

**Establishing robust chronologies for models of
modern human dispersal in Southeast Asia;
implications for arrival and occupation in Sunda and
Sahul**

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Abstract

Models that reconstruct modern human dispersal across the great arc from Africa to Australia require solid chronologies from key sites in Southeast Asia. Sunda, the continental landmass that connects Asia to Southeast Asia and Australasia, contains important evidence to constrain both arrival and occupation of humans en route to Australia. This evidence, however, is rarely associated with robust chronologies due to an absence of stratigraphic consistency, low precision, reproducibility or accuracy. In this research, optically stimulated luminescence (OSL) dating techniques were applied to three archaeological sites in Southeast Asia that encompass both arrival and occupation; Tam Pa Ling and Nam Lot in northern Laos and Tham Lod rockshelter in north-western Thailand. This application provided solid independent age estimates to confirm the integrity of the sequences. The timing of modern human arrival at Tam Pa Ling was identified as > 46 ka and arrival at Nam Lot after 50 ± 5 ka and before 46 ± 4 ka. Modern human occupation of Tham Lod was identified as occurring after 21 ± 4 ka and before 16 ± 2 ka. These robust chronologies have added evidence to understanding modern human arrival and occupation in Sunda. Furthermore these chronologies enable parallels to be drawn between the timing and archaeology of Late Pleistocene occupation in Sunda and Sahul. These similarities provide evidence to assess whether the Sunda occupants were the ancestors to the first Indigenous Australians.

Declaration

I hereby declare that this thesis is wholly my own work unless otherwise referenced or acknowledged. This document has not been previously submitted for qualifications at any other academic institution.



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List of Abbreviations and Symbols

BP	Radiocarbon ages expressed as Before Present
cal BP	Radiocarbon ages that have been calibrated
cm	centimetres
D _e	Equivalent dose
D _r	The rate of exposure of grains to ionizing radiation
Gy	Grays
IR	Infrared
IRSL	Infrared stimulated luminescence
ka	Thousand years ago (1ka = 1000 years ago)
LGM	Last Glacial Maximum
m	Metres
MIS	Marine isotope stage
OSL	Optically Stimulated Luminescence
SA	Single-aliquot
SAR	Single-aliquot regenerative
SG	Single-grain
TL	Thermoluminescence
uncal BP	Radiocarbon ages that have not been calibrated (uncalibrated)
U-Th	Uranium-Thorium
UV	Ultraviolet
¹⁴ C	Radiocarbon
±	Plus and minus an error margin
µm	Microns (unit of measurement for grain size)
σ	Sigma
>	Greater than
<	Less than

Chapter 1: Introduction

Homo sapiens, referred to collectively as modern humans, are the most recent branch of human evolution and are considered unique due to their wide spatial dispersal and ability to replace co-existing hominid populations (Lockwood, 2008, Falk, 2011). The origin of this species is centered in Africa around 200 thousand years ago (ka) (Stringer, 1988, White et al., 2003b, McDougall et al., 2005, Klein, 2008, Oppenheimer, 2009, Tattersall, 2009) with their spatial dispersal reaching as far south as Australia by 50 ka (Bird et al., 2002, Gillespie, 2002, Bowler et al., 2003b, Roberts et al., 1990, Roberts et al., 1994b, Thorne et al., 1999, Roberts et al., 2005). The exact route of dispersal out of Africa to Australia, however, is widely debated with multiple models in circulation attempting to piece together the discovery of modern human evidence around the world.

The validity of these models of dispersal is dependent on the strength of the chronologies from key sites in the region from which they derive their data. Chronologies provide timing for depositional events and when associated with modern human evidence can provide timing for the burial of paleoanthropological and archaeological evidence. Numerical dating techniques are methods of obtaining a numerical age estimate for depositional events and are essential for the establishment of chronologies. Each numerical dating technique differs in regards to the material being dated and as such each technique will constrain a different depositional event.

To be included in models of model human dispersal chronologies should be robust. A robust chronology should have stratigraphic consistency with a sequence of ages that reflects continual sediment deposition. There should be a direct association between the deposit dated and the paleoanthropological or archaeological material and age estimates produced should be accurate (close to the 'true' age), precise (low error margins) and reproducible (consistent results that can be regenerated if the procedure is replicated).

Considerable paleoanthropological and archaeological evidence requires robust chronologies, especially in regions that historically have not been a focus of research. Despite earlier nineteenth century discoveries, mainland Southeast Asia is a region that features little in narratives of modern human dispersal, due to a paucity of remains recovered from the region combined with poorly established chronologies. Important archaeological and paleoanthropological evidence in the region has been discovered in

limestone cave and rocks shelter environments. The Tam Hang caves in northern Laos, including cave sites of Tam Pa Ling and Nam Lot, and the Tham Lod rock shelter in north-western Thailand are two sites that contain crucial modern human evidence, with only preliminary chronologies. To ensure that models of human dispersal are accurate these preliminary chronologies must be developed into robust chronologies.

Optically Stimulated Luminescence (OSL) dating is a light sensitive dating technique that has become a useful chronometer for dating Quaternary sediment deposition; however, its value has not been fully recognised in Southeast Asia. This technique would provide a valuable independent age estimate for comparison with existing chronologies at Tam Pa Ling, Nam Lot and Tham Lod. Therefore this research aims to apply OSL dating to the sites of Tam Pa Ling, Nam Lot and Tham Lod in order to establish the integrity of the stratigraphic sequence and confirm the timing of modern human presence at each site; thereby providing increased confidence in the final chronology.

Arrival and occupation are the two main temporal parameters for modern human presence in a region. Even though the timing of arrival and occupation can vary, both are crucial for models of modern human dispersal. The existing chronologies at Tam Pa Ling and Nam Lot are argued to contain the earliest modern human evidence in mainland southeast Asia but a lack robusticity. Establishing robust chronologies for both sites will validate the timing of arrival for modern humans into mainland Southeast Asia.

The current chronology for Tham Lod indicates modern human occupation since $39,960 \pm 1050$ cal BP (Marwick, 2008, Marwick, 2013), however, the chronology for occupation just prior to and after the Last Glacial Maximum (LGM) presented by Shoocongdej (2006), requires additional dating to confirm preliminary estimates from thermoluminescence (TL) and radiocarbon dating techniques. As such a robust chronology at Tham Lod would confirm occupation around the LGM and enable correlations between the archaeological evidence from sites in Sunda and Sahul to reveal potential ancestral links between these two subcontinents.

1.1 Aims and objectives

The main aim of this research is to apply OSL dating to three sites within mainland Southeast Asia in order to develop robust chronologies from existing chronologies, for incorporation into models of modern human dispersal. To achieve this aim the objectives of this research are:

- (i) Provide new chronological evidence by applying OSL dating to sedimentary deposits containing paleoanthropological and archaeological evidence at three sites within mainland Southeast Asia.
- (ii) Use OSL dating to provide independent age estimates to compare with previous radiocarbon, Uranium-Thorium and luminescence dating; thus establish robust chronologies for each site.
- (iii) To test whether the chronologies for these sites agree with or challenge the current timing for modern human arrival and occupation in Southeast Asia.

1.2 Outline

Chapter 2 reviews the current literature on models of modern human dispersal that have been developed from interpretation of chronologies. Caves and rock shelters as repositories of paleoanthropological and archaeological evidence and the application of numerical dating techniques in these environments to establish chronologies for modern human evidence will also be reviewed; with an emphasis on investigating the value of a multidisciplinary approach.

Chapter 3 provides background information for all sites in this research including the type of evidence discovered and previous numerical dating techniques applied.

Chapter 4 will outline the methodology used in this research including geomorphological and sedimentological analysis at each site, as well as the OSL dating methods employed for sample collection, preparation and data analysis.

Chapter 5 will present the results of the application of OSL dating to the sites of Tam Pa Ling, Nam Lot and Tham Lod, providing new, more robust chronologies for each site.

Chapter 6 will encompass a discussion of the new age ranges for arrival and occupation at the sites, the robusticity of the newly established chronologies and an assessment of the implications of the timing of modern human arrival and occupation in mainland Southeast Asia for models of modern human dispersal.

Chapter 7 synthesises the findings of the research.

Chapter 2: Establishing modern human presence in mainland Southeast Asia; the need for robust chronologies

SECTION I: Current models of modern human dispersal and the paleoanthropological and archaeological record

2.1 Introduction

Models of modern human dispersal aim to explain the presence of modern human paleoanthropological and archaeological evidence around the globe and use this evidence to define probable routes. The most widely accepted model is *Out of Africa 2* or the *recent replacement model*. This model proposes a late Pleistocene eastern African origin of modern humans (Stringer, 1988, White et al., 2003b, McDougall et al., 2005, Klein, 2008, Oppenheimer, 2009, Tattersal, 2009) followed by the replacement of pre-modern humans in Africa and around the world; with dispersal reaching Australia around 50 ka. The focus of debate associated with this model is the route and timing of dispersal and the timing of arrival in the regions from Africa to Australia. Within the literature there is a focus on a MIS4-3 rapid coastal dispersal model. However, recent research is gradually providing evidence for more complex and earlier exit models around MIS5 (Petraglia et al., 2010, Dennell and Petraglia, 2012). This section will present a review of current models identifying the paleoanthropological, archaeological and genetic evidence at the core of their hypotheses as well as highlighting major gaps in evidence.

2.2 The start and end of *Out of Africa 2*

Available data from a variety of disciplines points clearly to the emergence of modern humans in Africa. Genetic research by Cann et al. (1987) and Ingman et al. (2000) has identified that all non-Africans were genetically derived from a common African ancestor present around 170 ka; which is consistent with paleoanthropological evidence in Africa. The earliest dated paleoanthropological modern human remains exist in eastern Africa including the Omo specimens dated to between 103.7 and 195.8 \pm 5 ka (McDougall et al., 2005) and the Ethiopian Herto crania dated to between 160 and 154 ka (White et al., 2003b). Modern human presence has also been established at 133 \pm 2 ka at Singa calvaria in Tanzania (McDermott et al., 1996) and 120-100 ka in southern

Africa at Klasies River Mouth (Feathers, 2002) suggesting a dispersal of modern humans through Africa after an eastern origin.

Early timing for modern human presence is also evident in Australia. Conservative estimates for modern human arrival in Australia have been proposed at 40 ka (O'Connell and Allen, 2004). Earlier age estimates for modern human occupation of Australia, however, are proposed from archaeological evidence at Malakunanja and Nauwalabila in Arnhemland dated to 50-60 ka (Roberts et al., 1990, Roberts et al., 1994b) and 53-60 ka (Roberts et al., 1994b) respectively; suggesting that modern human arrival into Australia occurred shortly after 60 ka. It is further suggested from archaeological evidence at Devils Lair that modern humans had reached the extreme southwest tip of the Australian continent by 48 ka (Turney et al., 2001, O'Connell and Allen, 2004). The only paleoanthropological evidence in Australia are the Lake Mungo remains dated to 40 ± 2 ka and Bowler et al. (2003) highlights that modern humans were present at Lake Mungo by 50-46 ka based on archaeological finds. Therefore based solely on archaeological evidence modern human arrival in Australia is inferred to have occurred prior to 50 ka (Bird et al., 2002, Gillespie, 2002, Bowler et al., 2003b, Roberts et al., 1990, Roberts et al., 1994b, Thorne et al., 1999, Roberts et al., 2005). These firmly established age estimates of modern human presence in eastern Africa and Australia have led to their locations being the start and end of a journey of modern human dispersal as part of *Out of Africa 2*.

2.3 MIS4-3 rapid coastal dispersal

There exists a general consensus view that modern human dispersal involved a single migration event out of Africa circa 60 ka followed by a rapid coastal dispersal to colonise Sunda and Sahul in a few thousand years (Macaulay et al., 2005, Blinkhorn and Petraglia, 2014, Stringer, 2000, Field and Lahr, 2006). Migration 60 ka along a coastal route is suggested to have been accelerated by previous adaption to marine environments during MIS5 from 150 - 100 ka (Oppo et al., 2001) in coastal south Africa and the Red Sea coast of Eritrea (Walter et al., 2000). As such a coastal route was a path of least resistance for migrating modern human populations especially due to increased aridity during MIS4 from 76-62 ka (Landais et al., 2004) in Africa and west Asia hindering an inland dispersal.

A single rapid coastal route of dispersal with an exit out of Africa 60 ka is embraced by some geneticists as it is said to be in agreement with DNA evidence (Macaulay et al., 2005). Review of DNA evidence within the literature, however, reveals that a 60 ka migration is often cited as a consensus without reference to the existence of a wide range of dates of migration out of Africa from DNA analysis, ranging from 85-45 ka. This large variation in timing of departure from Africa has been attributed to issues of calibration (Oppenheimer, 2009, Oppenheimer, 2011, Soares et al., 2009, Endicott et al., 2009, Boivin et al., 2013, Macaulay et al., 2005). As such further research in DNA analysis is required to improve the confidence in molecular estimates of human dispersal before a consensus date of migration out of Africa is firmly established by genetic evidence.

A major problem with the rapid coastal route of dispersal model is limited support from paleoanthropological evidence via the Indian Ocean Rim and Southern Asia. The region of South Asia is an integral part of the rapid coastal dispersal model as it is geographically located as a stepping stone from Africa to East Asia and Australia (Blinkhorn and Petraglia, 2014). Historical twentieth century research in South Asia has focused primarily on types of technological development. Association of identified technologies with modern humans remains implicit (Blinkhorn and Petraglia, 2014), as paleoanthropological modern human evidence is absent in mainland South Asia until after the Last Glacial Maximum (LGM), a period extending from at least 22 ka to 19 ka (Yokoyama et al., 2000). This absence of evidence has often been attributed to submergence of past inhabited coastal sites (Blinkhorn and Petraglia, 2014). The site of Jwalapuram in southern India is the earliest skeletal evidence of modern humans from the mainland dated to 20 – 16 ka (Clarkson et al., 2008). Earlier dated skeletal evidence from the region is only evident within Sri Lanka cave sites of Fa Hen at between 35 and 28 ka and Badatomba Lena at 28.5 ka (Kennedy and Deraniyagala, 1989, Deraniyagala, 1992). As such a confident timing of modern human arrival in the South Asian stepping stone is yet to be firmly established. Therefore the majority of the foundations for the timing of the MIS4-3 rapid coastal dispersal model have been drawn from paleoanthropological and archaeological evidence towards the end of the dispersal route in Sunda and Sahul (Petraglia et al., 2010).

2.4 Modern Human evidence in Sunda and Sahul

The current chronologies for sites in Sunda and Sahul indicate that a 60 ka African exit and rapid coastal dispersal is plausible (Figure 2.1). Paleoanthropological evidence from Tam Pa Ling in northern Laos and occupational evidence from Tham Lod and Lang Rongrien in Thailand suggest a modern human presence in the region around > 46-40 ka (Marwick, 2008, Anderson, 1997, Demeter et al., 2012a). Further south in island Southeast Asia the tibia bone fossil from Tabon cave in the Philippines dated to 48 ka (Oppenheimer, 2009, Mijares et al., 2010, Detroit et al., 2004); a modern human skull from Niah cave in Borneo dated to 45-39 ka (Barker et al., 2007); and cranial remains from Wajak Indonesia dated to 37.4-28.5 ka (Storm et al., 2013) suggest a Late Pleistocene modern human presence in the region. A similar timing for modern human presence is also evident for Sahul with evidence of modern human occupation in the form of marine shells and stone artefacts at both Jerimalai in East Timor (O'Connor, 2007) and Bismark Archipelago near PNG (Leavesley and Chappell, 2004) dated to around 40,000 BP and modern human presence being firmly established by at least 50 ka in Australia. Even though the timing for modern human evidence at these sites is said to support the timing of the MIS4-3 coastal route of dispersal; the majority of sites require additional age estimates to increase the confidence in the final chronology.

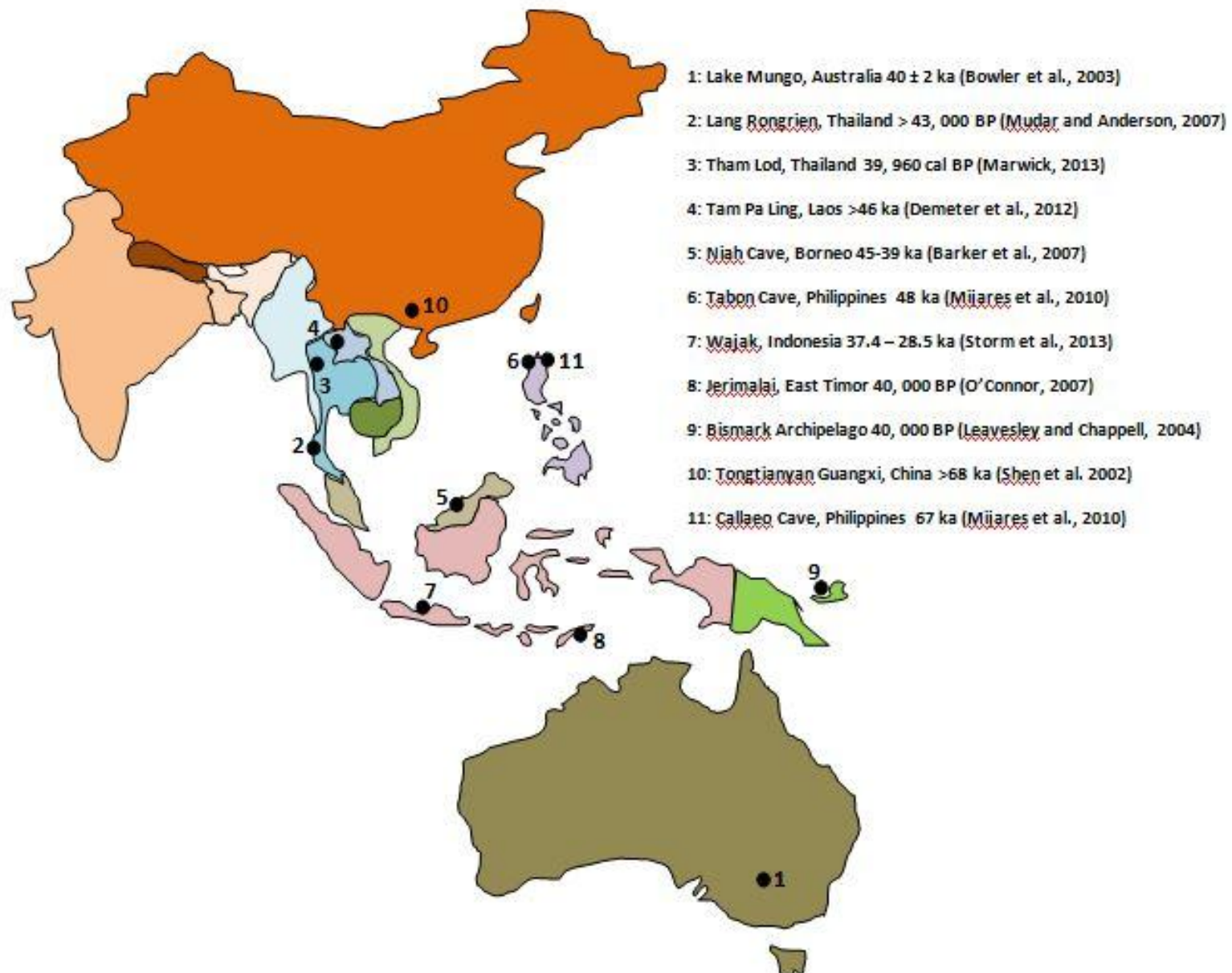


Figure 2.1 Map showing modern human evidence in Sunda and Sahul as referred to in section 2.4

Claims for a 60 ka migration out of Africa are weakened when considering early dated evidence from China and other parts of Asia. The earliest skeletal evidence of modern human presence in Asia is the Liujiang skull from Tongtianyan in Guangxi south China with a minimum age estimate of 68 ka proposed from repeated U-Th dating of flowstones (Shen et al., 2002), although the provenance of the material has been contested. Two other pieces of evidence have been proposed for supporting an earlier modern human arrival in Asia. It has been suggested that the mandible at Zhirendong in South China precedes the date of the Liujiang skull from U-Th dating of an overlying flowstone revealing an age estimate of greater than 100 ka (Liu et al., 2010). Also a metatarsal from Callao Cave in the Philippines has been dated to 67 ka (Mijares et al., 2010). However, in both of these cases there exists uncertainty regarding the identification of the evidence as modern human. In addition, other pieces of tantalising evidence include the stone tool evidence from New Guinea dated to 49 ka (Summerhayes et al., 2010) and the fully modern human faunal site of Song Gupuh in Indonesia suggesting a modern human influence since the early Last Interglacial (Morwood et al., 2008). As such sites where the provenance and identification of the evidence is insecure require robust chronologies to strengthen support for an earlier migration out of Africa.

2.5 The contribution of Middle Palaeolithic technologies to understanding the complexities regarding models of modern human dispersal

In contrast to the MIS4-3 rapid coastal dispersal model new evidence is providing support for a more complex modern human dispersal out of Africa to Australia, involving earlier and multiple dispersals. The first secure evidence for dispersal of modern humans out of Africa is paleoanthropological evidence from the Qafzeh caves in Israel (Stringer et al., 1989, Stringer, 1988, Valladas et al., 1988) dated to 100 – 85 ka (McDermott et al., 1993); suggesting a migration event out of Africa well before 60 ka. Further paleoanthropological evidence from the region, however, is absent after 70 ka (Petruglia et al., 2010). It is commonly suggested that cooler climatic conditions associated with the Toba Eruption (Petruglia et al., 2010) forced this population of modern humans back into Africa (O'Connell and Allen, 2004) or they went extinct (Dennell and Petruglia, 2012); identifying this as a failed dispersal (Quintana-Murci et al., 1999, Shea, 2008, Oppenheimer, 2011). However, archaeological evidence within the Arabian Peninsula is said to be indicative of a presence of modern human populations and their dispersal throughout the region since a MIS5 exit (Armitage et al., 2011).

Numerical dating of Middle Palaeolithic archaeological finds from coastal sites within the Arabian Peninsula is suggested to be indicative of an earlier coastal modern human dispersal out of Africa. The sites of Jebel Faya in the United Arab Emirates and Wadi Surdud in Yemen contain Middle Palaeolithic assemblages dating to MIS5, which display technological similarities to east and northeast Africa (Armitage et al., 2011, Delagnes et al., 2008, Macchiarelli, 2008). Associated with this evidence is lack of consensus for the location of exit out of Africa. A possible source of dispersal is suggested from the Sinai or Levent with populations expanding southwards to the Red Sea and Arabian Sea (Petraglia et al., 2010); facilitated by minimal dispersal barriers and habitable terrestrial environments (Fleitmann and Matter, 2009, Preusser, 2009, Petit-Maire et al., 2010, Rosenberg et al., 2013). The alternative exit location is identified as the Bab Al Mandab Strait, where populations would have expanded north and east (Petraglia et al., 2010). However, the lack of pre-Holocene paleoanthropological evidence within the Arabian Peninsula means that assignation of Arabian Middle Palaeolithic archaeological assemblages to modern humans during MIS5 remains elusive and as such the role of this region in modern human dispersal is contentious.

Similar to the Arabian Peninsula modern human presence within South Asia, in particular the Indian subcontinent, has been inferred from dated archaeological Middle Palaeolithic evidence, due to a paucity of paleoanthropological remains from the region. The most securely dated evidence of Middle Palaeolithic industries within South Asia arises from Jwalapuran, which displays a continual Middle Palaeolithic industry from 78 – 38 ka (Petraglia, 2007, Blinkhorn and Petraglia, 2014) inferred to indicate modern human occupation during this time period. Similar to the Arabian Peninsula there are two possible sources of dispersal to explain modern human presence within South Asia. The route of least resistance would be along coastlines (Field et al., 2007) as in the past the mountain chains of the Himalayas, Karhourmand and Hindu Kush were perceived to act as barriers to a transcontinental route of dispersal (Blinkhorn and Petraglia, 2014). The identification of technological affinities between the Middle Palaeolithic industry at Jwalapuran and the industry at Howiesons Poort in Africa (Mellars, 2006) have also been used as evidence within the literature to further support a west to east coastal route of dispersal from Africa. However, Korisettar (2007) has identified that past paleo-environmental conditions within South Asia could have facilitated an interior route of dispersal from the Levent and northern Arabia through mountainous terrain; but an absence of evidence means that a transcontinental dispersal route gains little attention.

