12 FIRST STABLE ISOTOPE RESULTS ON THE ECOLOGY OF THE STRAIGHT-TUSKED ELEPHANT (*PALAEOLOXODON ANTIQUUS*) FROM THE MIDDLE PLEISTOCENE MARATHOUSA 1 (PELOPONNESE, GREECE)

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12.1 INTRODUCTION

Carbon and oxygen stable isotope analysis of mammalian carbonate bioapatite is, nowadays, a well-established and widely used approach for past ecological investigations and paleoenvironmental reconstructions. Carbon is incorporated into mammalian tissues through their dietary intake. In this regard, the ratios of stable carbon isotopes in the tissues of primary consumers—hereafter expressed using the delta (δ) notation, wherein $\delta^{13}C=[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1] \times 1000$—reflect the isotopic composition of the ingested plant matter (DeNiro and Epstein, 1978), enriched by ~14.1 ± 0.5‰ in tooth enamel carbonate of large herbivores (Cerling and Harris, 1999; Passey et al., 2005), due to physiological and metabolic processes. In terrestrial ecosystems, variation in the isotopic signature of plant carbon permits a distinction between the two main photosynthetic pathways, i.e., C_4 and C_3 (Ehleringer and Monson, 1993), with the former group consisting of warm growth season grasses and forbs, which demonstrate higher average $\delta^{13}C$ value (~–13‰), and the latter incorporating trees, shrubs, and cool growth season grasses and sedges with a modern aver-

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age $\delta^{13}C$ value of ~–27‰ (Bender, 1971; Kohn, 2010). Within plant communities utilizing the C_3 photosynthetic pathway, additional environmentally controlled fractionation occurs, which is governed by multiple factors, such as degree of canopy closure, water availability, temperature, irradiance, or atmospheric CO_2 diffusion (van der Merwe and Medina, 1991; Heaton, 1999; Hofman-Kamińska et al., 2018). The interplay of these factors enables further habitat distinctions within the wide range of $\delta^{13}C$ values documented in C_3-dominated ecosystems, since carbon isotopic ratios of herbivores feeding under closed canopy conditions, i.e., dense forests, tend to be lower than for herbivores foraging in open woodlands, open parklands and grasslands, or at the top of the canopy (Drucker et al., 2008; Bocherens and Drucker, 2013).

Oxygen stable isotopic ratios in the skeletal tissues of large mammals essentially reflect those of ingested water. Variation in the isotopic composition of the latter occurs as a result of several geospatial, climatic, and environmental parameters, for instance degree of continentality, altitudinal differences, amount of precipitation, temperature, as well as differences in the hydrological processes of water bodies (for a detailed overview see Pederzani and Britton, 2019). In organisms that acquire water predominantly from drinking, i.e., obligate drinkers, oxygen stable isotopes track primarily the isotopic composition of the local meteoric water (Kohn and Cerling, 2002). In middle and high latitudes, the $\delta^{18}O$— provided by the equation $[(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{standard} - 1] \times 1000$ —of meteoric water is considered to be mainly associated with surface temperature and local precipitation (Fricke and O'Neil, 1996), where higher $\delta^{18}O$ values are observed in warmer and drier environments but lower values indicate colder or more humid periods (Bocherens and Drucker, 2013; Pederzani and Britton, 2019).

Figure 1: Map showing the location of European sites with available stable isotope data for *Palaeoloxodon antiquus* (made with Natural Earth, naturalearthdata.com).

Systematic excavations at the Middle Pleistocene open-air site Marathousa 1 (MAR-1) in the Megalopolis Basin (Peloponnese, Greece) revealed the partial skeleton of a straight-tusked elephant (*Palaeoloxodon antiquus*). The elephant was found at the base of the find-bearing sedimentary Unit 3 in Area A and is stratigraphically and spatially associated with lithic artefacts, and faunal (ostracods, molluscs, fishes, amphibians, reptiles, birds, mammals) and floral remains (see Harvati et al., 2018; Panagopoulou et al., 2018). The archaeological deposits are dated to ca. 450 ka and are correlated to the glacial Marine Isotope Stage 12 (Doukas et al., 2018; Jacobs et al., 2018; Karkanas et al., 2018; Tourloukis et al., 2018). The elephant skeleton belongs to a male individual with an estimated upper limit of its ontogenetic age between 64–71 years based on the tooth wear of the preserved upper third molars, which is also consistent with the extent of epiphyseal fusion of the skeletal elements (Konidaris et al., 2018). Additionally, the taphonomic study of the elephant's remains revealed cutmarks on some of the skeletal elements, indicating hominin exploitation of the carcass (Konidaris et al., 2018), while the traceological analysis of stone-tools further confirms that they were used in butchering activities (Guibert-Cardin et al., 2022).

