



Late Middle Pleistocene ecology and climate in Northeastern Thailand inferred from the stable isotope analysis of Khok Sung herbivore tooth enamel and the land mammal cenogram

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ABSTRACT

Paleoecological and paleoclimatic records based on the stable isotopes of mammalian tooth enamel are poorly known in mainland Southeast Asia during the Pleistocene. Khok Sung in Northeastern Thailand is a late Middle Pleistocene terrace deposit, tentatively dated either as 213 ka or 188 ka, yielding 15 described mammalian taxa with especially abundant and complete fossil remains. To investigate paleodiets and habitats of these ancient mammals and to understand the corresponding regional climate, we performed an analysis of stable carbon and oxygen isotopes extracted from tooth enamel carbonate of various mammalian taxa, coupled with the cenogram method. The enamel $\delta^{13}\text{C}$ values of Khok Sung mammals indicate a variety of diets, ranging from pure C_3 to C_4 plants, suggesting that C_4 grasses were a major component of local Thai ecosystems during the late Middle Pleistocene. The stable isotopic distinction between C_3 and C_4 plants suggests that the Pleistocene wildlife habitats ranged from closed forests to open grasslands for the Khok Sung area. Moreover, differences within sympatric Pleistocene herbivores such as proboscideans, rhinoceroses, and cervids characterize possible niche partitioning by minimizing interspecific overlap. Paleoclimatic interpretations based on the intra-tooth variability in enamel $\delta^{18}\text{O}$ values from large mammals and on the cenogram analysis reflect significant seasonal variations in precipitation and temperature, and humid conditions, for the Khok Sung locality. Compared to modern environments in Thailand, it is apparent that C_4 -dominated grasslands were more widespread at that time when anthropic impacts on the ecosystems were presumably absent or minimal.

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1. Introduction

Southeast Asia is known today as one of the biodiversity hotspots in the world, resulting from the complex interactions of its geological, biogeographical, and climatic events. In particular, changes in climate and sea levels in relation to repeated glacial cycles substantially impacted species diversification and faunal distribution in the region during the Pleistocene. A long history of paleontological excavations and research at numerous karstic sites

with a few terrace deposits has provided essential data in relation to changes in faunal communities and suggests diverse paleohabitat and paleoenvironmental conditions across mainland Southeast Asia throughout the Pleistocene glacial-interglacial cycles. Accordingly, our understanding of the terrestrial faunas and floras of the Pleistocene deposits has always played an important role in the reconstruction of these phenomena. However, the regional paleoclimate as indicated from the Pleistocene vegetation records remains questionable due to a scarcity of information from that period.

Stable isotope analysis and serial sampling of tooth enamel of terrestrial fossil mammals constitutes a powerful tool for exploring several aspects of paleoecology, vegetation cover,

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paleoenvironments, and paleoclimates (e.g., Cerling et al., 1989, 1997a, b; Quade et al., 1989, 1995; Quade and Cerling, 1995; Cerling and Harris, 1999; Kohn and Cerling, 2002). However, these advanced methods have not been widely applied to fossil mammals in mainland Southeast Asia. In Thailand, only three fossiliferous localities have been isotopically analyzed (Pushkina et al., 2010; Suraprasit et al., 2014; Bocherens et al., 2017): a late Middle Miocene coal mine of Mae Moh (13.4–13.2 Ma according to the magnetostratigraphy (Coster et al., 2010)) where diversified mammal faunas were recovered (Suraprasit et al., 2011, 2015a); the possible Early to Middle Pleistocene cave of Pha Bong where the giant fossil ape *Gigantopithecus* was documented (Bocherens et al., 2017); and a late Middle Pleistocene cave of Thum Wiman Nakin (older than 169 ka on the basis of the U-series geochronology (Esposito et al., 1998, 2002)) where a tooth of *Homo* sp. associated with abundant fossil mammals was found (Ginsburg et al., 1982; Tougard et al., 1998).

In 2005, the Khok Sung sand pit (Nakhon Ratchasima province, Northeastern Thailand) was excavated by the Thai-French paleontological team and the Department of Mineral Resources (Fig. 1).