As such current archaeological evidence in South Asia and also Arabia supports a coastal route of dispersal, however, evidence from both regions suggests that migration out of Africa occurred much earlier than the 60 ka consensus within the literature.

As demonstrated by this review the chronologies associated with archaeological and paleoanthropological evidence are instrumental to the development of models of modern human dispersal; as they reveal the timing of modern human presence in regions. There is a geographical bias in research on modern human sites resulting in many regions containing a lack of evidence with weak chronologies; predominately from the application of just one numerical dating technique in isolation. As such increasing the application of numerical dating techniques, as part of a multidisciplinary approach to sites will allow their evidence to be used in globalised models of modern human dispersal.

SECTION II: Chronometric techniques available to establish robust chronologies for modern human paleoanthropological and archaeological evidence

2.6 Introduction

The debate over the timing and routes of modern human dispersal has increased the need for numerical dating techniques to be applied to modern human evidence. Cave and rock shelters provide excellent environments for the preservation of both modern human evidence and deposits of material suitable for numerical dating. It is the ready availability of this material that will ultimately determine which numerical dating technique will be applied. This section will provide a brief overview of the basic principles and applications of chronometric techniques most commonly applied to date paleoanthropological and archaeological modern human evidence in cave and rock shelter settings.

2.7 Uranium-Thorium (U-Th) dating

An important deposit within cave environments is secondary carbonate speleothem deposits (Bosch and White, 2007), which are commonly associated with U-Th dating (Zhao et al., 2001, Morwood et al., 2004, Schwarcz, 1992, Jennings, 1985, Gillieson, 1996, Ford and Williams, 2007, Stock et al., 2005). U-Th dating is a radiometric dating technique able to determine the numerical age of uranium bearing materials by calculating the degree to which secular equilibrium has been restored between the parent isotope (^{234}U) and daughter isotope (^{230}Th). Therefore U-Th dating determines the time since precipitation of the calcite minerals, which represents the formation of the deposit.

The first successful U-Th dating on speleothems was achieved by Duplessy et al. (1970) and since then U-Th dating has been applied to a range of speleothem deposits. Laminar flowstones are favoured for establishing chronologies as they can overlie and underlie sedimentary layers providing minimum and maximum ages for the sedimentary unit. Successful application of U-Th dating of flowstones has been documented in Spain (Bischoff et al., 2003, Bischoff et al., 2007), Lebanon (Schwarcz, 1992), China (Shen et al., 2007, Shen et al., 2002, Zhao et al., 2001, Keates, 2010) and Indonesia (Westaway et al., 2007, Morwood et al., 2004, Roberts et al., 2005).

U-Th dating is advantageous in regards to its datable age range. Mass spectrometry has improved the precision of U-Th dating and as such it now has an age range from a few thousand years to 500 000 years (Shen et al., 2002); with lower precision in the upper age range. The closed system behaviour of speleothems creates an environment of equilibrium, meaning there is no loss of daughter isotopes after precipitation. This is considered an advantage for U-Th dating, enabling robust results. However, in individual cases speleothems may not conform to closed system behaviour, creating an environment of disequilibrium and results need to be checked to ensure reproducibility and accuracy. To agree with the laws of superposition U-Th ages of the upper layers must be younger than the layers below. If an age inversion occurs reliability of results can be cross checked through analysis of additional samples from the same horizon. The accuracy of results from U-Th dating on speleothems can be confirmed through comparison to individual age estimates from other numerical dating techniques.

The accuracy of U-Th age estimates can be affected by contamination. Contamination occurs when carbonates contain detritus sourced from wind blown or water borne sediments. This detrital material can contain daughter nuclides and in some cases uranium isotopes of ^{234}U and ^{238}U , which will influence the parent to daughter isotopic ratios from which U-Th age estimates are calculated (Walker, 2005). Therefore detrital contamination contributes to an unpredictable amount of uranium and thorium leading to erroneous and inaccurate results. Besides contamination another issue for U-Th dating is its application is limited to sites where material is firstly present and secondly present in a pure uncontaminated form and is chrono-stratigraphically relevant (Schwarcz, 1992, Pike et al., 2002, Wang et al., 2007). The absence of ideal speleothem material at some sites has prompted research into the direct U-Th dating of fossil material as a means of constructing a chronology.

U-Th dating on fossil material generally occurs on bone; however, it is also applicable to other material such as teeth and shells (Schwarcz, 1992, van der Plicht et al., 1989, Sambridge et al., 2012). The resulting age estimate represents the time since the fossil died and the decay of uranium commenced. As such U-Th dating on bone can only ever provide a minimum age as uranium uptake commences at an unknown time after death. The application of U-Th dating to fossil material is considered advantageous as it allows U-Th dating to be applied in contexts where speleothem deposits are absent. However, there are issues associated with the U-Th dating of bone. Bone does not conform to a

reliable closed system with uptake or loss of responding to geochemical changes in the burial environment (Pike et al., 2002, Sambridge et al., 2012, Hercman, Grün and McDermott, 1994). Delayed or recent uptake of uranium can lead to underestimated U-Th age estimates; alternatively leaching of uranium results in a thorium excess and overestimated U-Th age estimates (Pike et al., 2002). Attempts to identify, correct for and model uranium behaviour within bones with different uptake histories have been successful in increasing the understanding and accuracy of some U-Th dating (Millard and Hedges, 1996, Pike et al., 2002, Sambridge et al., 2012, Szabo, 1980, Grün and McDermott, 1994, Bischoff et al., 1995). This includes the most successful technique of U-series profiling, where the amount of uranium in the material is determined within an age depth profile (Storm et al., 2013). No attempt, however, has been completely successful at resolving these issues. Subsequently U-Th dating on bone can still yield erroneous results especially when applied to some paleoanthropological evidence (van der Plicht et al., 1989, Schwarcz, 1992, Michel et al., 2000). Therefore U-Th dating on bone is only considered accurate if used in association with independent age estimates from other numerical dating techniques.

2.8 Luminescence dating

A dating methodology that is widely applicable in cave and rock shelter environments is luminescence dating. Luminescence dating involves the light sensitive signal stored within the crystal lattice of mineral grains. The production and emission of a luminescence signal is dependent on a number of processes explained in figure 2.2. Exposure to light or heat results in the resetting to zero or “zeroing” of this luminescence signal. Once exposure ceases, as in a period of burial, mineral grains begin to trap energy within their crystal lattice from ionising radiation and cosmic rays in the surrounding environment (Aitken, 1998). Upon stimulation in the laboratory by heat (TL) or light (OSL) this trapped energy is released as a luminescence signal and its measurement is used to calculate a burial age estimate. As such luminescence dating involves calculating the time since mineral grains were last exposed to light or heat.

Application of luminescence dating to archaeological contexts can occur directly and indirectly. Direct dating is commonly associated with dating of artifacts such as chert and flint. When this material is heated by hominids for use as tools it results in a zeroing of the geological TL signal (Singhvi et al., 2005). Indirect luminescence dating is

commonly associated with sedimentary deposits containing modern human paleoanthropological and archaeological evidence. OSL dating applied to these sedimentary deposits measures the time since sediments were last exposed to sunlight; thus allowing a burial age to be calculated for modern human evidence.

OSL was established in the mid 1980's by Huntley et al. (1985) and since then has gained popularity over TL as it is more suited to measuring a light reset signal, providing more precise and accurate results. OSL dating is now considered an important tool used to establish the geochronology of sedimentary deposits containing quartz and feldspar minerals (Kars et al., 2008, Stokes, 1999, Wallinga et al., 2000). These mineral grains are ubiquitous in most sedimentary deposits (Stokes, 1999). Subsequently OSL dating can be applied to a range of sedimentary environments including caves and rock shelters, providing precise depositional chronologies up to hundreds of thousand years, depending on the sample (Stokes, 1999).

As with most dating techniques OSL dating has limitations with a prominent issue being partial bleaching of mineral grains. Complete resetting of the OSL signal of these minerals during sediment transport (Figure 2.2 (i)) is fundamental for accurate optical dating results (Singarayer et al., 2005, Thomsen et al., 2007, Bailey et al., 1997) and is a basic assumption of the technique. If minerals do not receive adequate sunlight exposure prior to deposition then the signal is only partially reset resulting in the deposition of mineral grains that are partially bleached (Aitken, 1998, Duller, 2004, Forman et al., 2000, Olley et al., 2004, Agersnap Larsen et al., 2000, Kuhns et al., 2000, Roberts et al., 2005). Therefore the equivalent dose measured in the laboratory will be the sum of the dose acquired since the sample was deposited plus the residual signal remaining at the time of deposition from partial bleaching. Partial bleaching is the most common problem associated with OSL dating and is associated with considerable age overestimations (Roberts et al., 2005) affecting accuracy of results. Other complications such as grain mixing, water content issues, beta micro-dosimetry and U-series disequilibrium can also affect the accuracy of OSL dating results. To improve accuracy of OSL results comparison with independent age estimates from other chronometric techniques is required.

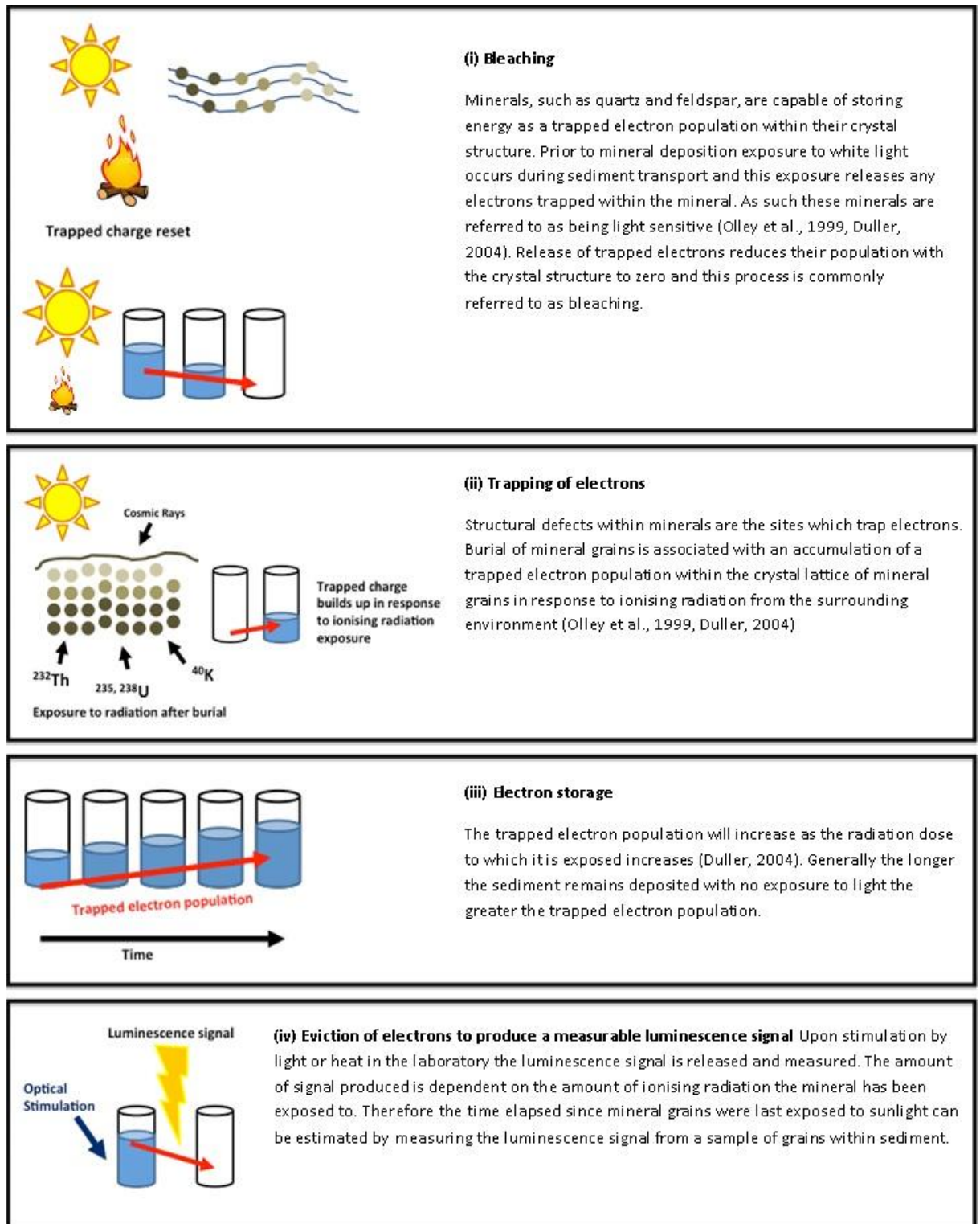


Figure 2.2: Processes involved in the production of a luminescence signal

2.9 Radiocarbon dating

Radiocarbon dating has historically been the main dating technique applied in cave and rock shelter environments to provide a time for modern human occupation. Tectonic uplift leads to the surface exposure of subterranean formed caves and rock shelters, which if suitable were occupied and inhabited by past hominids (Westaway et al., 2007). Cave or rock shelter environments contain evidence of occupation in the form of archaeological artifacts such as stone tools, in-situ charcoal deposits and burned bones from fire use (James, 1989). In-situ wood, charcoal and bones are ideal materials for radiocarbon dating, which estimates the time since the organic material was living. Generally wood degrades and the preservation of enough collagen in bone for radiocarbon dating is rare (Higham et al., 2006). As such charcoal is the dominant material used for establishing radiocarbon chronologies within the last 40 ka (Hua, 2009, Bird, 2007). Radiocarbon dating of in-situ charcoal deposits has proved successful in providing a time period for modern human occupation of cave and rock shelter environments in the Philippines (Mijares et al., 2010) and south-western Australia (Turney et al., 2001). Like U-Th and luminescence dating radiocarbon dating has certain limitations, in particular issues of calibration, upper age limits and contamination.

Long term atmospheric radiocarbon levels have changed over time. These variations, referred to as the 'de Vries' effect, were identified from discrepancies in results when comparing the age of wood based on dendrochronological dating to ages based on radiocarbon dating (Walker, 2005). To address the inconsistency between the results of these two techniques calibration was introduced which involves the conversion of radiocarbon years into calendar years. Furthermore calibration improves the accuracy of radiocarbon dating. The calibrated radiocarbon timescale has been produced based on dendrochronological records and more recently the timescale has been extended into the Late Pleistocene based on the U-Th measurements on marine coral.

The radiocarbon barrier is another limitation for radiocarbon dating as the upper age limits for establishing a chronology by radiocarbon dating affect the applicability of the technique to sedimentary environments (Higham et al., 2009, Chapell et al., 1996, Roberts et al., 1994a, Turney et al., 2001, Price et al., 2013, Grün and McDermott, 1994, O'Connell and Allen, 2004, Singhvi et al., 2005). Associated with the limits for radiocarbon dating is contamination by modern or older carbon, which can cause age overestimations or underestimations (Walker, 2005). The sorbent properties of carbon

materials absorb carbon-containing minerals in the surrounding environment producing significant errors in final age determinations. Elimination of contamination to obtain more accurate results has been attempted through pre-treatment protocols in particular acid base-acid pre-treatment with bulk combustion (ABA-BC) and acid based wet oxidation (ABOX). Bird et al. (1999) and Turney et al. (2001) propose that the ABOX pre-treatment extends the datable range of charcoal from samples in South Africa and Australia respectively. Paralleling developments in pre-treatment, the development of accelerator mass spectrometry (AMS) has improved the radiocarbon dating process by allowing the use of smaller samples of carbonised materials (Bird, 2007, Miller et al., 1999, Jull et al., 2013). As such the ABOX pre-treatment procedure combined with small sample capability of AMS is now the dominant method used for radiocarbon dating of charcoal (Bird et al., 2002, Jull et al., 2013).

Even with this combined method, however, radiocarbon age estimates cannot reliably be extended beyond 55 ka and in most cases results beyond 40 ka are inaccurate (Grun, 2000, St Pierre et al., 2009) limiting the use and applicability of radiocarbon dating to younger samples and chronologies. As such for radiocarbon dating to produce accurate results it needs to be used in conjunction with other dating techniques, especially when establishing chronological frameworks suspected to extend beyond 40 ka.

2.10 Implications for research in mainland Southeast Asia

The preceding sections have demonstrated that current chronological evidence does not conclusively support one model of human dispersal. It has been highlighted that some regions lack robust chronologies and mainland Southeast Asia is a region that has not been the focus of historical research into modern human presence, especially during the Late Pleistocene. Instead past research interests in this region have been directed towards monumental remains of more recent prehistoric populations (Marwick, 2009). Establishment of robust chronologies for modern human Late Pleistocene evidence within mainland Southeast Asia is important due to its geographical position as a path of modern human dispersal between evidence in China to the north and island southeast Asia and Australia to the south. Furthermore evidence from mainland Southeast Asia would be significant for understanding interactions between modern humans and their environments en route to Australia. As such mainland Southeast Asia would be an ideal

niche for research directed at increasing our understanding of modern human presence and dispersal.

Cave and rock shelter environments have been identified as ideal locations for the preservation of modern human evidence and deposits suitable for numerical dating. A multidisciplinary approach involves the application of more than one numerical dating technique which is advantageous as it provides multiple independent age estimates for comparison and cross checking. The applicability of numerical dating techniques to sedimentary environments, however, may limit the techniques that can be used as part of a multidisciplinary approach. For example, dating modern human evidence beyond 40 ka eliminates the use of radiocarbon dating. Subsequently the establishment of earlier chronologies requires the application of either U-Th or luminescence dating due to their ability to produce precise age estimates well beyond 40 ka. U-Th dating, however, is limited to sites containing uncontaminated secondary carbonate speleothem deposits. In the absence of speleothems, U-Th dating could be applied directly to fossil material however, erroneous results associated with delayed or recent uptake indicate it should not be utilised in isolation. OSL dating, in comparison, is globally applicable due to quartz and feldspar being ubiquitous in sedimentary environments and as such can be applied at sites lacking materials for U-Th and radiocarbon dating. Despite its wide applicability there has been limited application of OSL dating to many sites within mainland Southeast Asia that contain key modern human evidence. Therefore this research aims to apply OSL dating, where possible, as part of a multidisciplinary approach, to establish robust chronologies for modern human evidence within mainland Southeast Asia.

Chapter 3: Building from previous research at the sites of Tam Pa Ling, Nam Lot and Tham Lod to establish robust chronologies

3.1 Tam Hang caves Laos

The Tam Hang cave network includes the rock shelters of Tam Hang and caves Tam Pa Ling and Nam Lot that exist within the tower karst of Pa Hang which is located on the northern Annamitic Mountain Chain (Bacon et al., 2011, Duringer et al., 2012) in northern Laos (Figure 3.1). The geology of the mountain chain consists of weathered granite, schist and limestone, dislocated by vertical faults (Bacon et al., 2011; Duringer et al., 2012). The three Tam Hang caves differ substantially in morphology, sedimentology and paleoanthropological evidence.



Figure 3.1: Location of the Tam Hang cave network within northern Laos, mainland Southeast Asia

3.1.1 Tam Hang

Tam Hang is a group of 3 rock shelters approximately 100 metres long at the base of the Pa Hang tower karst (Bacon et al., 2011). Tam Hang was first discovered by Jacques Fromaget in 1934 who subdivided the Tam Hang site into three areas; Tam Hang south; Tam Hang central; and Tam Hang north (Bacon et al., 2011). Excavation at Tam Hang revealed fossil rich deposits containing Late Pleistocene and early Holocene paleoanthropological and archaeological evidence. Radiocarbon dating was applied to three of the seventeen skeletons buried below the surface of the rock shelter with only one skeleton containing enough collagen to produce an age estimate of $15,740 \pm 80$ BP

(Demeter et al., 2009). Further excavations in 2003 revealed cultural material consistent with a lithic industry associated with terrestrial foraging of hunter groups. Therefore the Tam Hang rock shelters are identified as being occupied by modern humans from the Late Pleistocene to early Holocene.

3.1.2 Tam Pa Ling

Tam Pa Ling (N20°12'36.0", E103°24'22.4" and 1110 m above sea level) is located at the top of the Pa Hang mountain approximately 50-60 meters above the Tam Hang rock shelters. Excavation of this site in 2009 was associated with the discovery of a partial modern human cranium (Demeter et al., 2012). Luminescence dating of the sediment, radiocarbon dating of the charcoal and U-Th dating of the partial human cranium was conducted by Demeter et al. (2012). The luminescence and radiocarbon dating revealed a minimum depositional age of ~46 ka and U-Th dating of the bone provided a maximum age for the remains of ~63 ka (Demeter et al., 2012). This chronology produced and published by Demeter et al. (2012) has been criticised due to the presence of a large chronological hiatus and reliance on radiocarbon age estimates from non in-situ charcoal that were close to the limits of radiocarbon dating. Further excavations at the site led to the discovery of a modern human mandible dated by U-Th to a minimum age of 44 ka (Demeter et al., Under review). As such additional supporting numerical dating evidence needs to be obtained to establish a robust chronological framework for both pieces of modern human evidence and increase the confidence in the timing of modern human presence at the site. This research applies OSL dating to the site in an attempt to improve the robusticity of the chronology and subsequently the OSL dating results have contributed to further research on the site conducted by Demeter et al. (Under review) (Appendix I).

3.1.3 Nam Lot

Nam Lot (N20°12'30.2", E103°24'26.6" and 1101 metres above sea level) is a cave consisting of multiple chambers and a passage located to the east of the Tam Hang rock shelters and Tam Pa Ling. A modern human tooth was discovered within a breccia sedimentary deposit located in the center of the cave along with faunal remains. Recent OSL and U-Th dating has been applied to the site to establish a chronology for the complex sedimentary deposits ranging from 72 – 46 ka with one sample being taken from each depositional layer (Bacon et al., 2015). As the tooth was deposited within the middle of the breccia deposit additional samples from the breccia would be beneficial to

establish a minimum and maximum age for the deposition for the tooth to establish the timing of modern human evidence at this site.

3.2 Tham Lod Thailand

Tham Lod is a small north facing rock shelter located at the base of an overhang of a Permian limestone cliff within Tham Lod village, Pang Mapha district in Mae Hong Son province north-western Thailand (Figure 3.2). The Pang Mapha district has a series of discontinuous limestone outcrops forming part of the Sham mountain ranges running north to south from Malaysia to Myanmar (Dunkley, 1985). The Tham Lod rock shelter is located approximately 150 metres away from the Lang River and is elevated 15 metres above current water levels (Marwick, 2013). The area was discovered by John Spies (Shoocongdej, 2006) and since then the site has been the focus of excavation. A combination of modern human skeletal and cultural material was recovered from three excavation areas in 2002 (Figure 3.3) (Shoocongdej, 2006), indicating occupation at the site. The most abundant cultural material recovered from the Tham Lod excavations consisted of flaked stone artifacts. Other material included organic sediment, charred material, shell, freshwater mussels remains and forest faunal remains.

Radiocarbon dating and thermoluminescence dating has been applied to the site and results are presented in Shoocongdej (2006) and Marwick (2013). Based on results in Shoocongdej (2006) a thermoluminescence age of $32,380 \pm 297$ ka exists for earliest evidence of occupation and the skeletal material is associated with radiocarbon ages of $12,100 \pm 60$ uncal BP and $13,640 \pm 80$ uncal BP and a thermoluminescence age of 13,422 ka (Shoocongdej, 2006). Marwick (2013) provides a radiocarbon estimate for first occupation at 39,960 cal BP. From these ages it is inferred that the Tham Lod rock shelter contains the oldest evidence of modern humans within the region of northern Thailand and as such has the potential to contribute greatly to the knowledge of Late Pleistocene archaeology and human occupation within northern Thailand. However, it is expressed that these results are preliminary (Shoocongdej, 2006) and there could be issues of contamination associated with radiocarbon dating due to acidic water infiltrating through the sediment matrix (Marwick, 2008). As such more dating needs to be applied to this site in order to obtain a robust chronology. OSL dating of the site would provide more accurate and precise results than previous TL dating. Furthermore application of OSL dating would provide the opportunity to independently test radiocarbon based chronologies (Briant and Bateman, 2009).



