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Late Pleistocene Mammalian Assemblages of Southeast Asia: New Dating, Mortality Profiles and Evolution of the Predator-Prey Relationships in an Environmental Context

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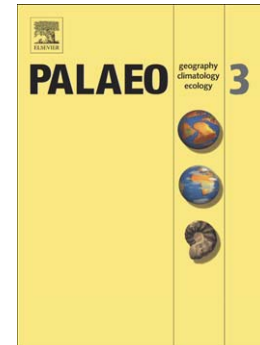
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**LATE PLEISTOCENE MAMMALIAN ASSEMBLAGES OF SOUTHEAST ASIA: NEW DATING,  
MORTALITY PROFILES AND EVOLUTION OF THE PREDATOR-PREY RELATIONSHIPS IN AN  
ENVIRONMENTAL CONTEXT**

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**Abstract**

Karstic sites have great potential for yielding data regarding changes in faunal communities in the Pleistocene of Southeast Asia. In this region, the majority of fossil-bearing deposits are karstic breccias, which generally demonstrate a complicated sedimentary history. While most of the mammalian assemblages recovered in these deposits are only composed of isolated teeth, their study remains essential for reconstructing palaeoecology and palaeoclimatology of the region. We analysed the assemblages recovered in three mainland and two insular karstic sites: Tam Hang South and Nam Lot in northern Laos, Duoi U’Oi in northern Vietnam, Punung in central Java and Sibrambang in western Sumatra and obtained new chronologies for three of these sites so that their significance could be discussed within their correct chronological context. The resulting age ranges place the sites in MIS5 and MIS4. The comparative analysis of the faunas, in terms of taphonomy, taxonomic diversity and abundance, and mortality profiles (*Cervus unicolor*, *Sus scrofa*, *Sus vittatus*, rhinocerotids and *Tapirus indicus*), reveals marked differences in prey-predators (carnivores and/or humans) relationships in relation to habitat. The study of hominines-bearing sites (Punung, Nam Lot, Duoi U’Oi) allows us to emphasize different interactions with large carnivores (felids, hyaenids, canids).

**Key-words:** Southeast Asian Faunas, Hominines, Geochronology, Taphonomy, Palaeoecology, Mortality profiles.

## 1. Introduction

The structure of populations and mortality profiles of mammals from Southeast Asian Pleistocene faunas have rarely been analyzed in their entirety (e.g., Tong, 2001; Schepartz et al., 2003, 2005; Schepartz and Miller-Antonio, 2010a, 2010b), as the faunal assemblages are often composed of a few isolated teeth, are not always well-preserved and often have unreliable chronologies. The assemblages encountered are most frequently cave or shelter accumulations that originate from karst breccias. In this region, the limestone karst system is subject to a tropical environment that is highly climate- and water-dependent. The processes of sedimentary deposits inside the network of caves and fissures lead to the formation of various deposits including breccias, some containing vertebrate remains. From living mammalian populations (biocoenosis) to fossil bone accumulations (thanatocoenosis) in the karsts, numerous pre- and post-depositional agents act on animals: diseases and old age, climates, flooding and other disasters, predators and scavengers, and bone collectors such as porcupines. All these processes contribute to the atypical composition and preservation of the vertebrate assemblages.

In this paper, we analyse assemblages recovered in five mainland and insular karstic sites in order to emphasize the characteristics of the Asian mammalian communities, and their evolution in the Late Pleistocene: Tam Hang South and Nam Lot in northern Laos, Duoi U’Oi in northern Vietnam, Punung in central Java and Sibrambang in western Sumatra (Fig. 1). The first three assemblages are not *in situ* deposits. The fossiliferous outcrops, most commonly breccias and clays, are found in fissures (Punung I), galleries and caves (Tam Hang South, Nam Lot, Duoi U’Oi, Punung II, and Sibrambang) (Storm et al., 2005; Storm and de Vos, 2006; Bacon et al., 2008a, 2008b, 2011, 2012; Durringer et al., 2012). The five assemblages share multiple characteristics, including several hundred isolated teeth, evidence of gnawing by

porcupines, presence of middle- to large-sized mammals, and an absence of small microvertebrates. These mammalian faunas are well-known and have already been discussed in the literature in terms of composition, taphonomy, biochronology, evolution, and palaeoecology (de Vos 1983, 1995; Sondaar, 1984; Leinders et al., 1985; Tougard, 1998; van den Bergh et al., 1996, 2001; Storm et al., 2005; Tougard and Montuire, 2006; Bacon et al., 2008a, 2008b, 2011, 2012; Louys and Meijaard, 2010; Antoine, 2012). Currently, only solid age estimates of two faunas have been proposed. The geochronology for the Duoi U’Oi faunal unit is consistent with its biochronological age ( $66 \pm 3$  ka, Bacon et al., 2008b), while Punung (I and II), based on a new comparable faunal assemblage recovered at the Gunung Dawung site (Punung III: luminescence, U-series,  $128 \pm 15$  ka /  $118 \pm 3$  ka; Westaway et al., 2007), is consistent with the oldest ages proposed until now (van den Bergh et al., 1996, 2001). At present the other faunas only have estimated chronologies, that is late Middle Pleistocene/Late Pleistocene for Tam Hang South and Nam Lot (Bacon et al., 2011, 2012; Durringer et al., 2012; Antoine, 2012) and Late Pleistocene for Sibrambang (de Vos, 1983; Skelton, 1985; Drawhorn, 1994; Antoine, 2012). We aim to improve the potential for faunal interpretation by establishing solid chronologies (combined OSL and U-series datings) for three of the five sites (Tam Hang, Nam Lot, and Duoi U’Oi).

The present comparative analysis of these fossil faunas, in terms of (i) taphonomy, (ii) taxonomic diversity and abundance, and (iii) mortality profiles of *Cervus unicolor*, *Sus scrofa*, *Sus vittatus*, rhinocerotids and *Tapirus indicus* (for four of the five assemblages), allows us to assess the events that acted during pre- and post-depositional processes inside the karst. In particular, mortality profiles are analysed in an attempt to emphasize the possible selectivity of large predators (carnivores and humans) on ungulate prey. Despite the atypical conservation of mammals with any skeletal elements showing evidence of butchery and the

lack of associated human artifacts in the sites (Duoi U'Oi, Nam Lot, and Punung), the assemblages of teeth are the only available material to infer eventual strategies of subsistence by humans. The two former sites yielded unidentified humans (*Homo* sp.; Bacon et al., 2008a; 2012). The latter produced isolated teeth assigned to *Homo sapiens* although their provenance remains uncertain, and the new dating tentatively suggests their presence at ca. 120 ka (Storm et al., 2005; Storm and de Vos, 2006; Westaway et al., 2007). The search of the possible causes of eventual changes in the structure of mammalian communities - climatic, latitudinal, ecological or anthropic - could offer some clues for understanding the past history of the region, with implications for the extinction of *Homo erectus* (“archaic *Homo sapiens*”) and the arrival of anatomically modern *Homo sapiens*.

## Figure 1

### 2. History and geological context

#### 2.1. Punung cave, Java

The Punung faunal assemblage was collected by von Koenigswald in the 1930s. First considered as a part of the much older Trinil assemblage (an archaic fauna of 0.9 Ma), it was distinguished as a “faunal entity” by Badoux (1959) who estimated its age to be late Middle Pleistocene. The Punung material comes from two 5 km-distant localities, Punung I near Mendolo Kidul and Punung II close to Tabuhan cave, the exact locations of which, in the vicinity of the Punung village, were not mentioned in the original reports. Due to the difficulty in separating the two sets of fossils, the Punung assemblages are since then considered together in all the publications (Badoux, 1959; de Vos, 1983).

Geological information on the site, however, was clarified when the exact place of the two localities (I and II) was relocated in 2003 by an Indonesian-Dutch team (see Storm et al., 2005 for a review of the site history). According to the observations of the authors in the



field, the Punung I outcrop consists of a yellow and a white fossiliferous cave breccia, which lies on the slope of a karstified limestone hill. During the survey, new fossilized teeth of mammals were found at Punung II with similar characteristics to the old Punung fauna. Despite observations on the nature and composition of the breccias from the two localities, it was not possible to distinguish between the two assemblages. Later, Westaway et al. (2007, p.710) defined the nature of the deposit: “*The sedimentary properties of the Punung breccias are remarkably similar, well weathered and composed predominantly of moderately sorted, unconsolidated, angular limestone and calcite clasts, with a 20% sandy-silt matrix*”.

We consider in the present analysis the updated Punung (I and II) faunal inventory reported by Storm and de Vos (2006). Concerning the age of the fauna, several estimates have been proposed (Table 1): 80-60 ka (de Vos, 1995), 110-70 ka (van den Bergh et al., 1996), or more inclusively 125-60 ka (van den Bergh et al., 2001), considering the most favorable eustatic (about 50 meters under the current sea level) and environmental conditions for a faunal dispersal across the Sundaland (de Vos et al., 1982; Leinders et al., 1985; de Vos and Sondaar, 1994; van der Kaars and Dam, 1995; van den Bergh et al., 1996; 2001). Recently, an age estimate of the Punung mammalian assemblage has been proposed by comparison with that of the new *in situ* assemblage discovered at Gunung Dawung site (Storm et al., 2005; Storm and de Vos, 2006; Westaway et al., 2007). This site Punung III close to the Tabuhan cave and in the same geological karstic context, yielded an original *in situ* fauna. Its composition was comparable to those of the two former localities of Punung, confirming the presence in Java of species clearly adapted to a wet and warm environment (amongst them *Pongo pygmaeus*, *Hylobates syndactylus*, or *Helarctos malayanus*) (de Vos, 1983). The age of the Punung III “yellow” breccia has been estimated between  $128 \pm 15$  ka and  $118 \pm 3$  ka using luminescence and uranium-series methods (Westaway et al., 2007). It is

clear now that a modern tropical fauna replaced an archaic fauna during the Marine Isotope Stage (MIS) 5e, as proposed previously (van den Bergh et al., 1996, 2001; Storm et al., 2005).

One hominid tooth is mentioned in the first report of von Koenigswald (1939). Five other teeth are also associated with the historical material (Badoux, 1959), which was assigned later by de Vos (1985) to *Homo sapiens*. Storm and co-workers did not find these human teeth again in the collection, but recognized a P3, long ignored but nonetheless assigned to “*Homo sp.*” by von Koenigswald. On the basis of its dimensions in comparison with those of prehistoric specimens from Australasia, Storm et al. (2005) confirmed the attribution to *Homo sapiens*, but the provenance of the tooth and its association with the Punung material is still uncertain. The Punung faunal turnover seems then to coincide with the replacement of *Homo erectus* by *Homo sapiens* in Java. The evidence which could certify the concomitant arrival of this species associated with a modern fauna around 120 ka are however tentative at best for the moment. For instance, the well-dated Gunung Dawung locality has not yet produced human remains.

## 2.2. Sibrambang cave, Sumatra

Numerous Sumatran caves contain rich fossil assemblages that were originally collected by Eugene Dubois between 1887 and 1890 (Dubois, 1891), and among the most prolific deposits are Lida Ajer, Sibrambang and Djamboe caves (Hooijer, 1947, 1948; de Vos, 1983). The exact location of the Sibrambang site was not mentioned in Dubois’ reports on excavations (de Vos, 1983). Despite recent attempts to relocate it in western Sumatra, its location and geological context are currently unknown. The faunal assemblages of two of the Sumatran caves, Lida Ajer and Djamboe, are estimated to be of the same age as Sibrambang, >81 ka and >70 ka, respectively, according to relative dating using amino-acid racemization

(AAR) on bone (Skelton, 1985; Drawhorn, 1994). For the purposes of this comparison we will therefore use the relative chronology of 81-70 ka for the Sibrambang site (Table 1). The composition of the fauna is comparable to that of Punung with only extant species. No human remains are mentioned in the locality of Sibrambang, but Lida Ajer yielded two modern human teeth.

### 2.3. Tam Hang South rockshelter, Laos

Tam Hang, in the Huà Pan province, northern Laos, is a “historic site” discovered during the 1930s by a French geologist, Jacques Fromaget. Tam Hang (TH) is a group of rock shelters situated along the wall of the limestone mountain Pà Hang. In a soft argillaceous sediment accumulated in the shadow of the rock shelters, Fromaget unearthed numerous archaeological and human remains from the Palaeolithic to the Neolithic (Fromaget, 1936, 1937, 1940a, 1940b; Fromaget and Saurin, 1936; Saurin, 1951; Demeter, 2000; Shackelford, 2007; Shackelford and Demeter, 2012; Patole-Edoumba et al., submitted).

Fromaget also located two distinct fossiliferous breccias that plastered the walls of the shelters, described in the literature as “tuf à *Hystrix*” (Arambourg and Fromaget, 1938; Fromaget, 1940; Beden et al., 1972). The “lower” breccias at TH Central and, in part, TH North, produced a mammal assemblage comprising 38 species, whereas the “upper” breccias at TH South produced a second assemblage encompassing 27 species. Both were considered as belonging to the Middle Pleistocene (Arambourg and Fromaget, 1938; Beden et al., 1972), and remained until recently among the only Middle Pleistocene palaeoecological data for the north of the Indochinese province (Tougaard and Montuire, 2006; Louys and Meijaard, 2010).

The site was re-located in the 1990s by T. Sayavonkhamdy. In 2003 and 2007, two fieldwork seasons conducted by a Lao-American-French team led to the collection of new faunal material from Tam Hang South (Bacon et al., 2008a, 2011, 2012). The remaining breccias from this locality were located at the basal part of the cliff (Fig. 2). Compared to the well-cemented and clasts-rich upper and middle breccias, the lower one has a softer cemented nature, is fine-grained, and is dark brown with mainly sandy/silty clay composition. As seen in Figure 2, two calcitic flowstones interrupt the sequence of the lower breccias, indicating at least two episodes of non-deposition. That suggests that the karstic gallery was flooded during deposition, and periodically dried up. The absence of pebbles supports an intrakarstic origin from inside to outside the karsts, rather than fluvial. The lower breccia contained isolated well-preserved teeth that form the new assemblage. The composition is comparable to the faunal list of Arambourg and Fromaget (1938), but new taxa are recorded for the first time, specifically several small carnivores and one rodent (Bacon et al., 2011). No human remains are recorded at Tam Hang South. This assemblage with modern and archaic species is characteristic of mammalian faunas from the late Middle Pleistocene to the early Late Pleistocene on the Asian mainland (Tougaard, 2001). In this paper we aim to improve this estimated chronology (Table 1).

## Figure 2

### 2.4. Nam Lot cave, Laos

The Nam Lot cave, discovered in 2007 in northern Laos, is located along the cliff of the Pà Hang Mountain, 250 m to the east of the Tam Hang site (Düringer et al., 2012; Bacon et al., 2012). The cave is a network of superimposed and interconnected galleries and chambers on four levels. The main chamber is about 60m long and contains a complicated depositional history due to several filling/reworking processes (Düringer et al., 2012, p.145-150). The

main sedimentary deposits, located in both lower and upper parts of the network, present a wide range of sedimentary rocks comprising true conglomerates, conglomeratic sandstones, sandstones, limestone-rich breccias, sandy and silty clays (Fig. 3). Except for the conglomerates, most of the sedimentary facies are rich in vertebrate remains, primarily isolated teeth. The majority of the remains derive from the breccia and from the silty/sandy clays in the lower part of the cave (Fig. 3). The internal structure of the sandstones with many large clasts shows that during the deposition, the flow was directed from inside to outside the cave (intrakarstic origin) (Düringer et al., 2012).

The composition of the Nam Lot assemblage consists of modern and extinct taxa (Bacon et al., 2012). Only one human incisor (*Homo* sp.) is recorded. The biochronological age of the assemblage was estimated between the late Middle Pleistocene and the Late Pleistocene, as that of Tam Hang South (Bacon et al., 2012) (Table 1). In this paper we aim to improve this estimated chronology with new combined OSL and U-series results.

### Figure 3

#### 2.5. Duoi U'Oï cave, Vietnam

The Duoi U'Oï cave is located in northern Vietnam, in the Man Duc village, 25 km away from the Hoà Bình city. It was excavated in 2003 by a Vietnamese-French-Japanese team (Bacon et al., 2008b). The cave is formed by two distinct and interconnected corridors about 25m long, one of which has an exceptionally well-preserved breccia. This cave deposit consists of the superimposition of two distinct fossiliferous layers, an argillaceous silty-clay at the base and a pisolite-rich calcareous breccia on the top, entirely encrusted with calcite (Fig. 4). The imbrication of clasts, the abundance of reworked speleothems (stalactites, calcitic floors) as well as the lack of alluvial sediments are evidence of water circulation from inside to outside the cave, i.e. intrakarstic origin (Bacon et al., 2008b: p.1631).

Both layers yielded numerous isolated teeth of middle- to large-sized mammals. The Duoi U’Oi fauna only consists of modern taxa, typical of the Late Pleistocene period (Bacon et al., 2008b). Two upper molars (*Homo* sp.) are recorded. The age estimate of the fauna is based on U-series dating from the calcitic floors ( $66 \pm 3$  ka) that cross the fossiliferous breccias (Bacon et al., 2008b) (Table 1). This estimate is thus considered the average age of the faunal unit. In this paper we aim to build on this one age estimate to produce a more robust chronology.

#### Figure 4

#### Table 1

### 3. Methods

#### 3.1. Luminescence and Uranium-series dating

Luminescence dating techniques (both red thermoluminescence (TL) and single grain optically stimulated luminescence (SG OSL) techniques were applied to isolated quartz grains, and U-series dating techniques were applied to flowstones for the three sites (Duoi U’Oi, Tam Hang, and Nam Lot) (see Supplementary Information). Initially, the site of Tam Hang proved difficult to date using U-series alone due to high levels of detrital contamination found in the speleothem deposits. To ensure the accuracy and reliability of the new chronologies, additional independent age estimates were obtained by employing luminescence techniques applied to the sediments/breccias, and this approach was also extended to the other sites. Most techniques display good agreement within their known-limitations.

*Luminescence dating:* Bulk breccia matrix was sampled from cleaned exposures in the stratigraphy using only red-filtered torch light. Quartz grains of 90–125  $\mu\text{m}$  and 180–212  $\mu\text{m}$  were separated from the matrix using standard purification procedures, including a final

etch in 40% hydrofluoric acid for 45 min (Aitken, 1985). Both a dual-aliquot protocol (DAP; Westaway and Roberts, 2006) using isothermal red TL emissions detected using a red sensitive photomultiplier tube (Electron Tubes Ltd S20 9658B) and cooling tower (LCT50 liquid-cooled thermoelectric housing) with Koop 2-63 and BG-39 filter combination, and a single-aliquot regeneration protocol (SAR; Wintle and Murray, 2000) using UV emissions detected using a standard blue PM (7.5 mm of Hoya U-340 filter) were applied to the smaller grain size fraction to obtain palaeodoses using a TL-DA-20 Risø unit. In addition, single-grain techniques incorporating a single-grain laser attachment and blue sensitive PM were applied to the larger grain size fraction employing a SAR methodology. A calibrated  $^{90}\text{Sr}/^{90}\text{Y}$  source was used to perform laboratory irradiations at a dose rate of between 10.62–10.38 Gy/min for the aluminium single-grain discs and 7.41 Gy/min for the stainless steel single-aliquot and red TL discs. Total dose rates were measured by in situ gamma spectrometry and laboratory beta counting, while concentrations of  $^{238}\text{U}$ ,  $^{235}\text{U}$ ,  $^{232}\text{Th}$  and  $^{40}\text{K}$  were measured by high-resolution gamma-ray spectrometry. We used an effective internal alpha dose rate of  $0.03 \text{ Gy ka}^{-1}$  and a long-term water content of between  $3\text{--}19 \pm 5\%$ .

*Uranium-series dating:* Calcite samples collected directly from flowstones using a hammer and chisel were submitted to the university of Queensland for U-series dating on a Nu Plasma multi-collector inductively coupled plasma mass spectrometry (MC-ICPMS) following analytical procedures described in detail elsewhere (Zhou et al., 2011; Clark et al., 2014). Their  $^{230}\text{Th}$  ages were calculated using Isoplot/EX 3.0 (Ludwig, 2003) and half-lives of 75,690  $\pm$  230 years ( $^{230}\text{Th}$ ) and 245,250 years ( $^{234}\text{U}$ ) after Cheng et al. (2000). As the samples are mostly impure calcite with relatively low U and very high levels of detrital Th (as reflected by high  $^{232}\text{Th}$  concentrations and low U/Th ratios), all  $^{230}\text{Th}$  ages must be corrected for non-radiogenic  $^{230}\text{Th}$ , that contributes to an age excess, making the  $^{230}\text{Th}$  age too old (see Zhao et

al., 2001). This is analogous to the marine reservoir age corrections for radiocarbon dates. In this study, the non-radiogenic  $^{230}\text{Th}$  correction was made assuming the detrital component has an initial  $^{230}\text{Th}/^{232}\text{Th}$  atomic ratio of  $4.4 \pm 2.2 \times 10^{-6}$  (bulk-earth value), and  $^{238}\text{U}$ ,  $^{234}\text{U}$ ,  $^{232}\text{Th}$  and  $^{230}\text{Th}$  in the detrital component are in secular equilibrium. This assumption is valid as the detrital component in impure speleothems was mainly derived from silts and clays washed into the caves through seepage water, with U/Th isotopic compositions within error of the bulk-earth value (St Pierre et al., 2012). Non-radiogenic  $^{230}\text{Th}$  correction often results in large age error magnifications in the corrected  $^{230}\text{Th}$  ages for samples with low  $^{230}\text{Th}/^{232}\text{Th}$  ratios (ca. 2-20 times larger than the uncertainties of the uncorrected  $^{230}\text{Th}$  ages). Nevertheless, two significantly purer samples, TAM-F2 from Tam Hang, and NL-F2 from Nam Lot, return precise and robust corrected  $^{230}\text{Th}$  ages of  $83 \pm 2$  and  $52 \pm 3$  ka, which dated the times of the flowstone formations, respectively. The other less pure samples from the two sites give much less precise corrected  $^{230}\text{Th}$  ages, statistically within error of the two more precise dates, respectively.

