



# Tooth enamel stable isotopes of Holocene and Pleistocene fossil fauna reveal glacial and interglacial paleoenvironments of hominins in Indonesia



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## ABSTRACT

The carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope compositions of fossilized animal tissues have become important proxies of paleodiet and paleoenvironment, but such stable isotope studies have not yet been extensively applied to the fossil assemblages of Sundaland (the biogeographical region comprising most of the Indonesian Archipelago). Here, we use the isotope composition of tooth enamel to investigate the diet and habitat of bovids, cervids, and suids from several Holocene and Pleistocene sites on Java and Sumatra. Our carbon isotope results indicate that individual sites are strongly dominated by either C<sub>3</sub>-browsers or C<sub>4</sub>-grazers. Herbivores from the Padang Highlands (Sumatra) and Hoekgrot (Java) cave faunas were mainly C<sub>3</sub>-browsers, while herbivores from *Homo erectus*-bearing sites Trinil and Sangiran (Java) utilized an almost exclusive C<sub>4</sub> diet. The suids from all sites show a wide range of  $\delta^{13}\text{C}$  values, corroborating their omnivorous diet. For the dataset as a whole, oxygen and carbon isotope values are positively correlated. This suggests that isotopic enrichment of rainwater and vegetation  $\delta^{18}\text{O}$  values coincides with an increase of C<sub>4</sub>-grasslands. We interpret this pattern to mainly reflect the environmental contrast between glacial (drier, more C<sub>4</sub>) and interglacial (wetter, more C<sub>3</sub>) conditions. Intermediate herbivore  $\delta^{13}\text{C}$  values indicating mixed C<sub>3</sub>/C<sub>4</sub> feeding is relatively rare, which we believe to reflect the abruptness of the transition between glacial and interglacial precipitation regimes in Sundaland. For seven *Homo erectus* bone samples we were not able to distinguish between diagenetic overprint and original isotope values, underlining the need to apply this isotopic approach to *Homo erectus* tooth enamel instead of bone. Importantly, our present results on herbivore and omnivore faunas provide the isotopic framework that will allow interpretation of such *Homo erectus* enamel isotope data.

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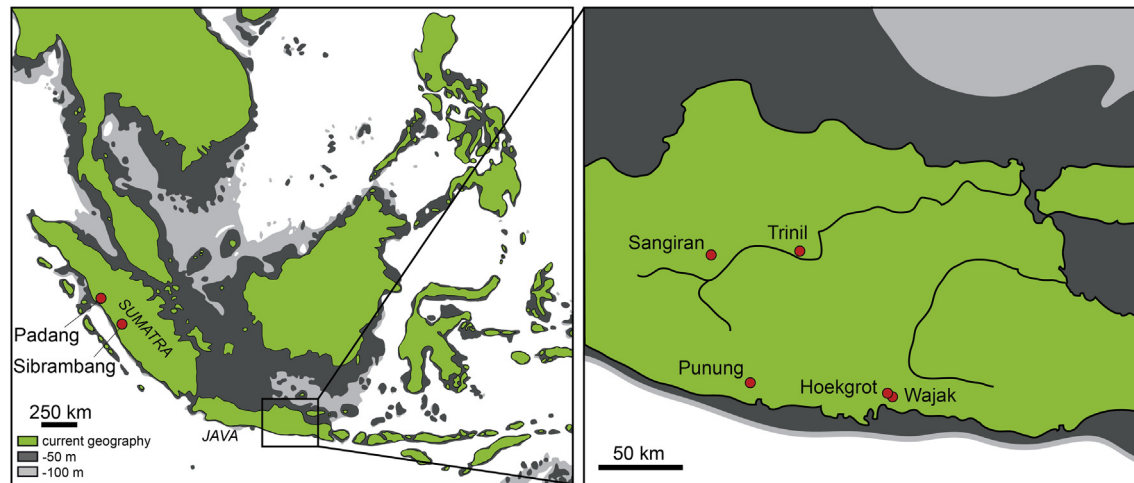
## 1. Introduction

Sundaland, a biogeographical region comprising Malaysia and the western part of Indonesia, is a well-studied biodiversity hotspot (e.g. Myers et al., 2000; den Tex et al., 2010; Lim et al., 2010). To a large extent, climate controls biodiversity dynamics in this region

(Woodruff, 2010). Glacial-interglacial cycles generate eustatic sea-level fluctuations, periodically turning the western islands of the Indonesian Archipelago into mountain ranges on the sub-aerially exposed Sunda Shelf (Hutchison, 1989; Voris, 2000, Fig. 1). The recurring land connection and greater extent of more open vegetation during glacial periods enabled repeated biotic migrations from mainland Asia into Sundaland. Subsequent isolation during interglacial periods encouraged genetic divergence and speciation of these faunas (von Koenigswald, 1935; Hanebuth et al., 2011; Slik

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**Fig. 1.** Map of Sundaland (left) and central Java (right), adapted from Voris (2000) and Sathiamurthy and Voris (2006), showing the extent of the Sunda plains sub-aerially exposed during glacial periods when the sea drops to respectively  $-50$  and  $-100$  m below its current level. The red dots indicate locations from which material sampled in this study originates, see Table 1.

et al., 2011; Leonard et al., 2015).