Figure 3.2: Location of the Tham Lod rock shelter in north western Thailand, mainland Southeast Asia

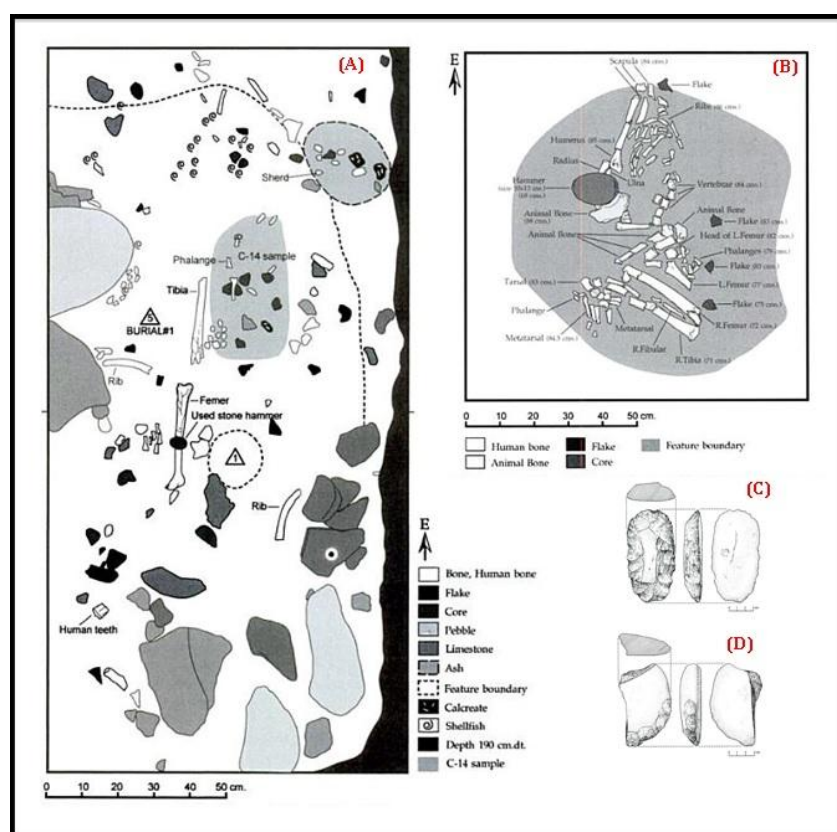


Figure 3.3: Skeletal remains and cultural material recovered from previous excavations at Tham Lod.

(A) Skeletal material recovered from a depth of 46 cm associated with the radiocarbon age of $12,100 \pm 60$ BP (Taken from Shoocongdej (2006) Fig. 3.4 pg 30).

(B) Skeletal material recovered from a depth of 94 cm and associated with the radiocarbon age of $13,640 \pm 80$ BP (Taken from Shoocongdej (2006) Fig. 3.5 pg 31).

(C) Example of a utilised core (Taken from Shoocongdej (2006) Fig. 3.6 pg 31).

(D) Example of a Sumatralith (Taken from Shoocongdej (2006) Fig. 3.7 pg 32).

3.3 Climatic conditions during modern human arrival and occupation in Southeast Asia

Modern humans transitioning through or occupying regions in Southeast Asia over the late Pleistocene and Holocene would have been exposed to changes in climate, vegetation and fauna due to glacial cycles (Hope et al., 2004). As outlined in Chapter 2 modern human arrival into Southeast Asia occurred within the Late Pleistocene and occupation continued throughout the Holocene. The LGM was associated with lower temperatures and precipitation (Hope et al., 2004) which would have affected modern human occupation in regards to a homogenization of vegetation, a changing food source and water supply. Also sea level fluctuations around the LGM led to the exposure of extensive areas of continental shelves. Post LGM was associated with an expanse of humid vegetation and increased moisture and warming of climates in Southeast Asia (Hope et al., 2004), increasing the mobility of modern humans in the region (Shoocongdej, 2000). The brief Younger Dryas period is said to have only slightly affected the local climates in Southeast Asia (Shoocongdej, 2000) having minimal impact on modern human populations.

Chapter 4: Methodology

4.1 Introduction

The type and availability of datable material in association with modern human evidence will ultimately determine the applicability of numerical dating techniques. The three most applicable chronometric techniques to limestone cave and rock shelter sites were reviewed in chapter 2. OSL dating was identified as the most applicable technique to a range of sedimentary deposits and the sediment available in cave and rock shelters for OSL dating is dependent on the sites morphology. Therefore this chapter will be divided into two sections. The first section outlines the techniques employed for a geomorphic analysis at each site, to gain an understanding of the context of sediment deposition. The second section outlines the application of OSL dating to the field sites and sample analysis methods employed.

SECTION I: Geomorphic Analysis

4.2 Geomorphic mapping

A reconstruction of cave and rock shelter morphology is essential to understand site formation and the processes responsible for sediment deposition. As such geomorphic mapping was conducted. Estimates of distance and elevation were made using a Stanley Ultrasonic Distance Estimator Measurer and measurements of bearing, angle and slope were made using a clinometer (Brunton compass). Significant cave deposits were recorded along with additional features including sources of water, potential source of sediment, temperature, entrance location, humidity and vegetation surrounding the site.

4.3 Sedimentology analysis

To reconstruct the sedimentary processes occurring at each site each, stratigraphic sections were analysed. At the sites of Tam Pa Ling and Tham Lod interpretation of the stratigraphy occurred in excavation pits. Interpretation of the stratigraphy at Nam Lot involved observations of sedimentary deposits on the cave wall and floor. Prior to sedimentological analysis the stratigraphic sections were cleaned using a trowel and if necessary a chisel, to remove any contamination. A detailed sketch of each stratigraphy was recorded along with a description of the sedimentary material including; grain size (using a G.V Chilingar - AAPG Bulletin grain sized card); colour (using a Munsell colour chart); and composition (matrix or clast dominated).

SECTION II: Optically-stimulated luminescence dating and its applications to sites in mainland Southeast Asia

OSL requires two variables to obtain an age estimate. The first is the equivalent dose (D_e), which is the dose the mineral grains received during burial. The second is the dose rate (D_r), which is the rate of exposure of grains to ionising radiation in the environment since burial. As such the burial age of sediments in this research was calculated using the following equation:

$$\text{Burial age (years)} = D_e \text{ (Gy)}^a / D_r \text{ (Gy/year)}^b$$

a: D_e is the equivalent dose estimated from the OSL signal

b: D_r is the rate of exposure of grains to ionising radiation in the environment since burial

4.4 OSL sample collection

4.4.1 Tam Pa Ling

Previous sample collection in 2009 resulted in three samples (TPL1, TPL2 and TPL3) being collected at Tam Pa Ling from trench 3, in order to produce a burial age for the partial modern human cranium. The need to establish a more secure chronological context for the depositional history of the site resulted in the subsequent collection of five samples between sample TPL1 and the top of the stratigraphic section (Figure 4.1). Samples TPL4 and TPL5 were taken beneath layers of powdery limestone precipitate at depths of 2 m and 1.8 m respectively, to establish a chronology below the precipitate layers. Sample TPL6 was taken above the shallowest limestone precipitate layer at a depth of 1.5 m to provide a minimum age for its formation. Samples TPL7 and TPL8 were taken at depths 1.2 m and 0.6 m to provide a comparison between the radiocarbon age estimates produced in Demeter et al. (2012) and to address the chronological hiatus for the upper section of the stratigraphy.

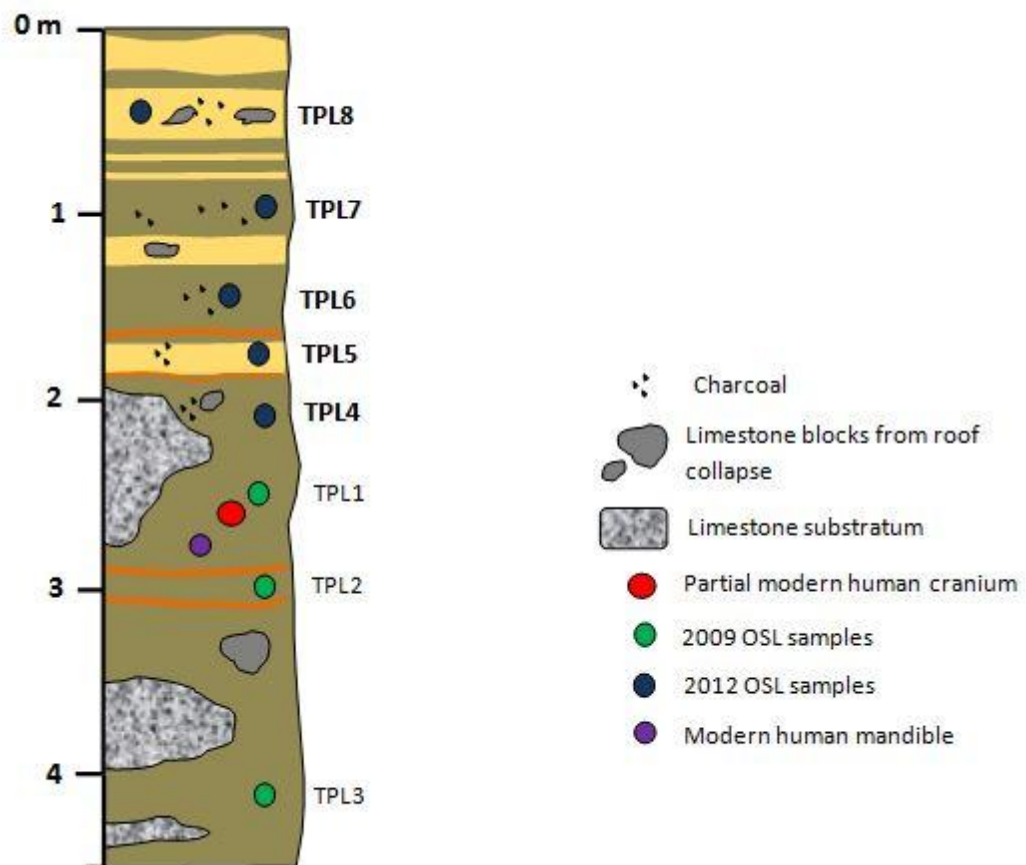


Figure 4.1 OSL sample locations in trench 3 at Tam Pa Ling

4.4.2 Nam Lot

The focus of previous OSL sampling at Nam Lot has been to constrain the faunal bones and complex depositional history. A modern human tooth was discovered in 2009 amidst faunal material within the breccia deposit in Nam Lot and a single OSL sample was taken from the breccia unit above the modern human tooth, to provide a minimum age for its deposition. This study has collected another OSL sample within the same breccia deposit but below the tooth (Figure 4.2) in order to provide a maximum age for the breccia deposition and another age to strengthen the chronological context for the modern human evidence at this site.

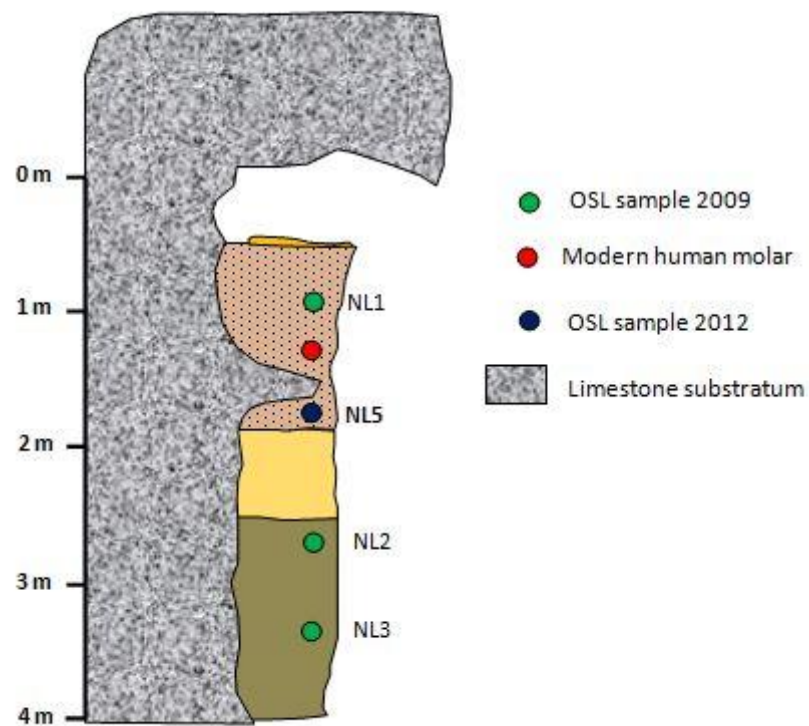


Figure 4.2 OSL sample locations at Nam Lot cave

4.4.3 Tham Lod

OSL sample locations at Tham Lod were chosen to establish a secure chronology for the depositional sequence and to provide independent OSL ages to compare with current radiocarbon and TL ages by Shoocongdej (2006). Due to the suspected disturbed nature of sediment deposition, especially within the upper profile, portable OSL dating was applied prior to OSL samples being collected. Nineteen portable OSL samples were taken between depths of 8 cm from the base of the profile to 306 cm. Results from portable OSL application led to the identification of a highly disturbed layer that was deliberately not sampled. As such seven samples were collected from varying depths (Figure 4.3) with samples TTL6 and TTL7 constraining the age of the layer containing the modern human skeletal material.

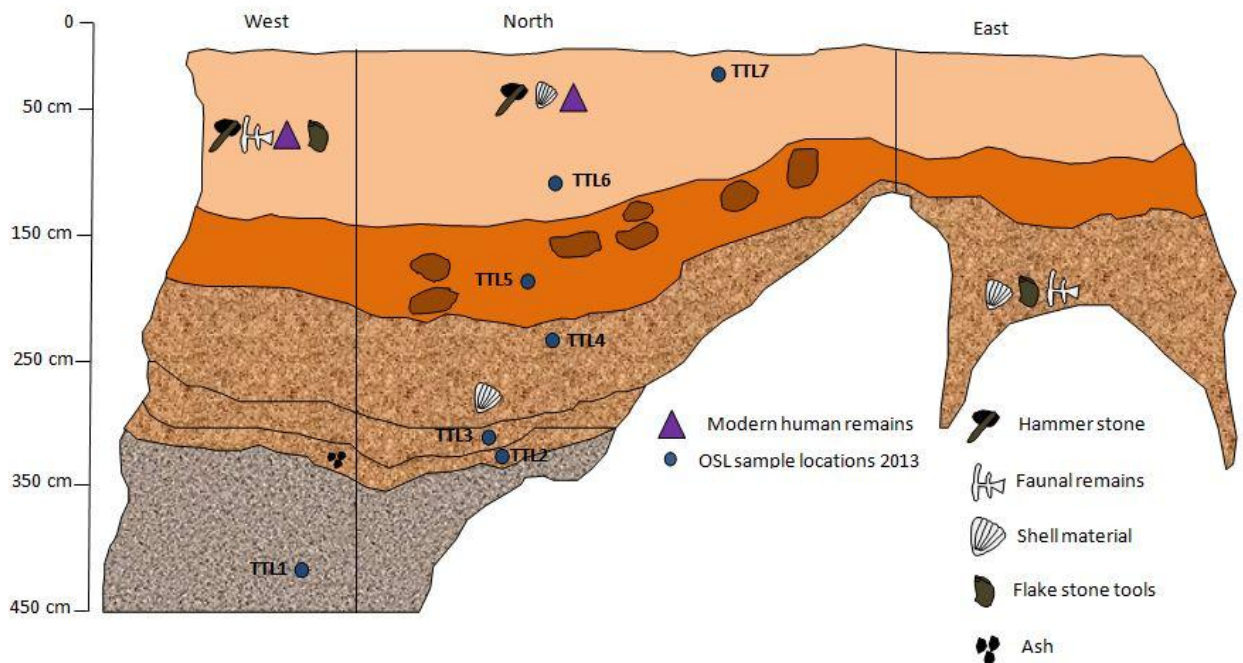


Figure 4.3: OSL sample locations at Tham Lod rock shelter. Sample TTL1 was taken at the base of the west profile and all other samples were taken from the north profile.

4.4.4 Sampling techniques implemented at each site

At the three sites either the tube or bulk sampling technique were applied depending on the dominant sedimentary composition of the units. The tube technique involved the hammering of light tight PVC cylinder tubes into exposed sections of unconsolidated deposits and was only applied at Tam Pa Ling for collection of samples TPL4, TPL5 and TPL6. A solid cap was placed on the hammering end and a reverse plunger placed inside the tube at the sampling end to prevent the mixing of the exposed bleached grains and unbleached grains. The open end of the tube was then placed flush against the exposed section and hammered in until the capped end was flush with the section of the wall. The tubes were removed, tightly double wrapped in black plastic, sealed with duct tape and labeled to ensure the transport and storage of the samples would be light-tight. Two tube cylinders were taken for each sample.

The bulk technique involved the collection of more consolidated sedimentary units, such as cemented breccias, sampled under red light conditions either under a cover or at night. A square section was marked with metal pins for sample collection under red light conditions. The section was cleaned using a chisel to remove any light exposed grains and then the sediment was sampled. The bag was tightly double wrapped in black plastic and secured by duct tape in red light conditions and labeled. Tam Pa Ling and Nam Lot samples TPL7, TPL8 and NL5 were collected using the bulk technique, plus all seven samples at Tham Lod due to the nature of the sediment and instability of the stratigraphic section, especially if exposed to hammering.

4.4.5 Portable OSL

The recent development of portable OSL makes it possible to perform luminescence measurements in the field which assist in OSL sample decisions (Sanderson and Murphy, 2010). Rather than a chronometric tool, portable OSL is a diagnostic tool that provides raw luminescence counts to demonstrate a potential increase in dose down section and identify changes in the source of sedimentation and suitable sampling locations (Muñoz-Salinas et al., 2011). Nineteen portable OSL samples were taken at Tham Lod by pressing short tubes into the sediment profile. The tubes were then extracted out of the profile and sealed with black plastic and tape to eliminate light exposure. Under subdued red light conditions samples were emptied from their tubes into plastic petri dishes and then inserted one at a time into a light tight sample chamber within the SUERC portable OSL reader. The portable reader stimulates the samples with photons

from arrays of light emitting diodes in the blue and infrared wavelengths (Muñoz-Salinas et al., 2011). A single counter multiplier registers the luminescence signals upon stimulation (Muñoz-Salinas et al., 2011). Results are then plotted in Microsoft Excel with the luminescence signal plotted against sample depth. Interpretation of the behaviour of the luminescence signal within the sedimentary profile at Tham Lod influenced bulk OSL sampling decisions.

4.5 Sample preparation

In the laboratory all sample preparation occurred under subdued red light conditions. Sample preparation consisted of an initial sieving to separate grainsize fractions into < 90 μm , 90-212 μm and > 212 μm . The < 90 μm and > 212 μm fractions were stored. The 90-212 μm fraction was exposed to a chemical treatment of 10% hydrochloric acid (HCl) to remove carbonate material followed by a 10% hydrogen peroxide (H_2O_2) treatment to remove organic materials. Each chemical treatment was left to stand for a minimum of 24 hours. Polytungstate of density 2.7g cm^{-3} and 2.62g cm^{-3} was used to separate firstly heavy minerals and secondly quartz and feldspars respectively. The separated quartz fraction was treated with 40% hydrofluoric acid for 40 minutes to remove the alpha contribution. The final step of sample preparation involved a final sieve to separate the quartz into < 90 μm , 90-125 μm , 125-180 μm , 180- 212 μm and > 212 μm fractions, and the 90-125 μm and 180-212 μm fractions were used for single-aliquot and single-grain analysis respectively.

4.6 OSL equipment

All OSL analysis was conducted at Macquarie University's luminescence dating facility, TRAPS. For all samples analysed, emissions were detected by an Electron Tubes Ltd 9235QA photomultiplier tube fitted with 7.5mm of Hoya U-340 filter fitted onto a Risø TL/OSL reader, model Risø OSL/TL-DA-20. Single-aliquot analysis involved a portion of single grains from the 90-125 μm fraction of a sample being mounted on to stainless steel discs and loaded into the Risø TL/OSL reader for analysis. In comparison, for single-grain analysis, aluminium discs with 100 precision-drilled 300 μm holes for 180-212 μm sized quartz were loaded into the Risø TL/OSL reader containing the single-grain attachment. Each of the 100 grains was stimulated for 2 seconds using a 10mW532 nm Nd:YVO₄ solid-state diode pumped green laser.

4.7 Dose recovery to determine preheat temperatures

A preheat procedure prior to the measurement of each natural and regenerated OSL

signal is necessary to remove electrons from thermally unstable traps that would not be present in the natural sample and may contribute to the OSL signal. Prior to SAR analysis, a dose recovery test was performed on four out of the seven samples from Tham Lod (TTL1, TTL3, TTL5 and TTL 7) to establish an appropriate preheat temperature for each sample from this site. Four 1 mm single-aliquot discs for each sample were prepared. The aliquots were initially bleached to remove the natural signal using the blue diodes. Bleaching occurred for 200 s and at room temperature to ensure minimal sensitivity changes. A dose similar to the expected natural was administered to the aliquots as a surrogate natural dose. Four different preheat temperatures of 220°C, 240°C, 260°C and 280°C were administered for 10 seconds, with the temperature that recovered a dose closest to the surrogate natural being identified as the most suitable measurement conditions. A dose recovery test was not performed on samples from Tam Pa Ling and Nam Lot as dose recovery tests for these two sites had been performed previously by Demeter et al. (2012) and (Bacon et al., 2015) respectively and as such the same preheat temperatures were used.

4.8 The use of the SAR protocol for single-aliquot and single-grain analysis

The single-aliquot regenerative dose (SAR) protocol was introduced as a method for determining the unknown burial dose of a sample of mixed grains as a single-aliquot (Murray and Wintle, 2003). The SAR procedure for single aliquot involves the measurement of both the OSL signal from the natural dose and the OSL signals from a number of laboratory doses from the same aliquot, to generate a dose response curve (Murray and Wintle, 2003). Any change in the sensitivity of the aliquot throughout the range of measurements is corrected by dividing the natural signal by a test dose (Murray and Wintle, 2003). The generalised SAR procedure applied to quartz in Murray and Wintle (2003) was adapted and used for single-aliquot analysis on four samples from Tham Lod from the lower, middle and upper stratigraphy (Table 4.1). A SAR procedure for samples from Tam Pa Ling and Nam Lot was previously applied by Demeter et al. (2012) and (Bacon et al., 2015).

Large variations in equivalent dose can occur when measuring an OSL signal from single aliquots, as multiple grains may have varying light exposure histories leading to partial bleaching (Duller, 2004). Consequently the contribution of partially bleached grains to the OSL signal will cause positively skewed distributions of equivalent dose values obtained from single aliquots, leading to an age overestimation (Olley et al., 1999, Olley

et al., 2004). Aeolian sediments have mostly been associated with full resetting of OSL signals (Stokes, 1992) and as such the SAR procedure for single aliquots has proved effective for obtaining an equivalent dose from aeolian samples. However, for samples with grains associated with different or insufficient light exposure during transport, an increase in accuracy can sometimes be obtained by measuring the equivalent dose of single grains, rather than single aliquots (Olley et al., 1999, Roberts et al., 1998).

Development of single-grain analysis has allowed the measurement of hundreds of individual grains from a sample. The SAR protocol has been applied to single-grain analysis in order to continue application of a measurement procedure that takes into account sensitivity of individual grains (Jacobs et al., 2006). Observations from field sites identified that the sedimentary deposits in Tam Pa Ling, Nam Lot and Tham Lod could potentially be associated with the deposition of partially bleached grains. These observations were confirmed by high statistical overdispersion values during single-aliquot analysis and as such single-grain analysis was the favoured method for application to all samples to obtain an accurate burial age.