### **3.2. The faunal analysis**

#### **3.2.1. The collections**

The new collections of Tam Hang, Nam Lot and Duoi U'Oi come from sites recovered by the authors. The old collections of Sibrambang and Punung are housed at the Natural Museum of Natural History in Leiden and the Senckenberg research Institute and Natural History Museum in Frankfurt.

#### **3.2.2. Definitions of NISP and MNI**

The number of specimens (NSP) and the number of identified specimens (NISP) have been estimated for the five assemblages. In localities studied by the authors, fragments were first



collected and matched for all taxa and for perissodactyls in either studied locality. Each tooth, or fragment of tooth, was then considered as one specimen.

In the analysis of taphonomic processes generated by porcupines, we used NISP for calculating gnawing frequency. Gnawing intensity has been defined using an estimate of the quantity of root gnawed by rodents: partially (1/4 to 3/4 of the root) or totally (the root is missing).

Two types of minimum number of individuals (MNI) have been calculated. The first one is based on the frequency of the most common tooth either left or right, upper or lower, by taxon (species, genus or family in some cases). This index is cited in the text as MNIf (frequency).

The second one is used in the analysis of mortality profiles, using a combination of different data. These combinations differ according to the methods used for reconstructing the profiles of species. For cervids, we considered all d4 and m1 or m3, either left or right, recorded in the samples. When one right d4 and one left d4 corresponded to the same age class, we counted one individual (MNlc=1). When one right d4 and one left d4 corresponded to different age classes, we counted two individuals (MNlc=2). For suids, we considered all left and right lower molars (m1/m2/m3), and selected the teeth in that same way. For rhinocerotids, the MNlc was calculated with all of the dentition in combining incompatible left/right and wear stage. This index is cited in the text as MNlc (combination).

The statistical tests (Fisher's test, permutation test, and Spearman's test) performed on NSP, NISP and MNIf were run in R version 2.14.1.

### **3.2.3. Mortality profiles**

Mortality profiles of large cervids, suids and perissodactyls have been analysed for four assemblages (Tam Hang, Nam Lot, Duoi U'Oi, and Sibrambang). We did not include the data from Punung in this analysis because the assemblage consists of a mix of teeth from two localities (I and II) (Badoux, 1959; de Vos, 1983).

We used wear criteria given by crown height measurements to estimate age classes for the large cervid, the sambar *Cervus unicolor/Rusa* sp. (Klein et al., 1981). Using this method, the selection of at least one milk tooth (d2/d3/d4) and one permanent molar (m1/m2/m3) is needed to cover all of the life of the species, from new born to old adult individuals. In relation to the mortality profiles of pigs (*Sus scrofa*, *Sus vittatus*), we used the crown formation sequences and occlusal surface wear patterns of the three lower molars (m1/m2/m3) to estimate age classes (Grant, 1982; Rolett and Chiu, 1994). For the rhinocerotid samples (including *Rhinoceros unicornis* and/or *R. sondaicus* and/or *Dicerorhinus sumatrensis*), we used wear stages of all teeth - permanent and deciduous, upper and lower - to characterize ages classes following a procedure adapted from Hillman-Smith et al. (1986) (see Supplementary Information).

The Kolmogorov-Smirnov test performed on mortality profiles was run in R version 2.14.1.

## 4. Results

### 4.1. Dating results

The resulting age estimates for the sites of Duoi U'Oi, Tam Hang and Nam Lot have been presented in Table 2 (luminescence) and Table 3 (U-series). The chronology of the Duoi U'Oi site ( $66 \pm 3$  ka; Bacon et al., 2008b) has been strengthened by a new age range of 70-60 ka. New chronologies have also been established for Tam Hang South (94-60 ka) and Lower Nam Lot (86-72 ka) (Tables 2 and 3). As previously discussed, the chronology for Punung III

(Gunung Dawung site; Storm et al., 2005) has been firmly established ( $128 \pm 15$  ka and  $118 \pm 3$  ka; Westaway et al., 2007) and a new chronological framework for the Sumatran caves (including Sibrambang) is currently under preparation (Westaway et al., in prep). About the latter site, we consider here the age of 81-70 ka (AAR on bone) (Skelton, 1985; Drawhorn, 1994), supported by both the biochronological age (de Vos, 1983) and taxonomic analysis of rhinocerotids (Antoine, 2012) (Table 1). The new established age ranges place the faunas of Nam Lot, Tam Hang, Sibrambang and Punung in the interglacial stage MIS5 (128-71 ka), whereas the age ranges place the Duoi U'Oi fauna in the relatively cooler period of MIS4 (71-59 ka) (Imbrie et al., 1984) (Fig. 5).

**Figure 5**

**Table 2**

**Table 3**

## **4.2. Composition of the mammalian assemblages**

### **4.2.1. Taxonomic diversity**

The five faunas are comparable only with respect to middle- to large-sized mammals (Artiodactyla, Perissodactyla, Proboscidea, Carnivora, Primates, and large Rodentia) (Table 4). All lack the whole category of small mammals (<1kg) (Scandentia, Pholidota, Erinaceomorpha, Soricomorpha, Chiroptera, and small Rodentia), and other microvertebrates.

Compared with the species diversity of Artiodactyla in living faunas from regions situated at different North to South latitudes (Corbet and Hill, 1992), the fossil faunas show remarkable similarities (S-Tables 2, 3). Taking into account only Perissodactyla defined at the species level and Proboscidea, the number of species identified in the fossil faunas is twice that in the living faunas (S-Tables 2, 3; Surovell et al., 2005; Antoine, 2012), a phenomenon

well documented not only in Southeast Asian faunas, but also in all of the faunas from the Pleistocene epoch world-wide (e.g. Surovell et al., 2005; Louys et al., 2007; Kahlke et al., 2011).

The inventory of primates in the recent mainland collections is affected by a taxonomic bias. All genera are represented, but it is difficult to distinguish the different species of *Macaca*, *Trachypithecus* and *Hylobates* (Bacon et al., 2008a, 2008b, 2011, 2012), because the inventory in old Indonesian collections uses old taxonomy (de Vos, 1983; Storm et al., 2005) (Table 4).

Fossil Carnivora are largely underestimated in terms of species diversity, especially at Tam Hang, Nam Lot, Duoi U'Oi and Sibrambang (Table 4), considering the 21 to 29 species inventoried in the living faunas at the North latitudes (0°-25°) (**S-Tables 2, 3**). Indeed, only half the potential species diversity is preserved (8 to 11 identified species). At Punung, Carnivora are few with two species recorded, compared with the 9 to 14 species inventoried south of the equator. It is evident that the ratio of the small-sized Carnivora species in fossil assemblages to supposed original species diversity is biased (only that of large-sized Carnivora, *Cuon alpinus*, *Pliocrocuta perrieri*, *Panthera tigris*, and *P. pardus*, is well represented).

For our excavations at Tam Hang, Nam Lot and Duoi U'Oi, we used systemic screens in an attempt to collect small animals. Therefore, the lack of small Carnivora is not due to recovery bias. The action of floods and loss during transport cannot be the only causes because other animals of comparable body size, namely Primates, are otherwise abundant in the assemblages. Several factors could have affected the composition of the Carnivora tooth collection prior to deposition in the karstic network: their relatively low abundance in any

mammalian guild or the selective role of porcupines we will examine in the taphonomic analysis.

The case is different for the historical sites of Punung and Sibrambang. The excavation techniques during these ancient surveys, with no sieving and the possible selection of the most complete and “beautiful” teeth could generate different biases, both in taxonomic diversity and abundance. In that respect, the low species diversity among Carnivora is particularly striking at Punung (S-Table 2).

#### **Table 4**

##### **4.2.2. Taxonomic abundance (NSP and NISP)**

The historic sites, Punung and Sibrambang, which produced 604 and 7090 identified specimens (NISP) respectively, are represented by teeth and rare, more complete elements such as mandibular fragments at Punung (Badoux, 1959; de Vos, 1983; observation by AMB and POA) (**Table 5**). This can be compared with the sites we studied. At Tam Hang, out of 673 specimens, only two fragments of mandibles were recovered (cervid and suid; Bacon et al., 2011); at Duoi U'Oi, among the 871 specimens, two fragments of jaws of macaque are recorded (one hemi-maxilla and one hemi-mandible; Bacon et al., 2008b); at Nam Lot, the assemblage is composed of 385 isolated teeth (Bacon et al., 2012), but no bones.

#### **Table 5**

##### **4.3. Taphonomy**

###### **4.3.1. Preservation of teeth**

All of the teeth from the five assemblages have intact crowns. Cusps and other relief on the enamel surface were not blunted.

#### 4.3.2. Action of porcupines

A large proportion of the isolated teeth in the five studied assemblages show roots with damage that is typical of porcupine gnawing. Rodents use their teeth to extract nutrients from bone, dentine or other tissues and continuously wear their incisors. The damages on teeth consist of characteristic chisel marks on roots, with some being partially gnawed and others totally gnawed (Fig. 6). Gnawing frequency is high in the assemblages with ~82% to ~94% of gnawed teeth (S-Table 4-8).

The state of preservation of teeth reveals differences between species within a site and differences between species from site to site (Table 6). The Tam Hang, Nam Lot and Punung samples are distinguished from the two other samples by percentages of gnawed roots, with up to 100% of the teeth in Carnivora, Primates, and ungulates (except perissodactyls which present a different treatment of remains in all sites). In these samples, most of the ungulate teeth have gnawed roots (99.3% to 100% at Tam Hang; 100% at Nam Lot; 97.4% to 100% at Punung), as do the teeth of Carnivora and Primates (98% to 100% at Tam Hang; 100% at Nam Lot) or those of Carnivora (100% at Punung), with high percentages of roots completely gnawed (S-Tables 5, 6, 8). In these sites, porcupines were active collectors of bones and collected available bones of species ranging from small monkeys to large bovids for their gnawing activities (see also Storm and de Vos, 2006). These data contrast with those from the Duoi U'Oi and Sibrambang samples, in which a significant part of the teeth belonging to Carnivora and Primates displays intact and ungnawed roots (12% to 50% at Duoi U'Oi; 5.8% to 48.6% at Sibrambang; Table 6). Porcupines were not the only accumulating agent for the small-sized species. At these sites, they collected available bones among a wide range of species, but ungulate bones remain their preference for gnawing activities (98.2% to 100% at Duoi U'Oi; 98.5% to 100% at Sibrambang; Table 6) (S-Tables 4, 7).

The proportion of gnawed teeth for rhinocerotids and tapirids ranges from low values at Nam Lot (11.8% and 25%, respectively, on few and fragmentary elements) up to very high rates at Sibrambang (93.4% and 92.9%, respectively) (Table 6). Rhinocerotid teeth show intermediate values in Tam Hang and Duoi U’Oi (51.2% and 39.0%, respectively), while tapirid teeth are much more gnawed in both assemblages (90.9%). In Punung, the situation is far different, with tapirid teeth again more gnawed than rhinocerotid teeth (73.3% vs. 10.7%). As far as gnawing intensity is concerned, the percentages of roots totally gnawed are null for both groups at Nam Lot, to 41.2% for rhinocerotids at Tam Hang and 90.9% for tapirids at Sibrambang (S-Tables 4-8). In these samples, the damages on tapirid teeth follow in this respect what it is observed for the other ungulate samples, while damages on rhinocerotids teeth show a different pattern (Table 6). To sum up, there is a continuum between Nam Lot (where very few perissodactyl teeth are gnawed: i.e. porcupines were not the main accumulating agent of these large animals) and Sibrambang (a majority of teeth are gnawed, mostly completely: i.e. porcupines were the major accumulating agent).

**Table 6**

**Figure 6**

#### **4.3.3. Frequency of teeth**

##### *The ratio of upper to lower teeth*

The ratios of upper to lower teeth are highly variable, with significant differences between some ungulate species within each site (Fisher's exact test,  $p < 0.05$ ) (Table 7). The values in the five assemblages demonstrate a better survivorship of lower teeth than upper teeth for the large species (>150 kg) among cervids, bovids, and rhinocerotids. In relation to the sambar *C. unicolor* and bovids *Bos/Bubalus*, we observe good preservation of premolars and molars and a lack of incisors and canines regardless of whether the site is a new

excavation (Tam Hang, Nam Lot, and Duoi U'Oi) or an old collection (Punung and Sibrambang), probably due to the fragility of anterior teeth in these taxa (Klein and Cruz-Urbe, 1984; Lyman, 2008) (S-Table 9). The presence of premolars and molars suggests that complete mandibles were preferentially accumulated in the sites before transport. When compared statistically (Fisher's exact test,  $p < 0.05$ ), there are significant differences in the proportions of teeth for *C. unicolor* between Duoi U'Oi and Tam Hang/Sibrambang and between Nam Lot and Tam Hang. The proportions of Sibrambang rhinocerotids are significantly different from those of Duoi U'Oi, Nam Lot, and Punung. These results suggest that different agents might have contributed to different accumulations.

Inversely, the ratio values for some small-sized species (<30kg) among primates (*Macaca* and *Hylobates*) and among ungulates (*M. muntjak*; except at Sibrambang, statistically different from the other sites for that species,  $p < 0.05$ ) indicate a better survivorship of upper teeth (Table 7). We also note differential preservation between primate and ungulate teeth in all sites (S-Table 9). In muntjacs, incisors and canines are lacking, most likely due to their fragility, whereas in small primates, all teeth are present (incisors, canines, premolars, molars). That suggests for both taxa the preferential accumulation of complete maxillae at the sites before transport.

The ratio values for pigs (*Sus* spp.), contrary to those of the other ungulates, show that upper teeth are preserved as frequently as lower teeth regardless of the site. The same inferences can be drawn for tapirids although sample sizes are smaller (Table 7). All types of teeth are represented in great numbers, and it seems reasonable, therefore, to suppose that complete jaws (maxillae and mandibles) were deposited in the sites (S-Table 9).

#### **Table 7**



*The ratio of permanent to deciduous teeth*

The lack of deciduous teeth of Carnivora is notable in the five assemblages (Table 7). Only the Sibrambang assemblage contains milk teeth of the bear *H. malayanus*, and that of Nam Lot contains some fragmentary milk teeth of the hyena *P. perrieri*. In the ungulate samples, the presence of both permanent and deciduous teeth is documented for most species except the serow *N. sumatrensis* (Table 7).

When ungulate species between recently excavated sites (i.e. Duoi U'Oi, Nam Lot and Tam Hang) are compared statistically, only proportions of *Cervus unicolor* and rhinocerotid teeth differ between Duoi U'Oi and the Tam Hang and Nam Lot sites (Fisher's test,  $p < 0.05$ ). The meaning of these differences can be explained by the action of different agents.

The ratio values calculated for the old collections of Sibrambang and Punung show marked differences with those estimated for the new collections of Tam Hang, Nam Lot, and Duoi U'Oi for all taxa (Table 7). In regards to pigs particularly, the values at Sibrambang (3741:6) and at Punung (113:0) are far from what would be expected based on the structure of populations in live herds (Biswas and Sankar, 2002). In regards to primates at Sibrambang and Punung, the absence or rarity of milk teeth among monkeys (613:0 and 52:1, respectively) and orangutans (1443:28 and 183:0) is also striking. At Sibrambang, only teeth of rhinocerotids are preserved in comparable frequencies (73:79) (Table 7). When ungulate species are compared statistically, the proportions of permanent and deciduous teeth from Sibrambang differ significantly from at least two among the four sites for *M. muntjak*, *C. unicolor*, *S. scrofa*, and rhinocerotids (Fisher's test,  $p < 0.05$ ). The most plausible explanation is that, in both historic sites (Punung and Sibrambang) the fragile deciduous teeth were often broken and fragmentary and therefore not preserved after excavation. We hypothesize that

only the well-preserved large and deciduous permanent teeth, with dense and solid enamel, were selected, resulting in recovery bias.

#### **4.3.4. Frequency of teeth and body size**

The correlation between the frequency of teeth (upper and lower/permanent and deciduous) and body size (mean weight; S-Table 10) within ungulates emphasizes two clear biases. At Nam Lot, there is a bias towards an accumulation of teeth of large ungulates: the heavier the animal, the more numerous the specimens (Spearman's test,  $r=0.82$  and  $r=0.96$ ,  $p<0.01$ , for upper and lower teeth respectively). At Sibrambang, the data reflects a bias towards an accumulation of teeth of small ungulates: the lighter the animal, the more numerous the specimens (Spearman's test,  $r=-0.89$ ,  $p<0.05$ , for permanent teeth). In the case of Nam Lot, the preferential accumulation of large species by one particular agent is significant, and the hyena probably played a major role (Kruuk, 1972; Brain, 1981; Palmqvist and Arribas, 2001; Fourvel et al., in press, accepted). In the case of Sibrambang, the results reflect the abundance of pigs. The species are most likely overrepresented in the assemblages due to the better survivorship of both upper and lower teeth and recovery bias.

#### **4.4. Taxonomic abundance (NISP and MNIf)**

##### **4.4.1. NISP and MNIf by family**

In regards to the assemblages from the new collections (Duoi U'Oi, Tam Hang and Nam Lot), NISP and MNIf by family provide general indications. The three faunas are dominated by cervids, bovids and suids. Cercopithecids are also abundant (Table 8).

The meaning of the NISP and MNIf from the Sibrambang and Punung assemblages are more problematic since they are largely biased due to the probable selection of well-

preserved teeth (Sibrambang in particular is differentiated from Duoi U'Oi for NISP and from Tam Hang for MNIf; permutation tests,  $p < 0.05$ , 20 000 permutations). Keeping in mind this bias, the relative predominance of suids and pongines over large ungulates (cervids, bovids, and rhinocerotids) is nevertheless notable.

## Table 8

### 4.4.2. NISP and MNIf by species

We compiled both indexes by species for ungulates and primates and by family for rhinocerotids and bovids in two-dimensional diagrams, which provide information on the representation of the group in each site (Klein and Cruz-Uribe, 1984; Lyman, 2008). Carnivora and humans have been excluded due to their relatively low abundance (Fig. 7).

The Figure 7 reveals that, at Tam Hang and Duoi U'Oi, four taxa are well-represented (*Macaca* sp., *S. scrofa*, *C. unicolor* and *M. muntjak*). The better survivorship of *Macaca* and *S. scrofa* in comparison with that of *C. unicolor* and *M. muntjak* might reflect the differential preservation of incisors and canines, preserved in the former and lost in the latter due to their fragility. *S. scrofa* is overrepresented due to the preservation of lower and upper teeth in equal numbers and to the great number of teeth on a row (the NISP varies in mammalian groups due to the different dental formulae: pigs have ten teeth on a row, monkeys eight teeth, rhinoceroses six to nine teeth). At Duoi U'Oi, the greater number of individuals of *C. unicolor* and rhinocerotids (large MNIf values for NISP) and *M. muntjak* to a lesser degree, in comparison with that of other ungulate species points to the possible action of external factors (carnivores and/or humans). That is also well demonstrated in the Tam Hang data.

At Nam Lot, we observe again a better survivorship of *S. scrofa* in comparison with all of the other species of ungulates or primates (Fig. 7). The bias observed in the preservation of

teeth exaggerates the abundance of the species. Large MNIf values for NISP of rhinocerotids and bovids also point to the possible action of external factors.

In relation to the Punung and Sibrambang assemblages, the diagrams emphasize the clear differential preservation of pigs and orangutans. The data most probably indicate the relative abundance of the populations in comparison with the other taxa. However, the representation of both species in the assemblages is exaggerated due to accumulated biases (the preservation of upper and lower teeth in pigs; the effects of the recovery bias, among the most significant of these). At Punung, the large MNIf values for NISP of pigs are notable.