In this study, we employ stable isotope analysis on enamel carbonates in order to reconstruct the average diet, and, subsequently, the preferred foraging habitat of the MAR-1 elephant. Since evidence of butchering directly associates the specimen with hominin activity, the resulting paleoenvironmental data can be used to infer the conditions surrounding hominin presence in the Megalopolis Basin. Because only one individual was available for analysis, we compared our results with published isotopic data for *Palaeoloxodon antiquus* from other European Middle Pleistocene localities, namely La Polledrara di Cecanibbio, Casal de' Pazzi (Palombo et al., 2005), and Poggetti Vecchi (Capalbo, 2018) in Italy; Neumark-Nord 1 (Grube et al., 2010), Steinheim an der Murr, and Mauer (Pushkina et al., 2014) in Germany (Fig. 1).

12.2 MATERIALS AND METHODS

We sampled the second distalmost lamella of the right upper third molar. The sample's surface was mechanically cleaned with a diamond-tipped handheld rotary tool to remove cementum and expose the enamel. Subsequently, the first few millimeters of the enamel layer were also removed to avoid contamination (Koch et al., 1997). Multiple samples were drilled perpendicularly across the tooth-growth axis, each yielding approximately 15 mg of enamel powder. Here, we present the average value obtained by analyzing the individual samples, to simulate a bulk-sampling strategy for the sake of comparison with other published records.

Following the pretreatment protocol described by Bocherens et al. (1994) and Koch et al. (1997), 1.35 ml of 2.5% sodium hypochlorite (NaOCl) was added to the sample vials, homogenized with high-speed vibration, and left to react for 24 hours to remove organic matter. Subsequently, the samples were centrifuged at 35000 rounds/minute for 3 minutes, the solution was removed, and the contents were rinsed repeatedly with MilliQ water. Next, a 1M Acetic Acid Buffer solution was added and left to react with the samples for 24 hours, to remove nonstructural carbonates. After the acetic acid buffer was extracted, the samples were rinsed three times with MilliQ H_2O and dried at 35°C for 72 hours. This process produced approximately 3 mg of purified biogenic apatite, which was reacted with concentrated orthophosphoric acid (H_3PO_4) to release CO_2. Stable isotope ratios were then obtained by analyzing the gaseous CO_2 with continuous multi-flow isotope ratio mass spectrometry (IRMS) at the University of Tübingen. Two international standards, IAEA-603 (Interna-

tional Atomic Energy Agency) and NBS-18 (National Bureau of Standards, now National Institute

$$\delta^{j}X = \frac{(^{j}X/^{i}X)_{sample}}{(^{j}X/^{i}X)_{standard}} - 1$$

of Standards and Technology or NIST), as well as three in-house standards were used for calibration. Results are expressed using the standard δ notation:

where ^{j}X is the heavier isotope and ^{i}X is the lighter isotope (Bond and Hobson, 2012). Measured ratios refer to $^{13}C/^{12}C_{VPDB}$ or $^{18}O/^{16}O_{VSMOW}$, wherein VPDB is Vienna Peedee Belemnite and VSMOW is Vienna Standard Mean Ocean Water.

12.3 RESULTS AND DISCUSSION

The mean $\delta^{13}C$ of the structural carbonate from the enamel of the straight-tusked elephant from MAR-1 is –11.2‰ (VPDB). The value falls within the expected range for a diet consisting purely of C_3 vegetation (–19.5‰ – –8.0‰ VPDB) after applying an enrichment factor of 1.5‰ (Koch et al., 2004; Tipple et al., 2010) to account for the difference in Pleistocene atmospheric CO_2 values relative to present day, due to the effects of fossil fuel burning. Furthermore, a mesic habitat consisting of open woodland can be deduced, considering that, in temperate environments, $\delta^{13}C$ values of Pleistocene herbivores lower than ~–14‰ indicate foraging under closed canopy forests, whereas values between –14‰ and –8‰ suggest more open landscapes (Farquhar et al., 1989; Ehleringer and Monson, 1993; Bocherens, 2003; Domingo et al., 2017; Metcalfe, 2021).