Table 4.1: Modified SAR procedure applied to Tham Lod samples

Step	Treatment for Tham Lod samples
1	Give dose ^a , D_i
2	Preheat of 220 degrees for 10 seconds
3	IRSL wash at 50°C for 100 seconds ^b
4	Measure OSL Stimulation by blue diodes for 100 seconds at 125°C
5	Give Test dose
6	Preheat of 160 degrees for 0 seconds
7	IRSL wash 50°C for 100 seconds
8	Measure OSL signal Stimulation by blue diodes For 100 seconds at 125 °C
9	Hot optical wash for 100 seconds at 240 degrees ^c
10	Give first regeneration dose and repeat steps 2-9
11	Give second regeneration dose and repeat steps 2-9
12	Give third regeneration dose and repeat steps 2-9
13	Give fourth regeneration dose and repeat steps 2-9 ^d
14	Give final regeneration dose and repeat steps 2-9 ^e

- For the natural sample D_i (Gy)
- An IRSL wash occurred prior to every OSL measurement to remove unwanted IR-sensitive signals from possible feldspar inclusions (Olley et al., 2004)
- A hot optical wash/bleach was included as the last step for each individual dose to reduce the level of recuperation build up through the repeated cycles (Murray and Wintle, 2003)
- The fourth regeneration dose = 0 in order to monitor any thermal transfer
- The final dose is the same as the first regeneration dose (a repeated dose) in order to monitor the ability of the aliquot to reproduce the same signal for the same dose (Murray and Wintle, 2003)

4.9 Rejection criteria for single aliquots and single grains

Rejections of aliquots or grains were based on criteria in Jacobs et al. (2003), Jacobs et al. (2006) and included:

- Natural signal that was less than 3 sigma the background value. Put simply, aliquots or grains that did not produce a measurable OSL signal (there was no evidence of decay on the shine down signal)
- Poor recycling ratio (if the recycling ratio was greater than 10% unity)
- Signals containing a large proportion of IR component (IR ratio $IR > 2\sigma$ signal)
- Aliquots or grains suffering from super saturation, where the decay curve does not come to within $\frac{3}{4}$ of the natural signal
- Saturation – when the traps become full and become unable to store additional electrons, causing an underestimation in OSL counts
- Recuperation

4.10 Single-grain analysis

Quartz grains in the size fraction 180- 212 μm were preheated to 260°C for 10 seconds for Tam Pa Ling and Nam Lot samples and 220 °C for 10 seconds for Tham Lod samples. The grains were then heated to 125°C and optically stimulated using a green laser for 2 seconds. A hot optical wash of 280°C for Tam Pa Ling and Nam Lot samples and 240°C for Tham Lod samples was applied for 100 seconds to eliminate any recuperation (as seen to be present in the dose recovery tests). As associated with SAR protocols a test dose was included for natural and regenerative measurements involving a cut heat of 160°C. The same regenerative cycles as the single-aliquot analysis were used but an additional two regenerative cycles were added for each sample to assess the IR component of each grain.

4.11 Single-grain distribution analysis

Radial plots allow visual evaluation of the equivalent dose within the context of its relative error and precision and indicate whether a sample is dominated by one population of equivalent dose values or suffers from overdispersion (Jacobs et al., 2006). Overdispersion of a sample plus an interpretation of the sedimentary environment will determine the choice of model used for calculation of an appropriate equivalent dose (Jacobs et al., 2006). An overdispersion between zero and 20 percent suggests the population of grains have the same or very similar equivalent doses, further suggesting that they were uniformly bleached prior to deposition. An overdispersion above 20

percent suggests a population of grains with a range of equivalent dose values and a possibility of partial bleaching of grains.

The central age model of Galbraith et al. (1999) provides an overdispersion parameter indicating the standard deviation of the distribution of single-grain equivalent dose values from a central equivalent dose value. Samples with an overdispersion of less than 20 percent can be considered to have been uniformly bleached at the time of deposition (Olley et al., 2004). As such for samples with an overdispersion less than 20 percent the central age model will provide an accurate estimate for the equivalent dose. However, samples with an overdispersion greater than 20 percent indicates a range of equivalent dose values and prompts the use of the minimum age model in order to produce an accurate estimate for the equivalent dose. It needs to be emphasised, however, that interpretation of the depositional environment is a major determining factor in the choice of model.

The minimum age model (MAM) (Galbraith et al., 1999) provides the most accurate estimate of equivalent dose for populations of grains that have been partially bleached. This model is based on the premise that within a population of partially bleached grains the most accurate equivalent dose value will be derived from grains producing the lowest measured equivalent dose values (Olley et al., 2004, Thomsen et al., 2007), as these values are representative of the well bleached population of grains. For all samples in this research high overdispersion values combined with deposition of sediment involving either slope-wash or rock fall processes identified the potential for partial bleaching of samples. This influenced the decision to use the MAM as the primary statistical model for estimating the equivalent dose.

4.12 Environmental Dose rate determinations

4.12.1 In-situ Gamma spectrometry

The field dose rates were estimated through the in-situ counting of radionuclides uranium, thorium and potassium within the sediment surrounding the OSL samples. Measurement was taken using a portable gamma-spectrometer (Inspector by Canberra) with a 2 inch Na-iodide scintillator probe. The holes created by the OSL tube and bulk samples were extended in diameter and length using a chisel to accommodate the shape of the gamma-spectrometer probe. It was placed inside the holes and covered with the

original sediment. Counting was undertaken for 30 minutes at each sample location. It was assumed that the dose rate measured in the field has prevailed throughout the burial period of the sediments.

4.12.2 Beta dose rate

Beta dose rates were obtained by using a Geiger-Muller Beta Multicounter system RISO GM-25-5A housed in a lead brick stack. The Beta Multicounter system detects the pulse from beta particles produced by samples in small measurement pots. Five samples are detected and counted during each measurement phase. Two standards including Magnesium oxide (MgO) to return a low beta count and to be used as a background signal, and SHAP a standard with a known beta dose rate (5.77 Gy/ka) measured by 3 different techniques were placed along side the three beta pots containing the finely milled sample for analysis. After detection the beta count rate is calculated in reference to the known standard and background values.

4.12.3 Alpha and cosmic ray contribution

The external alpha contribution was removed by the hydrofluoric acid treatment during sample preparation (section 4.5). For equivalent dose determinations an internal alpha dose rate of 0.032 ± 0.01 was assumed (Feathers and Migliorini, 2001). Estimation of the cosmic-ray dose rate involved analysis of the thickness of the overhang (in this case limestone) above the deposit, the sediment depth at the sample locations, altitude and geomagnetic latitude and longitude for each site, according to Prescott and Hutton (1994).

4.13 Moisture content corrections

Present day water content estimations were performed in the laboratory. Small amounts of sediment were extracted from each sample to determine the water content. Material collected was transferred to a pre weighed beaker to obtain a wet weight for the sample. The sample was dried in an oven at 70°C for seven days (or until completely dry) and the reweighed to determine the dry sample weight. The dry weight and weight of the empty beaker were subtracted from the wet weight to produce a value of the total weight of water loss from drying. The field water content for each sample was expressed as the weight of the water divided by the weight of the dry sediment. Before incorporation into age calculation, factors listed below were considered and field water content values were adjusted to incorporate the range of hydrological changes over time at each individual site.

Factors for consideration in field water content estimations:

- hydrology of the sites over time
- sediment composition
- sediment depth
- climatic conditions over time
- geomorphology of the site over time

4.14 Age Determination

To obtain a burial age the equivalent dose values of samples were divided by their dose rate determined from combining the internal alpha, beta, gamma and cosmic ray dose rates, according to the OSL age equation provided earlier. The age is considered to be equivalent to the time elapsed since mineral grains were last exposed to sunlight.

Chapter 5: Results

SECTION 1: Cave and rock shelter morphology, sedimentology and modern human evidence

5.1 Tam Pa Ling

Geomorphic mapping of Tam Pa Ling revealed the structure of the cave and provided evidence for its evolution and the dominant site formation processes. The cave is dominated by a main chamber (Figure 5.1) with the only entrance existing on the south facing side, which incorporates a steep sloped entrance, formed by collapse material (Figures 5.2). It is well decorated with speleothem drapery covering the cave walls. The sediments deposited on the cave floor consist primarily of sandy and silty clay layers with the presence of powdery calcite precipitate between some layers (Figure 5.3). Limestone casts and charcoal are also evident within the sediment profile.

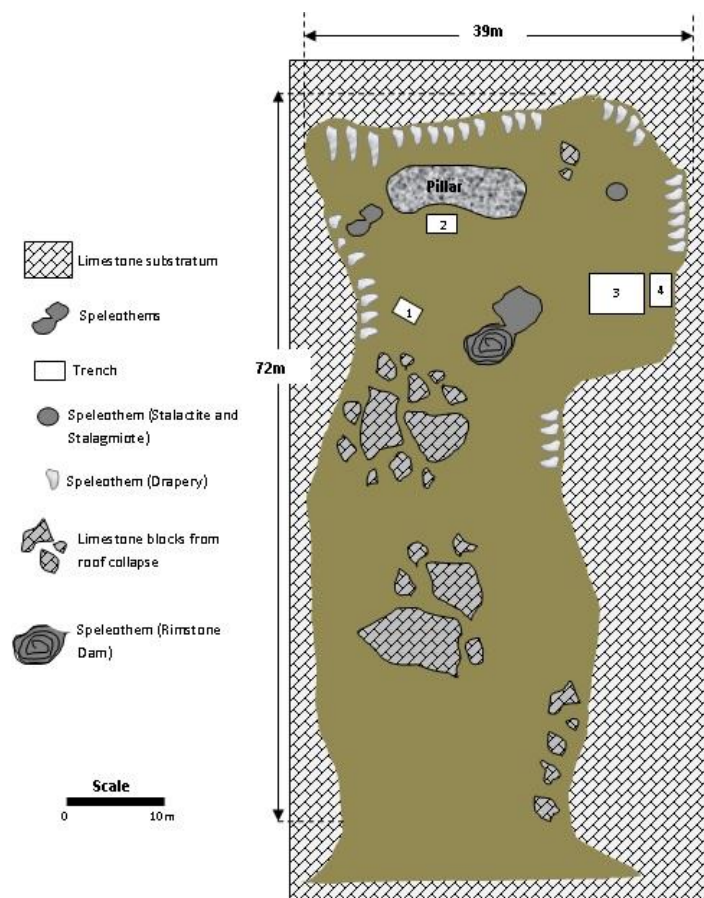


Figure 5.1: Planform view of the cave morphology at Tam Pa Ling

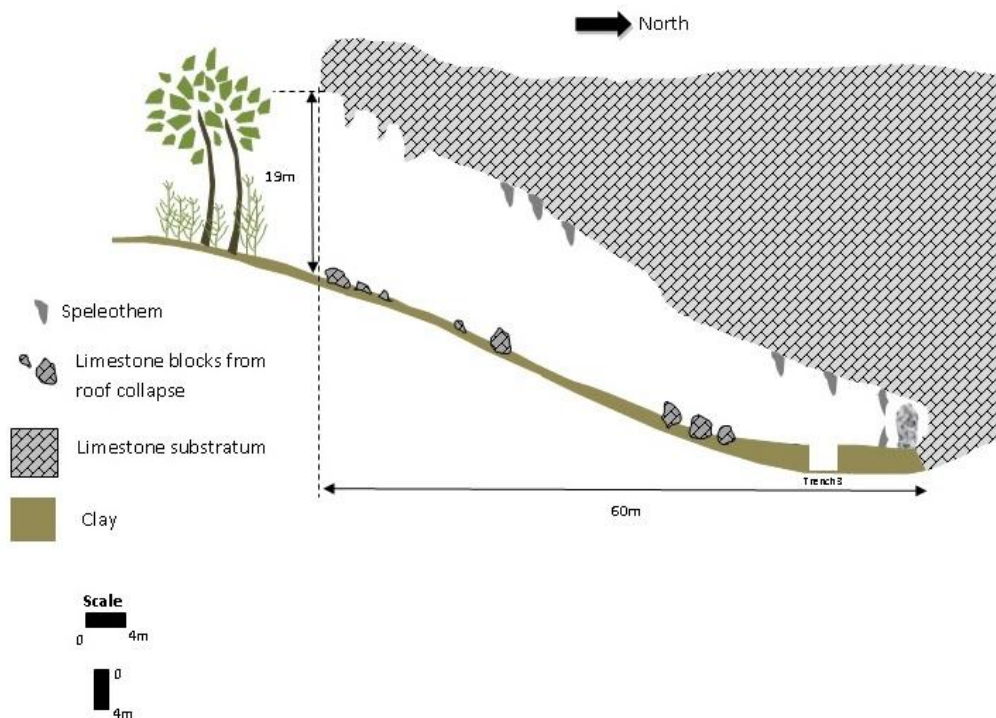


Figure 5.2: Profile view of the Tam Pa Ling cave. The entrance is on the south facing side and at a higher elevation than the cave floor

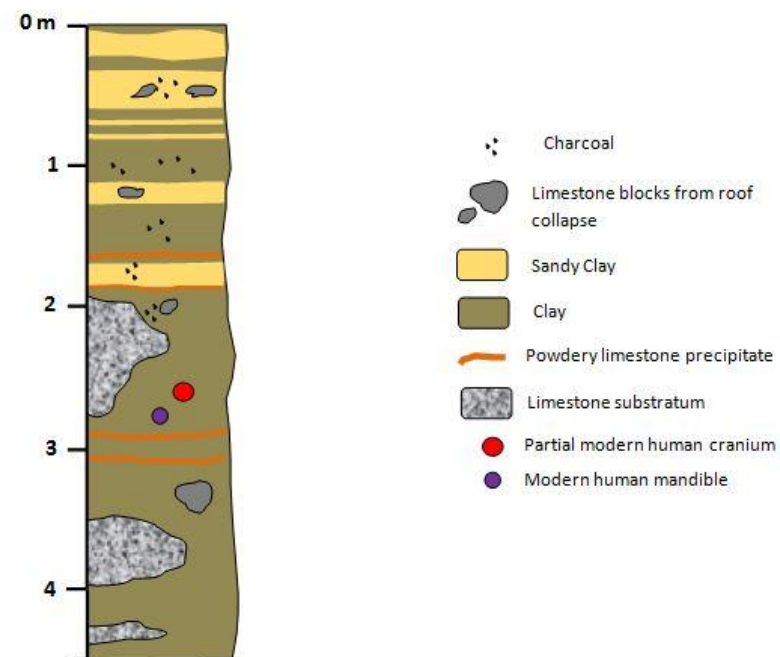


Figure 5.3: Sediment profile of trench 3 at Tam Pa Ling

5.2 Nam Lot

Geomorphic mapping at Nam Lot revealed multiple chambers and a connecting passage (Figure 5.4 and 5.5). Interpretation of the stratigraphic sections revealed a conglomerate deposit capped by a flowstone, high on the wall in chamber 3, and breccia and clay deposit low on the walls and cave floor in chamber 2 (Figure 5.6). Mapping revealed a flowstone blocking the end of passage 1 and the presence of sink holes as potential sources of sediment throughout the cave (Figure 5.7).

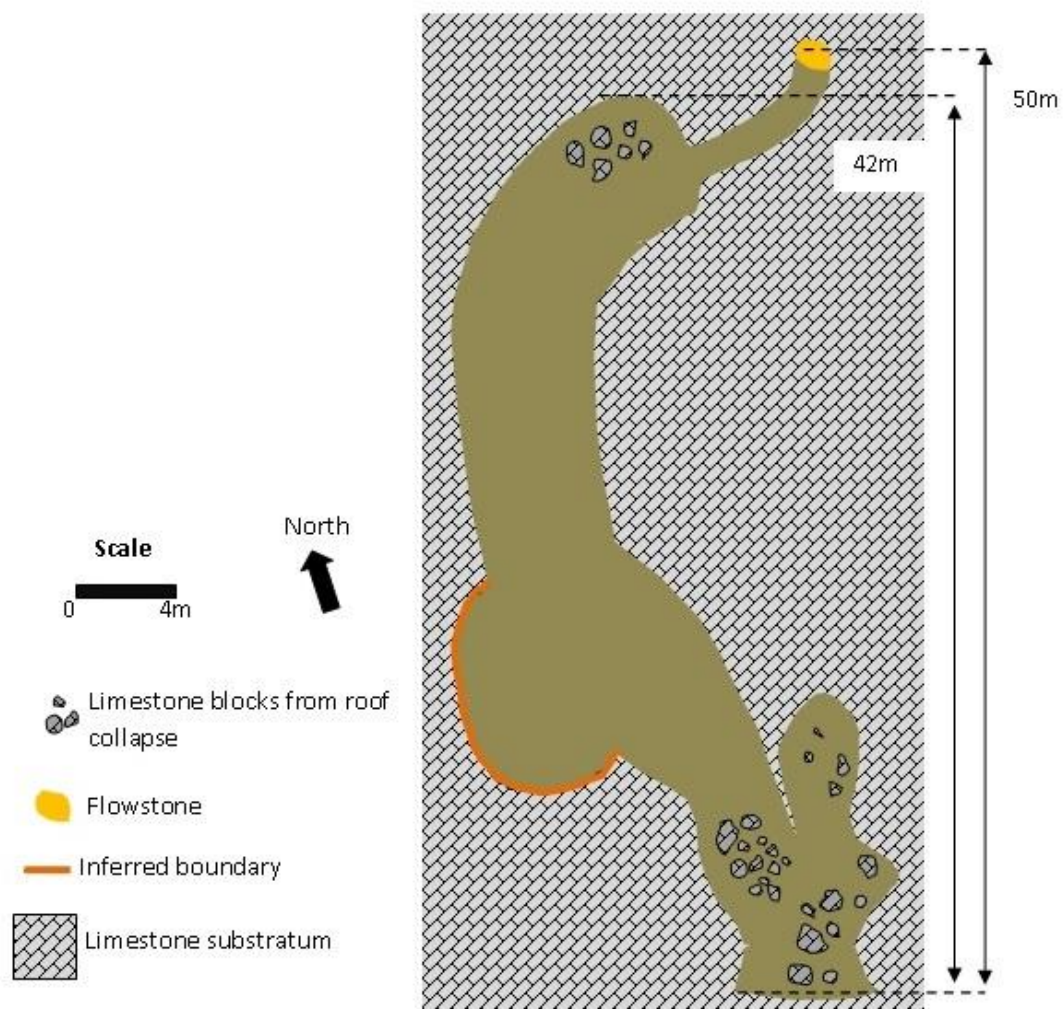


Figure 5.4: Planform view of the cave morphology of Nam Lot

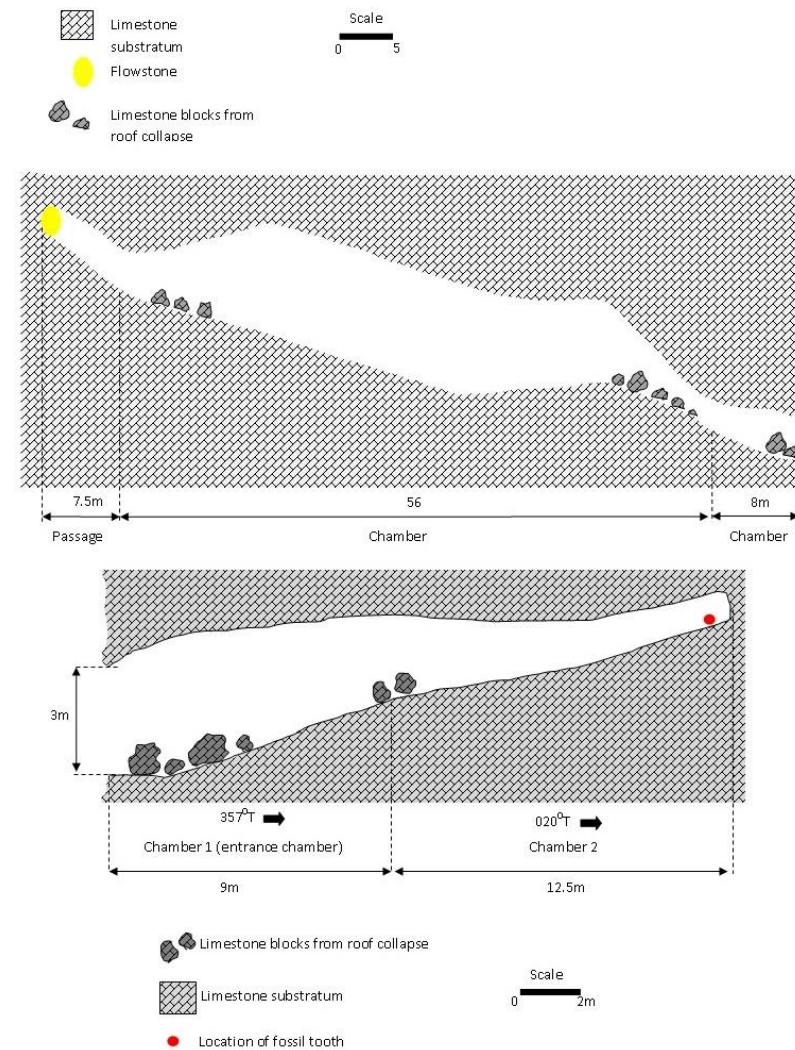


Figure 5.5: Profile view of Nam Lot cave from the west (top) and east (bottom)

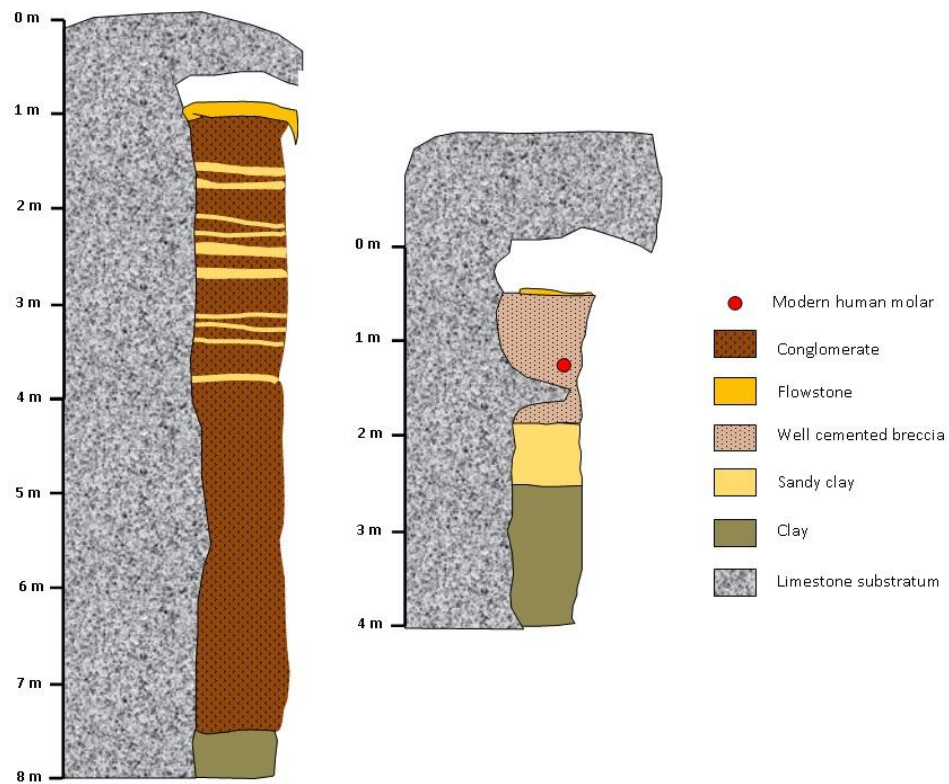


Figure 5.6: Sediment profile from chamber 3 in Nam Lot (left). Conglomerates consisting of rounded pebbles and cobbles are deposited on fine grained clays. Sediment Profile of Chamber 2 in Nam Lot (right). Clay and sand sediments overlain by well cemented breccia containing faunal bones and a modern human molar tooth.



Figure 5.7: Sinkhole above Breccia sedimentary deposit in chamber 2

5.3 Tham Lod

The limestone rock shelter of Tham Lod is located within a slightly elevated area within low density rainforest (Figures 5.8 and 5.9). The stratigraphic section has a sediment composition consisting predominately of gravel layers with varying clast sizes and a basal conglomerate layer (Figure 5.10). The conglomerate layer at the base of sequence is clast dominated containing large round boulders. The second stratigraphic layer, above the basal conglomerate, was also clast dominated consisting of gravel with some rounded cobbles. Clast sizes in this layer were smaller than the basal layer. The third and fourth stratigraphic layers contained similar gravel deposits with larger angular clasts being present in the third layer and smaller angular clasts present in the fourth layer. The fifth and sixth stratigraphic layers were highly disturbed with a mix of angular and rounded clasts. These disturbed layers contained the largest cobbles and boulders evident in the entire stratigraphic section. Towards the top of the sixth stratigraphic layer the sediment appears loose compared to the much more compacted layers at the base of the stratigraphic profile.