## Figure 7

### 4.5. Body-size and age category

#### 4.5.1. The ungulate populations

The distribution of the biomass of the ungulate species by age class in the five fossil faunas can be informative on the body-size category which predominates in each site (Fig. 8). With respect to the three sites we studied, Figure 8 shows that at Nam Lot 46.3% are large ungulates and 41.5% are medium-sized ungulates. Rhinoceroses, adult bovids and pigs are predominant in these categories (S-Table 12). The Tam Hang and Duoi U'Oi schemes present a biomass of large-sized animals (42.6% and 59.1%, respectively), that is greater than that of medium-sized (34.3% and 21.5%). These faunas are marked by the relative abundance of rhinoceroses (except new borns), juvenile sambars (*C. unicolor*) and adult pigs (*S. scrofa*) at Tam Hang, and rhinoceroses, adult sambars and adult pigs (*S. scrofa*) at Duoi U'Oi (S-Table 12). In both sites, pigs and muntjacs are well represented in their respective body-mass category (Fig. 8).

These three sites differ markedly from those of Punung and Sibrambang where we observe an overrepresentation of the medium-sized category, which represents 60.3% and

78.3%, respectively (Fig. 8). This category is dominated by pigs and is strongly exaggerated because of the conditions of preservation and old techniques of excavation, as we emphasized previously. Only the Sibrambang fauna contains new born rhinocerotines.

### Figure 8

#### 4.5.2. The large carnivoran populations

All of the faunas yielded few specimens of large Carnivora (Table 8; S-Table 11): canids (the dhole *Cuon alpinus*) and hyaenids (the hyena *Pliocrocuta perrieri*) at Nam Lot; canids (*C. alpinus*) and felids (the tiger *Panthera tigris* and the leopard *Panthera pardus*) at Duoi U'Oi and Sibrambang; canids (*C. alpinus*) and felids (*P. tigris*) at Tam Hang. At Punung, the tiger is the only predator. Humans are represented by one specimen each at Nam Lot, Punung and Duoi U'Oi, pointing to their relatively low abundance at the sites.

We used body mass predictions based on family regression to estimate the body mass of felids and canids in the fossil faunas (van Valkenburgh, 1990) (Table 9). According to this author, the m1 length produces the most accurate predictions in felids. The available data on *P. tigris* give a body mass estimate of 153.1 kg at Duoi U'Oi (one m1), and a range of 121.6-168.6 kg (mean=152 kg, 3 m1) at Punung (see also Hertler and Volmer, 2008). Contrary to modern populations, differences in body mass estimates between the Late Pleistocene tigers, from northern Vietnam (Duoi U'Oi) and from Java (Punung) are rarely observed. This body mass is intermediary between that of its modern counterparts in the mainland (~180-245 kg) and that of the smaller Sumatran or Javan tigers (~75-160 kg). The body mass estimate of *P. pardus* from Duoi U'Oi (20.5-26.1 kg on 2 m1) is smaller than that of living animals in the Asian mainland (45-65 kg SE Asia; 29-77 kg in India; Pocock, 1939; Francis, 2008). The body mass estimate of *C. alpinus* from Sibrambang (14-17.2 kg on 2 m1)

falls within that of the modern species on the mainland (10-21 kg; Francis, 2008). Only one P2 and one p3 can be clearly determined among the six specimens assigned to the hyena *P. perrieri*, but no m1. We will then refer to the body mass estimate used in the literature for the Pleistocene spotted hyena (60-80 kg; Dennell et al., 2008).

#### Table 9

### 4.6. Mortality profiles of species

#### 4.6.1. *Cervus unicolor/Rusa* sp.

The MNIc calculated on the basis of d4 and m1 or m3 are: 15 for Tam Hang, 25 for Duoi U’Oi, and 15 for Sibrambang (Tables 10 and 11). It was not possible to give such an estimate for the Nam Lot sample; due to the fragmentary nature of the 41 teeth assigned to the species, only two teeth were left after selection. We used wear criteria given by crown height measurements to determine age classes (Klein et al., 1981) (see Supplementary Information). Mortality profiles of sambars display differences between the three assemblages (Fig. 9), however, these differences are not statistically significant (Kolmogorov-Smirnov test). The underrepresentation of juveniles (<1 year), especially at Duoi U’Oi, is not an artefact of bad preservation of the assemblages (S-Table 13). Moreover, Tam Hang demonstrates that deciduous teeth can be well preserved in the fossil samples under relatively comparable post-depositional processes. The case of Sibrambang is different, since the small number of juvenile individuals might be due to recovery bias.

#### Table 10

#### Table 11

#### Figure 9

In the Tam Hang profile, the first age class (juveniles, <1.6yr) is predominant, and adult cohorts [3-8] contain both prime-aged (3 yrs-9 yrs) and old-aged individuals (>9 yrs up to ~13yrs old). Among cohorts of adult individuals in the Sibrambang profile, the presence of old-aged animals up to 13 years old is noted. The Duoi U'Oi profile displays differently a bias towards cohorts [3-6] that contain abundant prime-adult individuals (3yrs-9yrs), whereas juveniles are less represented and old individuals are lacking.

When the cohorts are grouped in three large classes, and compared with the demographic characteristics of *C. unicolor* of two Indian reserves (Fig. 9), the Tam Hang profile clearly displays an overrepresentation of juveniles (47%) in comparison with their abundance in living populations (19% in Nagarhole Park, 21% in Pench Park) (Karanth and Sunquist, 1995; Biswas and Sankar, 2002). The authors observed that 91% of group size is constituted by one (most often male) to three individuals, and 8.5% by 4 to 10 individuals. The Tam Hang profile resembles those generated by the social predator the dhole *C. alpinus*. Indeed, young sambars have their preference (85.7% of the kills for the dhole against 18% for the tiger) (Karanth and Sunquist, 1995). Any clear selective predation can be assessed from the Sibrambang profile (Fig. 9).

The Duoi U'Oi mortality profile illustrates a pattern of possible human selective hunting. Figure 9 shows that, despite the absence of old individuals (>9 yrs), the profile is characterized by an overrepresentation of adult individuals (76%) in comparison with their abundance in modern populations (59.3% to 73.2%) (Karanth and Sunquist, 1995; Biswas and Sankar, 2002). Adult *Cervus* have the preference of tigers (70.6%) rather than that of dholes and leopards (Karanth and Sunquist, 1995: Table 5), but among adult animals killed, old-aged individuals are usually present (6.9%) (Karanth and Sunquist, 1995: Table 9). Therefore, the Duoi U'Oi pattern, with the lack of all old-aged individuals and the elevated

proportions of prime-adult individuals, diverges from the typical prey selection by tigers. The study of archaeological sites shows that humans appear to be the only predators likely to generate such a mortality pattern that is dominated by prime-aged prey (Klein and Cruze-Urbe, 1984; Stiner, 1990; Steele, 2003, 2004).

#### 4.6.2. *Sus scrofa/Sus vittatus*

We calculated the MNIC on the basis of lower molars (m1/m2/m3): 23 for Tam Hang, 21 for Duoi U'Oi, 15 for Nam Lot (*Sus scrofa*), and 164 for Sibrambang (*Sus vittatus*) (Tables 10 and 12). We used the two eruption stages of germs [T, U], the thirteen wear stages defined for m1 and m2, and the ten stages for m3, to determine age classes of individuals (Grant, 1982; Rolett and Chiu, 1994) (see Supplementary Information). Mortality profiles of pigs display differences between the four assemblages (Fig. 10). The Sibrambang profile is statistically different from those of Tam Hang, Nam Lot and Duoi U'Oi (Kolmogorov-Smirnov test, each  $p < 0.001$ ).

#### Table 12

The two first cohorts of new borns and immature individuals up to 5/8 months old [T-U] are absent in all assemblages (Fig. 10). The cohorts [A-C] are also underrepresented, considering the litter size of piglets and their high rate of mortality in living species (the social unit is one or more females and their last litters with subadults from previous litters, each litter size reaching sometimes 10 piglets; Biswas and Sankar, 2002). All samples were biased towards low proportions of very young individuals. In new collections, it is most probably due to the fragility of carcasses and their rapid destruction by predators or other agents or to the fact that the small and light m1s were lost during transport in the karsts. In the old collection of Sibrambang, the recovery bias adds to these factors. It is particularly



marked for the cohorts [A-B] only defined on small m1s, whereas the cohort [C] is defined on larger m2s.

**Figure 10**

Keeping in mind these biases, the mortality profiles of Tam Hang and Nam Lot display comparable proportions between cohorts [D-F, 1 yr-2 yrs] of young adult individuals and those of mature adult individuals [G-K, >2 yrs]. Both profiles lack the cohorts of old-aged individuals [M-N, >6 yrs]. In contrast, in the Duoi U'Oi profile (Fig. 10), the cohorts of mature adult individuals [G-N] are well represented and include a significant number of old-aged animals [M, >6 yrs]. The Sibrambang profile diverges from those of Tam Hang, Nam Lot and Duoi U'Oi, by the presence of elevated cohorts of piglets and young adult [C-F] and mature adult individuals [G], and very old-aged individuals up to ~10 yrs [N] (Fig. 10).

When the cohorts are grouped in three large age classes and compared with the demographic characteristics of modern *Sus scrofa* populations (Fig. 10), only the Duoi U'Oi fauna resembles the living populations with the predominance of mature and old adult individuals up to 200kg (62% to 66%/71.6%) (Karanth and Sunquist, 1995; Biswas and Sankar, 2002). This mortality pattern might also reflect the predation of the tiger, particularly in habitats of rich prey biomass densities (in that case prey selection determined by chance encounter matches the demographic profile) (Schaller, 1967; Stiner, 1990). Indeed, the hunt of the tiger is preferentially directed towards either immature (34.8%) or mature adult individuals (64.2%), and among them the largest ones (~200 kg) (Karanth and Sunquist, 1995). This behavior is plausible according to the body mass estimate of the Duoi U'Oi tiger (153.1 kg). We can't however rule out two alternatives: the presence of very old animals observed at Duoi U'Oi (Fig. 10) might be associated with scavenging activities by humans on

carcasses abandoned by the tigers or that died naturally; or selective hunting on this category of prey by humans (Faith, 2008).

In relation to Sibrambang, the profile displays different representations within the cohorts from the oldest piglets to the youngest adult individuals [C-G]. In the three-cohorts profile, the corresponding age class is overrepresented (42% vs 28.4% in a modern population; Biswas and Sankar, 2002) (Fig. 10). In current mammalian communities (without human hunting), this type of selection of animals of ~30-60kg is characteristic of habitats with prey biomass-depleted densities (for example, in that case, the tiger prefers animals of medium body size such as pigs and chital (*A. axis*) (Reddy et al., 2004). At Sibrambang, the predation of the large carnivores (tiger, leopard, and dhole) could generate this profile.

The Tam Hang and Nam Lot profiles also differ from those of living populations with a predominance of young adult animals in the former (43%) and mature adult animals in the latter (40%) (Fig. 10). At Nam Lot, both the hyenas and dholes could generate this profile. In African savannas, hyenas act as a “solitary scavenger and predator of small mammals or as a group-living hunter of ungulates” (Nowak, 1999). Depending on their behavior, the kills involve either preferentially small prey (<50kg) or medium-sized prey (100-200kg) (Cooper et al., 1999). In Indian habitats, the dhole acquired prey in a body mass range of ~30-60 kg (Johnsingh, 1982; Karanth and Sunquist, 1995; Selvan et al., 2013a, 2013b). At Tam Hang, the predominant age class of pigs with a body mass range of 30-60 kg might also be preferred by the dhole.

#### **4.6.3. Perissodactyla**

##### *Rhinoceroses*

In relation to rhinoceroses (Table 10), we calculated the MNlc on the basis of upper and lower, permanent and deciduous dentition: 25 for Tam Hang, 59 for Duoi U'Oi, 8 for Nam Lot, and 152 for Sibrambang (Table 13). We used sixteen tooth wear stages to characterize individual ages following a procedure adapted from Hillman-Smith et al. (1986). This protocol seems to be the most accurate for comparing the rhinocerotid samples, even if it does not allow any direct comparison with living populations (*R. unicornis*) (see Supplementary Information). The mortality profiles of the four rhinocerotid samples (including *Rhinoceros unicornis* and/or *R. sondaicus* and/or *Dicerorhinus sumatrensis*; Fig. 11) display marked differences between assemblages. The mortality profiles statistically differentiate the samples from each other (Kolmogorov-Smirnov test, statistical differences were considered significant at the 0.05 level), except the Duoi U'Oi profile which is not statistically different from that of Sibrambang, and that of Tam Hang is not statistically different from that of Nam Lot. With respect to Sibrambang, the sample of young individuals is much less affected by recovery bias in comparison with the other species (*Rusa* sp. and *Sus vittatus*).

#### **Table 13**

The Duoi U'Oi sample (Fig. 11c) displays a profile in which almost all cohorts are represented: calves [II-V], subadult [VI-VIII], and adult individuals [IX-XVI]. The Tam Hang (Fig. 11a) and Nam Lot (Fig. 11b) profiles consist essentially of juveniles up to 3 years old [II-V], conversely. The Sibrambang profile appears intermediate between both clusters (Duoi U'Oi vs Tam Hang and Nam Lot) with a majority of calves (including newborns [I, up to 1.5 months]), but with subadult, adult and old individuals fairly well represented as well (Fig. 11e).

We compared the profiles with that of the natural demographic composition observed in a modern population of *Rhinoceros unicornis* in the Royal Chitwan National Park, Nepal (26.6% calves; 21.2% subadults; 52.2% adults; Laurie, 1982; Laurie et al., 1983), which roughly coincide with the age classes [I-V], [VI-VIII], and [IX-XVI] as defined by Hillman-Smith et al. (1986) (Fig. 12). To our knowledge, no vital statistics exist for Sumatran rhinoceroses. In all four samples, juveniles are far more numerous than expected in a natural population ranging from 36.2% in the Duoi U’Oi population to 87.6% in that of Nam Lot (Fig. 12). Taking this into account, the Duoi U’Oi sample is closer to a “natural” calf+subadult+adult population than other rhinocerotid samples. In this respect, it resembles the population of Panxian Dadong, a Middle Pleistocene site in China where the *Rhinoceros sinensis* dental sample (121 teeth) points to a classical “U-shaped” attritional profile with 41.3% of juveniles, 9.1% of subadults, and 49.6% of adults (Schepartz and Miller-Antonio, 2010a, 2010b). Dinerstein and Price (1991) also observed the population of *R. unicornis* from the Nepalese Park and calculated that 62% of the individuals were less than 12 years-old, which grossly corresponds to the age classes of infants, juveniles and subadult individuals [I-X] defined by Hillman-Smith et al. (1986). Here again, the Duoi U’Oi (59.4%) sample is closer to the modern natural population than other rhinocerotid samples studied here.

The Sibrambang profile shows the predominance of infants and juveniles [I-V] (Fig. 11d). In the three-cohort mortality profile, these ages correspond to 55.4% in comparison with 26.6% in a living population (Fig. 12). Among the three Carnivora species, only the tiger is known to prey on young calves (Laurie et al., 1983).

Both profiles of Tam Hang and Nam Lot are significantly different from those of Duoi U’Oi and Sibrambang in the relative overrepresentation of juveniles and youngest subadult individuals [II-VII] (Fig. 11). The other cohorts [VIII-XVI] have few of the former represented,

whereas they are lacking in the latter. Considering age classes [I-X, < 12yrs], the percentages reach 78.9% at Tam Hang and 100% at Nam Lot. The samples are, however, by far the smallest ones (11 and 19 specimens, respectively), which is likely to somewhat lessen their significance. The carnivoran guild from Tam Hang includes two large flesh eaters, tiger and dhole, but only the tiger, known to prey on young rhinocerotid calves (Laurie et al., 1983), could generate this profile. Nam Lot is quite distinct, with the co-occurrence of scavengers and/or opportunistic predators such as hyenas, dholes and humans. Considering a body mass estimate of 60-80 kg (Dennell et al., 2008), it is conceivable that the hyena killed such large prey, (the body weight of a young rhinoceros reaches 400 kg (Kruuk, 1972). Today when hunting by packs, significant percentages of the kills also involve large prey like buffaloes (200-400kg - up to 13%) and even elands (>400kg - up to 2%) depending on their availability (Kruuk, 1972; Cooper et al., 1999; Höner et al., 2002; Palmqvist et al., 2011). In the case of Nam Lot, the formation of large hunting packs most certainly compensated for their small body size (~60-80 kg) (today young rhinoceros up to 6 months are hunted by packs of about 15 hyenas; Kruuk, 1972). Contrary to tigers, hyenas have been observed to bring back to the dens only the lighter carcasses of their kills (Klein and Cruz-Urbe, 1984), which could also explain the presence of only juveniles at Nam Lot.

**Figure 11****Figure 12***Tapirs*

A sample of nineteen teeth of the Malayan tapir *Tapirus indicus* from Sibrambang allow us to reconstruct a three-cohort mortality profile (Fig. 13). The tapir samples from Tam Hang, Nam Lot, and Duoi U'Oi are too small for being included in this comparison, most likely due to low population density (four, four, and 11 teeth, respectively; Bacon et al., 2008a,

2008b, 2011, 2012). Moreover, in the Tam Hang and Nam Lot samples, they only consist of permanent teeth, pointing to a probable underrepresentation of juvenile (and subadult?) individuals.

The population structure of tapirs, especially that of the Malayan tapirs (*T. indicus*), is far from known. Tapirs are considered to be solitary animals, with the only attested groups being generally one mother and its offspring (*Tapirus terrestris*, Bolivia; Maffei, 2003) or two adults (*T. indicus*, Sumatra; Novarino, 2005). Nevertheless, based on dental eruption sequence and wear stages, Maffei (2003) assessed that a natural lowland tapir population from Bolivian Amazonia (64 individuals) could be comprised of 25% juveniles (<1 year-old), 19.5% subadults (between 1 and 2 years), and 55.5% adults (2 years and more). The mortality curve of tapirs (*T. indicus*) from Sibrambang based on similar wear stages is tentatively compared to this “J-shaped” pattern (Fig. 13). At Sibrambang, adult individuals are overrepresented (73.7%) (Fig. 13). The body weight of adult individuals is estimated between 250 and 350 kg (Francis, 2008), a category more accessible to tigers than to leopards and dholes (O’Brien et al., 2003).

## Figure 13

### 5. Discussion

#### 5.1. A new chronological framework

Despite being major fossil sites in the Southeast Asian Pleistocene record, Tam Hang and Nam Lot have only ever been discussed using estimated chronologies (Bacon et al., 2008a; 2011; 2012; Düringer et al., 2012). However with the combined use of OSL and U-series methods, the sites can be now discussed within their correct chronological context. The new age range for Tam Hang proved to be slightly younger than anticipated, returning an age that is Late Pleistocene (94-60 ka), while the numerical age range of Nam Lot agrees with its

estimated age (86-72 ka). The new luminescence chronology for the base of Duoi U'Oi (70-60 ka) agrees with the previously obtained age for the overlying breccias ( $66 \pm 3$  ka; Bacon et al., 2008b).

Despite complications regarding Thorium contamination in some of the flowstone samples (especially from Tam Hang South) there is good agreement between the red TL, SG OSL and U-series techniques. Despite some apparent chronological inversions that are mostly within error limits (e.g., the flowstones and the breccias from Tam Hang), the results describe an increase in age with depth for all sites. For Tam Hang South (Fig. 2), there is no statistical significance between the ages for the lowest and middle levels of the breccias but the upper level appears to be younger. Whereas in Nam Lot (Fig. 3) the older stratigraphic units are divided from the younger via two clear episodes of flowstones precipitation at 60-62 ka and 52 ka. The SG OSL results are consistently younger than the SA OSL and red TL results as observed at other sites (e.g., Demeter et al., 2012), but bearing in mind the limitations of each technique (e.g., SA averages the signal from many grains and red TL represents a maximum age for deposition), the results are remarkably consistent and contribute to establishing a more robust chronological framework for the region.

These new chronologies (combined with the Westaway in preparation work on the Sumatran caves) significantly contribute to our understanding of the age of many of the key fossil sites in Southeast Asia, and enable valid comparisons and correlations to be made between sites. Different ages estimates (ESR/U-series) of faunas in the Indochinese subregion (Corbet and Hill, 1992) are few. At the transition MIS5-MIS4 (~130-60 ka), one can cite in southern China Wuyun cave (350-200; Wang et al., 2007; 279-76 ka; Rink et al., 2008) and Upper Pubu cave (280-88 ka; Rink et al., 2008), Ma U'Oi cave in northern Vietnam (>49 ka; Bacon et al., 2004; 2006), Thum Wiman Nakin cave in Thailand (>169 ka; Esposito et al.,

1998, 2002), and Batu cave in peninsular Malaysia (66-33 ka; Ibrahim et al., 2013). Consequently, the biochronological timescale being far from complete, the reconstruction of palaeoecological changes on the basis of faunal composition poses a real challenge. We propose that the application on the multi-disciplinary approach to additional key sites in this region will start to address the gaps in the chronological framework for the SEA fossil sites.

