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A complete skull of *Crocuta crocuta ultima* indicates a late Middle Pleistocene age for the Khok Sung (northeastern Thailand) vertebrate fauna

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ABSTRACT

The locality of Khok Sung, Nakhon Ratchasima province, which corresponds to an ancient river terrace, has yielded the richest Pleistocene fauna of Thailand with a thousand of fossil vertebrate remains. This fauna has been previously dated between the Early Pleistocene and the Middle Pleistocene. We describe here a nearly complete hyaenid skull and associated mandible identified as belonging to spotted hyaena *Crocuta crocuta ultima*. The spotted hyaena *C. c. ultima*, which extended its maximum latitudinal distribution from northern China to Peninsular Thailand, is a characteristic component of Southeast Asian Middle Pleistocene faunas. These new biochronological data, coupled with a magnetostratigraphic study of the lithological section, provide a powerful multiproxy approach for the dating of Khok Sung fauna, pinpointing rather a late Middle Pleistocene age than the Early Pleistocene. In addition, the occurrence in the Khok Sung section of a short reverse excursion of the magnetic field within the Brunhes normal Chron can be tentatively identified as corresponding either to the "Iceland Basin" (188 ka) or to the "Pringle Falls" (213 ka) excursion, suggesting an even more precise dating of the locality. According to the presence of a spotted hyaena, the Khok Sung fauna may illustrate an open canopy habitat in a floodplain with abundant and diversified herbivores, close to the main river channel. This interpretation contrasts with the paleobotanical data which indicate wet and dry tropical forests and may instead describe the surrounding upland vegetation.

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1. Introduction

Biogeographically, Thailand occupies a key position in Southeast Asia because of its intermediate location between Indochinese and Sundaic provinces. This major biogeographical region is predominantly identified by climatic, floristic, and faunistic data (Lekagul and McNeely, 1988; Corbet and Hill, 1992; Chaimanee and Jaeger, 1993; Tougard and Montuire, 2006). Previous studies of late Middle Pleistocene faunas in Southeast Asia including Vietnam (Olsen and Ciochon, 1990; Long et al., 1996), Laos (Bacon et al., 2011), Cambodia (Beden and Guérin, 1973; Thein, 1974), and Thailand (Pope et al., 1981; Ginsburg et al., 1982; Chaimanee and Jaeger, 1993; Tougard et al., 1996; Chaimanee, 1998; Tougard, 1998, 2001) have shown that these faunas include widely distributed mammalian species across the Indochinese and Sundaic provinces. Some were involved in migration and were likely to be relevant for the understanding of the migration of *Homo erectus* and of its settlement patterns (Marwick, 2009).

Concerning the Middle Pleistocene of Thailand, most of the large mammal assemblages were described from the main caves of which are Thum Phra Khai Phet (Chaimanee and Jaeger, 1993; Tougard, 2001), Cave of the Monk in Ban Fa Suai (Zeitoun et al.,

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2005), Thum Phedan (Yamee and Chaimanee, 2005), and Kao Pah Nam (Pope et al., 1981). The ages of Thai Pleistocene caves have been mostly defined on the basis of their mammalian assemblages as for instance the "*Ailuropoda-Stegodon*" fauna (Kahlke, 1961; Zeitoun et al., 2005). Unfortunately, this association is characteristic of a long period, from the Early Pleistocene to the beginning of the Late Pleistocene (Rink et al., 2008; Bacon et al., 2011), rendering imprecisely all biochronological datations. In Thum Wiman Nakin, where a tooth of *Homo* sp. was collected (Tougard et al., 1998), the U-series methods extracted from numerous samples of calcite and tooth enamel have been performed (Esposito et al., 1998). The obtained ages from tooth enamel, ranging from 8 to 350 ka, have demonstrated the weakness of this method applied on teeth for localities under tropical humid climates (Esposito et al., 2002). Nevertheless, a stalagmitic floor sealing the fossiliferous layers has been securely dated back to 169 ± 11 ka (Esposito et al., 2002). The fossiliferous cave filling is therefore older than this stalagmitic floor (see Supplementary data—Table A1 for the mammalian fauna list reported from Thum Wiman Nakin).