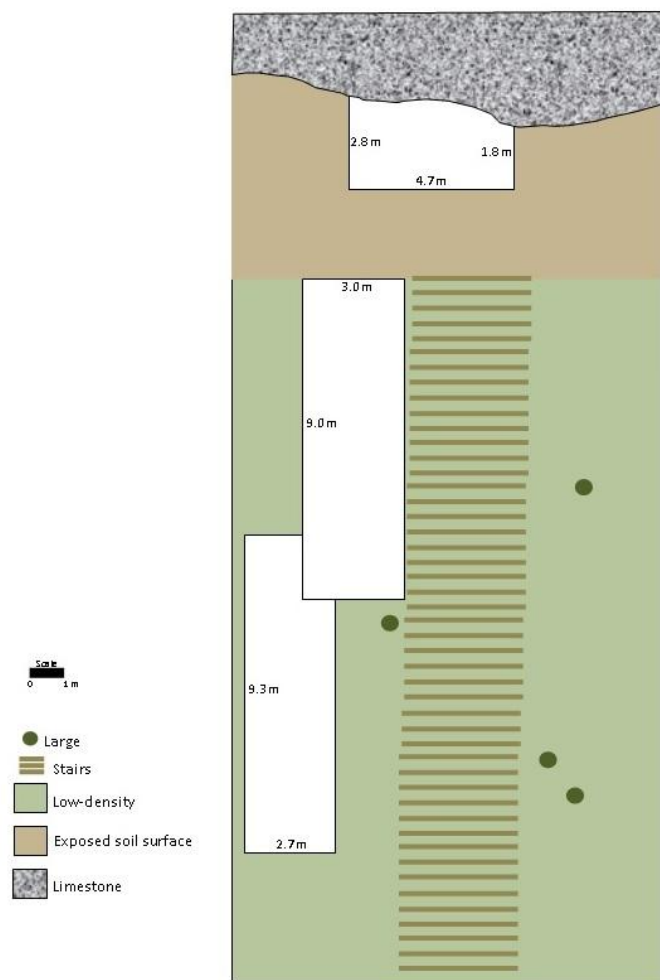


Figure 5.8: Planform view of Tham Lod rock shelter

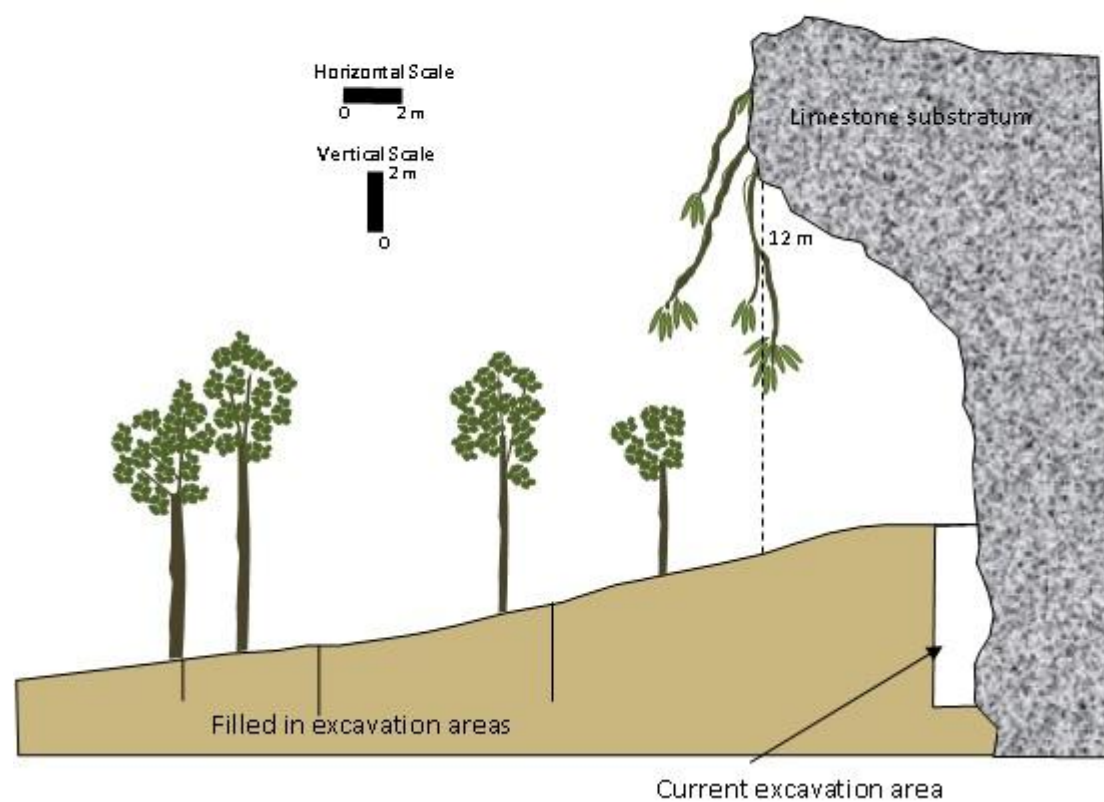


Figure 5.9 Profile view of Tham Lod rockshelter

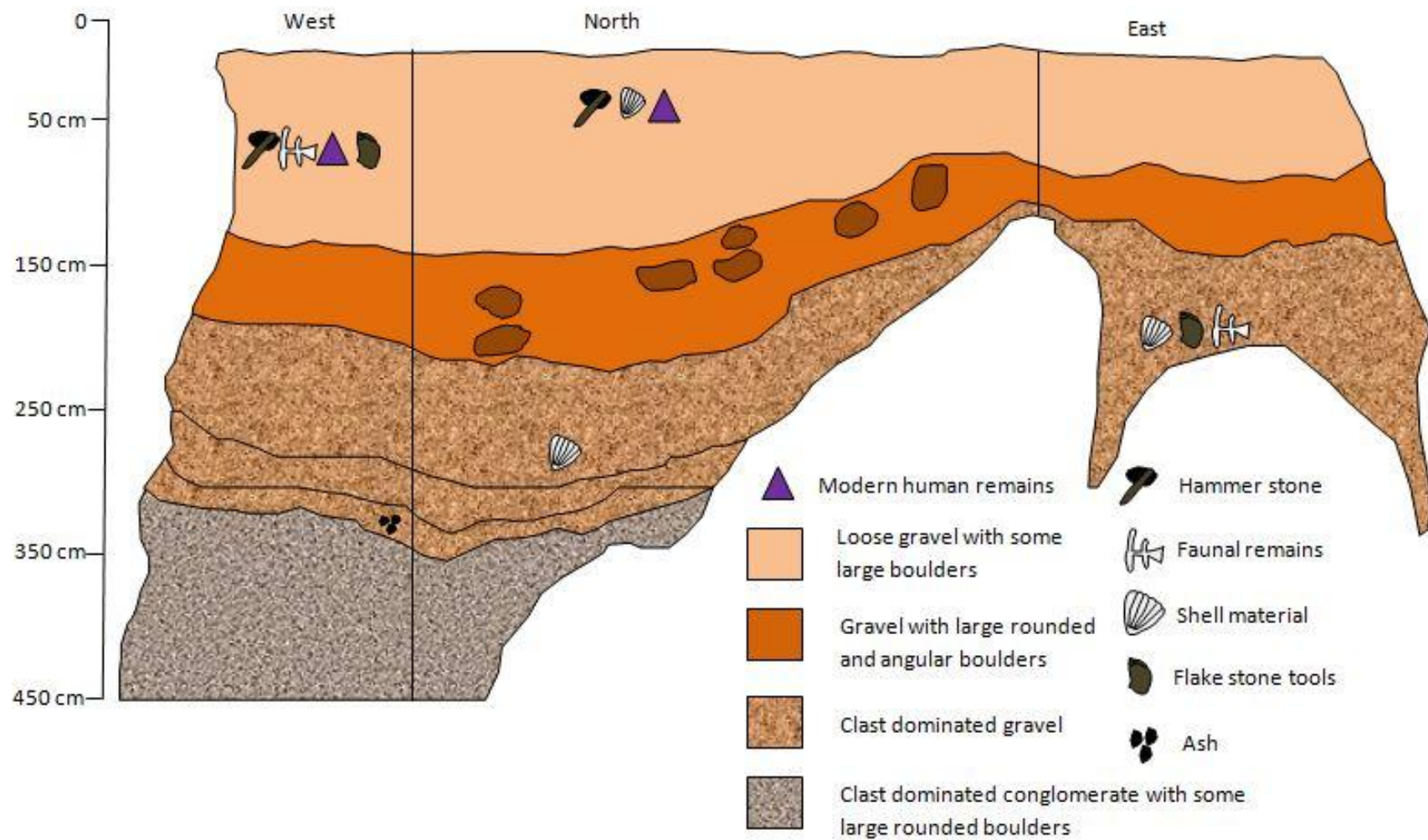


Figure 5.10 Stratigraphic sections for the west (left), north (middle) and east (right) profiles at Tham Lod

SECTION II: Results from the application of OSL dating

5.4 Portable OSL results

Results from portable OSL analysis within the field at Tham Lod (Figure 5.11) show that the OSL counts decrease from the top of the sequence towards the base. Above 1 meter the luminescence signal becomes scattered with scattering escalating throughout the upper profile. As such OSL samples were directed away from the upper disturbed section of the profile.

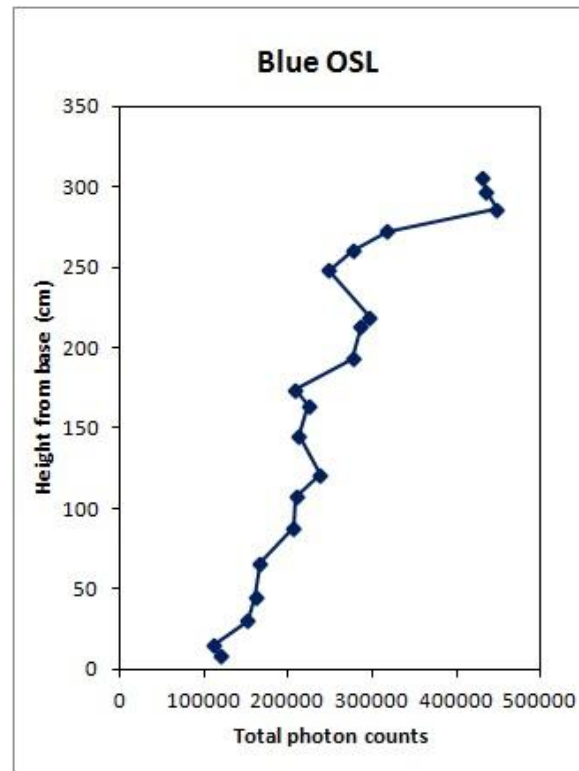


Figure 5.11: Portable OSL results showing changes in luminescence signal throughout the sedimentary profile

5.5 Identifying the appropriate preheat temperature and TL peaks

In order to identify the most appropriate preheat temperature a sequence of glow curves were measured directly after a sequential increase in preheat procedures (Figure 5.12). The preheat temperature of 220°C performed best in the dose recovery and therefore was the chosen preheat temperature for samples from Tham Lod.

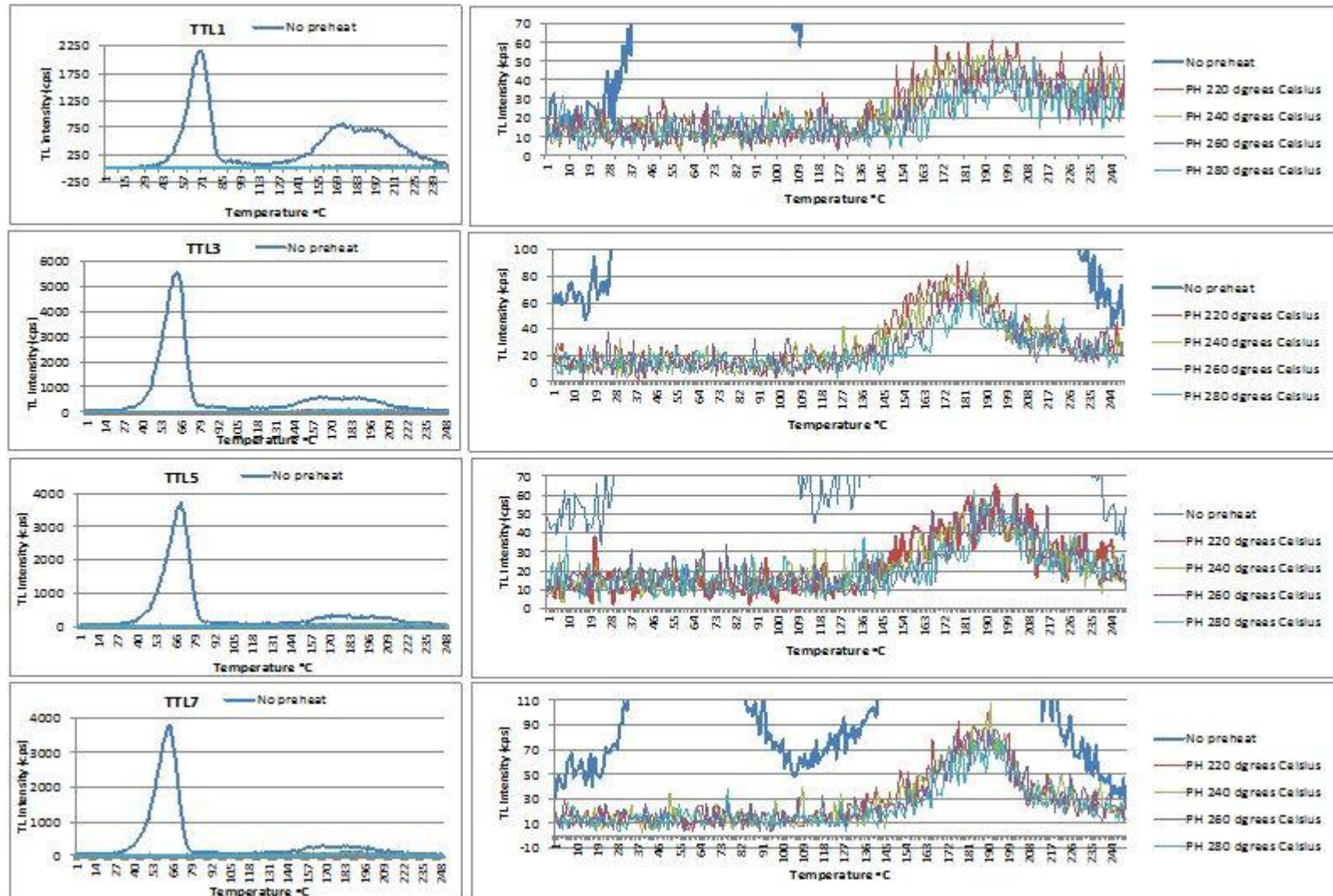


Figure 5.12: TL glow curves for four Thailand samples. The contribution of electrons from thermally unstable traps is plotted in the smaller diagrams to the left with the diagrams on the right showing any thermal erosion of OSL peaks associated with different preheat temperatures.

5.6 Single-aliquot dose response for Tham Lod

Single-aliquot analysis for Tham Lod revealed that samples towards the base of the stratigraphy had grains suffering from super saturation. Sample TTL1 had a low acceptance rate with all rejected aliquots suffering from super saturation. As such only 1 aliquot was accepted for which an overdispersion and age could not be estimated. Sample TTL4 had two rejected aliquots from super saturation and samples TTL5 and TTL7 within the upper stratigraphy had no rejected aliquots. The statistical overdispersion was below 20% for sample TTL5 but above 20% for samples TTL4 and TTL7 (Table 5.1). The ages produced for 3 samples (Table 5.2) are not stratigraphically correct with sample TTL4 associated with a younger rather than older age estimate compared to sample TTL5. Due to the inconsistency in age estimates, the contribution of super saturated grains evident in samples TTL1 and TTL4 and high overdispersion for samples TTL4 and TTL7 single-grain analysis was chosen as the preferred option to obtain an equivalent dose.

5.7 Determining the equivalent dose

5.7.1 Single-grain measurements – OSL decay and dose response curves

OSL decay curves for each sample showed variation in grain brightness and signal luminescence intensity. Each sample contained bright grains and the decay curve of such bright grains is evident in figure 5.13. These typical bright grains were dominated by the 'fast' decay component. Measurement of grains included a range of regenerative doses and a fixed test dose to produce dose response curves that grows with increased dose. The ideal shape of dose response curves is evident in figure 5.13 and non-growth facilitated the rejection of some single grains.

Table 5.1: Results from SAR procedure for Tham Lod samples

Sample	Single aliquots processed	Single aliquots accepted	Single aliquots rejected	Overdispersion (%)	Statistical model
TTL1	24	1	23	Could not be calculated	MAM
TTL4	24	22	2	28.9	MAM
TTL5	24	24	0	9.5	MAM
TTL7	24	24	0	32.4	MAM

Table 5.2: Table of single-aliquot OSL burial ages for samples from Tham Lod with associated dose rate and equivalent dose data

Sample Code	Sample depth (cm)	Grain size (um)	Field gamma dose rate (Gy/ka)	Beta dose rate (Gy/ka)	Cosmic-ray dose rate (Gy/ka)	Water content (%)	Total dose rate (Gy/ka)	Statistical model	Equivalent dose (Gy)	Age (ka)
TTL4	210	90-125	0.346 ± 0.04	1.263 ± 0.043	0.064	3/ 10 ± 7	1.704 ± 0.05	MAM	26 ± 3	15 ± 2
TTL5	170	90-125	0.343 ± 0.04	1.018 ± 0.04	0.059	6/21 ± 15	1.451 ± 0.35	MAM	41 ± 2	23 ± 2
TTL7	39	90-125	0.468 ± 0.04	1.131 ± 0.06	0.049	81/50 ± 30	1.680 ± 0.40	MAM	15.2 ± 1.3	9 ± 3

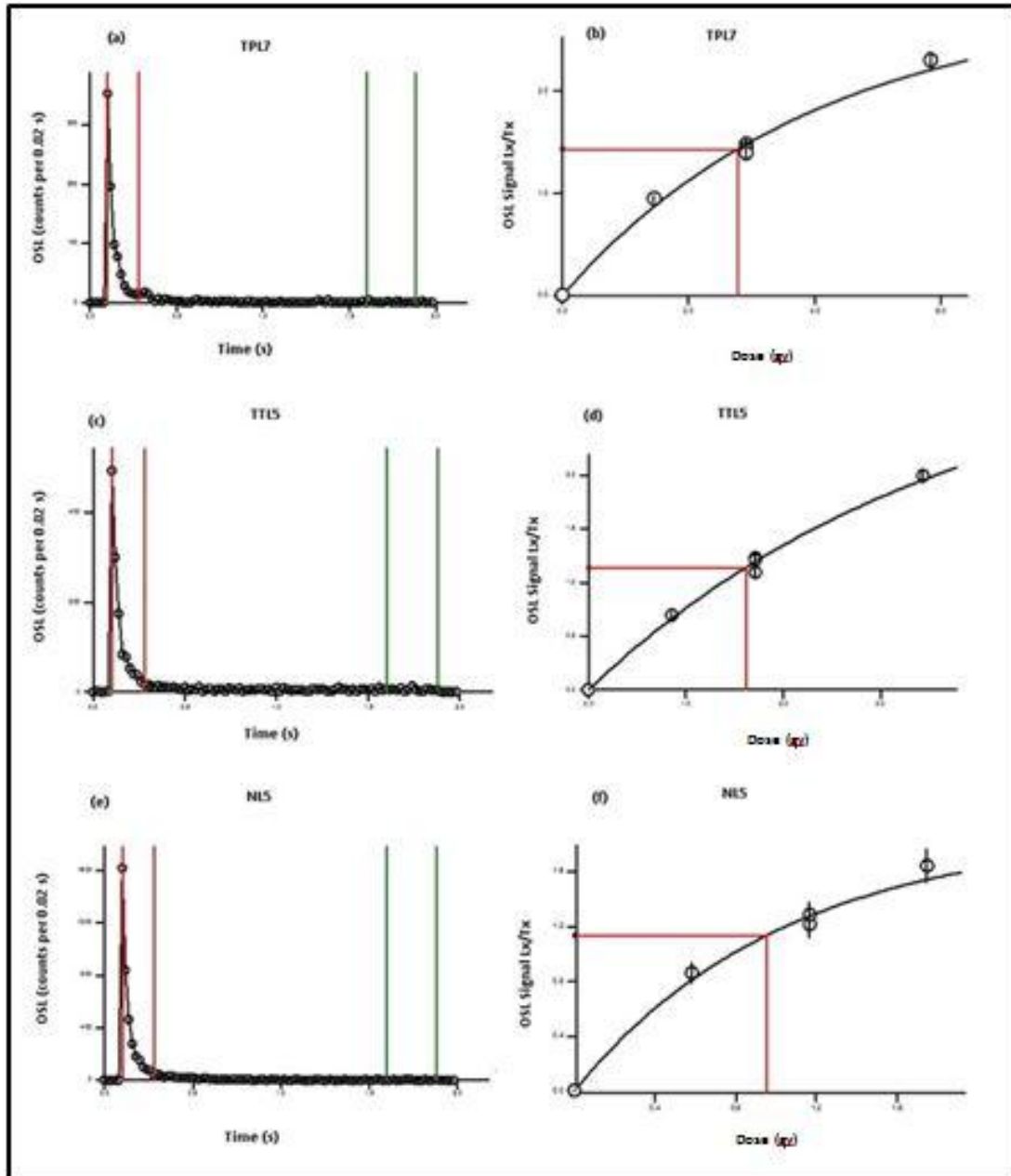


Figure 5.13: Decay curves (a)(c)(e) and dose response curves (b)(d)(f) for a bright grain from samples TPL7, TTL5 and NL5

5.7.2 Single-grain rejections

Determining the equivalent dose values for samples followed the procedure outlined in section 4.10 with grains being rejected for reasons outlined in section 4.9. Rejected grains were not considered for equivalent dose estimations and as such only grains that demonstrated characteristics of a bright grain (Figure 5.13) and were not rejected for reasons specified in section 4.9, were considered for equivalent dose estimation (Table 5.3). Initially 400 grains for each sample were measured and based on rejections (Table 5.4) some samples required the measurement of extra grains. Sample TTL2, however, returned low amounts of quartz within the 180-212 μm size fraction after processing, which meant that only 400 grains could be initially measured. The majority of grains for all samples were rejected due to a low signal to background ratio. Samples from Tham Lod had a large proportion of grains being rejected for super saturation and samples from Tam Pa Ling and Nam Lot had a greater proportion of grains rejected for saturation.