## 5.2. The evolutionary frame

On the basis of (i) the evolutionary stages in lineages of modern mammals (subspecies defined on dental dimensions showing more or less advanced stages among the well-documented species), (ii) the presence of species such as *Megatapirus augustus* and *Stegodon orientalis* to be specific, and also (iii) the occurrence of new incomers, we first considered the Tam Hang South fauna as rather characteristic of the late Middle Pleistocene (Bacon et al., 2011). The new age range of 94-60 ka is slightly younger than we anticipated. We also hypothesized that the Nam Lot fauna could be more recent than that of Tam Hang, on the basis of more advanced evolutionary stages in *Muntiacus muntjak* and *Sus scrofa*, among the best preserved remains (Bacon et al., 2012). The new age range of 86-72 ka for Nam Lot does not confirm, nor reject, this hypothesis. Age estimates for both faunas document the presence of archaic and modern species during the interglacial stage MIS5 (128-71 ka), in the northern Indochinese subregion (Corbet and Hill, 1992) (Fig. 1 and 5).

Both Punung and Sibrambang faunas are exclusively composed of modern species. The age estimate of the Punung fauna, between  $128 \pm 15$  ka and  $118 \pm 3$  ka (MIS5) (Westaway et al., 2007), shows that the “continental” fauna which reached the southernmost land of Java, at the time of low sea level, was totally modern in its composition (Voris, 2000; van den Bergh et al., 2001; Louys and Turner, 2012). It is envisageable that climate and habitat,



globally at the south of the equator, were not favorable to *Megatapirus* and *Stegodon* species, as also shows the securely dated Badak fauna in Peninsular Malaysia devoid of both archaic species since at least 208 ka (274-208 ka; Ibrahim et al., 2013). Indeed, during that time, and so far as 72 ka as demonstrate the Nam Lot-type faunas in northern Laos (and so far as 76 ka, in Southern China; Rink et al., 2008), archaic species (*S. orientalis*, *M. augustus*) still lived in this northern part of the Indochinese area.

Drastic changes occurred in the faunas which succeeded those of Tam Hang and Nam Lot during the second half of the Late Pleistocene in northern Indochina. Indeed, the Duoi fauna from northern Vietnam is totally modern in its composition and characterized by more advanced evolutionary stages in mammalian lineages and by the occurrence of *Dicerorhinus sumatrensis* (Bacon et al., 2008; Antoine, 2012). The solid chronology of the fauna ( $66 \pm 3$  ka), strengthened by two independent age estimates (70-60 ka), clearly dates that these evolutionary changes were established by MIS4 (71-59 ka), during a relatively cool climate (Fig. 1 and 5). At the state of knowledge, the securely dated Batu cave fauna documents in the same way the first occurrence of *D. sumatrensis* in Peninsular Malaysia at 66-33 ka (Ibrahim et al., 2013), whereas its southernmore presence at Sibrambang around 81-70 ka remains questioned (Antoine, 2012).

### 5.3. Review of pre- and post-depositional factors

The preservation of remains in the five fossil assemblages depends on several agents which acted during pre- and postdepositional processes (Table 14). In an attempt to trace these processes, the present taphonomic analysis shows that the last agent is the excavators who created a bias in choosing only the most complete and well-preserved teeth. This

recovery bias clearly distinguishes the assemblages of the old collections (Punung and Sibrambang) from the three others (Tam Hang, Nam Lot, and Duoi U'Oi).

#### **Table 14**

In the sites we studied, Tam Hang, Nam Lot, and Duoi U'Oi, the lack of very small and light teeth of microvertebrates (<3mm) is striking. The sedimentological analysis shows that the sites are not formed in situ (Bacon et al., 2008a, 2008b; Düringer et al., 2012). All remains of mammals accumulated in breccia deposits originated somewhere upwards in the karstic network (Düringer et al., 2012). In the three sites, the formation of the fossiliferous deposits was endokarstic and not fluvial, and these processes of transport inside the karsts clearly selected only the teeth of middle- to large-sized mammals (Table 14). In the case of endokarstic deposits, bones and teeth together with clasts, speleothems and argillaceous sediments are transported and deposited by powerful floods, which act as selective agents in relation to the density of remains (Düringer et al., 2012). Taking into account the state of preservation of teeth with intact crowns, these agents were most likely selective rather than destructive. In all cases, only isolated teeth with rare bones are preserved, suggesting that the transportation was long and that most of the small and light remains were lost during the water circulation inside the network. These deposits are mostly carried and reworked from cave to cave over long time-scales, so it is difficult to evaluate the rate of bone accumulation. This type of assemblage is the most frequently encountered in Southeast Asia (Tougaard, 1998; Zeitoun et al., 2005, 2010; Rink et al., 2008; Ibrahim et al., 2013), even if some assemblages present different preservation (Chaimanee, 1998; Bacon et al., 2004, 2006). The present analysis shows, however, that it is difficult to emphasize the effects of the drainage in the karsts on the composition of the preserved assemblages, and some questions remain unresolved (is the lack of small Carnivora due to the action of floods? Can

we also attribute some aspects of the differential preservation of teeth, i.e. upper vs. lower or permanent vs. deciduous, to that action?).

The taphonomic analysis shows that, before transport, the main accumulating agent in the five assemblages is the porcupine *Hystrix brachyura* (Table 14). About ~82% (Duoi U'Oi) to ~94% (Tam Hang) of teeth have gnawed roots (S-Tables 4-8). These percentages are higher than those observed by Brain (1981) in South African sites, with 22% to 100% of gnawed objects (horns, bones and teeth) collected in lairs and by O'Regan et al. (2011), with 54.6% to 93.6% of gnawed objects (bones and isolated teeth). The phenomenon is also more frequent than that observed in cave sites from northern China (Wu and Poirier, 1995; Tong et al., 2008).

It is clear that porcupines (*Hystrix brachyura*, 15-20 kg; Francis, 2008) collected remains from a wide range of taxa: in the faunal lists (Table 4), the smallest species weighs ~2 kg (*Martes flavigula*; Francis, 2008) and the largest species weighs ~4250 kg (*Elephas maximus*; Francis, 2008), as observed in South African sites (Brain, 1981; O'Regan et al., 2011). The results suggest that, in all sites, rodents collected a large quantity of available, transportable remains preferentially choosing either mandibles of large herbivores (rhinocerotids, bovids, *C. unicolor*) or maxillae of small animals (Carnivora, Primates, *M. muntjak*) or both (suids). The differences we observe in the frequency of gnawed teeth belonging to Carnivora and Primates at Tam Hang, Nam Lot and Punung (~100%) versus at Duoi U'Oi and Sibrambang (50% to 100%) could be linked to the fact that, in the latter sites, porcupines were not the only accumulating agents. Differential damages are also observed between species of rhinocerotids from site to site, with ~11% of gnawed teeth at Nam Lot and Punung, ~45% at Tam Hang and Duoi U'Oi, and up to ~93% at Sibrambang. At Nam Lot and Punung, porcupines were not the only accumulating agents. The data suggest that the sites might

have been co-occupied by porcupines and predators of small animals at Duoi U’Oi and Sibrambang (leopards and/or dholes) and porcupines and predators of large animals (hyenas at Nam Lot and tigers at Punung). This variability in rhinocerotids damage is also noted in some other Asian Pleistocene sites. In the analysis of the late Middle Pleistocene Panxian Dadong locality (MIS6-8), in China, Schepartz et al., (2003) conclude there is “minimal post-mortem damage from animal processing”, with only 10% of the rhinocerotid sample being gnawed by porcupines. In contrast, the rate is very high in Lang Trang, Vietnam (Late Pleistocene; Vu The Long et al., 1996), and in the “Cave of the Monk”, Ban Fa Suai, Thailand (Middle Pleistocene; Zeitoun et al., 2005).

The behavior of porcupines in accumulating a wide range of available remains suggests that the assemblages can be used as indicators of abundance and diversity of middle- to large-sized species living in the areas surrounding the sites (Brain, 1981; Skinner et al., 1986). Furthermore, the taxonomic diversity shows that there is a rather good representation of large Carnivora and ungulate species (Lyman, 2008; and references therein). In relation to the sites studied, the analysis of mortality profiles of some ungulate species reveals that the carcasses might be those of prey consumed and abandoned by large predators (carnivores and/or humans) (Table 14).

#### **5.4. Reconstruction of the environmental context during MIS5 and MIS4**

##### **5.4.1. MIS5: Punung, Sibrambang, Tam Hang, and Nam Lot**

According to the taphonomic analysis of the northern and southern sites, it is most likely that differences in relative species abundance reflect firstly differences in habitat. The Tam Hang (94-60 ka) and Nam Lot (86-72 ka) faunas are diversified, and rich in the ungulate biomass of both modern and archaic species. The few differences in the relative abundance

of some ungulate species reflect differences in the behavior of hypercarnivores (tiger and dhole at Tam Hang vs hyena and dhole at Nam Lot), rather than differences in habitat (Table 14). Both faunas are dominated by cervids, bovids, and suids, documenting open seasonal deciduous forests, a mixed habitat with trees and grassy covers. In India, different types of deciduous forest, gallery forest and alluvial plain carry the highest ungulate biomasses, with browsers and grazers (Eisenberg and Seidensticker, 1976). Cercopithecids are also abundant in these forests dominated by open canopy. In this respect, the rare pongines and hylobatids in the faunas support the presence of reduced areas with large fruit trees in the surrounding localities, as observed today in some degraded habitats in Indonesia (Felton et al., 2003; Morrogh-Bernard et al., 2003). Around stage MIS5, the Tiangyang pollen sequence reveals elements indicating a dense forest and warm climate (Leizhou Peninsula, southern China; Zheng and Lei, 1999), which is in accordance with the composition of the mammalian communities of Tam Hang and Nam Lot. For Sun and colleagues (2003), the vegetation was dominated by monsoon evergreen forests, with a great proportion of *Catanopsis* and *Quercus*.

The Punung fauna from central Java (128-118 ka; Westaway et al., 2007), while impoverished in mammalian species, is typical of faunas living in aseasonal rain forests. At the onset of MIS5, a modern tropical fauna replaced the archaic fauna (Leinders et al., 1985; de Vos and Sondaar, 1994; Storm et al., 2005; Storm and de Vos, 2006). In the Punung fauna, the array of potential ungulate prey is poorly diversified, but so is that of the large predators with only the occurrence of the tiger. The composition of the new fauna of Gunung Dawung (Punung III) also points to this pattern, with seven ungulate species but no large predators (Storm et al., 2005; Storm and de Vos, 2006). The data are in agreement with the presence of humid and warm climate in Java (and more largely in the Lesser Sunda Islands of

Indonesia) based on sedimentological, palynological, and palaeoecological data (van der Kaars and Dam, 1995, 1997; van den Bergh et al., 1996; 2001; Wang et al., 1999; Tougard and Montuire, 2006; Louys and Meijaard, 2010). The Sibrambang fauna from northwest Sumatra (81-70 ka) shows that, at the end of MIS5, a diversified modern fauna was present on the western margin of the Sundaland. The fauna is rich in large predators (tiger, leopard, and dhole), but the data suggest that the biomass of large ungulates (especially bovids and cervids) could be depleted, as is observed in tropical evergreen forests with meadows (Eisenberg and Seidensticker, 1976). Due to the specialized diet of orangutans, around 60% of which is comprised of fruits and leaves, a large population density is a good indicator of the presence of regular and abundant fruit resource (Eisenberg and Seidensticker, 1976; Galdikas, 1988; Delgado and van Schaik, 2000). Regarding modern populations of wild pigs in Asia, the highest atypical densities of individuals have also been observed in aseasonal lowland dipterocarp rain forests with abundant food resource (Ickes, 2001). The recent palaeoecological interpretation based on palynological evidence indicates that southwest Sumatra during that period (~83-71 ka) was dominated by “species- and fern-rich closed-canopy rainforest, with a substantial presence of open herbaceous swamps and mangroves along the coast line” (van der Kaars et al., 2010, p.67), which is in accordance with the composition of the faunal community of Sibrambang.

However, two rhinocerotid teeth from Nam Lot (Rhinocerotidae indet.: one lower milk molar and one lower molar), one tapir tooth from Tam Hang (*Tapirus indicus*: m2), two teeth from Sibrambang (*T. indicus*: two M2s) and two teeth from Punung (*T. indicus*: one P4 and one M2) show linear enamel hypoplasia. This testifies to a non-congenital physiological stress, hypothetically pointing to malnutrition during juvenile stages in a similar proportion (2/17, 1/11, 2/19, and 2/21, respectively), i.e. for ~10% of the corresponding samples. Food

resource was therefore not continually available at local scale, at least in sufficient amounts, for such large hindgut fermenters during MIS5 in the Sundaland.

#### 5.4.2. MIS4: Duoi U’Oi

On the basis of the analysis of the Duoi U’Oi fauna from northern Vietnam, both climate and habitat may explain the relative abundance of species. The fauna is typical of those living in open seasonal forests, with a particular importance on ungulate biomass. Considering megaherbivores, the Duoi U’Oi fauna is slightly less diversified than those of Tam Hang and Nam Lot, but the carnivore guild is enriched with one additional species, the leopard (*P. pardus*) (the predator-to-prey ratio in species diversity is 2:14 at Tam Hang, 3:11 at Duoi U’Oi, and for comparison 3:3 in south Indian intact tropical forests; Karanth and Sunquist, 1995). Its age,  $66 \pm 3$  ka, strengthened by two independent age estimates, 70-60 ka, places it in the Periglacial stage (MIS4). The marine record from South China Sea shows that this period was characterized by quantities of herbs, Poaceae and *Artemisia*, clearly indicating cooler and drier conditions than Interglacials (Sun et al., 2003). During that cooling period, the Duoi U’Oi fauna shows that notable changes occurred in mammalian communities: the composition in megaherbivores illustrates a small “turnover” and the appearance of more advanced stages implies changes in body size and then biology of mammals (Bacon et al., 2008b, 2011; Antoine, 2012).

One may notice that during the Periglacial stage 4 (~71-52 ka, MIS4) and the earliest part of MIS3, in southwest Sumatra both vegetation and climate remained similar to those of MIS5a (van der Kaars et al., 2010). It is conceivable that a Sibrambang-type fauna with no significant changes continued to occupy Sumatra during MIS4. In addition, it seems that the Toba eruption did not modify the palaeofaunas of Sundaland (Louys, 2007, 2012). Thus, the

Duoi U'Oi and Sibrambang faunas show how similar faunas evolved when exposed to very different latitudinal and environmental conditions on the Sundaland (Table 14). Both faunas are quasi identical in species diversity, but clearly differ by the relative abundance of ungulate species, and the nature of prey-predator relationships relative to habitat (open seasonal forest vs aseasonal rain forest).

### 5.5. Evolution of the prey-predator relationships

What emerges from the present analysis is that each fauna most probably represents a complex mix of different sources of accumulation, as observed in some other sites (Bekken et al., 2004) (Table 14). Nevertheless, it is possible on the basis of mortality profiles of some ungulates to identify the primary agent of prey selection: Tam Hang is a dhole site, Nam Lot is a hyena site, and Duoi U'Oi is a human site. The primary agent at Sibrambang could be the tiger, but the results are less obvious, probably due to the large overlap of food items consumed by the three large predators (Table 14). Regarding recent mammalian communities, among a wide variety of prey, ungulate species constitute around 80% or more of the kills made by predators (Schaller, 1967; Kruuk, 1972; Brain, 1981; Karanth and Sunquist, 1995; Biswas and Sankar, 2002). Regarding Late Pleistocene mammalian communities that were richer in ungulate and large carnivore guilds, it is highly conceivable that remains accumulated at the sites, or in the areas surrounding the sites, reflect the importance of prey hunting and/or scavenging.

What can be inferred is that one of the consequences of the evolution of the climate-habitat context between northern and southern Sundaland during MIS5, was a dramatic change in the predator-prey relationships. Indeed, the present analysis suggests different prey-biomass categories available to predators. Particularly when the Duoi U'Oi and



Sibrambang faunas are compared, we observe that tigers did not have the same access to prey. In the rich ungulate community of Duoi U'Oi, the predation of the tiger (153 kg) is biased towards mature adult pigs and among them the larger ones were preyed upon (~200kg). It seems that young rhinoceroses (~400 kg), while abundant, were under low predation pressure, only preyed upon in rare cases. In the depleted ungulate community of Sibrambang, young adult pigs and piglets (<30 kg to 60 kg) might be consumed due to their great availability by the tigers, but also by leopards and dholes. The predation of the tigers might be also directed towards large animals like mature adult tapirs (250-350kg) and young rhinoceroses (~400kg), that are nevertheless less abundant in the record. Thus, as observed today in the Sub-Indian continent, the Pleistocene tigers most likely had great plasticity in their behavior regarding the type and body-mass category of prey hunted (Karanth and Sunquist, 1995; Ickes, 2001; Biswas and Sankar, 2002; Reddy et al., 2004; Ramesh et al., 2012; Selvan et al., 2013a).

The comparative analysis of the Duoi U'Oi and Sibrambang faunas points to another aspect: the coexistence of the three large predators (tiger, dhole, and leopard) in mammalian communities. The body mass estimate of the leopard *P. pardus* from Duoi U'Oi reveals its small size (20-26 kg), smaller than that of the living leopard in Asia (from China to India, 22-77 kg, Table 9), whereas the body mass estimate of the dhole *C. alpinus* from Sibrambang (14-17 kg) reveals a size comparable to that of the living dhole in Asia (in southeast area, 10-21 kg, Table 9). The complex interaction and competition between them for prey hunting and scavenging, characterized in Indian mammalian communities by a large overlap of prey items (Karanth and Sunquist, 1995; Biswas and Sankar, 2002; Ramesh et al., 2012; Selvan et al., 2013a, 2013b), was most probably less marked during the Late Pleistocene. Indeed, considering the body-mass estimates, they could occupy different

ecological niches. Whereas the dhole, which hunts by packs, might have focused on medium-sized prey, the small leopard, a solitary hunter, might have preferentially killed small-sized prey, either on the ground or in the trees, depending on the habitat type. Thus, at Duoi U'Oi, the leopards might have preferred the muntjacs (20-28 kg, *M. muntjak*; Francis, 2008) (Table 14). At Sibrambang, thanks to a comparable small size, the leopard was likely able to hunt monkeys, such as gibbons (8-11 kg, *S. syndactylus*; Francis, 2008) in arboreal strata, as it is observed today in forests with continuous canopy cover (Galdikas, 1988).

Tam Hang shows that, like today in Asia, wild dogs used dens excavated in caves or rocky sites, also occupied by porcupines. Dholes are social predators which hunt in paks from 5 to 11 individuals usually at night, early in the morning, or in the daytime (Johnsinh, 1982; Selvan et al., 2013b). In regards to prey species and age class, no interaction with the tiger emerges from the analysis of Tam Hang (Table 14). Dholes might be able to kill a large range of medium-sized prey (muntjac, young sambar, and young adult pig).

At Nam Lot, the data clearly reflect the bone-collecting behavior of the hyena, which focused primarily on rhinocerotids (mortality profiles) and bovids (large values of MNIF for NISP) (Table 14). Given the composition of the fauna, both in predators and prey, it is likely that the site represents accumulations in a hyena den (Fourvel et al., in press, accepted). Like today in Africa, natural cavities of caves such as that of Nam Lot could be used as dens for the hyenas and their offsprings (Kruuk, 1977; Brain, 1981; Turner and Anton, 1997). In this respect, the Nam Lot site is highly informative as to the behavior of the hyena *P. perrieri* during MIS5 in Southeast Asia. The Nam Lot hyena (60-80 kg; Dennell et al., 2008) was an efficient hunter of large-sized prey, adult mature pigs (up to ~200 kg), young rhinoceros (up to ~400 kg) and large bovids (> 500 kg). In this respect, it resembles the modern spotted hyena *Crocuta crocuta*. In the absence of other hypercarnivores in the site, only the hyenas

are able to kill such prey. Thus, hyenas hunted the largest animals and consumed their carcasses in prime condition (Kruuk, 1972; Blumenschine et al., 1987).

What also emerges from the comparative taphonomic analysis with the Tam Hang fauna is that the hyena and the tiger occupied comparable open landscapes, but in the case of no interaction, the hyena killed a larger range of large prey than the tiger. Unlike the tiger (~150 kg), the spotted hyena (60-80kg), generally nocturnal or crepuscular, hunts alone, in small groups or sometimes in large packs up to 25 individuals (Kruuk, 1972; Boitani and Bartoli, 1984; Turner and Anton, 1997; Nowak, 1999; Cooper et al., 1999; Höner et al., 2002; Francis, 2008). At Nam Lot, it is obvious that only the formation of large packs compensated for their small body size, when hunting large ungulates. The present analysis shows that during MIS5 in that region of Southeast Asia, the hyena was an efficient hunter that needed an important prey biomass (that suggests a greater vulnerability than that of the tiger faced with changes in ungulate populations). Its behavior seems to differ from that of the large-sized hyena *Pachycrocuta brevirostris* which rather relates to that of modern brown and striped hyenas (Palmqvist and Arribas, 2001). Indeed, *P. brevirostris* (~110kg; Palmqvist et al., 2011) is considered predominantly a bone-cracking scavenger which fed on carcasses killed and partially consumed by other hypercarnivores (Palmqvist et al., 1996; Palmqvist and Arribas, 2001 *contra* Turner and Anton, 1997; Galobart et al., 2003; Dennell et al., 2008; Louys, 2014).