This locality, which corresponds to an ancient fluvial terrace, today constitutes a very rich Pleistocene vertebrate fauna in Thailand where most of the mammal and reptile remains (skulls, isolated teeth, and postcranial bones) are well-preserved. All vertebrate fossils were collected from layers of sand and gravels rich in organic matter, around 6–8 m below the surface (see Duangkrayom et al. (2014) and Suraprasit et al. (2015b) for the detailed sedimentology and stratigraphy). Fossils recovered at the Khok Sung site are often articulate and *in situ* at their original level of deposition (e.g., nearly complete skeletons of stegodontids and wild water buffaloes) (Suraprasit et al., 2016). The mammalian assemblage is diverse (at least 15 recognized species in 13 genera) and contains extinct and extant large-sized taxa including a primate, carnivores, proboscideans, rhinoceroses, a suid, cervids, and bovids (Chaimanee et al., 2005; Suraprasit et al., 2015b, 2016). An approximate age of the Khok Sung fauna is attributed to the late Middle Pleistocene, either 213 ka or 188 ka, based on the occurrence of a paleomagnetic short reversal and on the presence of *Crocota crocuta ultima* that represents an accurately calibrated biochronological index (Suraprasit et al., 2015b). Plant remains

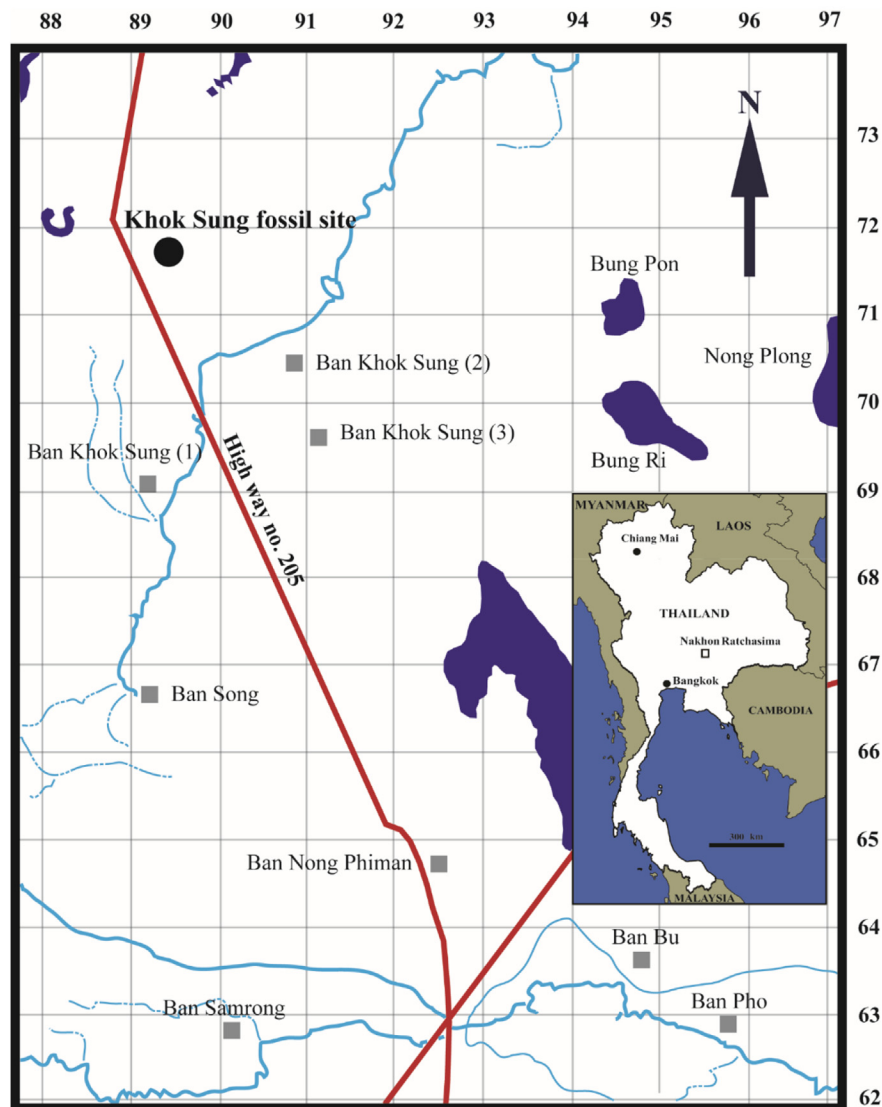


Fig. 1. Map of Thailand showing the location of the Khok Sung fossiliferous site in Nakhon Ratchasima province, Northeastern Thailand. Red lines indicate roads or highways. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

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