Table 5.3: Summary of single grains accepted for equivalent dose measurements for Tam Pa Ling, Nam Lot and Tham Lod

Sample	Single grains processed	Single grains accepted	Single grains rejected	Proportion of luminescence emitting grains (%)	Rejection rate (%)	Overdispersion (%)	Statistical model
TPL4	900	121	779	13	87	32.5	MAM
TPL5	800	136	664	17	83	32.8	MAM
TPL6	900	178	722	20	80	41	MAM
TPL7	1400	121	1279	9	91	32.7	MAM
TPL8	1800	101	1699	6	94	45.4	MAM
NL5	900	60	840	6.6	93.4	32.5	MAM
TTL1	2000	82	1918	4.1	95.9	44.0	MAM
TTL2	400	37	363	9.3	90.7	47.1	MAM
TTL3	800	100	700	10.0	70.0	32.8	MAM
TTL4	700	125	575	17.9	82.1	43.0	MAM
TTL5	1000	110	890	11.0	89.0	32.1	MAM
TTL6	1000	114	886	11.4	88.6	32.8	MAM
TTL7	400	155	245	38.8	61.2	57.5	MAM

Table 5.4: Summary of single-grain rejections based on individual criteria for samples from Tam Pa Ling, Nam Lot and Tham Lod

Criteria for rejection	TPL 4	TPL5	TPL6	TPL7	TPL8	NL5	TTL1	TTL2	TTL3	TTL4	TTL5	TTL6	TTL7
Signal $<3\sigma$ BG	297	280	300	697	918	430	997	178	350	260	409	440	137
Recycling ration $>10\%$ unity	194	158	109	142	145	181	303	44	96	61	138	159	44
IR ratio IR $>2\sigma$ signal	148	119	216	55	98	145	130	47	71	66	149	88	15
Saturated grains	98	85	82	91	86	44	0	0	1	0	10	5	0
Supersaturating grains	37	17	4	52	9	12	458	88	164	177	157	186	43
Recuperation $>5\%$	2	2	10	4	34	15	16	3	4	7	5	3	2
No Decay	1	0	0	235	406	8	10	2	12	3	18	2	3

5.7.3 Equivalent dose distributions

The equivalent dose distributions and equivalent dose value chosen for age calculation are presented in tables 5.5 and 5.6 and radial plots (Figures 5.14 and 5.15). For all samples more than 20 percent of equivalent dose values lie outside of the 2σ error shaded bar on radial plots indicating that the distributions are overdispersed. Values of overdispersion for each sample are evident in table 5.3. Overdispersion for all samples combined with the sedimentological context prompted the use of the MAM to estimate an equivalent dose for age calculation. Precision is generally higher for samples from the upper stratigraphy at Tam Pa Ling (TPL7 and TPL8) and Tham Lod (TTL5, TTL6 and TTL7) as the radial plots for these samples show equivalent dose values closer to the radial axis, compared to samples TPL4, TPL5 and TPL6 and TTL1-4 respectively from the lower stratigraphy.

5.8 Obtaining burial OSL ages

Dose rates were estimated using the techniques outlined in section 4.12 and the individual gamma, beta and cosmic dose rates along with the total dose rate and subsequent burial ages are listed in tables 5.5 and 5.6. For both Tam Pa Ling and Tham Lod there was no identified trend in changes in dose rates with depth. Burial ages at Tam Pa Ling, Nam Lot and Tham Lod are stratigraphically correct increasing in age towards the base of the sediment profiles (Figures 5.16, 5.17 and 5.18). For Tam Pa Ling the stratigraphy has been constrained by the age estimate of 48 ± 5 ka at the base of the sediment profile to 2.4 ± 0.3 ka at the top of the profile, with the partial modern human cranium and mandible being deposited around 46 ± 5 ka. As such deposition of sedimentary material at Tam Pa Ling has occurred from the Late Pleistocene into the Holocene. Deposition occurring from the Late Pleistocene to the Holocene is also evident at Tham Lod with deposition of the site constrained to between 21 ± 4 and 3 ± 1 ka. In comparison the time scale of sediment deposition of Nam Lot does not transition into the Holocene with the youngest age for sediment deposition in the Late Pleistocene at 46 ± 4 ka. Based on OSL age estimates for the deposition of the breccia at Nam Lot the modern human tooth was deposited after 50 ± 5 ka and before 46 ± 4 ka. For Tam Pa Ling and Nam Lot the burial ages are in good agreement with ages from past numerical dating, with exception of the radiocarbon age estimates from the upper profile at Tam Pa Ling. The burial ages from the application of single-grain OSL at Tham Lod are not in agreement with past radiocarbon and TL dating.

Table 5.5: Table of OSL burial ages for samples from Tam Pa Ling and Nam Lot with associated dose rate and equivalent dose data

Sample Code	Sample depth (cm)	Grain size (um)	Field gamma dose rate (Gy/ka) ^a	Beta dose rate (Gy/ka) ^b	Cosmic-ray dose rate (Gy/ka) ^c	Water content (%) ^d	Total dose rate (Gy/ka) ^e	Statistical model	Equivalent dose (Gy) ^f	Age (ka)
TPL4	200	180-212	1.108 ± 0.04	1.513 ± 0.07	0.015	30/25 ± 5	2.67 ± 0.16	MAM	86 ± 5	32 ± 3
TPL5	180	180-212	1.008 ± 0.04	1.393 ± 0.06	0.015	31/25 ± 5	2.45 ± 0.13	MAM	54 ± 4	22 ± 2
TPL6	160	180-212	0.844 ± 0.05	1.295 ± 0.06	0.014	47/30 ± 10	2.19 ± 0.22	MAM	29 ± 3	13 ± 2
TPL7	120	180-212	0.436 ± 0.05	1.143 ± 0.06	0.014	38/30 ± 5	1.63 ± 0.10	MAM	20 ± 1	12 ± 1
TPL8	60	180-212	0.852 ± 0.04	1.609 ± 0.07	0.015	28/20 ± 5	2.51 ± 0.14	MAM	6 ± 0.5	2 ± 0.3
NL5	140	180-212	1.862 ± 0.04	1.570 ± 0.07	0.015	10/10 ± 5.0	3.479 ± 0.12	MAM	175 ± 15	50 ± 5

a: Determined from U, Th and K concentrations measured using a portable gamma spectrometer

b: Concentrations determined from beta counter measurements of dried and powdered sediment samples

c: Time averaged cosmic-ray dose rates for dry samples. From Prescott and Hutton (1994), each assigned an uncertainty of ± 10%. d: Field/time averaged water contents. Water content expressed as (mass of water/mass of dry sample) × 100. Water content was used to calculate the total dose rate.

e: Mean ± total (1σ) uncertainty, calculated as the quadratic sum of the random system uncertainties (including photo counting errors, errors associated with variance in the background signal, instrument reproducibility, errors associated with D_e determination derived from Monte Carlo stimulation)

f: Includes an assumed internal alpha dose rate of 0.032 ± 0.01 Gy/ka

Table 5.6: Table of OSL burial ages for samples from Tham Lod with associated dose rate and equivalent dose data

Sample Code	Sample depth (cm)	Grain size (um)	Field gamma dose rate (Gy/ka)	Beta dose rate (Gy/ka)	Cosmic-ray dose rate (Gy/ka)	Water content (%)	Total dose rate (Gy/ka)	Statistical model	Equivalent dose (Gy)	Age (ka)
TTL1	431	180-212	0.321 ± 0.06	1.086 ± 0.05	0.049	20/25 ± 5	2.65 ± 0.16	MAM	31.0 ± 5.0	21 ± 4
TTL2	310	180-212	0.387 ± 0.04	1.188 ± 0.05	0.057	9/16 ± 7	1.665 ± 0.06	MAM	31.0 ± 4.0	19 ± 3
TTL3	290	180-212	0.387 ± 0.04	1.235 ± 0.06	0.058	7/15 ± 8	1.712 ± 0.08	MAM	28.0 ± 3.0	16 ± 2
TTL4	210	180-212	0.346 ± 0.04	1.263 ± 0.043	0.064	3/ 10 ± 7	1.704 ± 0.05	MAM	25.7 ± 21.9	15 ± 1
TTL5	170	180-212	0.343 ± 0.04	1.018 ± 0.04	0.059	6/21 ± 15	1.451 ± 0.35	MAM	19.5 ± 1.2	13 ± 4
TTL6	108	180-212	0.293 ± 0.04	1.017 ± 0.05	0.064	0.5 /15± 14.5	1.406 ± 0.22	MAM	13.7 ± 1.1	10 ± 2
TTL7	39	180-212	0.468 ± 0.04	1.131 ± 0.06	0.049	81/50 ± 30	1.680 ± 0.40	MAM	4.7 ± 0.4	3 ± 1

a: Determined from U, Th and K concentrations measured using a portable gamma spectrometer

b: Concentrations determined from beta counter measurements of dried and powdered sediment samples

c: Time averaged cosmic-ray dose rates for dry samples. From Prescott and Hutton (1994), each assigned an uncertainty of ± 10%. d: Field/time averaged water contents. Water content expressed as (mass of water/mass of dry sample) x 100. Water content was used to calculate the total dose rate.

e: Mean ± total (1σ) uncertainty, calculated as the quadratic sum of the random system uncertainties(including photo counting errors, errors associated with variance in the background signal, instrument reproducibility, errors associated with D_e determination derived from Monte Carlo stimulation)

f: Includes an assumed internal alpha dose rate of 0.032 ± 0.01 Gy/ka

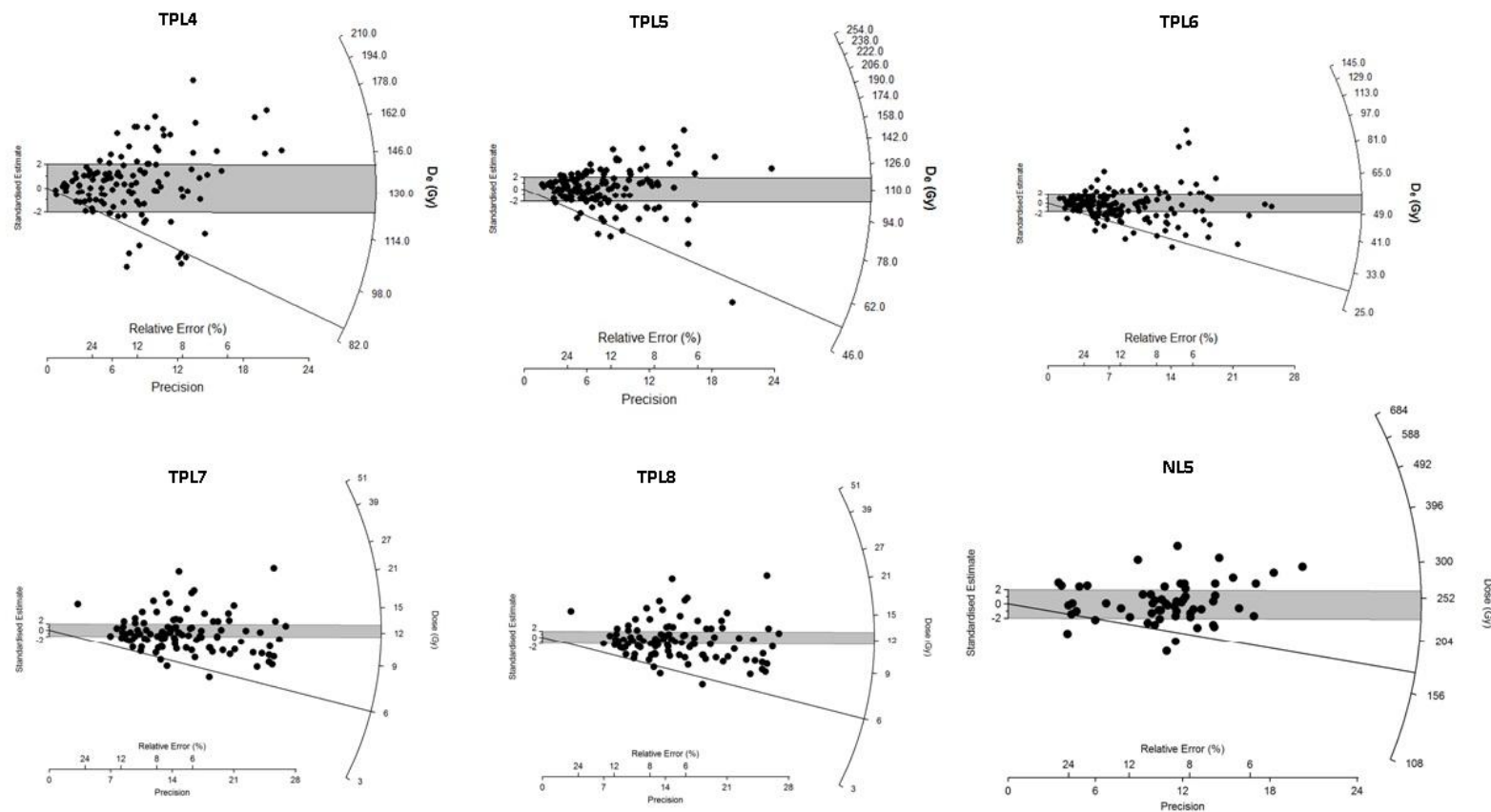


Figure 5.14: Equivalent dose values displayed in radial plots for samples from Tam Pa Ling and Nam Lot. Each dot is representative of an equivalent dose value (Gy) for an individual grain. The measured equivalent dose for each grain can be interpreted by extrapolating a line from the y-axis origin, though the data point until it intersects the radial axis on the right hand side (Olley et al., 2004). Equivalent doses with highest precision and smallest relative error lie closest to the radial axis. The least precise estimates of equivalent dose lie closer to the left (Galbraith et al., 1999). The left hand side y-axis shows the central age and 2 σ error with the shaded bar showing the equivalent dose values that yield ages consistent with the 2 σ error confidence interval. The straight line from the centre of the y-axis to the radial y-axis represents the equivalent dose calculated through the MAM.

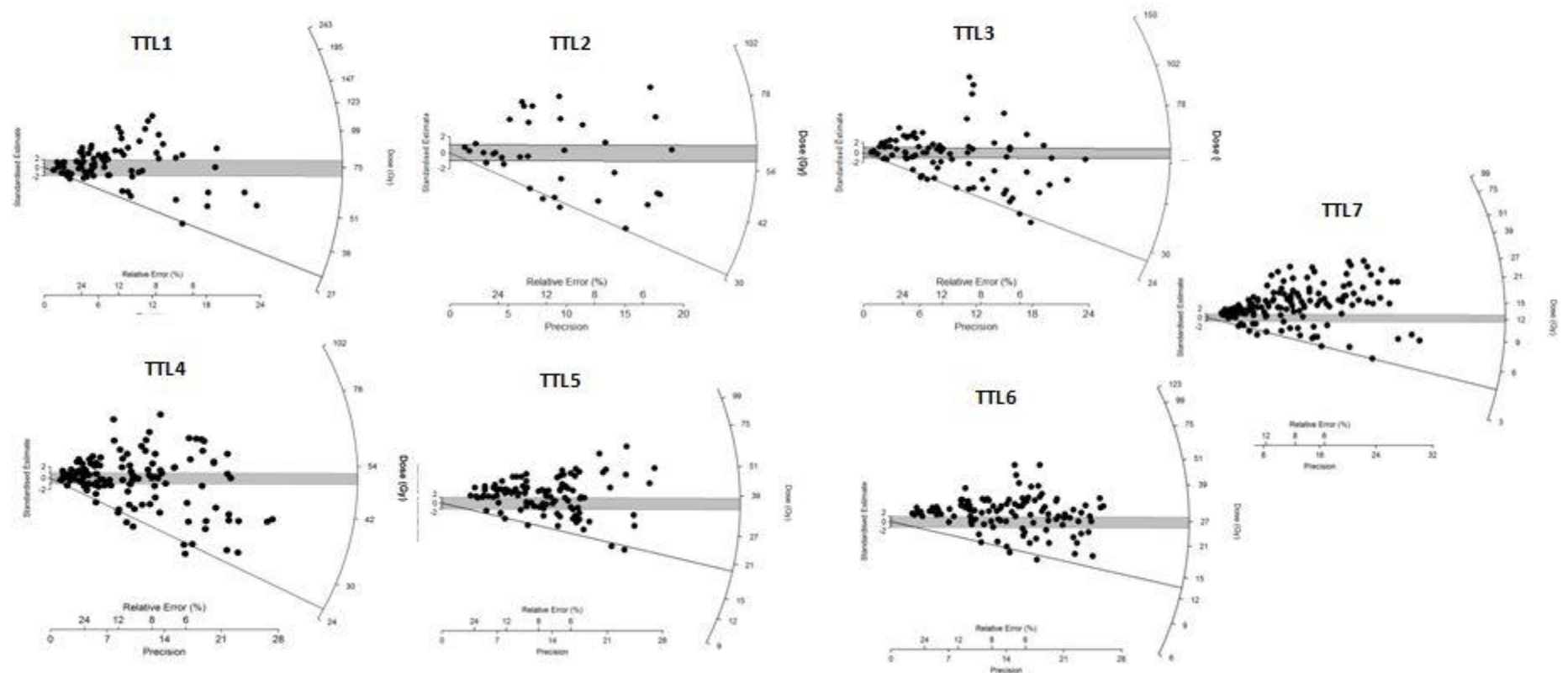


Figure 5.15: Equivalent dose values displayed in radial plots for samples from Tham Lod. Each dot is representative of an equivalent dose value (Gy) for an individual grain. The measured equivalent dose for each grain can be interpreted by extrapolating a line from the y-axis origin, though the data point until it intersects the radial axis on the right hand side (Olley et al., 2004). Equivalent doses with highest precision and smallest relative error lie closest to the radial axis. The least precise estimates of equivalent dose lie closer to the left (Galbraith et al., 1999). The left hand side y-axis shows the central age and 2 σ error with the shaded bar showing the equivalent dose values that yield ages consistent with the 2 σ error confidence interval. The straight line from the centre of the y-axis to the radial y-axis represents the equivalent dose calculated through the MAM.

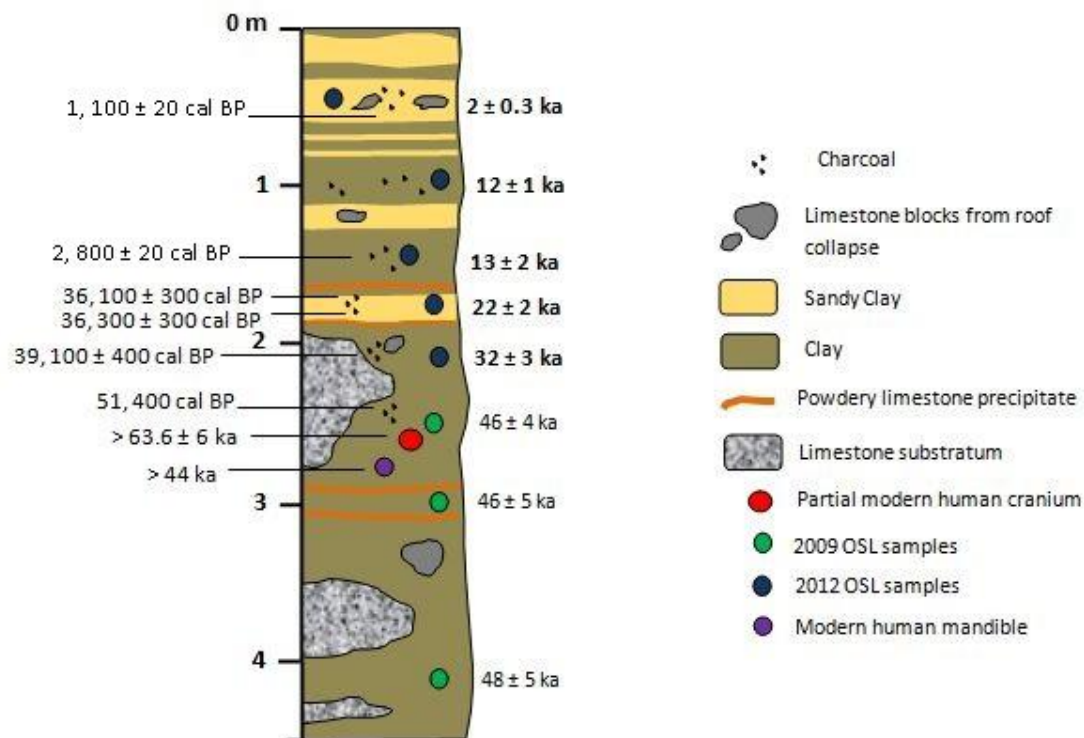


Figure 5.16: Stratigraphic sequence for Tam Pa Ling depicting single-grain OSL ages from 2009 and 2012 with radiocarbon and U-Th age estimates

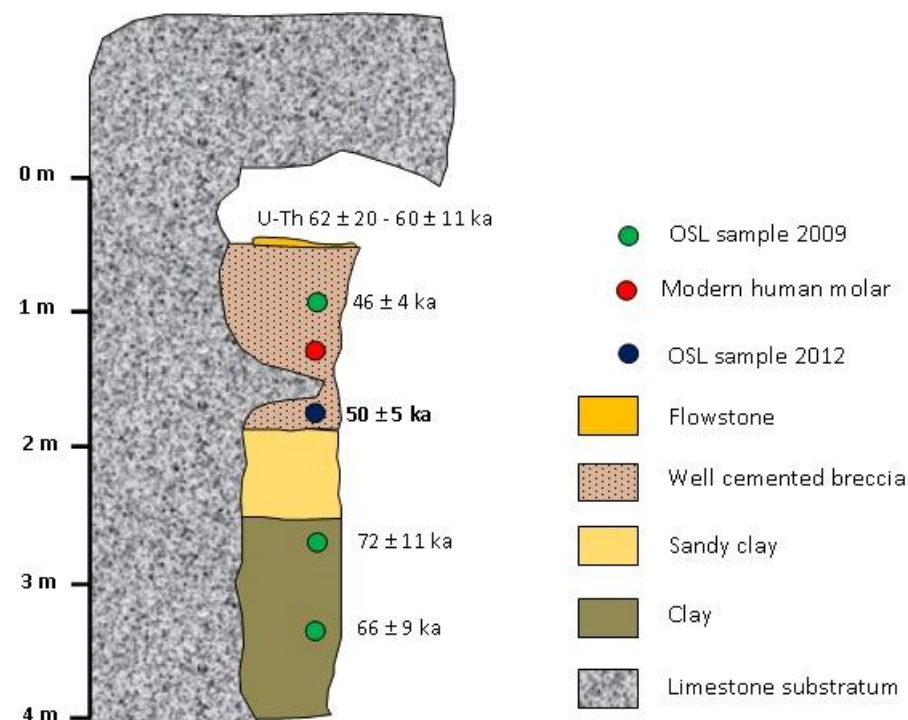


Figure 5.17: Stratigraphic sequence for Nam Lot depicting the new single-grain OSL age for sample NL5 in relation previous single-grain OSL ages and the U-Th age for the capping flowstone. There is a chronological inversion between single-grain OSL results and the U-Th results from dating of the capping flowstone. This inversion, however, is within error limits and the results still reflect an increase in age with depth.