Similar results were obtained from the carbon stable isotope analysis of a *Palaeoloxodon antiquus* individual from the Middle Pleistocene site of Poggetti Vecchi (Italy, MIS 7), which yielded an average $\delta^{13}C$ value of –11.05‰ VPDB (Capalbo, 2018). Additionally, the $\delta^{13}C$ value of the MAR-1 specimen falls within the range of $\delta^{13}C$ values (from –13.7‰ to –9.9‰ VPDB) obtained for the straight-tusked elephant population of Casal de' Pazzi (Italy, MIS 7; Palombo et al., 2005). In contrast, results from La Polledrara di Cecanibbio (Italy, MIS 9) demonstrated higher $\delta^{13}C$ values (from –9‰ to –10.9‰ VPDB) (Palombo et al., 2005), suggesting that this population was feeding in a drier environment with more open C_3 vegetation compared to the MAR-1 elephant, and the majority of the specimens from Italy correlated with MIS 7. The $\delta^{13}C$ values of *P. antiquus* specimens from three sites in Germany, namely Neumark-Nord 1 (MIS 5; Grube et al., 2010), Steinheim an der Murr (MIS 11; Pushkina et al., 2014), and Mauer (MIS 15; Pushkina et al., 2014), appear to be lower than those of the MAR-1 specimen (Fig. 2), suggesting more forested and humid environments for the German localities.

With respect to oxygen isotope ratios, the average $\delta^{18}O$ value of the enamel bioapatite for the MAR-1 elephant (+23.5‰ VSMOW) plots lower than those of the Italian *P. antiquus* specimens correlated with MIS 7 and MIS 9, with values ranging between +24.8‰ and +27.6‰ VSMOW (Fig. 2). Higher oxygen isotopic values (+25.5‰ – +28.0‰ VSMOW) were also obtained for the specimens of Neumark-Nord 1 in Germany during MIS 5. However, in juxtaposition with the results obtained for the elephants of Steinheim an der Murr and Mauer, the MAR-1 elephant demonstrates a higher $\delta^{18}O$ value. This likely indicates that the interglacial specimens from La Polledrara, Casal de' Pazzi, and Poggetti Vecchi in Italy, as well as those of Neumark-Nord 1, experienced warmer or more arid climatic conditions compared to the MAR-1 elephant, whereas cooler or more humid conditions characterize the environment of the interglacial populations from Steinheim an der Murr and Mauer in Germany. The influence of continentality may have also contributed in part to this pattern, specifically concerning the comparison of