#### **5.6. Subsistence behavior of humans**

In relation to Nam Lot (Bacon et al., 2012), human (*Homo* sp.) diet can not be reconstructed on the basis of the taphonomic analysis of the assemblage, and there is no

evidence for human-hyena interaction at this site (Table 14). At Punung, we can not assume that humans (*Homo sapiens*; Storm et al., 2005) contributed to the accumulation of bones.

In contrast, at Duoi U'Oi where humans (*Homo* sp.; Bacon et al., 2008b) might have had a non-negligible role in the accumulation of remains, selective hunting was focused on the mature adult sambar, selected by age (180-260 kg for modern *C. unicolor*; Francis, 2008). The comparative analysis of Tam Hang and Duoi U'Oi indicates that climatic changes between interglacial and glacial stages (MIS5-4) did not modify species abundance of the sambar locally in the Indochinese region. In comparably rich mammalian communities in Central India, Biswas and Sankar (2002) observed that 91% of group size is constituted by one to 3 individuals and 8.5% by 4 to 10 individuals. In some particular ecological conditions, Ramesh et al. (2012) observed aggregations of 36-45 individuals in swampy grasslands during the wet season in a deciduous habitat of Southern India. The Duoi U'Oi hunters might have found this species relatively accessible in this type of environment. With respect to rhinoceroses, no particular predation by man on age class can be recognized, at least under high pressure, at this site. Abilities for humans to hunt large and dangerous prey such as old pigs (~200 kg) are plausible but not demonstrated (Milo, 1998; Faith, 2008). There is no reliable evidence supporting scavenging behavior by humans (Binford, 1985; Chase, 1989; Stiner, 1992; Klein and Cruze-Urbe, 1996; Marean, 1998; Bar-Yosef, 1998; Marean and Assefa, 1999; McBreaty and Brooks, 2000).

The behavior of people present at Duoi U'Oi (MIS4) with a low selection pressure on megaherbivores (three species of rhinoceros are present) and a deliberate choice of the sambar, seems to differ from that of their Middle Pleistocene predecessors (*H. erectus*/archaic *Homo sapiens*) in Southern China (~MIS6-8). Indeed, Tong (2001) demonstrated a possible organized hunting of calves *Dicerorhinus mercki* at the Nanjing site,

whereas Schepartz et al. (2003, 2005) and Schepartz and Miller-Antonio (2010a, 2010b) emphasized a selection by hominins either hunting or scavenging of prime age adults (*Rhinoceros sinensis*) and young stegodonts *Stegodon orientalis* at the Panxiang Dadong site.

The identity of the hominins (late archaic *Homo sapiens* vs early modern *Homo sapiens*) present at Duoi U’Oi, could not be determined by the few isolated teeth (Bacon et al., 2008b), but the time interval (70-60 ka) coincides with some important events in the evolution of *Homo sapiens* supported by recent securely dated discoveries in the area such as Zhirendong in Southern China dated to ~100 ka (U-series) (Liu et al., 2010), and Tam Pà Ling, one of the localities of “Tam Hang” in Northeast Laos, dated to 63-46 ka (TL, U-series) (Demeter et al., 2012). A possibly more ancient emergence of archaic/modern *H. sapiens* remains is debated on the basis of the age estimate of the Liujang cave site, 132-111 ka (Shen et al., 2002). However, the fauna from Zhirendong has not been analysed through a comparable taphonomic approach (Liu et al., 2010), and the modern human of Tam Pà Ling is neither associated with large mammals nor with any artifact assemblage (Demeter et al., 2012). Therefore, we can not assume that the selective hunting of sambar by humans from Duoi U’Oi originated from that of early modern *Homo sapiens* present in Asia since around 100 ka, or from that of new migrants represented by anatomically modern *Homo sapiens*, arriving from Africa at ca. 70-60 ka (Stringer and Andrews, 1998; Wu, 2004; Macaulay et al., 2005; Mellars, 2006a, 2006b; Oppenheimer, 2009; Boivin et al., 2013). Based on our current state of knowledge, the oldest evidence of the emergence of such foraging abilities in East Asia is situated in MIS3 and associated with morphologically modern *Homo sapiens* in northern China, at Tianyuan cave (42-39 ka) (Shang et al., 2007) and later fully modern *Homo sapiens* at Zhoukoudian Upper cave (34-10 ka) (Pei, 1934). Indeed, the mammalian faunas shows an elevated mortality of young and prime-adult *Cervus nippon* at Tianyuan (Shang and

Trinkaus, 2010), and of *C. nippon* and *C. elaphus canadensis* at Zhoukoudian (Norton and Gao, 2008). In the latter site, this behavior is one of the components of the modern human behavioral package (Henshilwood and Marean, 2003; Norton and Jin, 2009; Richter et al., 2012). Thus, it appears that the hunting behavior of cervids by age-class seen at Duoi U'Oi (~66 ka) in northern Vietnam precedes that in northern China (~40 ka) by ca. 26 ka. For the moment, only three other sites in Australasia, also from MIS3, provide such association showing modern behavioral traits: the Wajak site in Java dated to 37-29 ka (Storm et al., 2013), the Niah cave site in Borneo dated to around 45-39 ka (Barker, 2005; Barker et al., 2007) and the Callao site on the island of Luzon, Philippines, dated possibly over 65 ka (Mijares et al., 2010).

Information provided by the analysis of the Duoi U'Oi site is all the more important since Southeast Asia lacks evidence on this pre-Upper Palaeolithic period. In particular, there are no data which demonstrate behavioral shifts, changes in culture and associated foraging adaptations (in prey selection particularly), at the time of the presumed emergence of modern humans (70-60 ka). Considering the processes of transport through the cave system and the formation of the breccias, the fossiliferous layer formed within a relatively short time period during a unique depositional event (only one phase of stagnation, with no reworking and redeposition), which makes this site exceptional compared to other karstic sites with multiple phases of deposits (Düringer et al. 2012).

The rate of uplift/incision calculated in the surrounding of the Duoi U'Oi site (Düringer et al. 2012), which is 2 to 10 times lower than the estimated rate in China, around 0.1m per ka and 0.5m per ka (Yang et al., 2011), suggests a very small change in the topography of the site (the entry of the cave is now situated at 3 meters above the alluvial plain). Around 70 ka the site was opened on the alluvial plain at the same elevation and close to riverine areas

(Bacon et al., 2008; Düringer et al., 2012). Humans most probably occupied margins between the plains and karst limestone hills. There are no steep slopes, canyons or other landscapes which could have been used as traps for animals, which implies that hunters may have obtained deer mainly by stalking (Stiner, 1990). Carnivores either tigers, or leopards and dholes, also used the site or the vicinity of the site as short-term dens.

Due to the state of conservation of the Duoi U'Oi assemblage, with most of the elements probably destroyed by intrakarstic mechanisms, uncertainties surround most of the possible skills by humans at this site. We can not determine if the selective hunting on prime-age adult deer is due to the deliberate strategy of a small forager group (Stiner et al., 1999, 2000; Speth, 2004). The hunting appears concentrated upon one specific large animal but, in the array of available prey species, we can't rule out possible procurement of small games, such as muntjacs, monkeys or other small-sized animals including birds, reptiles and river fishes.

## 6. Conclusion

Although there are problems relating to karst complexity (*i.e.* understanding the process and duration of infilling, constraining the breccias etc.), and to understanding the role of all taphonomic agents which might affect the accumulations, the study of deposits containing exclusively isolated teeth of mammals can be useful for reconstructing the palaeoecology and palaeoclimatology of Southeast Asia during the Pleistocene. Indeed, the present comparative analysis of five fossil faunas revealed a great flexibility in predator-prey dynamics, with important changes in predator niches according to prey abundance during the interglacial and glacial stages MIS5-4. We emphasized particularly how the degree of forest cover (open deciduous forest vs tropical evergreen forest) due to latitudinal variations in the Sundaland, could affect the disponibility of the biomass of large ungulates,

constraining large carnivores and hominins to adopt different hunting and scavenging strategies. Further zooarchaeological data are needed to refine the knowledge of human subsistence behavior, especially that related to the emergence of modern *Homo sapiens* in Southeast Asia around ~70-60 ka.

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**Highlights**

1. Fossiliferous deposits from five karstic sites are used to reconstruct palaeoecology in Southeast Asia during the Late Pleistocene (MIS5-4).
2. The combined use of OSL and U-series methods allow us to place the sites in a new chronological context.
3. The analysis of the faunas reveals a great flexibility in predator-prey relationships in the Sundaland.
4. The site of Duoi U'Oi (northern Vietnam) reveals at 66 ka a selective hunting by humans focused on mature adult sambar.

**Figure captions**

**Figure 1:** Location of Pleistocene sites (stars).

**Figure 2:** Stratigraphy of the Tam Hang South locality (see Tables 2 and 3 for dating results).

**Figure 3:** Stratigraphy of the Nam Lot locality, Upper and Lower sections (see Tables 2 and 3 for dating results).

**Figure 4:** Stratigraphy of the Duoi U'O'i locality (see Tables 2 and 3 for dating results). The results of the U-series datings are from Bacon *et al.* (2008b).

**Figure 5:** New chronological framework based on numerical ages for quartz grains (luminescence) and flowstones (U-series) for Tam Hang, Nam Lot and Duoi U'O'i sites. The chronology for Punung has been previously established by Westaway *et al.* (2007) and that for Sibrambang by de Vos (1983), Skelton (1985), Draworn (1994) and Antoine (2012). Definition of Marine Isotopic Stages (MIS) is from Imbrie *et al.* (1984).

**Figure 6: A.** General view of tower karst morphology in the mainland of Southeast Asia; **B.** Endokarstic breccias that plastered the walls of a cave (Nam Lot, northern Laos), with geochronologists measuring the radioactivity; **C.** Example of deposits with argillaceous sandy breccias interrupted by horizontal flowstones; **D.** Fossiliferous karstic breccias with isolated teeth of rhinoceroses; **E-F.** Teeth showing different damages on roots gnawed by porcupines; **E.** left m1/m2 of *Cervus unicolor* almost totally gnawed (3/4 of the root); **F.** left

p3 of *Pliocrocota perrieri*; **G.** right m1 of *Ursus thibetanus*; **H.** left I3 of *Ursus thibetanus* partially gnawed (1/4 of the root).

**Figure 7:** Two-dimensional diagrams with NISP on abscissa and MNIf on ordinate by species (circles) or family (stars) of ungulates and Primates in the five samples. In order to correct the sampling effect between the Sibrambang assemblage and the other assemblages, we used the logNISP/logMNIf.

**Figure 8:** Percentage by body-size category for the species of Artiodactyla, Perissodactyla and Proboscidea in the fossil faunas studied here: small size (SS: <30kg), medium size (MS: 31-175kg), large size (LS: >176kg). See S-Table 12 for the distribution of individuals (juvenile/adult) in each body-size category. The number of individuals by category is as follows: Tam Hang (SS: n=14, MS: n=21, LS: n=26); Nam Lot (SS: n=5, MS: n=17, LS: n=19); Duoi U'Oi (SS: n=18, MS: n=20, LS: n=55); Punung (SS: n=7, MS: n=35, LS: n=16); Sibrambang (SS: n=26, MS: n=249, LS: n=43).

**Figure 9: I.** Mortality profiles of *Cervus unicolor* from Tam Hang and Duoi U'Oi and *Rusa* sp. from Sibrambang. Age classes [1-10] are defined by Klein et al. (1981): [1] young (<1.6 year), [2] yearling (<3.2 years), [3-6] prime-adult, and [6-10] old adult individuals (up to 16 years). **II.** The three-cohort profiles are compared with the natural demographic composition observed in two Indian mammalian communities: (A) Nagarhole National Park (Karanth and Sunquist, 1995) and (B) Pench National Park in India (Biswas and Sankar, 2002).

**Figure 10: I.** Mortality profiles of *Sus scrofa* from Tam Hang, Nam Lot, and Duoi U'Oi, and *Sus vittatus* from Sibrambang. Age classes [T-U, A-N] are defined by Grant (1982) and Rolett and

Chiu (1994): [T-U] piglets <5-8 months and [A-C] piglets <10-14 months, [D-F] young adult (<18-26 months), [G-L] mature adult and [M-N] old adult individuals. **II.** The three-cohort profiles are compared with the natural demographic composition observed in two Indian mammalian communities: (A) Nagarhole National Park (Karanth and Sunquist, 1995) and (B) Pench National Park (Biswas and Sankar, 2002).

**Figure 11:** Mortality profiles of rhinocerotids from (A) Tam Hang, (B) Nam Lot, (C) Duoi U’Oi, and (D) Sibrambang based on dental remains (at family level) and following a protocol modified from Hillman-Smith et al. (1986) by one of the author POA (Bacon et al., 2008a). Age classes [I-XVI] and corresponding individual ages in months (m) and years (y) are defined by Hillman-Smith et al. (1986).

**Figure 12:** Three-cohort profiles of rhinocerotids from Tam Hang, Nam Lot, Duoi U’Oi, and Sibrambang compared with (A) the natural demographic composition observed in one modern population of *Rhinoceros unicornis* from Chitawan Valley, Nepal (Laurie, 1982). Calves are less than 3 years-old [0-V], subadults between 3 and 6 years-old [VI-VIII], and adults more than 6 years-old [VIII-XVI].

**Figure 13:** Three-cohort profiles of *Tapirus indicus* from Sibrambang compared with (A) the natural demographic composition observed in one modern natural population of *Tapirus terrestris* at Chaco, Bolivia (Maffei, 2003). Calves are less than 1 year-old, subadults between 1 and 2 years-old, and adults 2 years-old or more.

**Table captions**

**Table 1:** Location, estimated ages <sup>(e)</sup>, and numerical age estimates (OSL, U-series, AAR) of the five fossil mammalian faunas considered in the study. Main corresponding references are noted.

**Table 2:** Blue OSL and red TL dating of sediments from fossiliferous caves in SEA: dose rate data, equivalent doses, and ages.

**Table 3:** Uranium-series dating of flowstone from breccias cave sites in SEA: ages and supporting data. Ratios listed in the table refer to activity ratios. <sup>230</sup>Th ages are calculated using Isoplot/Ex 3.0 (Ludwing, 2003). Non-radiogenic <sup>230</sup>Th correction was applied assuming non-radiogenic <sup>230</sup>Th/<sup>232</sup>Th atomic ratio =  $4.4 \pm 2.2 \times 10^{-6}$  (bulk-earth value), and <sup>238</sup>U, <sup>234</sup>U, <sup>232</sup>Th and <sup>230</sup>Th are in secular equilibrium. Non-radiogenic <sup>230</sup>Th correction results in large age error magnifications in the corrected <sup>230</sup>Th ages for samples with low <sup>230</sup>Th/<sup>232</sup>Th ratios.

**Table 4:** Summary table of the full faunal lists of the five fossil assemblages. The Punung (I and II) faunal inventory is from Storm and de Vos (2006) and that of Sibrambang is from de Vos (1983) and the inventory of the Natural Museum of Leiden. (\*) The Perissodactyls of Punung and Sibrambang have been revised by POA. *Rhinoceros* sp. refers to either *R. unicornis* or *R. sondaicus*. Rhinocerotina indet. refers to *Rhinoceros* (*R. unicornis* and/or *R. sondaicus*) and/or *Dicerorhinus sumatrensis*. Taxa synonymous to: <sup>(1)</sup> *Cervus* sp., <sup>(2)</sup> *Naemorhedus sumatrensis*, <sup>(3)</sup> *Bos javanicus*, <sup>(4)</sup> *Felis temmincki*, <sup>(5)</sup> *Helarctos malayanus*, <sup>(6)</sup> *Hystrix brachyura*, <sup>(7)</sup> now assigned to *Pliocrocota perrieri* (Werdelin and Lewis, 2012).

**Table 5:** Number of Specimens (NSP) and Number of Identified Specimens (NISP) by mammalian orders in the five fossil assemblages: Punung (Badoux, 1959; Vu The Long et al., 1996; observation of AMB and POA), Sibrambang (Inventory of the Natural History Museum of Leiden; observation of AMB and POA), Tam Hang (Bacon et al., 2008a, 2010; Antoine, 2012), Nam Lot (Bacon et al., 2012), and Duoi U’Oi (Bacon et al., 2008b; Antoine, 2012). Using permutation tests, the Sibrambang fauna is statistically different from that of Nam Lot ( $p < 0.05$ , 20 000 permutations).

**Table 6:** Percentages of teeth with ungnawed and gnawed roots in some taxa of the five faunas. Germs which only consist of crowns are not considered. <sup>(1)</sup> number of teeth  $\leq 3$ ; <sup>(2)</sup> data not observed. The grey zones represent the absence of the taxon in the samples.

**Table 7:** Frequency of teeth by species, family or Order in the fossil assemblages. U: upper; L: lower; P: permanent; D: deciduous. The proportions of ungulate teeth have been statistically compared (all p-values resulting from paired comparisons were adjusted by Fisher’s exact test, statistical differences were considered significant at the 0.05 level).

**Table 8:** NISP and MNIf by taxon. Punung (Vu The Long et al., 1996; observation of AMB and POA); Sibrambang (Inventory of the Natural History Museum of Leiden and observation of AMB and POA); Tam Hang (Bacon et al., 2008a, 2010); Nam Lot (Bacon et al., 2012); Duoi U’Oi (Bacon et al., 2008b). In relation to large Carnivora, the data of the Felidae/Hyaenidae correspond to one species at Tam Hang (*P. tigris*), Nam Lot (*P. perrieri*) and Punung (*P. tigris*), two species at Duoi U’Oi (*P. tigris*: NISP=7, MNIf=1; *P. pardus*: NISP=8, MNIf=2) and



Sibrambang (*P. tigris*: NISP=6, MNIf=2; *P. pardus*: NISP=15, MNIf=4). The Canidae correspond to one species for all sites (*C. alpinus*).

**Table 9:** Body mass estimates of predators based on family regression of body mass (BM) against length of first lower molar (m1l) of felids and canids (van Valkenburgh, 1990). Equations used:  $\log_{10}(\text{BM})=3.05\log_{10}(\text{m1l})-2.15$  for felids (n=3, Prediction Error=28%);  $\log_{10}(\text{BM})=1.82\log_{10}(\text{m1l})-1.22$  for canids (n=27, Prediction Error=27%). <sup>(1)</sup>Francis (2008), <sup>(2)</sup>Smith and Yan Xie (2008), <sup>(3)</sup>Pocock (1939). For canids from Sibrambang, the body mass prediction by size category (10-100 kg; van Valkenburgh, 1990) overestimates the body mass of individuals (28.6-32.8 kg).

**Table 10:** Taxa used for reconstructing mortality profiles within fossil faunas.

**Table 11:** MNIC calculated by using the combination of tooth (left and right d4/m1/m3) with age class (10 cohorts) for the analysis of the mortality profiles of *Cervus unicolor/Rusa* sp. The m2 being more massive than m1, we used the maximal mediolateral breadth to discriminate the teeth (Klein et al., 1981) in the Tam Hang and Sibrambang samples (packs 809/738/844 when necessary). It clearly separates two sets of teeth with no overlap: Tam Hang (m1=13.9–15.1mm, m2=16.1–18mm); Sibrambang (m1=10.8–14mm, m2=14.7–16.2 mm).

**Table 12:** MNIC calculated by using the combination of two stages of germ formation for m1 with 13 wear stages of left or right m1/m2/m3 for the analysis of mortality profiles of suids. Due to the large number of teeth (N=1581), we only used the left molars in the Sibrambang

sample (packs 739AJ, 836E, 841AO, 845A/AA/E/G, 950CC). We distinguished m1 from m2 on the basis of the maximal mediolateral breadth of crowns for the Tam Hang, Nam Lot and Duoi U'Oi samples, and for the Punung and Sibrambang samples when necessary. Tam Hang and Duoi U'Oi (m1=10–13 mm) and (m2=14–17 mm); Sibrambang (m1=8–12.50 mm) and (m2=12.50–17 mm); Punung (m1=9–13.50 mm) and (m2=14–17 mm).

**Table 13:** MNIC calculated on permanent and deciduous teeth in rhinocerotids for the analysis of mortality profiles.

**Table 14:** Summary table of pre- and post-depositional factors assessed in the present analysis for the five assemblages. <sup>(1)</sup> Results based on few observations; <sup>(2)</sup> based on bi-dimensional diagrams (large MNIf for NISP); <sup>(3)</sup> based on mortality profiles; <sup>(4)</sup> defined as *Crocota crocuta* in the original description (Bacon et al., 2012).