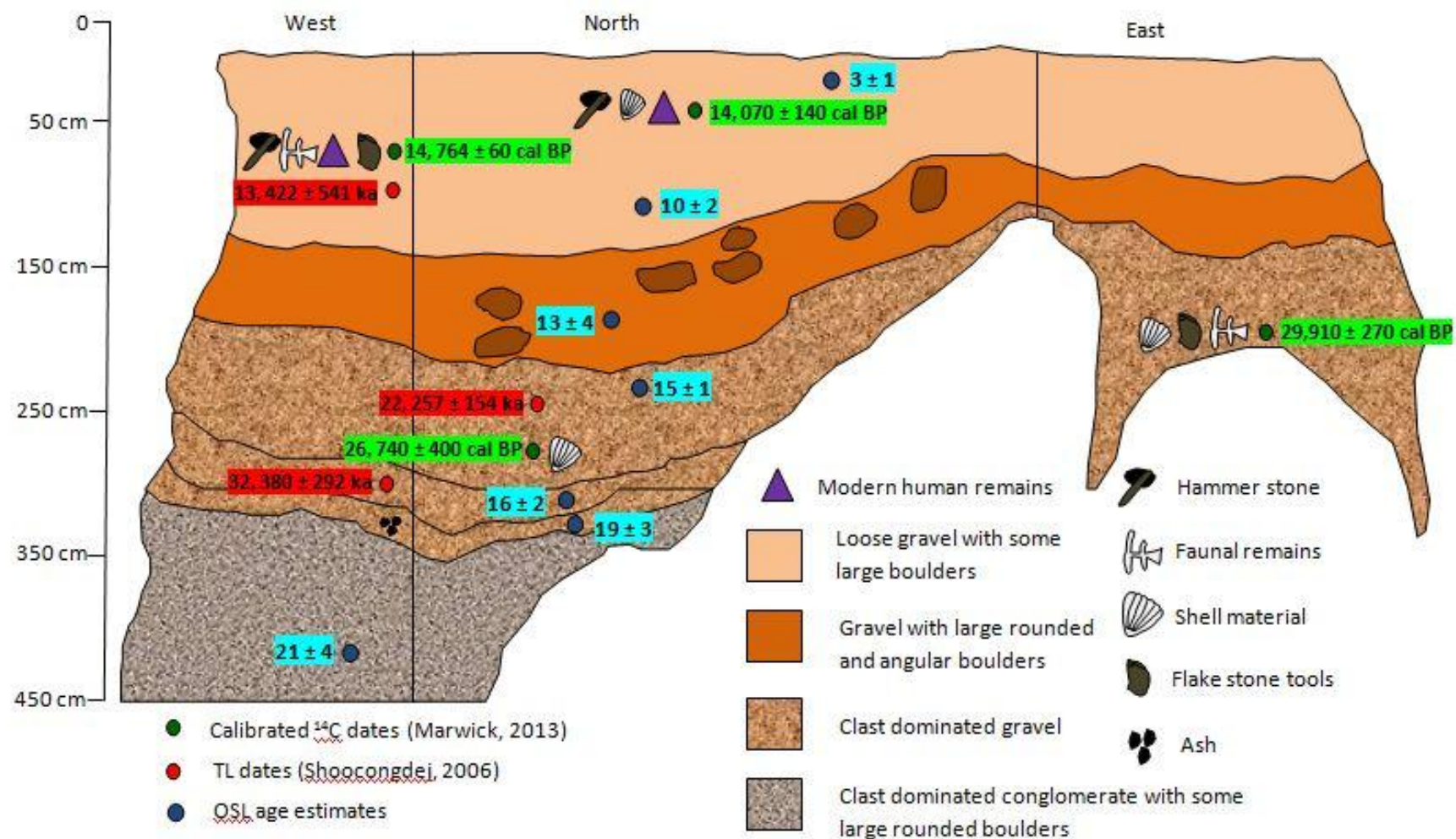


Figure 5.18: Stratigraphic sequence for Tham Lod depicting single-grain OSL age estimates and previous radiocarbon and TL ages estimates

Chapter 6: Discussion

6.1 Introduction

Providing independent age estimates for sites with existing preliminary chronologies has proved an effective approach to establish robust chronologies that further define the timing of modern human presence in mainland Southeast Asia. The established chronologies for Tam Pa Ling and Nam Lot reveal a modern human arrival earlier than Marine Isotope Stage 3 (MIS3) while the chronology at Tham Lod indicates occupation during MIS 2, around the timing of the LGM. However, radiocarbon estimates from Marwick (2013) indicate that occupation at Tham Lod extends back to 39,960 cal BP. Based on the results presented, the aim of this chapter is to demonstrate the robust nature of the new chronologies for each site and discuss the implications to models of modern human dispersal in mainland Southeast Asia.

SECTION I: Secrets of sedimentology: reconstruction of site history from stratigraphic analysis

As chronologies provide timing for depositional events, an understanding of sediment deposition at sites is crucial to provided contextual information for interpretation of results from numerical dating techniques. Based on the results from geomorphic and sedimentological analysis this section will discuss the stratigraphic sequence of each site, focusing on links between sediment deposition and paleoanthropological and archaeological evidence.

The limestone caves of Tam Pa Ling and Nam Lot in northern Laos do not contain any in-situ occupational evidence within their stratigraphic sections. As such the means of deposition of paleoanthropological material within each cave is determined by the caves morphology and dominate depositional processes. At Tam Pa Ling geomorphic analysis reveals that the only source for sediment input in the cave is the elevated south facing entrance (Figure 5.2) as there is an absence of any connecting sinkholes within the cave. As such it is inferred that the clay dominated sedimentology and deposition of fossil material (Figure 5.3) at the base of the sloped entrance into the cave is attributed to slope-wash processes transporting sediments and fossils from the landscape outside the cave to the cave floor. As such Tam Pa Ling is classified as a 'wash-in' cave, which has implications for the interpretation of the chronology.

Unlike Tam Pa Ling the current cave entrance to Nam Lot is at a lower elevation than the sedimentary deposits (Figure 5.5), eliminating it as a source area for sediment input. Geomorphic analysis at Nam Lot revealed the only other source for sediment is the presence of sinkholes throughout the cave (Figure 5.7). As such Nam Lot is classified as a sink cave (Westaway et al., 2009), with sinkholes in the cave acting as passageways for the transport of sediments and fossil material channeled from the land surface. Subsequently the presence of the modern human tooth within the breccia deposit indicates that the angular breccia material and tooth were once present on the landscape and were transported into the cave via a sinkhole, assumed to be the sink hole located above the breccia sedimentary deposit (Figure 5.7). Interpretation of the stratigraphic sections at Nam Lot also suggests that sinkholes must have acted as solution channels as the sedimentology of Nam Lot indicates an alluvial influence for the sediment deposition of the clays and conglomerate deposits (Figure 5.6), varying from pooled water to high powered flow, respectively. The capping flowstones are suggestive of dry periods within the cave.

In contrast to the wash-in and sink caves of Tam Pa Ling and Nam Lot the stratigraphic section of Tham Lod rock shelter contains archaeological material that is in-situ in the form of a 'living floor' and as such is inferred to be occupational. Interpretation of the stratigraphy has revealed a change in the mode of deposition from fluvial to mass movement. The basal conglomerate layer containing well rounded boulders is indicative of fluvial deposition and this is supported by Khaokiew (2004) who suggests the cobbles were deposited by an ancient river bed. The sedimentary deposits above this layer contain archaeological material and generally consist of poorly sorted angular clast dominated gravels (Figure 5.10), indicative of sediment deposited by mass movement (Owen, 1991, Spedding and Evans, 2002). The presence of archaeological material above the basal conglomerate layer suggest that first occupation of Tham Lod was associated with a change in hydrology and the lateral movement of an ancient stream away from the rock shelter.

It has been agreed upon within the literature that the large rounded boulders within the upper section of the stratigraphy at Tham Lod are likely to have been placed there by modern humans due to the absence of a high energy fluvial system required for their deposition (Shoocongdej, 2006, Marwick, 2013, Pureepatpong, 2006). Mass movement could be an alternate explanation for their presence, but due to the placement of the

boulders discovered in a circular pattern (Pureepatpong, 2006) it is more likely that modern humans placed these boulders in such a manner as to reflect a ceremonial burial and hence modernity.

Analysis of the sedimentary units has enabled a reconstruction of past processes operating at each site. The slope-wash nature of sediment deposition at Tam Pa Ling, deposition via sink holes for Nam Lot and a mix of fluvial and mass movement processes for Tham Lod suggests a potential for partial bleaching of grains associated with sediment deposition processes at each site. Therefore to provide a conservative age estimate single-grain analysis and use of the MAM was implemented to address partial bleaching. Additionally sedimentological analysis at Tam Pa Ling and Nam Lot has revealed an allogenic source of paleoanthropological evidence from the surrounding landscape and for Tham Lod sedimentological analysis has identified the influence of lateral stream movement on the occupation of the site. Furthermore an understanding of the history of sediment deposition will provide context and data for the interpretation of the results from numerical dating techniques at each site.

SECTION II: Establishing the validity of chronologies

The chronologies presented in the results must be classified as robust in order for their significance and resulting implications to be firmly and unquestionably established. Criteria for robust chronologies was outlined in chapter 1 and will be used in this section to discuss the validity of each chronology. As the establishment of robust chronologies is dependent on the application of more than one dating technique, outlined in chapter 2, the robusticity of each chronology will differ due to the availability of material at each site.

The application of OSL dating to the upper stratigraphy at Tam Pa Ling has established a chronology of sediment deposition from the Late Pleistocene at 32 ± 3 ka to the late Holocene at 2.4 ± 0.3 ka (Figure 5.16), which agrees with previous Late Pleistocene OSL age estimates from the lower stratigraphy in Demeter et al. (2012). OSL ages for the upper stratigraphy demonstrate a range of precisions (Table 5.5). Reproducibility is demonstrated as a similar equivalent dose for each disc was produced, from replication of the same procedure for each sample, on over 8 discs containing 100 grains as part of the single-grain analysis approach. The OSL ages are also stratigraphically correct with

age increasing with depth and consistent with slope-wash deposition of sediment over time. As such the age of the sediment in direct association with paleoanthropological evidence will reflect the time of burial.

Stratigraphic consistency of OSL ages within the upper profile has confirmed sediment accumulation was continuous at the site. This stratigraphic consistency was challenged due to the presence of a supposed sedimentary hiatus of 44 ka (Demeter et al. 2012) which was argued to reduce the confidence in the entire chronology. This hiatus has been reduced to 10 ka between samples TPL4 and TPL5 and 9ka between samples TPL5 and TPL6. Associated with these hiatuses is a layer of powdery calcite precipitate (sometimes referred to as 'moonmilk') (Figure 5.16), which is suggested to be indicative of drier conditions and as such a cessation of sediment deposition by slope-wash processes into the cave. A hiatus of 10 ka is also evident between samples TPL7 and TPL8 within the vicinity of limestone blocks that have been interpreted as representing a temporary blockage of the cave entrance, limiting sedimentary inputs. Even though the chronological hiatus has been reduced and the results have been identified to be precise, reproducible and stratigraphically consistent, comparison of OSL ages to independent dating techniques is required to confirm accuracy and the robusticity of the Tam Pa Ling chronology.

Originally radiocarbon dating of charcoal was attempted by Demeter et al. (2012) and Demeter et al. (Under review) with the aim of producing an in-situ chronology for sediment deposition. Throughout the stratigraphy, results from radiocarbon dating were generally older than the OSL age estimates for sediment deposition (Figure 5.16). This combined with an absence of in-situ burning features to explain charcoal presence, such as hearths, suggested that the organic matter was not derived from occupation. From interpretation of the cave morphology (Figure 5.2) and slope-wash depositional processes identified in section I, it is assumed that charcoal within the stratigraphic section was most likely washed into the cave from elsewhere on the landscape. Subsequently it is expected that radiocarbon results would be older than the timing of deposition of the sedimentary layers. The younger radiocarbon age estimates towards the top of the profile are suggested to be from mixing of the upper profile. As OSL establishes the time since minerals were last exposed to sunlight, the OSL ages are identified as the most accurate representation of the timing of sediment deposition and thus the most appropriate age estimate for the associated fossil material.

Demeter et al. (Under review) attempted to establish independent U-Th age estimates for the deposition of powdery calcite precipitate layers within the stratigraphy (Figure 5.16). However, the results were unsuccessful as the material was precipitated and suitable calcite for dating could not be obtained. Consequently overlying and underlying calcite layers providing maximum and minimum ages for sediment deposition were unavailable for comparison with OSL ages. The only other independent age estimates available for comparison are based on U-Th ages for paleoanthropological material including a minimum age of 63 ka for the partial modern human cranium (Demeter et al. 2012) and a minimum age of 44 ka for the modern human mandible (Demeter et al., Under review).

These U-Th dating results have been presented as minimum ages for bone formation due to the possibility that the bone represents an open system with uranium migrating into the bone after deposition. The porous nature of the bone fragment used for U-Th dating of the mandible prevented the application of microdrilling for U-Th profiling. As such, the analysis was conducted on small handpicked fragments that contained inseparable post-fossil secondary calcite overgrowths. Subsequently the individual fragment ages represent minimum ages for the fossil itself and as such time of death should be much earlier than 44 ka (Demeter et al., Under review). Due to the inability to conduct U-Th profiling on both of these samples, there is limited confidence in the U-Th age estimates. However, minimum ages of 44 ka and 63 ka, are still in agreement with OSL burial ages, within errors. It is probable that the partial modern human cranium was present on the landscape for a few thousand years prior to deposition in Tam Pa Ling.

The partial agreement between independent U-Th age estimates combined with the precision, and reproducibility of the OSL results indicates an accurate OSL chronology and based on the discussion of robusticity above, namely stratigraphic consistency and integrity, the chronology at Tam Pa Ling is considered robust. Therefore it can be said with confidence that modern human presence at Tam Pa Ling in northern Laos occurred in the Late Pleistocene prior to 46 ka, confirming previous statements in Demeter et al (2012) for Tam Pa Ling containing the earliest modern human evidence in mainland Southeast Asia.

A Late Pleistocene modern human presence within northern Laos is also indicated by the chronology at Nam Lot. The age estimates constraining deposition of the modern human tooth to after 50 ± 5 ka and before 46 ± 4 ka are associated with low error margins, and agree with other OSL and red TL age estimates and the independent U-Th age estimate of capping flowstones dated by Bacon et al. (2015), within error margins (Figure 5.17). As such the OSL ages are accurate and the chronology is stratigraphically consistent. When taking into account error margins there are no large hiatuses in sediment deposition, demonstrating stratigraphic consistency for the chronology. The reproducibility of sample NL5 could be improved by increasing the grains contributing to the equivalent dose estimate to 100, however, this was prevented due to a low quartz yield for this sample. The identified reworking of the modern human tooth in Nam Lot however, suggests that the OSL chronology should represent a minimum age for the fossil with the potential for the tooth to be older and the need for it be directly dated to resolve its true age. Based on the discussion above the chronology at Nam Lot meets the criteria for a robust chronology and compares favourably with the chronology from Tam Pa Ling. Therefore these two sites provide a confident timing for modern human presence before 46 ka within the region of northern Laos.

The site of Tham Lod is known to have evidence of occupation from 39,960 cal BP (Marwick, 2013) but for this research the stratigraphic section with maximum occupation age of $32,380 \pm 292$ ka based on samples in Shoocongdej (2006) was targeted to produce a more robust chronology. The application of OSL dating to this section at Tham Lod confirms that a Late Pleistocene occupation occurred in this rock shelter, however, there is a great disparity between recent OSL ages and previous radiocarbon and thermoluminescence results (Figure 5.18), which casts doubt on the validity of the sites original chronology.

OSL results indicate that first occupation occurred after deposition of the ancient stream bed around 21 ± 4 ka and prior to 16 ± 2 ka, potentially around 19 ± 3 ka. Even though the sample TTL2 provides an age for the first occupation layer within the stratigraphy, it is less reliable compared to other OSL ages as a low quartz yield led to the acceptance of less than 80 grains for equivalent dose estimates during single-grain analysis. OSL ages are consistently younger than all radiocarbon and TL ages throughout the stratigraphic section. The younger OSL ages within the upper stratigraphy challenge the timing of a transition to a burial site in the Late Pleistocene just prior to $14,764 \pm 60$ cal BP at Tham

Lod, proposed by Shoocongdej (2006). OSL samples TTL6 and TTL7 confine the sediment deposit containing the skeletal material and indicate burial of material between 10 ± 2 and 3 ± 1 , which is Holocene in age. The lack of agreement between previous radiocarbon and TL and recent OSL results within the entire stratigraphy is attributed to issues associated with TL and radiocarbon dating.

The three TL ages at Tham Lod are not in agreement with the OSL ages from the same stratigraphic layers and it is hypothesised that the limitations of the TL dating technique for sediment dating are affecting the accuracy of the TL ages. As explained in chapter 2, partial bleaching is an issue affecting the accuracy of results in luminescence dating and the main benefits of single-grain OSL analysis is the ability to rapidly bleach without leaving a residual signal and provide more accurate and precise results through the selective removal of individual grains. In comparison TL analysis involves the measurement of luminescence signals from single aliquots and the contribution of partially bleached or undesirable grains to the equivalent dose determination cannot be isolated or removed (Feathers, 2003). This is further emphasised when comparing burial age estimates from single-grain analysis (Table 5.6) to single-aliquot analysis (Table 5.2), with the latter showing much earlier depositional ages. Also an exposure time of minutes to hours is required to remove any residual signal prior to burial for TL dating (Godfrey-Smith et al., 1988, Feathers, 2003); compared to OSL dating which requires exposure to sunlight for only a few seconds to minutes for resetting (Roberts, 1997, Roberts et al., 1998). Therefore optical rather than TL techniques provide more accurate results for burial age estimates of grains that were reset by sunlight.

The application of TL and OSL techniques at Jinmium rock shelter in Northern Australia (Roberts et al., 1999) is a good example of this disparity. Samples from the site used for the TL estimates of age suffered from partial bleaching (from unbleached grains in the roof spall) and produced a significant age overestimations in the Late Pleistocene. The application of single-grain OSL was able to detect and remove insufficiently bleached grains from age calculation and in turn produced a more accurate younger Holocene timing for the 'true' burial age and modern human occupation (Roberts et al., 1999, Galbraith et al., 1999, Roberts et al., 1998). Evidently it is hypothesised that insufficient bleaching is likely to be the case at Tham Lod, as sediment deposition is attributed to fluvial and mass movement processes. Therefore burial ages proposed from the

application of TL at Tham Lod should be viewed as maximum age estimates and OSL ages should be considered as a more parsimonious estimation of the 'true' burial age.

Like the TL age estimates, radiocarbon ages at Tham Lod are earlier than associated OSL ages within the sampled stratigraphic layers. Unlike TL, radiocarbon and OSL techniques are dating different events, however, as Tham Lod is an occupational site it is assumed that the radiocarbon estimates performed on organic sediment, charred material and shell would be in-situ materials and present results similar to the timing of sediment deposition from OSL dating. However, it has been inferred that radiocarbon sampling techniques and contamination at the site has potentially led to overestimated radiocarbon ages.

The radiocarbon estimates within the upper profile were performed on organic sediment, of which sampling involves the bulk collection of organic material. Bulk sampling leads to isotopic heterogeneity of carbon material being masked. Subsequently the proportion of non in-situ reworked older carbon within the sample is unknown (Eglinton et al., 1996) and cannot be selectively removed; resulting in a potential age overestimation. As the radiocarbon ages within the top layer of the stratigraphy at Tham Lod were estimated from organic sediment it is inferred that the sample contained a contribution from older carbon leading to a potential age overestimation.

Other than bulk sampling, contamination is another possibility that accounts for overestimated radiocarbon ages, as explained in chapter 2. As limestone is of geological origin it has an age greatly in excess of archaeological material. When calcium carbonate is dissolved by water it can introduce additional carbon to the soil and be absorbed by organic material, making the material appear older than its true age (Boudin et al., 2013, Wang et al., 1996). Marwick (2013) identifies that in the past it is highly likely that water has flowed through the sedimentary deposits beneath the rock shelter at Tham Lod leading to a poor organic preservation. It is likely that this water also contributed old carbon from the overlying limestone to organic material within the stratigraphic section. Therefore there is a possibility that material used for radiocarbon dating at Tham Lod could be contaminated by older carbon, creating an age overestimation and leading to discrepancies between OSL and radiocarbon ages. It also needs to be noted that the radiocarbon age estimate of $26,740 \pm 400$ cal BP for shell material could

potentially be overestimated if the shell material used for dating was present on the landscape for a period of time prior to being brought to the site.

Based on comparison of OSL ages to independent age estimates from TL and radiocarbon it could be said that there is poor agreement. However, based on the discussion of the known limitations of TL and radiocarbon dating techniques it is evident that the OSL ages represent the most parsimonious result and potentially the 'true' burial age. The OSL ages are stratigraphically consistent, increasing with depth and there are no large hiatuses in sediment deposition, indicating the OSL chronology has stratigraphic consistency. The ages are also associated with low error margins demonstrating precise estimates of burial age and besides sample TTL2, all ages are reproducible as replication of the same procedure on at least 4 discs each with 100 grains as part of the single-grain analysis approach produced similar results for equivalent dose estimates. In addition, by dating the burial sediments there is a direct association between the material being dated and the archaeological evidence, with no questions over the in-situ nature of the datable material. As such the new OSL chronology for Tham Lod confining the Late Pleistocene to late Holocene periods of occupation is robust.

SECTION III: Implications of robust chronologies to understanding modern human dispersal

1. Timing of modern human arrival in Southeast Asia

The robust chronologies for Tam Pa Ling and Nam Lot indicate the earliest modern human evidence for mainland Southeast Asia and as such imply that modern human arrival into the region occurred earlier than 46 ka. Before this evidence from northern Laos the earliest evidence for modern human presence on the mainland was from Lang Rongrien in Thailand with archaeological evidence dated to > 43, 000 BP (Anderson, 1997, Mudar and Anderson, 2007). Early modern human presence is also evident in island Southeast Asia with arrival suggested to have occurred by at least 50 ka to be able to explain archaeological evidence in the highlands of New Guinea dated to 49 ka (Summerhayes et al., 2010), the presence of a tibia in the Philippines dated to 48 ka (Oppenheimer, 2009, Mijares et al., 2010, Detroit et al., 2004) and a modern human skull from Niah cave in Borneo dated to 45-39 ka (Barker et al., 2007). With arrival occurring

in Southeast Asia earlier than 46 ka and potentially earlier than 50 ka it indicates that an earlier than 60 ka exit out of Africa is plausible, but requires more convincing evidence.

Evidence for an earlier exit has been argued by Dennell and Petraglia (2012) and has been suggested by genetic evidence defining a modern human presence in Southeast Asia at 79-75 ka (Oppenheimer, 2002). However, a lack of well dated paleoanthropological remains from the region of East Asia > 60 ka means that a 60 ka exit and rapid dispersal is still plausible to explain a modern human arrival before 46 ka on the mainland and 50 ka in island Southeast Asia. The confirmed early evidence from Tam Pa Ling and Nam Lot, along with current evidence from island Southeast Asia and new evidence from Sumatra dating modern human presence to between 83-71 ka (Westaway et al., under review) is becoming a collective of evidence weakening a 60 ka exit and supporting alternate models that advocate for an earlier exit out of Africa. Evidence from Arabia also supports an earlier exit from Africa (Petraglia, 2007, Armitage et al., 2011, Delagnes et al., 2008, Macchiarelli, 2008, McDermott et al., 1993). However, before this evidence is identified as indicative of the first migration of modern humans out of Africa, more research is needed to prove that modern humans were the species responsible for cultural deposits in Arabia.

2. Implications for dispersal routes from Africa to Southeast Asia

Even though there is increasing evidence to support the possibility of an earlier exit from Africa, an exit location is yet to be confidently identified. As outlined in chapter 2 current evidence supports two possible exit locations out of Africa. The first at the north end of the Red Sea, crossing over to the Levent, based on evidence from the Qafzeh caves (Stringer et al., 1989, Stringer, 1988, Valladas et al., 1988). An alternate location is at the southern end of the Red Sea at the Bab al Mandab, supported by evidence from Wadi Surdud in Yemen (Delagnes et al., 2008). Paralleling discourse concerning the exit location out of Africa are debates surrounding the routes travelled by modern humans from Africa to reach Southeast Asia and Australia.

Marwick (2009) evaluates three possible models for hominid movements into Southeast Asia, however, only 2 are based on modern human evidence. The first possibility is the commonly accepted coastal route of dispersal based on genetic and geographical analysis (Macaulay et al., 2005), involving eastward migrations along the coast of the

Indian ocean and then the coast of South Asia and Myanmar. The chronologies for modern human arrival into mainland Southeast Asia > 46 ka in no way challenges the route of migration along the coastline as it is still feasible that modern humans exited Africa earlier and migrated eastward along the coastline to reach mainland Southeast Asia by > 40 ka and potentially earlier. However, as identified in chapter 2, and further demonstrated by Marwick (2009) defining this route is problematic as post LGM sea level rise has led to submergence of the majority of the route and any associated evidence of modern human presence.

The second migration possibility is based on the work of Demeter et al. (2003) and Shackelford and Demeter (2012) involving the identification of two populations within mainland southeast Asia, based on the analysis of modern human crania from the Asia region. They propose that a northern population from China migrated southwards along the east coast of Southeast Asia and encountered a second group of modern humans from mainland Southeast Asia, including the Tam Pa Ling modern humans. Marwick (2009) identifies that these conclusions should be received with caution as the sample used for analysis is small and the geographic distribution of sites could reflect the focus of research interest rather than actual modern human migration patterns. As such more research is needed to make confident conclusions about the paths travelled by modern humans to reach Southeast Asia.

3. Establishing a Late Pleistocene cultural connection between Sunda and Sahul

Robust chronologies for occupational evidence at certain sites assist in understanding pathways for modern human dispersal; as they enable correlations between similar archaeology and patterns of occupation at similar times, suggesting a cross fertilisation of ideas and technologies. Dispersal into Sahul is the final stage of migration for the great arc of modern human dispersal during the Late Pleistocene and it is generally accepted that modern humans travelled from Sunda, due to its close geographical proximity to northern Sahul. Occupational evidence at Tham Lod indicates that modern humans were migrating through inland river regions in Sunda since around 39,960 cal BP (Marwick, 2008, Marwick, 2013). Similar occupation of inland river regions during similar timing in the Late Pleistocene at sites in Sunda and Sahul suggests that occupation by modern humans occurred concurrently. A comparison of these sites will contribute to the debate concerning whether modern humans in tropical Sunda were

well equipped with subsistence strategies to enable them to successfully disperse to and colonise the tropical environments of Sahul. Put more simply – is there enough agreement between the archaeologies of both regions to suggest that modern humans in mainland Southeast Asia were the ancestors of the first Indigenous Australians?