A long history of paleontological research in the Indonesian Archipelago has captured the resulting biodiversity changes in rich and well-documented faunal collections (e.g. Van den Bergh et al., 2001). Arguably among the most iconic discoveries are specimens of the hominin *Homo erectus* found at Trinil, Sangiran, and several other locations on Java (e.g. Dubois, 1894, 1896; Sartono, 1968, 1971; Kaifu et al., 2005a,b; Huffman et al., 2006; Kaifu, 2006; Indriati and Antón, 2008; Huffman et al., 2010; Zaim et al., 2011; Antón, 2013). Altogether the Indonesian fossil collections contain a wealth of Pleistocene and Holocene terrestrial faunas, with taxonomic compositions suggesting diverse paleohabitat conditions.

In this study, we aim to further expand our knowledge of available resources and ecological niches in Sundaland paleohabitats, and examine what this reveals about the climatic background of these environments inhabited by early humans. To achieve this we use carbon and oxygen isotope ratios in tooth enamel of seven Sundaland fossil fauna sites as a proxy for paleodiet and paleoecology of the faunas under study. This is the first time that such an extensive isotopic approach is applied to fossil faunas from Sundaland sites.

## 2. Background

The carbon isotopic composition ( $\delta^{13}\text{C}$ ) in mammalian bones and teeth records dietary  $\delta^{13}\text{C}$  values, with a fixed fractionation factor of  $\sim 13\text{‰}$  for the tooth enamel of most large mammalian herbivores (Lee-Thorp et al., 1989; Passey et al., 2005) and  $\sim 14.1\text{‰}$  for the tooth enamel of ungulates (hoofed animals) in particular (Cerling and Harris, 1999). For enamel there is limited, if any  $\delta^{13}\text{C}$  fractionation as one moves to the carnivores higher up the food chain (Lee-Thorp and Sponheimer, 2006). The  $\delta^{13}\text{C}$  of animal tissue thus ultimately records the  $\delta^{13}\text{C}$  value of the vegetation at the base of the food chain (DeNiro and Epstein, 1978). Trees and shrubs utilize the  $\text{C}_3$  photosynthetic pathway, whereas many tropical grasses and sedges are  $\text{C}_4$ -type photosynthesizers (Calvin and Bassham, 1962; Hatch and Slack, 1966). The  $\delta^{13}\text{C}$  ranges of  $\text{C}_3$  plants and  $\text{C}_4$  grasses differ by on average  $\sim 14\text{‰}$  and do not overlap (Smith and Epstein, 1971; Cerling et al., 1997). The  $\delta^{13}\text{C}$  values of  $\text{C}_3$  plants are considerably influenced by environmental factors: water stress results in higher  $\delta^{13}\text{C}$  values (Ehleringer and Cooper, 1988; Farquhar et al., 1989; Stewart et al., 1995; Abram et al., 2009;

Kohn, 2010), whereas a closed canopy environment shifts  $\delta^{13}\text{C}$  to very low values (Medina and Minchin, 1980; van der Merwe and Medina, 1991; Cerling et al., 1997; Kohn, 2010). More positive  $\delta^{13}\text{C}$  values in vegetation and animal tissues can thus be taken to indicate a habitat with more open vegetation. For this reason, tooth enamel  $\delta^{13}\text{C}$  has become an increasingly important paleodietary and paleoenvironmental proxy in southern and eastern African paleoanthropological studies (Lee-Thorp et al., 1994; Sponheimer et al., 2003; Sponheimer and Lee-Thorp, 2006; Levin et al., 2008; Cerling et al., 2013, 2015).

Previous studies suggest that the cycling between colder and drier glacials and warmer and more humid interglacials affect the relative abundance of open habitats on Sundaland. For instance, leaf wax records from Sulawesi in central Indonesia record a shift to more positive  $\delta^{13}\text{C}$  values during the Last Glacial Maximum (LGM), an indication of an increasingly open habitat and possibly an increase in  $\text{C}_4$  grasses (Russell et al., 2014; Wicaksono et al., 2015). Palynological evidence from Java indicates an increase of open swamp vegetation and grasslands in this time period (van der Kaars and Dam, 1997; van der Kaars et al., 2000). Leaf wax and palynological records from northwestern Sumatra do not show this LGM-Holocene vegetation contrast, which is likely due to the fact that this particular area remains relatively wet during glacial periods (Maloney, 1980; Morley, 1982; Newsome and Flenley, 1988; Niedermeyer et al., 2014). Paleoclimate simulations suggest that tropical rainforests in other parts of Sumatra and the adjacent shelf were significantly reduced during the LGM, with the glacial increase in open vegetation and  $\text{C}_4$  grasses taking place in a geographically delimited 'savanna corridor' (Bird et al., 2005; Cannon et al., 2009). Overall the available data suggest that, although local microclimatic effects deserve careful consideration, the larger part of the region comprising Java, Sumatra and Sulawesi experiences significant vegetation changes during glacial interglacial transitions.

The oxygen isotopic composition ( $\delta^{18}\text{O}$ ) in animal tissue is largely determined by  $\delta^{18}\text{O}$  values in food and drinking water (Longinelli, 1984; Luz and Kolodny, 1989), which are in turn dependent on ecological, climatic and geographical factors (Craig, 1961; Dansgaard, 1964). The  $\delta^{18}\text{O}$  value of rainwater decreases with increasing distance from the moisture source, increasing altitude, decreasing temperature, and high intensity precipitation (Dansgaard, 1964). Arid conditions enrich leaf water and surface

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