Figure 1

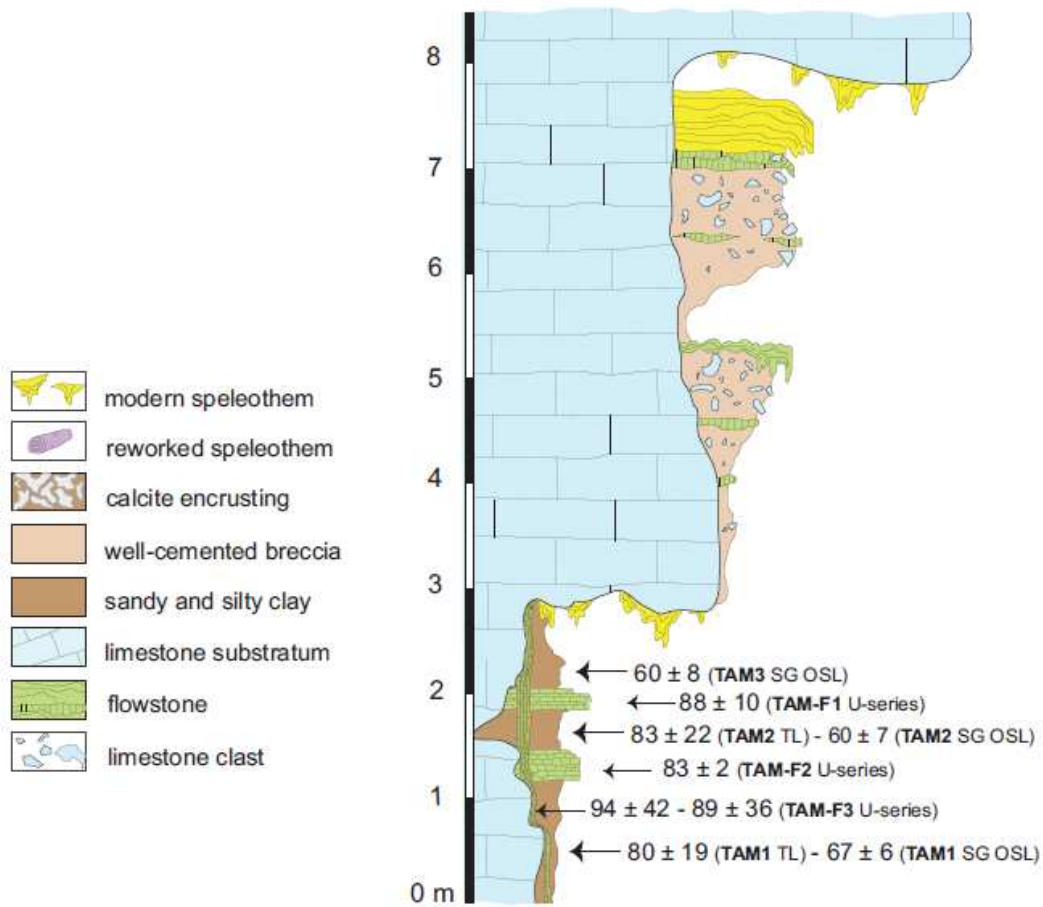


Figure 2

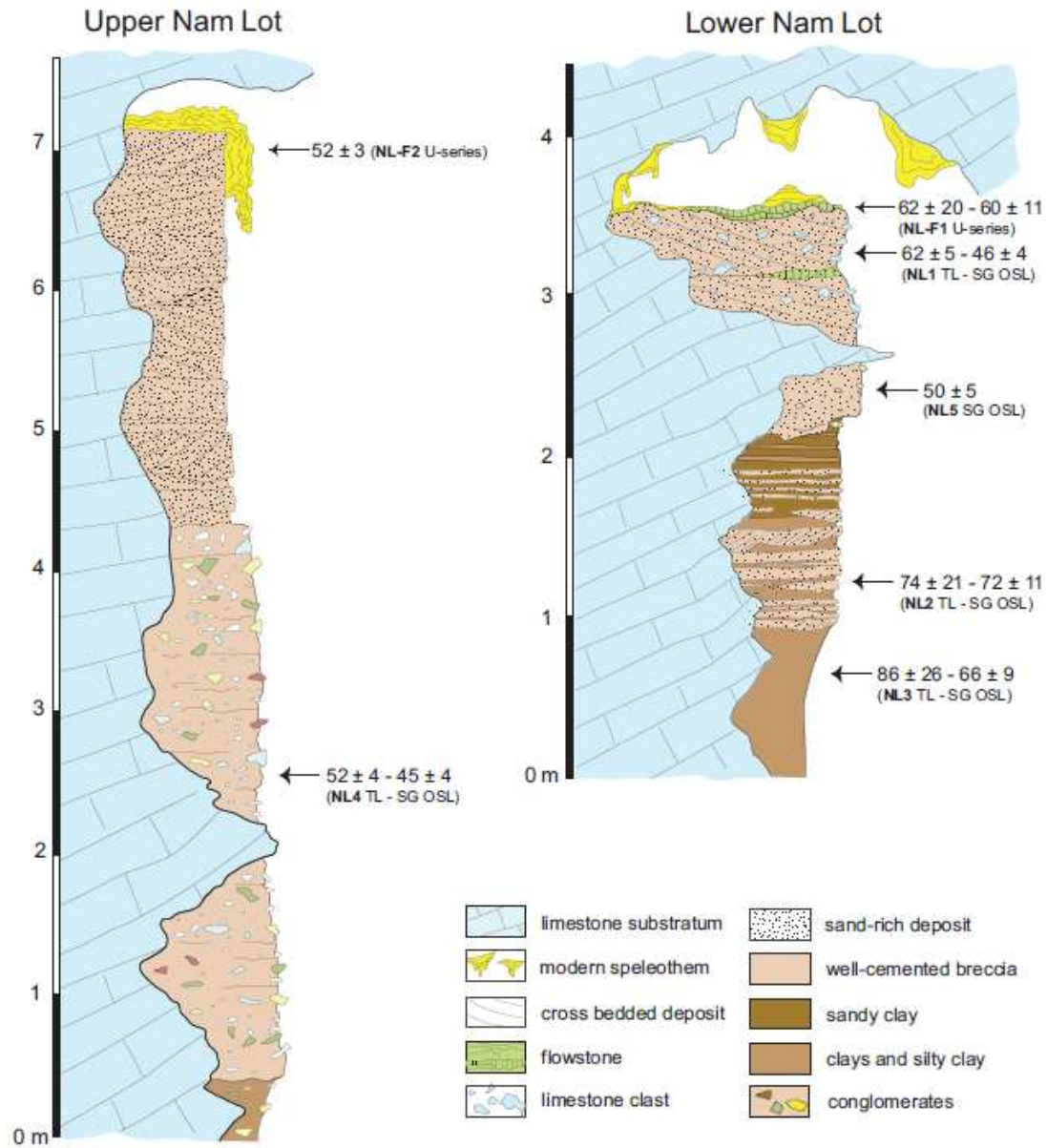


Figure 3

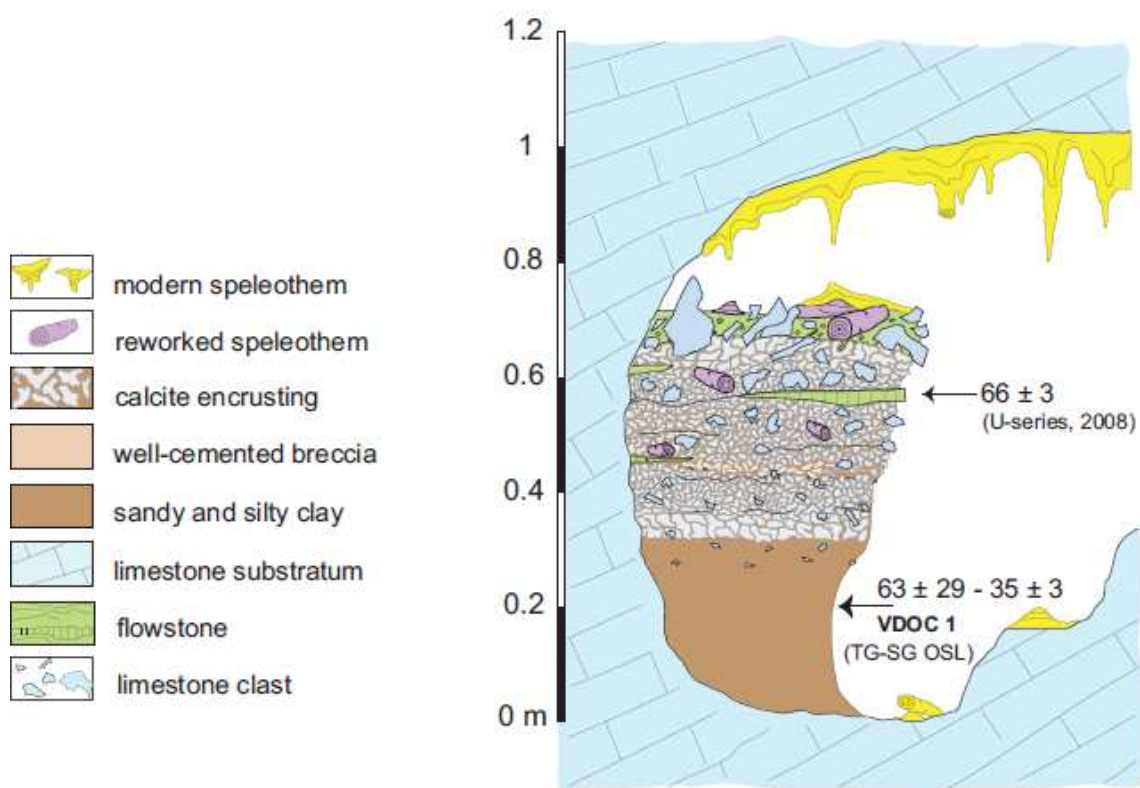


Figure 4

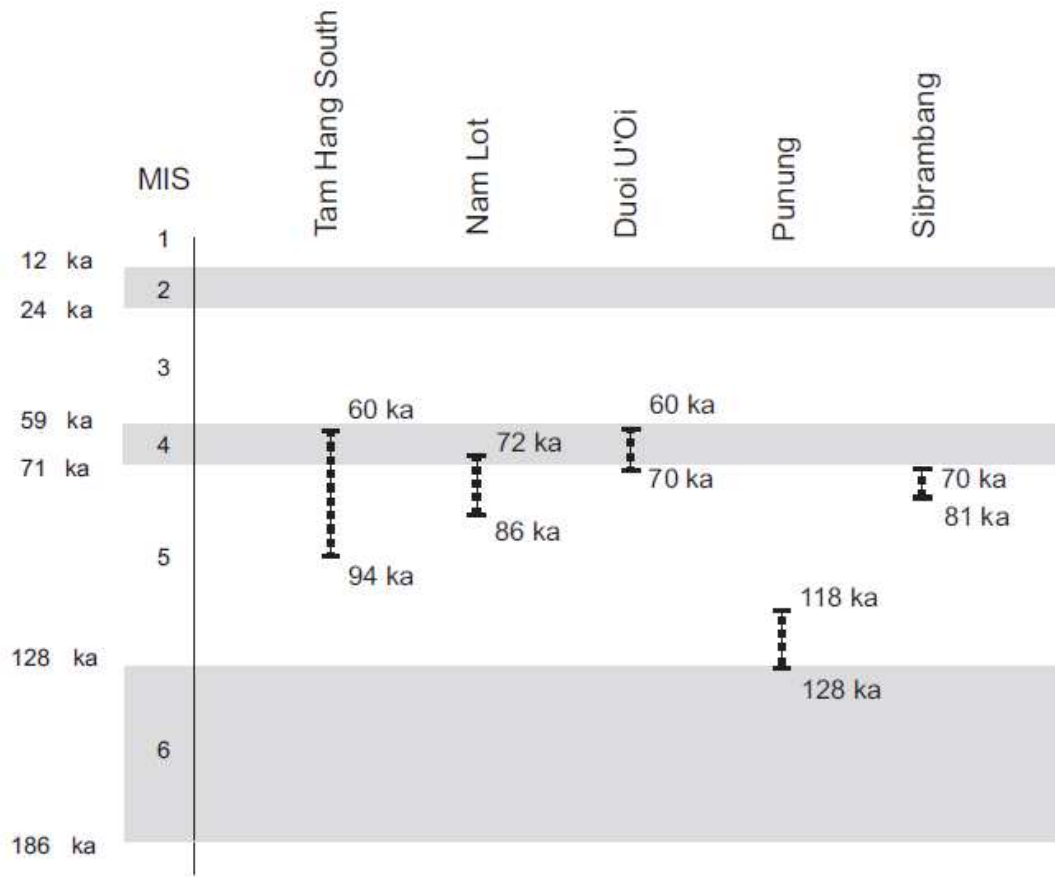


Figure 5



Figure 6



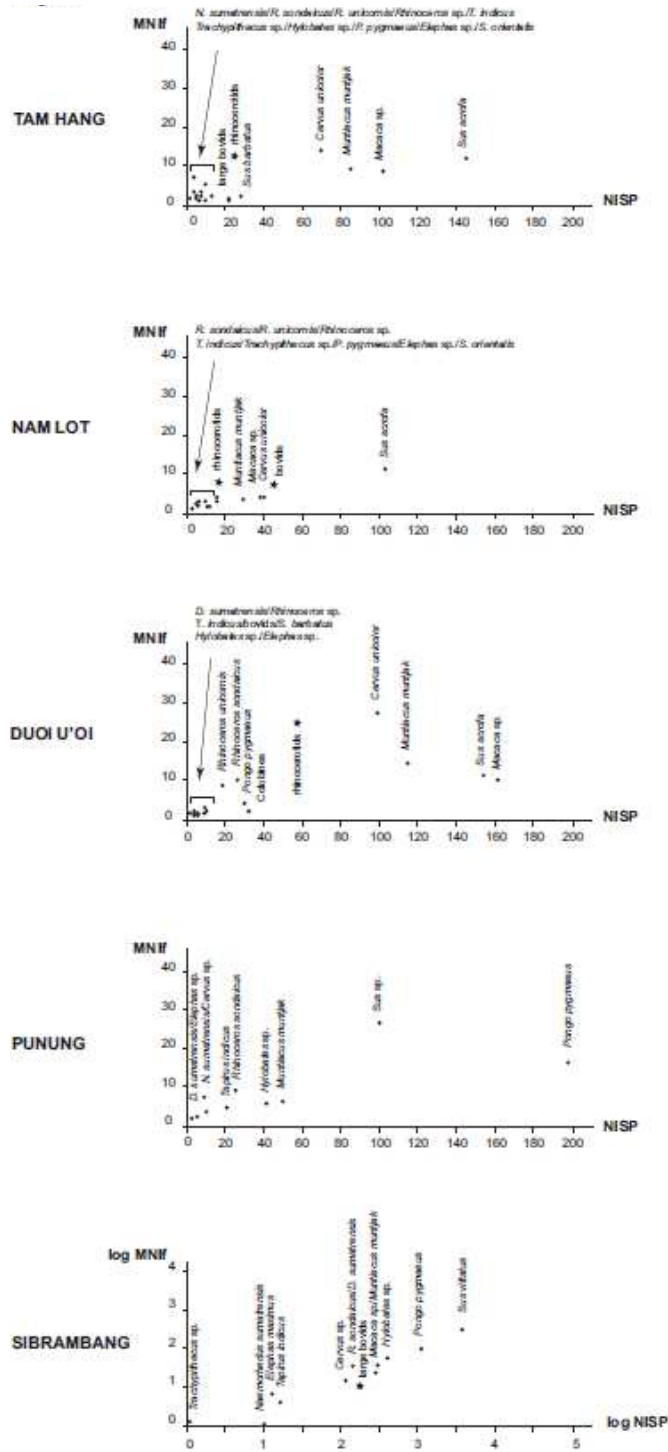


Figure 7

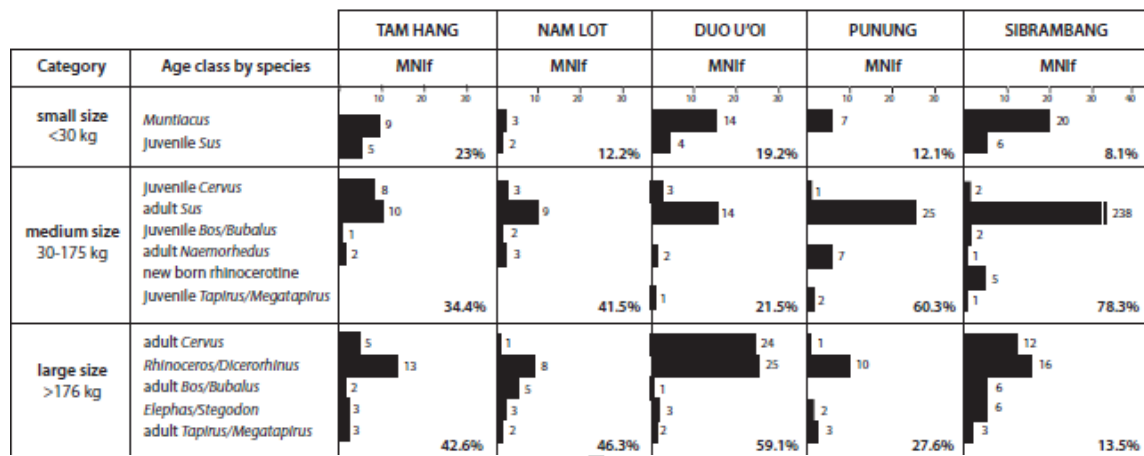


Figure 8

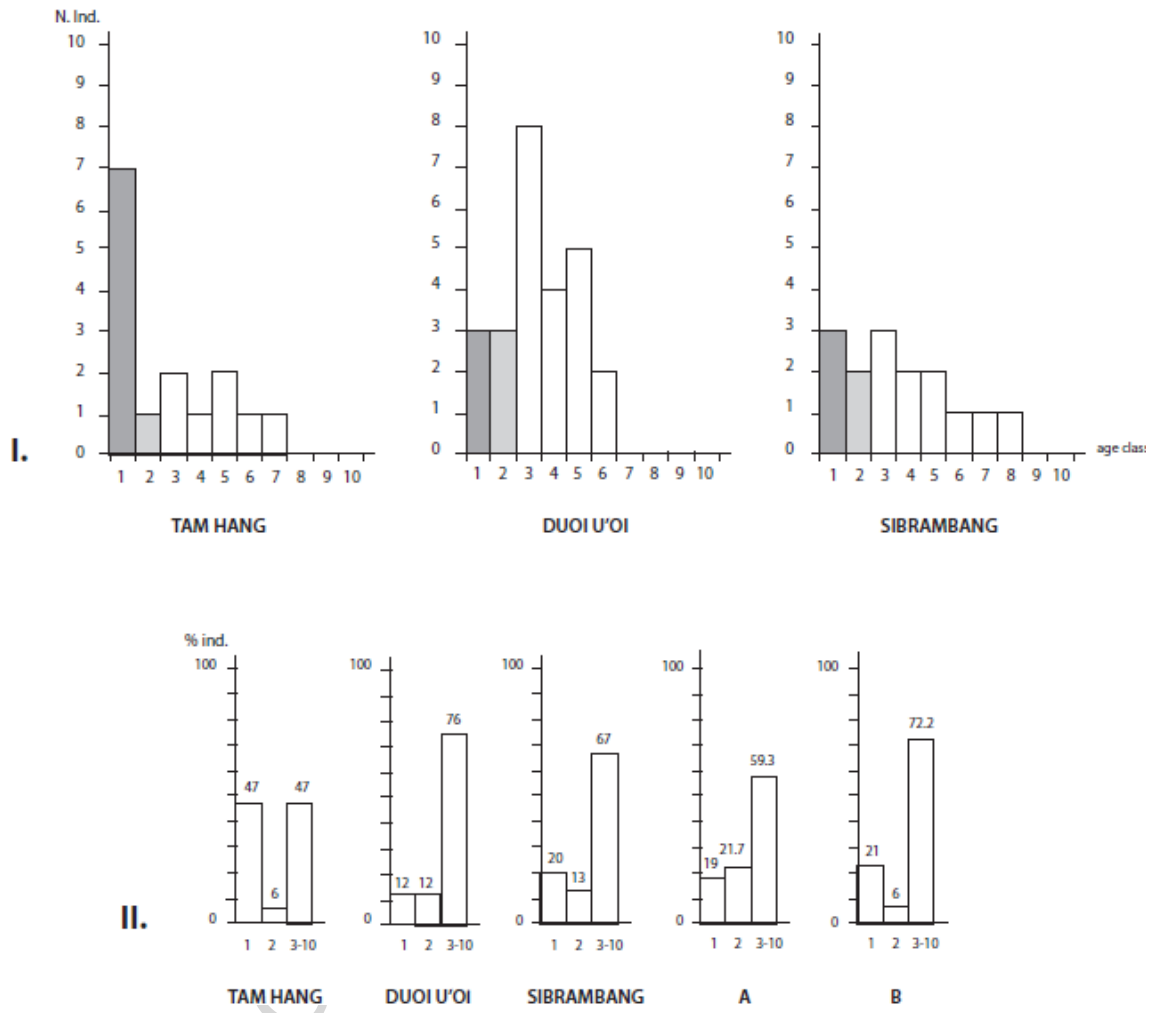


Figure 9

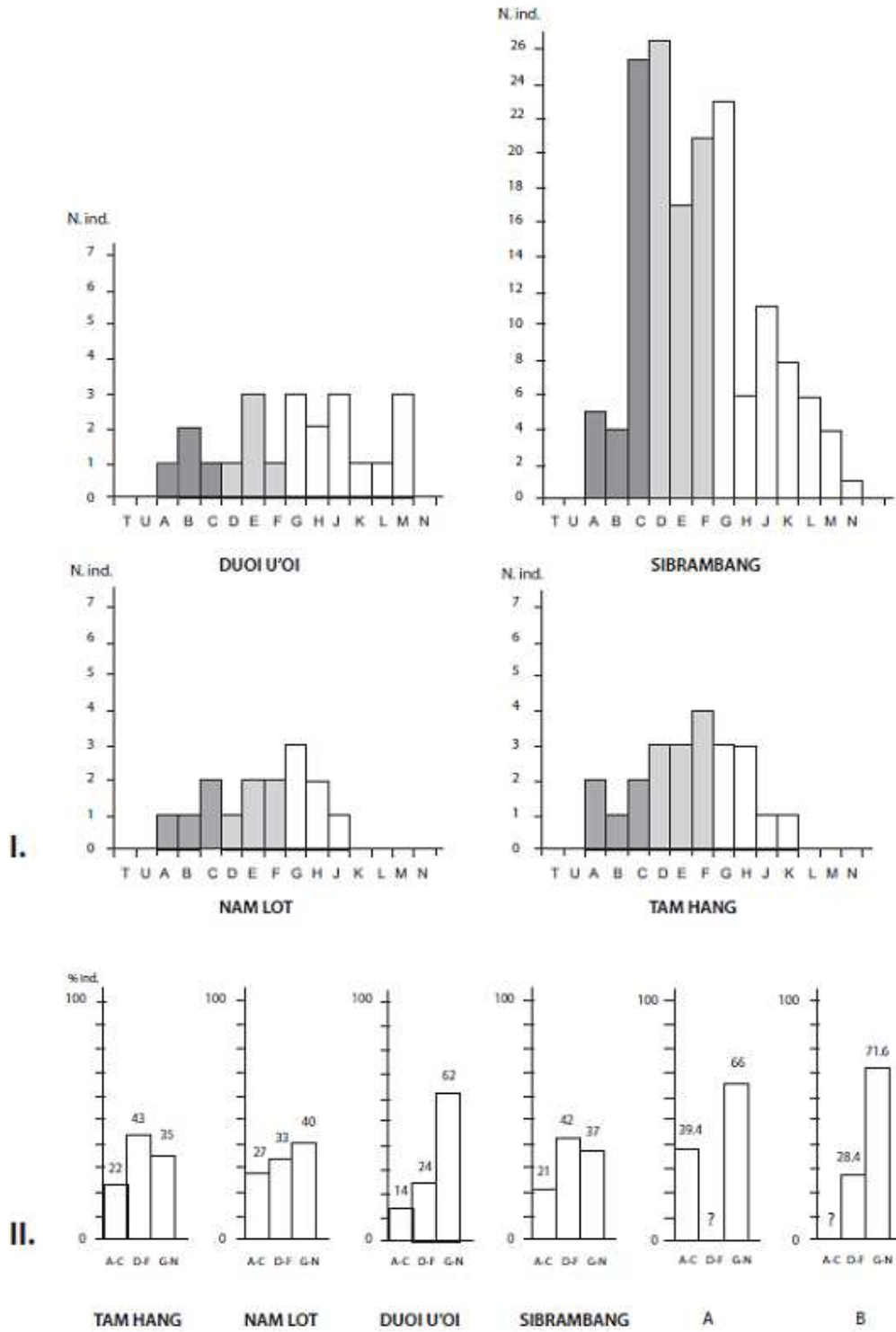


Figure 10

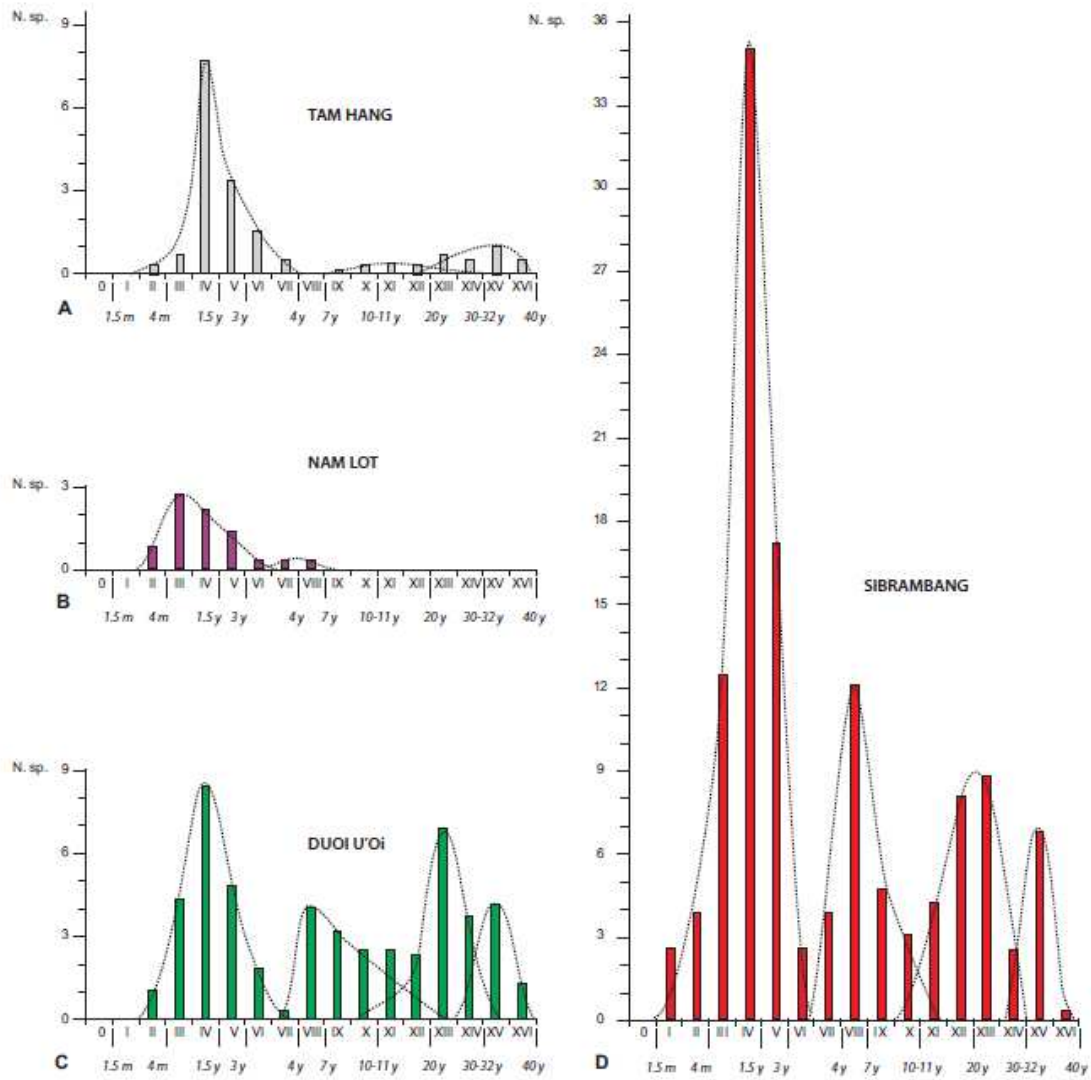


Figure 11

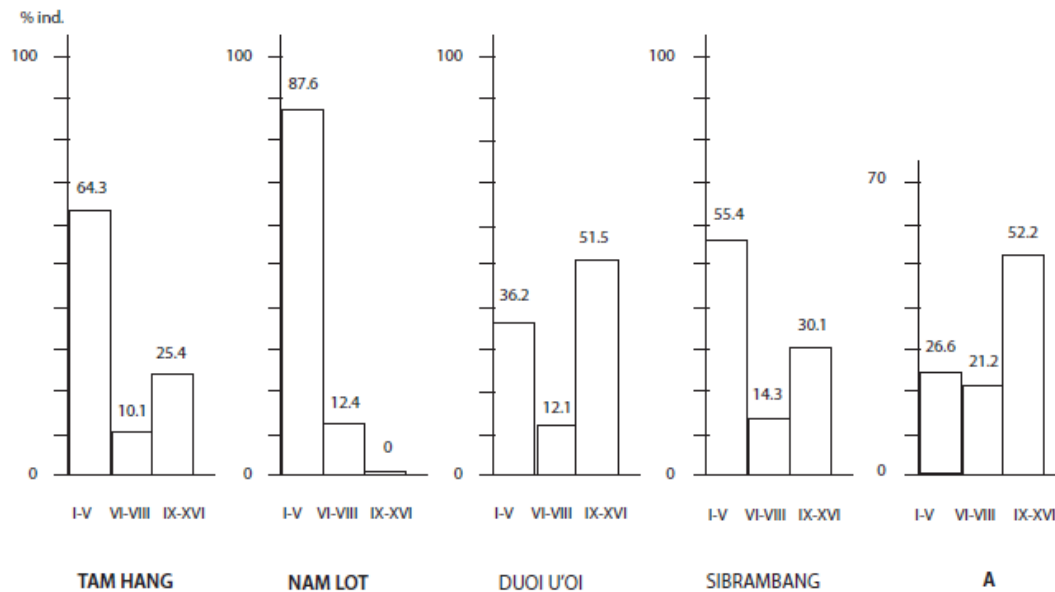


Figure 12

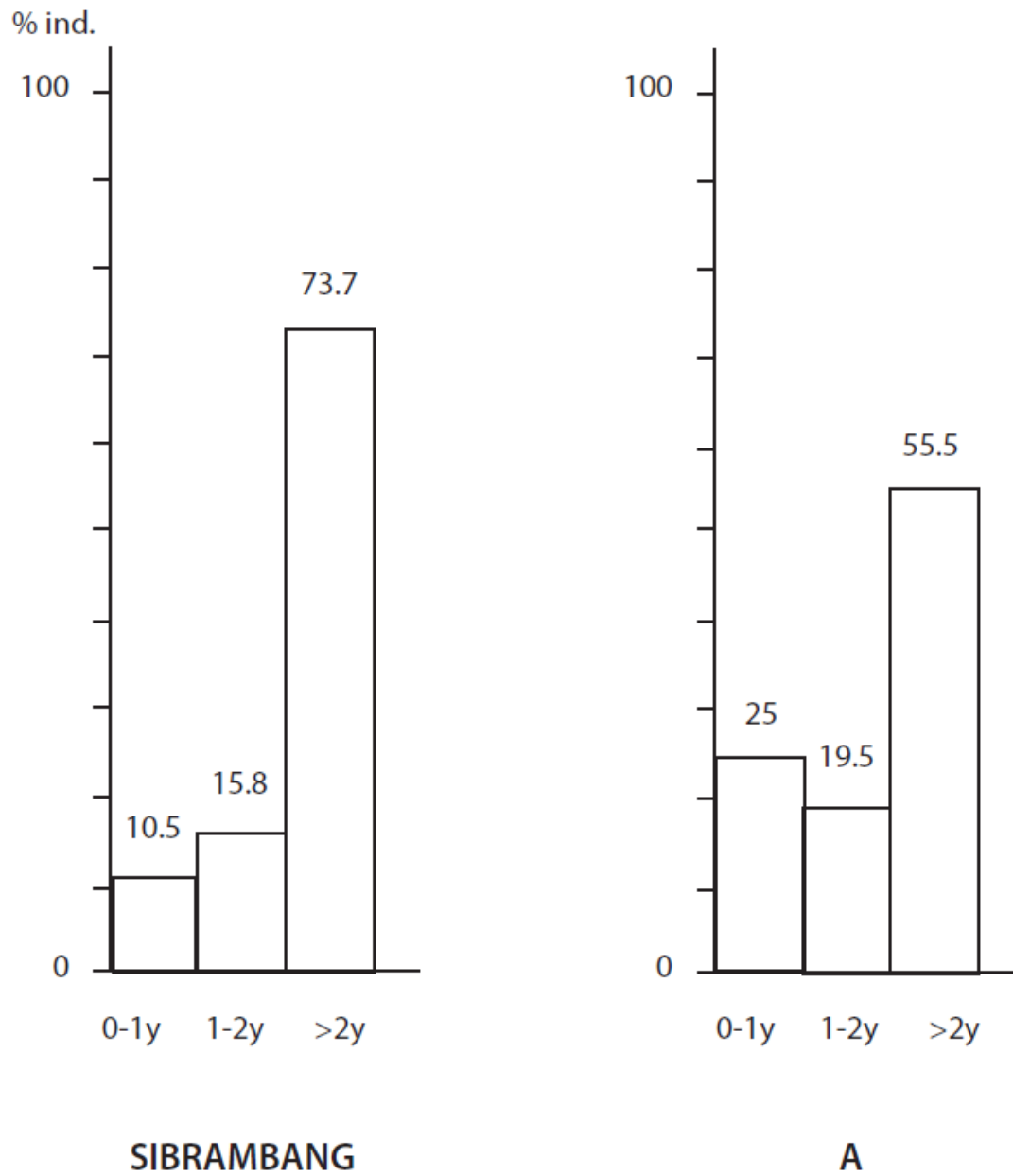


Figure 13

Table 1

Sites	Location	Age	References
Duoi U'Oi	Northern Vietnam Hoà Binh province	<b>66 ± 3 ka</b> (U-series) Late Pleistocene	Bacon et al. (2008b) Antoine (2012)
Nam Lot	North East Laos Huà Pan province	Late Middle Pleistocene/Late Pleistocene <sup>(e)</sup>	Duringer et al. (2012); Bacon et al. (2012)
Tam Hang South	North East Laos Huà Pan province	Late Middle Pleistocene <sup>(e)</sup>	Bacon et al. (2008, 2010); Duringer et al. (2012) ; Antoine (2012) ; Bacon et al. (2012)
Sibrambang	Northwest Sumatra Padang Highlands	80-60 ka <sup>(e)</sup> > <b>70 ka</b> (AAR, Djamboe site) > <b>81 ka</b> (AAR, Lida Ajer site) Late Pleistocene	de Vos (1983) Skelton (1985), Drawhorn (1994) Skelton (1985), Drawhorn (1994) Antoine (2012)
Punung	East Java	80-60 ka <sup>(e)</sup> 110-70 ka <sup>(e)</sup> ca. 125-60 ka <sup>(e)</sup> <b>128 ± 15 ka/118 ± 3 ka</b> (OSL, U-series)	de Vos (1995) van den Bergh et al. (1996) van den Bergh et al. (2001) Westaway et al. (2007)



Table 2

Sample code	Depth (from surface) (m)	Grain Size ( $\mu\text{m}$ )	Beta dose rate <sup>a</sup> ( $\text{Gy ka}^{-1}$ )	Field gamma dose rate <sup>b</sup> ( $\text{Gy ka}^{-1}$ )	Cosmic-ray dose rate <sup>c</sup> ( $\text{Gy ka}^{-1}$ )	Water content <sup>d</sup> (%)	Total dose rate <sup>e</sup> ( $\text{Gy ka}^{-1}$ )	Technique <sup>f</sup>	Statistical Model <sup>g</sup>	Equivalent dose <sup>h,i</sup> (Gy)	Age <sup>j</sup> (ka)
<i>Tam Hang</i>											
TAM1	8.05	180-212	1.336 ± 0.059	1.029 ± 0.002	0.016	13 / 5 ± 2	2.41 ± 0.08	UV <sub>SG</sub>	MAM	162 ± 14	67 ± 6
	8.05	90-125	1.413 ± 0.061	1.029 ± 0.002	0.016	14 / 5 ± 2	2.49 ± 0.09	red TL	DAP UNBL DAP BL	428 ± 4 199 ± 46	172 ± 7 80 ± 19
TAM2	7.00	180-212	1.261 ± 0.064	1.140 ± 0.002	0.015	15 / 10 ± 5	2.45 ± 0.15	UV <sub>SG</sub>	MAM	146 ± 14	60 ± 7
	7.00	90-125	1.334 ± 0.066	1.140 ± 0.003	0.015	16 / 5 ± 2	2.52 ± 0.15	red TL	DAP UNBL DAP BL	463 ± 4 210 ± 54	184 ± 12 83 ± 22
TAM3	6.20	180-212	1.294 ± 0.064	1.029 ± 0.002	0.016	7 / 5 ± 2	2.37 ± 0.09	UV <sub>SG</sub>	MAM	142 ± 11	60 ± 8
	6.20	90-125	1.368 ± 0.065	1.029 ± 0.002	0.016	7 / 5 ± 2	2.44 ± 0.09	red TL	DAP UNBL DAP BL	808 ± 4 /	331 ± 14 /
<i>Nam Lot</i>											
NL1	0.14	180-212	2.420 ± 0.086	2.420 ± 0.004	0.015	15 / 15 ± 5	4.201 ± 0.231	UV <sub>SG</sub>	MAM	192 ± 10	46 ± 4
	0.14	90-125	2.559 ± 0.091	1.8862 ± 0.004	0.015	15 / 15 ± 5	4.331 ± 0.239	UV <sub>SA</sub>	MAM	231 ± 8	53 ± 4
	0.14	90-125	2.559 ± 0.091	1.8862 ± 0.004	0.015	15 / 15 ± 5	4.331 ± 0.239	red TL	DAP UNBL DAP BL	267 ± 15 /	62 ± 5 /
NL2	2.60	180-212	1.433 ± 0.047	1.353 ± 0.004	0.017	6 / 5 ± 2	2.834 ± 0.082	UV <sub>SG</sub>	MAM	204 ± 31	72 ± 11
	2.60	90-125	1.515 ± 0.050	1.353 ± 0.004	0.017	6 / 5 ± 2	2.915 ± 0.085	red TL	DAP UNBL DAP BL	297 ± 13 217 ± 61	102 ± 6 74 ± 21
