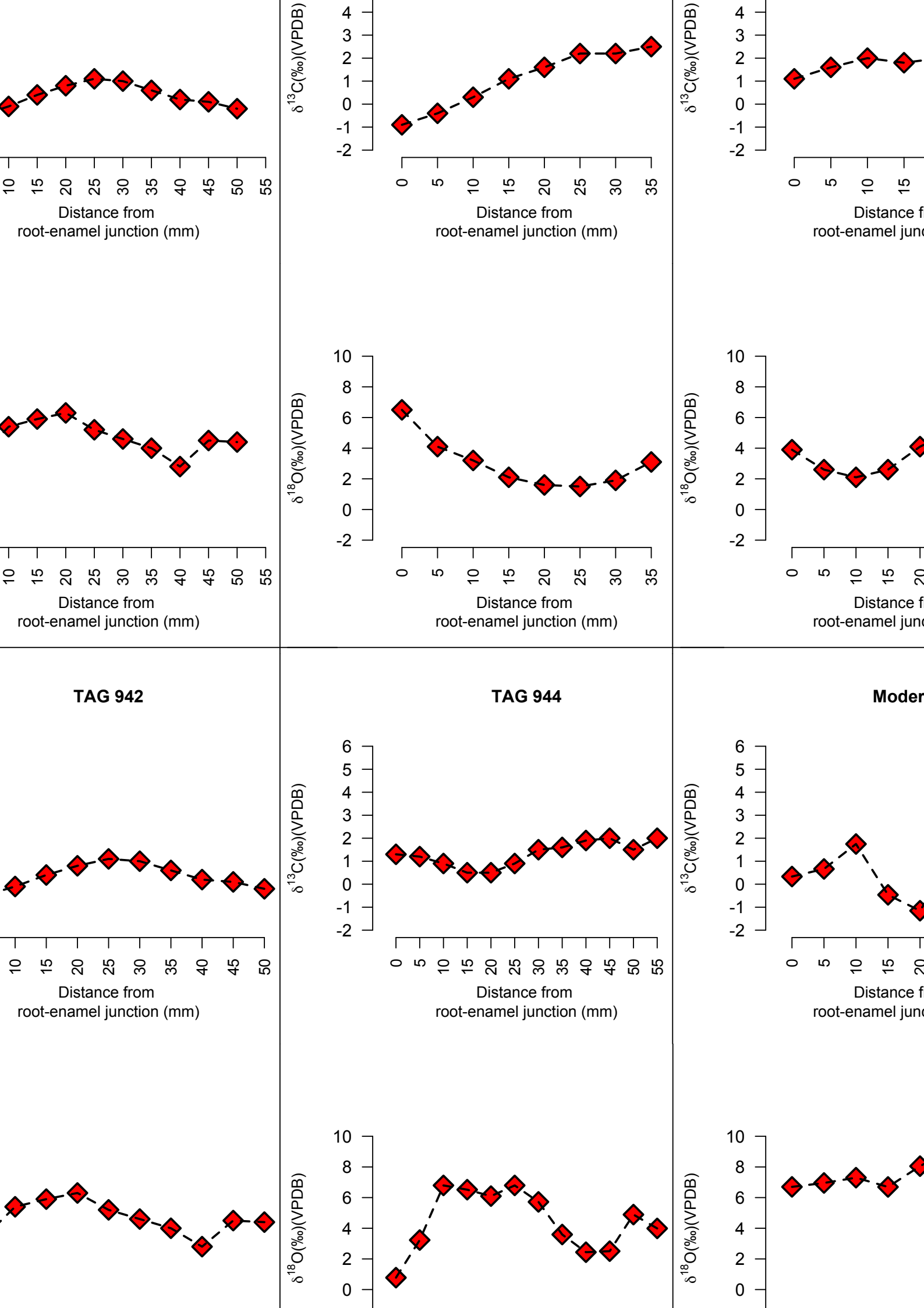

hadah (b)
Mahazat as-Sayd
Protected Area
N
0
500
km

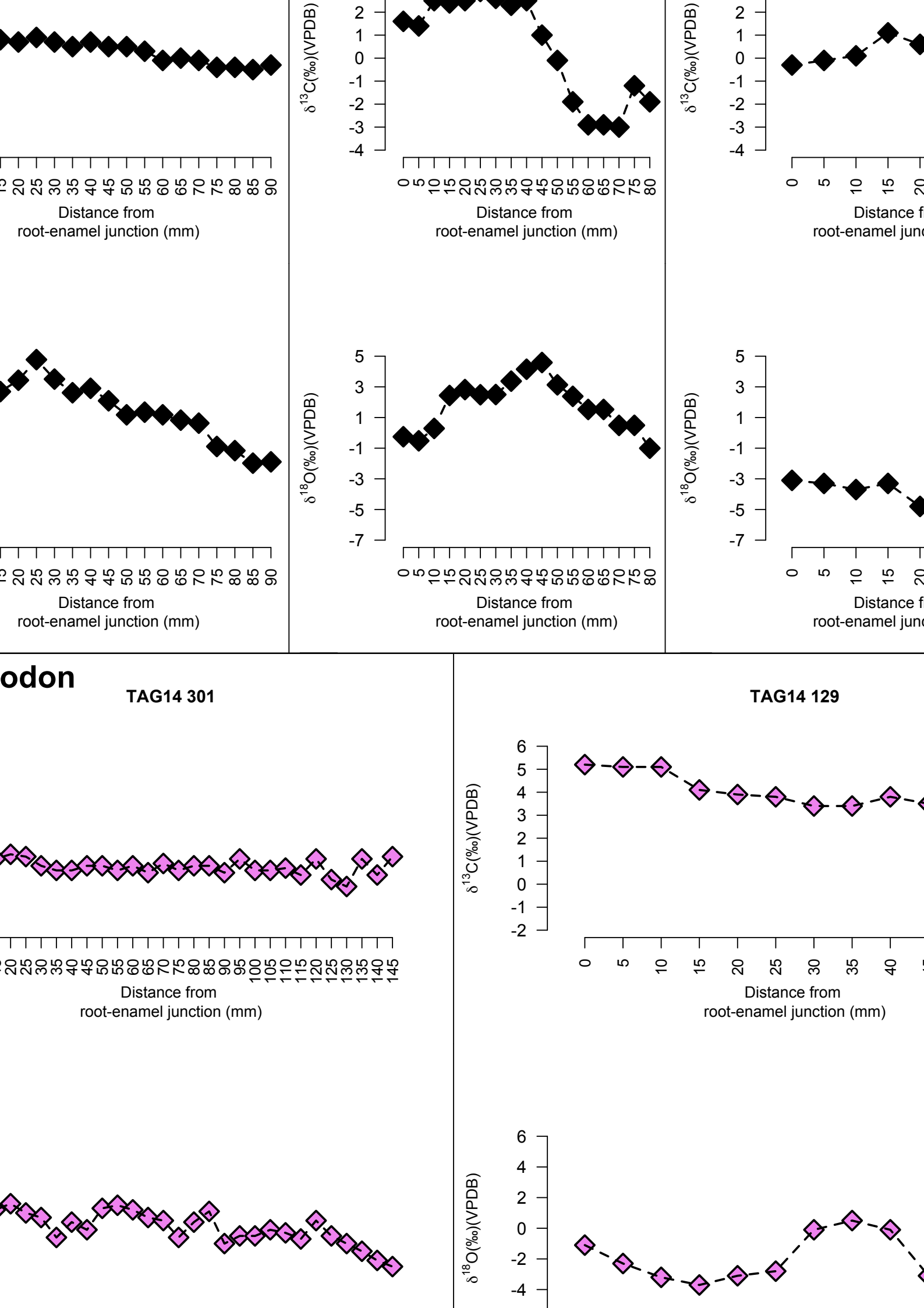

b
Tis' al Ghada
Palaeolake
overlying
0
500




δ 18O(‰)(VPDB)
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
-6
-7
-8
Bovid
Palaeoloxodon reckii
Equid
Oryx


Laikipia
Tsavo
Modern Arabia
TAG


TAG 942
TAG 944
Moder
δ13C(‰)(VPDB)
δ18O(‰)(VPDB)
Distance from
root-enamel junction (mm)


odon
TAG14 301
TAG14 129
δ13C(‰)(VPDB)
δ18O(‰)(VPDB)
Distance from
root-enamel junction (mm)