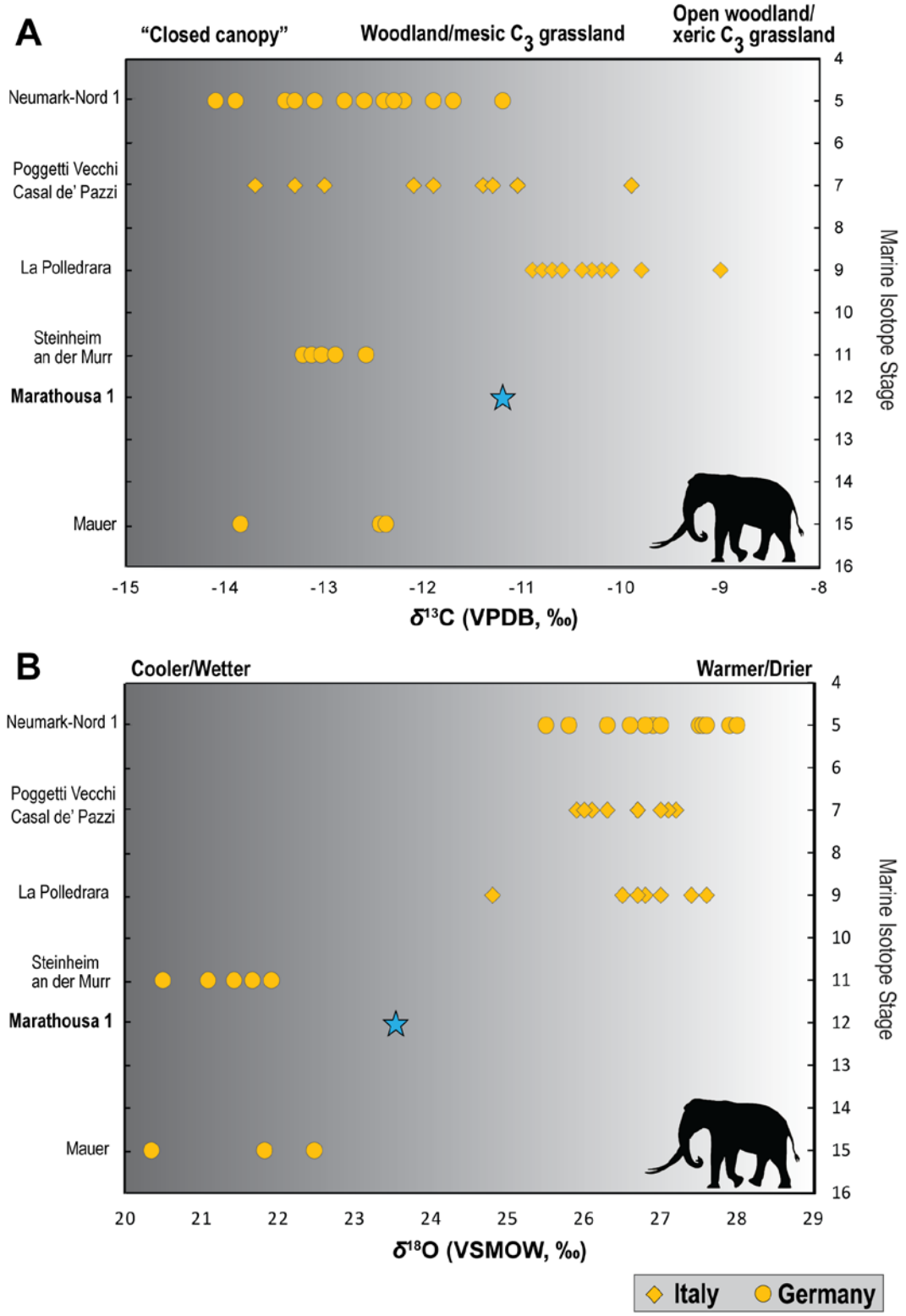

Figure 2: A, mean $\delta^{13}C$ values and B, mean $\delta^{18}O$ values for the straight-tusked elephant (*Palaeoloxodon antiquus*) of Marathousa 1 (MAR-1) compared to published *Palaeoloxodon* isotopic data from other European Middle Pleistocene localities. Marathousa 1 is the single locality correlated with a glacial stage.

the Mediterranean sites with data from Germany, wherein values are expected to become more ^{18}O-depleted as distance from the coast increases.

Overall, the results are compatible with the correlation of the archaeological sequence from MAR-1 with a glacial stage (MIS 12; see also Boni et al., this volume; Butiseacă et al., this volume; Kyrikou et al., this volume), reflecting colder conditions in the eastern European peri-Mediterranean region during glacial stages. Nevertheless, the carbon and oxygen isotopic composition of the studied elephant individual suggests that moderately humid conditions likely persisted in the Megalopolis Basin, which, in turn, supported abundant C_3 vegetation cover. This indicates that the effects of the glaciation in the area were less severe, creating conditions that provided essential subsistence resources to both fauna and hominins, therefore aiding their survival.

CONCLUSIONS

The preliminary results of the stable isotope study on the *Palaeoloxodon antiquus* from the Middle Pleistocene of Marathousa 1 highlight the significance of the method in obtaining important palaeoecological insights from an individual organism with the prospect of addressing broader paleoenvironmental concepts. The present study provides additional support to the hypothesis that the region acted as a refugium for fauna and hominins through the palaeoecological characterization of the individual. Future research will focus on the investigation of intra-tooth isotopic profiles with the aim to obtain temporally high-resolution palaeoecological data and investigate in greater detail potential sources of variation in the isotopic composition of the individual, such as possible seasonal fluctuations in resource availability.

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