In 2005, a rich and diversified vertebrate fauna has been excavated, by the Thai-French paleontological research team with the Department of Mineral Resources, from the Khok Sung sand pit in Nakhon Ratchasima province, northeastern Thailand (Fig. 1A). These excavations have provided a unique assemblage of fossil plants, reptiles, fishes, and mammals. Fossil plants including fruits (Rhamnaceae, Dipterocarpaceae, and Anacardiaceae), seeds, leaves, woods, tubers (Cyperaceae), and ambers, of the Khok Sung assemblage have been studied by Grote (2007). Some reptilian fossils have been also described, including turtles (*Batagur* cf. *trivittata*, *Heosemys annandalii*, *Heosemys* cf. *grandis*, and *Malayemys* sp.) and soft-shelled turtles (*Chitra* sp. and cf. *Amyda* sp.) by Claude et al. (2011) and a gharial, *Gavialis* cf. *bengawanicus* by Martin et al. (2012). Remains of fishes (pectoral spines) are represented predominantly by large silurids and some indeterminate snake vertebrae are observed (Claude et al., 2011). The Khok Sung site also represents a fluviatile terrace deposit where the vertebrate fossils are on average rather complete (e.g., skulls, jaws, and postcranial bones). The postcranial skeletons have been rarely found in connection due to some limited transport and predation having dissociated the bones. The mammalian assemblage is generally represented by Middle Pleistocene taxa including a rhinoceros, boars, bovids, cervids, a spotted hyaena, and an advanced form of the extinct proboscidean *Stegodon* (Chaimanee et al., 2005, 2007), whose generic and/or specific attribution are poorly known. The fossil preservation in the Khok Sung sand pit is exceptional when compared to that of Thai Pleistocene caves where fossils, having been displaced and altered by predators and porcupines (Chaimanee et al., 2007), are very fragmentary (isolated teeth). Moreover, the fossils of Khok Sung have been collected *in situ*, whereas most of the fossils recovered from adjacent sand pits along the Mun River are uninformative because they were *ex situ* and collected by local workers (Duangkrayom et al., 2014) without stratigraphic control. The Khok Sung site, bearing abundant well-preserved vertebrate fossils, is therefore of critical importance to contribute to the knowledge and datation of the fossil mammalian communities, to the understanding of their evolution, paleobiogeography, and paleoenvironments.

The age of Khok Sung fauna has been previously established as either being of Early Pleistocene age on the basis of the dispersal patterns of *Gavialis* (Martin et al., 2012) or ranging from Early to Middle Pleistocene based on the presence of an advanced form of *Stegodon* (Chaimanee et al., 2005; Chaimanee, 2007) and on well-dated tektites from adjacent localities (Charusiri et al., 2002). Tektites in Southeast Asia result from an impact event dated of about 700 ka (Gentner et al., 1969) but have never been recorded in this locality.

The spotted hyaena *Crocuta crocuta* has played an important role in the evolutionary history of the Pleistocene mammalian faunas in Eurasia since it has been commonly recorded from cave deposits of several Pleistocene sites of mainland Southeast Asia (e.g., Louys et al., 2007), China (e.g., Pei, 1934; Tseng and Chang, 2007), and Europe (e.g., Sardella and Petrucci, 2012). On the other hand, the study of ancient mtDNA of spotted hyaenas by Sheng et al. (2014) has indicated that extinct and living spotted hyaenas originated

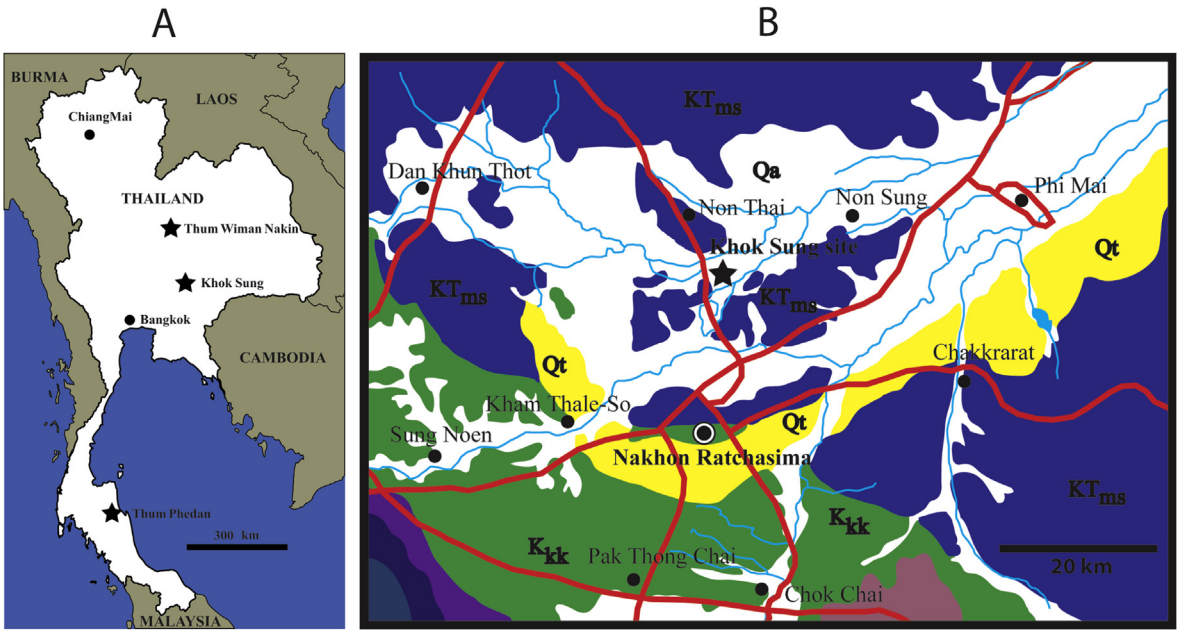

Fig. 1. The locality of the Khok Sung sand pit: A—map of Thailand and B—geological map of Nakhon Ratchasima province. Stars indicate late middle Pleistocene sites and red lines refer to main roads. Abbreviations: **Qa** (Quaternary alluvium), **Qt** (Quaternary terrace), **KTms** (Late Cretaceous to Early Palaeogene? Mahasarakam Formation), and **Kkk** (Early to Late Cretaceous Khok Kruat Formation) (modified from DMR, 2007).

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