NL3	2.90	180-212	1.390 ±	1.525 ± 0.004	0.015	22 / 20 ±	2.961 ±	UV <sub>SG</sub>	MAM	196 ± 25	66 ± 9

			0.067			5	0.158					
	2.90	90-125	1.470 ± 0.069	1.525 ± 0.004	0.015	22 / 20 ± 5	3.040 ± 0.163	<b>red TL</b>	DAP UNBL	325 ± 16	107 ± 8	
									DAP BL	263 ± 78	86 ± 26	
<b>NL4</b>	2.00	180-212	2.224 ± 0.071	2.155 ± 0.004	0.016	3 / 2 ± 5	4.427 ± 0.080	<b>UV<sub>SG</sub></b>	MAM	197 ± 17	45 ± 4	
	2.00	90-125	2.352 ± 0.075	2.155 ± 0.004	0.016	3 / 2 ± 5	4.554 ± 0.084	<b>UV<sub>SA</sub></b>	MAM	238 ± 17	52 ± 4	
	2.00	90-125	2.352 ± 0.075	2.155 ± 0.004	0.016	3 / 2 ± 5	4.554 ± 0.084	<b>red TL</b>	DAP UNBL	554 ± 30	122 ± 7	
									DAP BL	238 ± 24	52 ± 5	
<b><i>Duoi U'Oi</i></b>												
<b>VDOC 1</b>	2.00	180-212	3.121 ± 0.113	2.633 ± 0.003	0.023	19 / 15 ±5	5.809 ± 0.317	<b>UV<sub>SG</sub></b>	MAM DAP	150 ± 11	35 ± 3	
	0.60	90-125	3.301 ± 0.119	2.633 ± 0.004	0.023	19 / 15 ±5	5.987 ± 0.328	<b>red TL</b>	UNBL	515 ± 25	101 ± 7	
									DAP BL	318 ± 147	63 ± 29	

- a Concentrations determined from beta counter measurements of dried and powdered sediment samples.
- b Determined from U, Th and K concentrations measured using a portable gamma-ray spectrometer at field water content
- c Time-averaged cosmic-ray dose rates (for dry samples), each assigned an uncertainty of ± 10%.
- d Field / time-averaged water contents, expressed as (mass of water/mass of dry sample) x 100. The latter values were used to calculate the total dose rates and OSL/TL ages
- e Mean ± total (1σ) uncertainty, calculated as the quadratic sum of the random and systematic uncertainties. An internal dose rate of 0.03 Gy ka<sup>-1</sup> is also included
- f Three luminescence techniques were applied to these samples; UV<sub>SG</sub> = UV single-grain, UV SA = UV single-aliquot and red TL = red thermoluminescence
- g Statistical models used to determine the dose distribution between aliquots -MAM - Minimum Age Model
- h Palaeodoses include a ± 2% systematic uncertainty associated with laboratory beta-source calibrations
- i UV<sub>SG</sub> UV OSL signal measured using single-grains of quartz - at least 1000 grains were run for each sample with x% of the grains emitting an acceptable luminescence signal, with the De derived from a MAM.
- j Uncertainties at 68% confidence interval

Table 3

Sample Name	Sample depth <sup>a</sup>	U (ppm)	<sup>232</sup> Th (ppb)	( <sup>230</sup> Th/ <sub>b</sub> <sup>232</sup> Th)	( <sup>230</sup> Th/ <sup>238</sup> U)	( <sup>234</sup> U/ <sup>238</sup> U) <sup>b</sup>	Uncorr. 230Th Age (ka) <sup>b</sup>	Corr. 230Th Age (ka) <sup>b</sup>	Corr. Initial ( <sup>234</sup> U/ <sup>238</sup> U)
<i>Tam Hang</i>									
TAM-F1	7.00 m	0.006	33.26	2.54	0.836 ± 0.006	1.260 ± 0.003	113 ± 2	88 ± 10	1.46 ± 0.08
TAM-F2	7.60 m	0.1750	39.4	10.45	0.777 ± 0.003	1.370 ± 0.001	87 ± 1	83 ± 2	1.50 ± 0.02
TAM-F3-R1	7.40 m	0.010	70.56	1.41	0.981 ± 0.006	1.273 ± 0.002	148 ± 2	89 ± 36	1.82 ± 0.47
TAM-F3-R2	7.40 m	0.011	72.48	1.42	1.007 ± 0.005	1.284 ± 0.002	153 ± 2	94 ± 42	1.89 ± 0.52
TAMC-F1		0.011	17.94	2.71	0.267 ± 0.002	1.302 ± 0.001	25 ± 1	18 ± 3	1.35 ± 0.02
<i>Nam Lot</i>									
NL-F1-R1	0 m	0.011	153.22	2.23	1.150 ± 0.004	2.023 ± 0.002	84 ± 1	62 ± 20	3.12 ± 0.67
NL-F1-R2	0 m	0.011	153.44	3.11	1.162 ± 0.004	2.236 ± 0.003	74 ± 1	60 ± 11	3.11 ± 0.41
NL-F2	0 m	0.022	7.94	5.00	0.600 ± 0.006	1.392 ± 0.002	60 ± 1	52 ± 3	1.50 ± 0.03

<sup>a</sup> Measured from base of the cave floor to sampling height.

<sup>b</sup> Uncertainties at 95% confidence interval.

Table 4

	TAM HANG	NAM LOT	DUOI U'OI	PUNUNG	SIBRAMBANG
<b>ARTIODACTYLA</b>	<i>Cervus unicolor</i> <i>Muntiacus muntjak</i> ssp. <i>Bos</i> cf. <i>sauveli</i> <i>Bubalus bubalis</i> <i>Naemorhedus sumatrensis</i> ? <i>Sus scrofa</i> ssp. <i>Sus</i> cf. <i>barbatus</i>	<i>Cervus unicolor</i> <i>Muntiacus muntjak</i> <i>Bos</i> sp. <i>Bubalus bubalis</i> Bovidae indet. <i>Naemorhedus sumatrensis</i> <i>Sus scrofa</i>	<i>Cervus unicolor</i> <i>Muntiacus muntjak</i> <i>Bubalus</i> cf. <i>bubalis</i> <i>Naemorhedus sumatrensis</i> <i>Sus scrofa</i> <i>Sus barbatus</i>	<i>Cervus</i> sp. <i>Muntiacus muntjak</i> Bovidae indet. <i>Capricornis sumatrensis</i> <sup>(2)</sup> <i>Sus</i> sp.	<i>Rusa</i> sp. <sup>(1)</sup> <i>Muntiacus muntjak</i> <i>Bibos javanicus</i> <sup>(3)</sup> <i>Bubalus bubalis</i> <i>Capricornis sumatrensis</i> <sup>(2)</sup> <i>Sus vittatus</i> <i>Sus barbatus</i>
<b>PERISSODACTYLA</b>	<i>Rhinoceros unicornis</i> <i>Rhinoceros sondaicus</i> <i>Rhinoceros</i> sp. Rhinocerotina indet. <i>Megatapirus augustus</i> <i>Tapirus indicus</i> cf. <i>intermedius</i>	<i>Rhinoceros unicornis</i> <i>Rhinoceros sondaicus</i> <i>Rhinoceros</i> sp. Rhinocerotidae indet. <i>Tapirus</i> sp.	<i>Rhinoceros unicornis</i> <i>Rhinoceros sondaicus</i> <i>Dicerorhinus sumatrensis</i> <i>Rhinoceros</i> sp. Rhinocerotina indet. <i>Tapirus indicus</i>	<i>Dicerorhinus sumatrensis</i> * <i>Rhinoceros sondaicus</i> * <i>Tapirus indicus</i> *	<i>Rhinoceros sondaicus</i> * ? <i>Dicerorhinus sumatrensis</i> * <i>Tapirus indicus</i> *
<b>PROBOSCIDEA</b>	<i>Elephas</i> sp. <i>Stegodon orientalis</i>	<i>Elephas</i> sp. <i>Stegodon</i> cf. <i>orientalis</i>	<i>Elephas</i> sp.	<i>Elephas</i> sp. ( <i>maximus</i> )	<i>Elephas maximus</i>
<b>CARNIVORA</b>	<i>Arctonyx collaris</i> cf. <i>rostratus</i> <i>Meles meles</i> <i>Melogale personata</i> ? <i>Martes</i> cf. <i>flavigula</i> <i>Cuon alpinus</i> cf. <i>antiquus</i> <i>Viverra zibetha</i> <i>Paradoxurus hermaphroditus</i> <i>Prionailurus</i> cf. <i>bengalensis</i> <i>Panthera tigris</i> <i>Ursus thibetanus</i> cf. <i>kokeni</i> <i>Helarctos malayanus</i>	<i>Meles meles</i> <i>Martes flavigula</i> <i>Cuon alpinus</i> <i>Viverra zibetha</i> <i>Ursus thibetanus</i> cf. <i>kokeni</i> <i>Ailuropoda melanoleuca</i> <i>Crocota crocuta ultima</i> <sup>(7)</sup> cf. <i>Felis temmincki</i>	<i>Arctonyx collaris</i> <i>Meles meles</i> <i>Cuon alpinus</i> <i>Viverra zibetha</i> <i>Viverra</i> cf. <i>megaspila</i> Viverridae indet. <i>Neofelis nebulosa</i> <i>Panthera tigris</i> <i>Panthera pardus</i> <i>Ursus thibetanus</i> <i>Helarctos malayanus</i>	<i>Panthera tigris</i> <i>Helarctos malayanus</i>	<i>Arctonyx</i> sp. <i>Cuon</i> sp. <i>Neofelis nebulosa</i> <i>Panthera tigris</i> <i>Panthera pardus</i> <i>Profelis temmincki</i> <sup>(4)</sup> <i>Ursus malayanus</i> <sup>(5)</sup> Carnivora indet. <i>Paguma</i> sp.
<b>PRIMATES</b>	<i>Macaca</i> sp. ? <i>Trachypithecus/Presbytis</i> <i>Hylobates</i> sp. <i>Pongo pygmaeus</i>	<i>Macaca</i> sp. ? <i>Trachypithecus/Presbytis</i> <i>Pongo pygmaeus</i> <i>Homo</i> sp.	<i>Macaca</i> sp. Colobinae indet. <i>Hylobates</i> sp. <i>Pongo pygmaeus</i> <i>Homo</i> sp.	<i>Macaca</i> sp. <i>Hylobates syndactylus</i> <i>Hylobates</i> cf. <i>leuciscus</i> <i>Pongo pygmaeus</i> <i>Homo sapiens</i>	<i>Macaca</i> sp. <i>Symphalangus syndactylus</i> <i>Hylobates</i> sp. <i>Trachypithecus cristatus</i> <i>Presbytis</i> sp. <i>Pongo pygmaeus</i>
<b>RODENTIA</b>	<i>Hystrix brachyura</i> <i>Leopoldamys sabanus</i>	<i>Hystrix brachyura</i>	<i>Hystrix brachyura</i>	<i>Hystrix brachyura</i>	<i>Acanthion brachiurus</i> <sup>(6)</sup>

Table 5

	TAM HANG	NAM LOT	DUOI U'OI	PUNUNG	SIBRANGBANG
	NSP 979	NSP 434	NSP 1189	NSP >613	NSP ~10 000
	NISP	NISP	NISP	NISP	NISP
<b>Artiodactyla</b>	379	233	386	169	4305
<b>Perissodactyla</b>	30	21	69	48	>171
<b>Proboscidea</b>	7	8	10	4	17
<b>Carnivora</b>	53	34	76	26	139
<b>Primates</b>	117	45	235	257	>2078
<b>Rodentia</b>	87	44	95	>100	>380
<b>Total</b>	<b>673</b>	<b>385</b>	<b>871</b>	<b>604</b>	<b>7090</b>

Table 6

		Ungulates							Carnivora				Primates		
		Rhinocerotidae	Tapiridae	Suidae	<i>Cervus unicorn</i>	<i>Muntiacus muntjak</i>	<i>Bos/Bubalus</i>	<i>Naemorhedus sumatrensis</i>	small Carnivora	large Felidae	Ursidae	<i>Cuon alpinus</i>	<i>Macaca sp.</i>	<i>Pongo pygmaeus</i>	<i>Homo sp.</i>
DUOI U'OI	ungnawed	61.0	9.1	1.2 <sup>(1)</sup>	-	1.8 <sup>(1)</sup>	-	-	50	13.3	16.6	42.8	34.8	12	-
	gnawed	39.0	90.9	98.8	100	98.2	100 <sup>(1)</sup>	100	50	86.7	83.4	57.2	65.2	88	100 <sup>(1)</sup>
TAM HANG	ungnawed	48.8	9.1	0.7	-	-	-	-	-	11	-	-	3.1	-	
	gnawed	51.2	90.9	99.3	100	100	100	100	100	89	100	100	96.9	100 <sup>(1)</sup>	
NAM LOT	ungnawed	88.2	75 <sup>(1)</sup>	-	-	-	-	-	-	-	-	-	-	-	-
	gnawed	11.8	25 <sup>(1)</sup>	100	100	100	100	100	100	100	100	100	100	100 <sup>(1)</sup>	100 <sup>(1)</sup>
SIBRAMBANG	ungnawed	6.6	7.1	-	-	1.5	-	-	5.8	18.1	10.4	8.3	-	48.6	
	gnawed	93.4	92.9	100	100	98.5	100	100	94.2	81.9	89.6	91.7	-	51.4	
PUNUNG	ungnawed	89.3 <sup>(1)</sup>	26.7	2.6	-	(2)	2.6 <sup>(1)</sup>	-		-	-		(2)	(2)	-
	gnawed	10.7 <sup>(1)</sup>	73.3	97.4	100	(2)	97.4	100		100	100		(2)	(2)	100 <sup>(1)</sup>

Table 7

	TAM HANG				NAM LOT				DUOI U'OI				PUNUNG				SIBRAMBANG			
	U	L	P	D	U	L	P	D	U	L	P	D	U	L	P	D	U	L	P	D
<i>C. unicolor</i>	12	60	51	19	14	26	23	17	39	60	88	11	5	7	11	1	25	85	110	6
<i>M. muntjak</i>	51	36	70	16	24	13	36	-	81	33	99	15	30	18	43	6	165	176	236	2
Suidae	82	91	136	8	40	60	90	11	>81	>80	146	10	>63	>50	>113		1977	1770	3741	6
<i>N. sumatrensis</i>	5	3	8		6	8	14		5	5	10		5	26	31		7	5	12	
Large Bovidae	19	29	46	2	12	37	47	4	-	2	2		-	-	-	-	30	76	109	5
Rhinocerotidae	8	18	6	19	1	9	2	15	14	32	31	24	7	19	18	9	66	84	73	79
Tapiridae	1	4	5	1	2	4	6		6	5	10	1	10	7	13	7	10	9	17	2
Proboscidea	5	2	3	4	6	-	4	4	7	3	7	3	1	-	1		11	6	12	5
Small Carnivora	14	15	29		9	4	13		16	12	28		-	-	-	-	38	12	50	
Ursidae	18	7	26		7	7	14		18	6	24		3	8	11		45	21	64	2
Felidae/Hyaenidae	6	3	9		1	>1	2	frgt	4	11	15		2	9	11		10	12	22	
Small primates	>69	>36	102	4	18	21	38	1	>157	>51	208		34	19	52	1	382	231	613	
<i>P. pygmaeus</i>	2	-	2		2	1	3		2	20	20	2	112	71	183		781	677	1443	28

Table 8

Order	Subfamily/Family	TAM HANG		NAM LOT		DUOI U'OI		PUNUNG		SIBRAMBANG	
		NISP	MNif	NISP	MNif	NISP	MNif	NISP	MNif	NISP	MNif
Artiodactyla	Cervidae	156	22	76	7	213	41	61	9	354	34
	Bovidae	51	5	56	11	12	3	8	7	204	9
	Suidae	172	15	101	11	161	18	>100	25	3747	244
Perissodactyla	Rhinocerotidae	25	13	17	8	58	23	27	10	152	21
	Tapiridae	5	3	4	2	11	5	21	5	19	4
Proboscidea	Elephantidae	4	2	3	1	10	3	4	2	17	6
	Stegodontidae	3	1	5	2	-	-	-	-	-	-
Carnivora	Felidae/Hyaenidae	9	2	6	1	15	3	15	3	21	6
	Ursidae	14	4	16	3	24	5	11	3	67	12
	Canidae	12	2	5	2	23	4	-	-	12	3
	Others	18	12	6	5	14	8	-	-	51	19
Primates	Cercopithecidae	108	10	41	5	198	18	16	4	209	17
	Hylobatidae	6	3	-	-	3	2	41	6	398	39
	Ponginae	3	1	3	1	32	4	199	14	1471	74
	Homininae	-	-	1	1	2	1	1	1	-	-
Rodentia	Hystricidae	87	-	44	-	95	-	>100	-	>380	-
	<b>Total</b>	<b>673</b>	<b>&gt;95</b>	<b>385</b>	<b>&gt;60</b>	<b>871</b>	<b>&gt;138</b>	<b>&gt;604</b>	<b>&gt;89</b>	<b>&gt;7090</b>	<b>&gt;488</b>



Table 9

		Measurement (m1 length)	Body mass (kg)	Range of body mass in modern species (kg)
<b>Duoi U'Oi</b>	<i>Panthera tigris</i>	26.3	153.1	180-245 kg (Southeast Asia) <sup>(1)</sup> 90-306 kg (China) <sup>(2)</sup> ~75-160 kg (Sumatra)
<b>PUNUNG</b>	<i>Panthera tigris</i>	24.4	121.6	
		27.1	166.3	
		27.2	168.6	
<b>Duoi U'Oi</b>	<i>Panthera pardus</i>	13.6	20.5	45-65 kg (Southeast Asia) <sup>(1)</sup> 37-90 kg (China) <sup>(2)</sup> 29-77 kg (Inde) <sup>(3)</sup>
		14.7	26.1	
<b>SIBRAMBANG</b>	<i>Cuon sp.</i>	19.9	14	
		22.3	17.2	10-21 kg (Southeast Asia) <sup>(1)</sup>

Table 10

TAM HANG SOUTH	NAM LOT	DUOI U'OI	SIBRAMBANG
<i>Cervus unicolor</i>	-	<i>Cervus unicolor</i>	<i>Rusa sp.</i>
<i>Sus scrofa</i>	<i>Sus scrofa</i>	<i>Sus scrofa</i>	<i>Sus vittatus</i>
<i>Rhinoceros sondaicus</i>	<i>Rhinoceros sondaicus</i>	<i>Rhinoceros sondaicus</i>	<i>Rhinoceros sondaicus</i>
<i>Rhinoceros unicornis</i>	<i>Rhinoceros unicornis</i>	<i>Rhinoceros unicornis</i>	-
<i>Rhinoceros sp.</i>	<i>Rhinoceros sp.</i>	<i>Rhinoceros sp.</i>	-
-	-	<i>Dicerorhinus sumatrensis</i>	<i>Dicerorhinus sumatrensis</i>
Rhinocerotina indet.	Rhinocerotidae indet.	Rhinocerotina indet.	-
-	-	-	<i>Tapirus indicus</i>

Table 11

<b>Sites</b>	<b>Number of teeth</b>	<b>MNlc (m1/m3, cohort)</b>	<b>MNlc (d4, cohort)</b>
<b>TAM HANG</b>	N = 18 9 m1, 9 d4	N = 9 4 lm1, 5 rm1	N = 6 4 ld4, 2 rd4
<b>DUOI U'OI</b>	N = 41 37 m3, 4 d4	N = 22 22 lm3	N = 3 3 ld4
<b>SIBRAMBANG</b>	N = 19 17 m1, 2 d4	N = 14 12 lm1, 2 rm1	N = 1 1 ld4

Table 12

<b>Sites</b>	<b>Number of teeth</b>	<b>MNIc Type (m1/m2/m3), side (left/right) of tooth</b>
<b>TAM HANG</b>	N = 39 16 m1, 7 m2, 16 m3	N = 23 3 lm1, 13 rm1, 2 rm2, 5 rm3
<b>DUOI U'OI</b>	N = 45 7 m1, 14 m2, 24 m3	N = 21 3 lm1, 8 lm2, 10 lm3
<b>NAM LOT</b>	N = 25 6 m1, 6 m2, 13 m3	N = 15 2 lm1, 2 rm1, 5 lm2, 5 lm3, 1 rm3
<b>SIBRAMBANG</b>	N = 1581 1154 m1/m2, 427 m3	N = 164 27 lm1, 45 lm2, 92 lm3
<b>PUNUNG</b>	N = 53 10 m1, 6 m2, 37 m3	N = 20 5 rm1, 1 rm2, 1 lm3, 13 rm3

Table 13

Sites	Number of teeth	MNlc (permanent teeth)	MNlc (deciduous teeth)
TAM HANG	N = 25	N = 7 P/M, M3; m1-m3	N = 18 D2-D3; d1-d2, d4
DUOI U'OI	N = 59	N = 25 M1-M3; p2-p4/m1-m3	N = 34 D1-D4; d1, d3
NAM LOT	N = 8	-	N = 8 1 upper; 7 lower D2; d1-d4
SIBRANG	N = 152	N = 74 32 upper; 42 lower P2-P4/M1-M3; p2-p4/m1-m3	N = 78 36 upper; 42 lower D1-D4; d2-d4
PUNUNG	N = 27	N = 18 4 upper; 14 lower M2-M3; m1-m3	N = 9 3 upper; 6 lower D2, D4; d2-d4

Table 14

		Southern latitudes	Northern latitudes	Northern latitudes	Southern latitudes	Northern latitudes
		MIS 5 128-118 ka	MIS5 94-60 ka	MIS5 86-72 ka	MIS 5 81-70 ka	MIS 4 70-60 ka
		PUNUNG	TAM HANG	NAM LOT	SIBRAMBANG	DUOI U'OI
<b>Action of excavators</b>	Selection of teeth	present	absent	absent	present	absent
<b>Action of floods</b>	Selection of large mammals vs microvertebrates	large-sized mammals	large-sized mammals	large-sized mammals	large-sized mammals	large-sized mammals
<b>Action of porcupines</b>	Gnawing intensity by porcupines	high (moderate in rhinocerotids) <sup>(1)</sup>	high (moderate in rhinocerotids)	high (moderate in Perissodactyla) <sup>(1)</sup>	moderate (high in ungulates)	moderate (high in tapirs + Artiodactyla)
<b>Action of predators</b>	Primary agent of prey selection	-	dhole ( <i>Cuon alpinus</i> )	hyena ( <i>Pliocrocota perrieri</i> ) <sup>(4)</sup>	? tiger ( <i>Panthera tigris</i> )	humans ( <i>Homo</i> sp.)
	Predation pressure on <i>Muntiacus muntjak</i> <sup>(2)</sup>	-	dhole ( <i>Cuon alpinus</i> )	-	-	leopard ( <i>Panthera pardus</i> ) dhole ( <i>Cuon alpinus</i> )
	Predation pressure on large bovids <sup>(2)</sup>	-	-	hyena ( <i>Pliocrocota perrieri</i> )	-	-
	Predation pressure on <i>Cervus unicolor</i> <sup>(2+3)</sup>	-	dhole ( <i>Cuon alpinus</i> )	-	-	humans ( <i>Homo</i> sp.)
	Predation pressure on suids <sup>(3)</sup>	-	dhole ( <i>Cuon alpinus</i> )	hyena ( <i>Pliocrocota perrieri</i> ) dhole ( <i>Cuon alpinus</i> )	tiger ( <i>Panthera tigris</i> ) leopard ( <i>Panthera pardus</i> ) dhole ( <i>Cuon alpinus</i> )	tiger ( <i>Panthera tigris</i> ) ? humans ( <i>Homo</i> sp.)
	Predation pressure on rhinocerotids <sup>(2+3)</sup>	-	tiger ( <i>Panthera tigris</i> )	hyena ( <i>Pliocrocota perrieri</i> )	tiger ( <i>Panthera tigris</i> )	not clearly identified (low predation pressure)
	Predation pressure on <i>Tapirus indicus</i> <sup>(3)</sup>	-	-	-	tiger ( <i>Panthera tigris</i> )	-

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