There is a general consensus within the literature that a coastal route was exploited to facilitate eastward migration of modern humans from Africa to Australia (Macaulay et al., 2005, Blinkhorn and Petraglia, 2014, Stringer, 2000, Field and Lahr, 2006). Furthermore there is a consensus that migration from Sunda to Sahul involved a series of water crossings and island hopping across the Wallacean Archipelago to reach western New Guinea (Summerhayes and Ford, 2014, Lilley, 1994). Coastal occupational evidence in Sunda, however, is absent making any similarities and direct connections between modern humans and their coastal occupation behaviours in Sahul and Sunda difficult to prove. This absence of evidence, however, does not indicate that Late Pleistocene modern humans in Sunda were not utilising coastal resources; rather the lack of coastal cultural sites is attributed to their location on the exposed Sunda continental shelf that was subsequently submerged during post LGM sea level rise. As such it can be assumed that modern humans were most likely occupying coastal sites of Late Pleistocene Sunda. The cultural evidence from coastal occupational sites throughout Sahul further suggests that modern human populations in Sunda were equipped with necessary skills to survive in and colonise the coastal areas of Sahul.

For example, It has been identified that the Bismark Archipelago and near by sites of Yombom, Matenkupkum and Buang Merabak were colonised soon after the mainland in northern Sahul and cultural assemblages are indicative of a migration facilitated by the exploitation of marine resources (Lourandos, 1993, Lilley, 1994). The sites of Matenkupkum and Buang Merabak, which were never located more than a few hundred metres from the coast, contain shell fish and fish species in their assemblages demonstrating exploitation of marine resources of the reef zone and inshore areas from 41 100- 38, 950 cal BP and 44, 890 – 43, 100 cal BP respectively (Summerhayes and Ford, 2014).

Other sites of marine exploitation from Sahul are from Australia at Brremangurey rock shelter (Morwood et al., 2012), Mandu Mandu Creek rock shelter in northwest Cape (Morse, 1988) and Koolan rockshelter 2 within the Buccaneer Archipelago on the

northwest Kimberley coast (O'Connor, 1989). All of these sites contain evidence of Late Pleistocene exploitation of marine species from 36 ka, 25, 000 BP and 27, 500 BP respectively. Exploitation of the Kimberley coastline is also evident in occupational evidence at sites within the southern Kimberley from Riwi dated to > 40, 000 BP and Carpenters Gap I dated to 33, 992 -32, 970 cal BP (O'Connor, 1995). The presence of marine species at these sites, located hundreds of kilometers inland from the Late Pleistocene coastline, suggest that modern human groups were inhabiting coastal areas of Western Australia during the Late Pleistocene and trading with inland groups through social networks. Other than coastal environment interactions, Sunda and Sahul have occupational evidence that indicates modern humans in both regions were versatile hunter-gatherers able to move beyond the coastal fringes into lowland forest by following the path of least resistance along inland rivers.

The first similarity between inland Late Pleistocene occupational sites in Sunda and Sahul is interaction with inland rivers and streams for subsistence. The cultural assemblage at Tham Lod contains a range of forest fauna but is dominated by freshwater mussels. Shoocongdej (2000) suggests this is indicative of intermittent occupation dependent on the close proximity of freshwater sources during dry phases, as this is when freshwater mussels experience maximum growth. Close proximity to a freshwater source is said to also have influenced the occupation of the Lang Rongrien rock shelter in Thailand. Lang Rongrien's cultural assemblage, dating back to > 43, 000 BP, indicates exploitation of freshwater species. Close to half of the faunal assemblage is dominated by freshwater turtles (Mudar and Anderson, 2007); which is said to be sourced from the Huai Lum Phu Thong Stream close by (Shoocongdej, 2000). Similarly the high diversity of freshwater species consisting of shellfish and species of freshwater fish within the 40, 000 BP occupational cultural assemblage at Niah cave indicates reliance on close by streams and swamps for food resources (Mudar and Anderson, 2007).

Interaction between modern human and inland rivers and streams for sustenance is also a feature of modern human occupation in Sahul. The Late Pleistocene occupation sites of Carpenters Gap 1 and Carpenters Gap 3 in the southern Kimberley in Western Australia contain freshwater fish and mussels respectively which, like sites in Sunda, is most likely attributed to the proximity of the freshwater source of the Lennard River (O'Connor et al., 2014, O'Connor, 1995). Shellfish and fish are also evident in cultural assemblages at Willandra Lakes (Allen and O'Connell, 2003) indicating a dependence on freshwater

resources for the colonisation of the southern half of the Australian mainland during the Late Pleistocene.

A second similarity between inland Late Pleistocene occupational sites in Sunda and Sahul is interactions between modern humans and their environment to construct stone tools. In both regions artifact assemblages are made up almost entirely of flaked stone tools sourced from rivers and streams. The source of material for flaked stone tools at Tham Lod and Lang Rongrien in Thailand is attributed to freshwater sources transporting materials downstream (Shoocongdej, 2000, Marwick, 2013). Further south in Sahul the site of Collapsed Shelter in the Kimberley, with occupational evidence from 36 ka, contains flaked stone artifacts of which the cobbles of the Mitchell River are identified as a potential source (Ross et al., 2010). Also the sites of Carpenters Gap 3 and Upper Swan with occupational evidence from 33,847 – 32,970 cal BP and 38,000 BP respectively, both contain artifacts inferred to be sourced from river gravels and manufactured on site (O'Connor et al., 2014, Pearce and Barbetti, 1981).

This discussion has demonstrated evidence for inland exploitation capabilities exercised by modern humans upon immediate arrival in Sahul. Similarities in the timing and archaeology of inland occupational sites in Sunda to Sahul indicate that modern humans in both regions were interacting with their environments at similar times and in similar ways. Based on these similarities it is inferred that modern humans in Sunda were well equipped with hunter-gatherer skills to facilitate the colonisation of and dispersal through Sahul. As such this evidence could support a Sunda origin for the first ancestors of Sahul with a cross-fertilisation of occupation patterns and technologies.

4. Recommendations for future research

This research has demonstrated that by improving the robusticity of existing chronologies the significance of evidence for models of modern human dispersal is confirmed. Many sites within Southeast Asia are preliminarily dated, usually involving the application of a single numerical dating technique, and would benefit from a similar dating approach involving comparison to independent age estimates, as applied in this research. The sites of Tabon cave, Niah cave and Lang Rongrien rock shelter contain some of the earliest modern human evidence but require comparison to independent age estimates to confirm their robusticity and significance to be included in models of

modern human dispersal. It is suggested that these sites would benefit from a single-grain OSL dating approach.

At Tabon cave OSL dating combined with U-Th dating of in-situ speleothems would help identify whether results from recent U-Th dating of bone are accurate. Similarly OSL dating at Lang Rongrien rock shelter would identify whether radiocarbon age estimates towards the upper limits of the radiocarbon barrier are accurate and subsequently whether the site is suffering from a compressed chronology. Single-grain OSL dating at Niah cave in Borneo would be beneficial to target partial bleaching in the single-aliquot OSL results, originally implemented to address unreliable radiocarbon estimates on bone (Higham et al., 2009, Stephens et al., 2007).

Chapter 7: Conclusion

This research applied OSL dating to key modern human sites to improve the robusticity of existing chronologies for arrival and occupation in mainland Southeast Asia. Furthermore this research aimed to define the significance of these sites for models of modern human dispersal. The application of OSL dating to the existing chronologies at Tam Pa Ling, Nam Lot and Tham Lod has not drastically changed the previously established chronologies, but instead has significantly improved the robustness of each chronology and as a consequence has increased the confidence in the age range to enable valuable interpretations to be made and implications assessed.

The resulting chronologies for Tam Pa Ling and Nam Lot have been used to demonstrate the stratigraphic consistency of the deposits, with OSL age estimates being stratigraphically consistent, reproducible, precise and accurate when compared to independent age estimates. Therefore the robusticity of these chronologies provides more confidence in the timing of modern human arrival in the region of northern Laos at > 46 ka or when considering errors > 49 ka. This represents the earliest dated modern human evidence in mainland Southeast Asia, and when combined with similar early modern human evidence from island Southeast Asia weakens the credibility of a 60 ka exit out of Africa associated with the commonly accepted MIS4-3 rapid coastal dispersal model.

The application of OSL dating to the existing chronology at Tham Lod has emphasized the necessity for independent age estimates to establish a robust chronology for a site. OSL age estimates were stratigraphically correct, mostly reproducible and precise, but lacked agreement with past TL and radiocarbon dating. Based on a comparison of single-aliquot and single-grain analysis results from the site, it was evident that grains for age estimation were suffering from partial bleaching. This clarified that TL age estimates were overestimations as, like single-aliquot analysis, the technique cannot selectively remove partially bleached grains. It was also identified that contamination and bulk sampling techniques were contributing to age overestimations for some radiocarbon samples. Due to these known limitations of TL and radiocarbon dating techniques, the OSL age estimates were identified as the most accurate results and representative of a 'true' burial age.

The OSL age estimates at Tham Lod confirmed a Late Pleistocene occupation with earliest evidence of occupation occurring between 21 - 16 ka. Based on a radiocarbon age estimate of 39,960 cal BP by Marwick (2013), however, Tham Lod is known as a 40 ka occupational site. The sample location of this radiocarbon estimate was not evident in Shoocongdej (2006) and as such comparison to independent OSL age estimates from this research was difficult and should be considered in the future to further constrain the timing of occupation at Tham Lod. As a 40 ka occupational site comparison between Tham Lod and other inland river occupational sites in Sunda and Sahul with similar archaeology revealed that modern humans in both regions were interacting with their environments in similar ways at similar points in time. Subsequently this evidence could indicate that modern humans in Sahul migrated from Sunda, bringing with them sustenance capabilities to survive and flourish in inland river environments.

Overall this research has demonstrated the benefits of applying OSL dating as an independent age estimate to improve the robusticity and significance of existing chronologies. As the region of Southeast Asia has a paucity of well dated modern human sites it is important to confirm the validity of currently established chronologies by developing a robust framework and defining their significance for modern human arrival and occupation. Then and only then can this evidence be useful to construct accurate and valid models of modern human dispersal.

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Appendix: Publications

The first paper is under review for the journal Plos One and the second paper has been published in the journal Palaeogeography, Palaeoclimatology, Palaeoecology. These papers have been included, as research from this thesis has contributed to OSL chronology presented in both papers. As the first paper is under review it has been presented in the same format as the submitted manuscript.

Early modern humans and morphological variation in Southeast Asia: fossil evidence from Laos

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Abstract:

Little is known about the timing of modern human emergence and occupation in Eastern Eurasia. However a rapid migration out of Africa into Southeast Asia by at least 60 ka is supported by archaeological, palaeogenetic and palaeoanthropological data. Recent discoveries in Laos provide the first possible evidence for the coexistence of archaic and modern human morphology at a single site, Tam Pa Ling, between 63-44 ka. The fully modern human morphology of the TPL1 cranium supports an early migration of modern humans out of Africa while the mandible of a second individual (TPL2) demonstrates mosaic morphology. The TPL2 mandible has a chin and discrete traits consistent with early modern humans, but it retains a robust lateral corpus and internal corpus morphology that is typical of archaic humans across the Old World. Archaic traits of TPL2 and the fully modern human morphology of TPL1 suggest that a large range of morphological variation was present in early modern human populations residing in the region by MIS 3.

Introduction

In December 2009, a partial human cranium with fully modern morphology (TPL1) was recovered from Tam Pa Ling (Demeter et al., 2012a). In December 2010, a complete human mandible (TPL2) was recovered from the same site. Based on non-alignment between the maxilla of the TPL1 cranium and the TPL2 mandible, these remains represent two separate individuals. These fossils are the first Pleistocene human remains discovered in Laos since 1934 (Fromaget, 1936, Fromaget, 1940), and they establish the definitive presence of early modern humans in mainland Southeast Asia by a minimum of 46 ka and likely as much as 20,000 years earlier (Demeter et al., 2012a)

Tam Pa Ling is one of only a handful of well-dated, early modern human fossil sites in eastern Asia and Australasia. The partial skeleton from Tianyuandong, northern China, is dated to ~ 40 ka (Shang et al., 2007), as is the partial cranium from Laibin, southern China and the Niah 1 cranium from Sarawak, Malaysia (Barker et al., 2007b, Jia and Wu, 1959, Shen et al., 2007b). Other fossils such as Liujiang and Ziyang from China may be as old, but their provenance is uncertain (Shen et al., 2002b, Wu and Poirier, 1995, Yuan et al., 1986, Woo, 1958, Woo, 1959a, Woo, 1959b). The oldest modern human remains from south Asia at Fa Hein in Sri Lanka are modestly younger at ~36 ka cal BP (Kennedy et al., 1987, Kennedy, 1999). Modern human fossils are present in Australia by at least 40 ka though the timing of the earliest remains is uncertain (Bowler et al., 2003a). Fossils from Callao Cave, Luzon, Philippines have been dated to ~ 67 ka, although their specific attribution is unclear (Salvador Mijares et al., 2010). A partial mandible from Zhirendong, southern China, which is dated to ~ 100 ka, shows a mixture of archaic and modern human morphology (Liu et al., 2010b), and late archaic humans fossils from the Chinese sites of Maba and Xuyiyao are dated to 125-69 ka (Wu and Poirier, 1995, Yuan et al., 1986, Woo and Peng, 1959, Gao et al., 2007, Wu and Trinkaus, 2013). This slowly accumulating record of human fossils from the Late Pleistocene of Eastern Eurasia lends additional data to questions about modern human origins at the eastern periphery of the Old World.

The purpose of the current analysis is first to strengthen and extend the chronological framework for the TPL deposits with additional dated geological samples. Secondly, TPL2 is described with an emphasis on its mosaic morphology. Its affinity is determined on the basis of discrete traits and geometric morphometrics in order to place the fossil in its appropriate evolutionary context and to determine the position of this site, northern Laos and the Southeast Asian mainland more generally in Late Pleistocene human evolution.

Context and dating

Tam Pa Ling is located in Huà Pan Province, Laos, approximately 260 km NNE of Vientiane (20°12'31.4'' N, 103°24'35.2''E, elev. 1,170 m). The cave is part of the Annamite Mountains, which straddle the Laos-Vietnam border (Fig. 1). The landscape consists of tower karsts derived from the dissolution of Upper Carboniferous to Permian limestone beds, with a dense network of caves and galleries. Tam Pa Ling has a single, south-facing opening that descends 65 m to the main gallery. This gallery measures 30 m in length along a north-south axis and 40 m in width along an east-west axis. The TPL excavation is located at the east end of the gallery at the base of the sloped entrance (Figs. S1, S2). Sediments at the base of the slope represent periodic, slopewash deposition from the argillaceous-dominated bank from the entrance of the cave, and the stratigraphic integrity of these layers has been established (Demeter et al., 2012b).

The site was discovered in 2008 and has been excavated since November 2009. In December 2009, cranial remains of a single, modern human were found at a depth of 2.35 m (TPL1, Fig. S3) (Demeter et al., 2012b). Analysis of these remains reveals completely modern anatomy with no archaic features. In December 2010, a complete human mandible

(TPL2) was recovered at a depth of 2.65 m and approximately one meter from the source of the TPL1 cranium (Figs. 2, S4, S5). It was broken at the symphyseal plane, and the right and left halves were recovered approximately 20 cm apart. Despite their proximity in the excavation, differences in size and morphology, non-alignment between the maxilla of the TPL1 cranium and the TPL2 mandible and the difference in the degree of occlusal attrition of the TPL1 teeth and the TPL2 M₃ indicate that these remains represent two separate individuals. Some micromammal and reptile remains were also recovered in the TPL trench, and collected at a depth between 0.74 and 4.5 m. The preliminary analysis of the rodent material reveals that the fauna is dominated by three taxa, *Leopoldamys* cf. *sabanus*, *Niviventer* sp. and *Rattus* sp. (77% of the identifiable remains), the remaining material being composed of *Berylmys* sp., *Chiropodomys* sp., *Hapalomys* sp., *Belomys pearsonii* and some unidentified Arvicolinae (SI, Table S7). Most of the taxa are still present today in the Tam Pa Ling region, except for *Belomys pearsonii*, and the Arvicolinae. The latter taxon might indicate some cooler component. No artifacts have been found at the site, and there is no evidence of an occupation surface within the stratigraphic section or within the cave. As is the case with TPL1, the source of the fossil is unknown but the state of preservation and the absence of water-rolling evidence suggest that it originated at the entrance of the cave and was subsequently carried into the cave via slopewash transport and buried within the cave stratigraphy.

The stratigraphy of the site has been described elsewhere (Demeter et al., 2012b) and is described in detail in the Supplementary Information (SI) text. As previously reported, luminescence ages for the surrounding sediments provided a minimum age of 46 ka for sedimentary deposition and the associated fossils, and direct U/Th-series dating of the frontal bone provided a maximum age of ~ 63 ka. Radiocarbon results presented supporting data to suggest antiquity but were outside the generally accepted age range for this method. Despite this, the chronology has been contested (Pierret et al., 2012) with questions raised by a potential sedimentary hiatus of ~ 44 ka in the upper stratigraphy. Therefore, in 2012, additional OSL, U/Th-series and radiocarbon samples were collected throughout the 4.5 m section to extend the chronology, confirm the integrity of the deposits and reduce the age range of the unknown hiatus period (see SI text for dating strategy, sampling locations and sample characteristics). In addition, a bone fragment from the left condyle of TPL2 was sampled for U/Th-series dating to confirm the dating of the fossil itself.

The extended OSL chronology agrees with and builds on the previous chronology (Fig. 1, Tables 1, 2). It has reduced the sedimentary “hiatus” of ~ 44 ka that was previously identified at the top of the stratigraphic column, decreasing the measured time to ~10 ka between samples TPL4-OSL and TPL5-OSL and ~ 9 ka between samples TPL5-OSL and TPL6-OSL. Both of these sections are separated by a layer of powdery calcite precipitate (‘moonmilk’), which may represent a cessation of sedimentation in the cave or an arrival of calcium-rich water. Between samples TPL1-OSL and TPL4-OSL, and between TPL7-OSL and TPL8-OSL there are hiatuses of ~ 14 ka and 10 ka, respectively, which represent the largest gaps in sedimentary accumulation with no obvious record of a break in the stratigraphy (see SI text). However, in both of these locations there is a large amount of rockfall that may represent a period of collapse and the temporary blockage of the cave from allochthonous sedimentary inputs.

The OSL age estimates (TPL4-8-OSL, Fig. 1, Table 1) display a steady increase in age with depth, are stratigraphically consistent over the 4.5 m of excavation but show little agreement with the calibrated radiocarbon results within known limitations of the techniques. The radiocarbon results are generally older than the timing of sedimentary deposition according to the OSL chronology. We attribute this difference to older carbon that has washed in from the landscape, and while the radiocarbon dates may be useful for displaying the antiquity of the deposits, they are not reliable for establishing the timing of fossil deposition. Efforts to obtain calcite suitable for U/Th-series dating from the powdery moonmilk layers

were unsuccessful, but the tip of an overhanging stalactite (LS12-F3, Table 2) corresponding to the level of the human cranium provided a useful maximum age of ~64 ka for sedimentary infilling at that depth (Fig. 1). The U/Th-series dating of the TPL2 bone fragment (LS12-B1-B5) proved equally challenging and could not be microdrilled for U/Th-series profiling due to its porous nature. As such, the analysis was conducted on small handpicked fragments, which gave a minimum age for the fossil of ~44-36 ka. As the bone fragments used for U/Th-series dating are porous and contained inseparable, post-fossil, secondary calcite overgrowths, the individual fragment ages represent minimum ages for the fossil, i.e., the fossils cannot be any younger than ~44 ka, and should in fact be older. These ages estimates are in agreement with the OSL burial ages within errors (Demeter et al., 2012b), but due to the sedimentary nature of the cave as a wash-in environment it is expected that the fossils were on the landscape for a time before being washed into the cave so should in fact be older than the depositional ages as suggested by the initial dating of TPL1 (Demeter et al., 2012b). However, these new U/Th results still place a useful minimum constraint on the age of the fossils themselves, implying that they cannot be Holocene or last glacial maximum in age.

The radiocarbon chronology also displays an increase in age with depth, but is consistently older than the OSL chronology throughout the upper part of the section. As the burning that created the charcoal, which was used for the radiocarbon chronology, did not occur *in situ* there is a strong likelihood that the charcoal represents old carbon that was washed into the cave (from natural or anthropogenic fires) (Fig. 1, Table 2). Thus the radiocarbon chronology is consistently older than the OSL chronology throughout the upper section and has been presented to demonstrate the problems linked with radiocarbon dating in ‘sink’ or ‘wash-in’ (non-occupation) caves (see SI text).

This new chronology confirms the validity of the previous chronological framework for the TPL1 cranium, confirms the integrity of the stratigraphic section and supports a greater antiquity for the TPL2 mandible than is suggested by the minimum age range of 44 to 36 ka.

Results

TPL2: Preservation. The mandible is largely complete with a well-preserved corpus that is broken at the symphyseal plane and the inferior right and left rami (Fig. 2). The corpus has significant damage to the alveolar bone immediately surrounding the break at the midline symphysis, but otherwise shows only minor post-mortem scratching and abrasions. The right ramus is broken at the level of the sigmoid notch and is missing the mandibular condyle and coronoid process. The left mandibular condyle is broken at the level of the sigmoid notch although the coronoid process is complete and the anterior portion of the sigmoid notch is present. A remaining portion of the condyle was used for U/Th-series dating (see “Context and dating”). Additional details about the preservation of the specimen and its reconstruction are provided in the SI text.

The TPL2 mandible represents a mature adult individual, with complete formation of the corpus, alveolar bone, rami and condylar subchondral bone. Both third molars have erupted. The apices of all the roots, including those of the M₃s, are completely closed (stage Ac¹⁹ as indicated on CT scans (Moorrees et al., 1963)). All the teeth have been broken *post-mortem*, except M₃, which shows advanced occlusal attrition. The combination of mandibular maturity, complete molar formation and significant occlusal wear on the M₃ suggests a minimum age for this individual at the end of the third decade. Sex of the individual is unknown.

The mandible has no skeletal lesions. The right M₃, the only preserved dental crown, shows significant occlusal attrition but there is no indication that this is pathological.

Overall dimensions. Linear and angular measurements and details of discrete traits of TPL2 are provided in Tables S1 and S2. The overall dimensions of TPL2 are small, with an inferior

mandibular length of 77.0 mm and an estimated superior length of 87.0 mm, well below that of all other Pleistocene archaic or early modern human samples (Table 3). Mandibular breadth across the condyles cannot be assessed given their complete absence, but it is estimated to be between 92-100 mm. More reliably, bigonial breadth of TPL2 is 81.0 mm, and the dental arcade breadth at the M_2 is 48.3 mm. There are no significant differences between any early modern human and archaic samples in estimated dental arcade breadth (Table 3), but TPL2 has a significantly smaller dental arcade breadth than all modern and archaic samples, including the closely contemporaneous mandible from Tianyuan cave (64.5 mm) or any other East Asian early modern humans (66.4 ± 2.2 , $n=5$) (Shang and Trinkaus, 2010). The only other *Homo* fossils that are similarly small in bigonial breadth and dental arcade breadth at the M_2 are LB1 (83.0 mm (estimated) and 55.0 mm, respectively) and LB6 (71.0 mm and 53.0 mm, respectively) from Liang Bua, Flores (Brown and Maeda, 2009).

Modern human features: discrete traits. Due to post-mortem damage, the superior symphysis is unobservable; only the inferior half of the symphysis is visible (~ 16.4 mm from the basal margin). TPL2 has a clear chin, with a midline *tuber symphyseos* and paired lateral tubercles and a *mentum osseum* category rank 4 (Liu et al., 2010b, Dobson and Trinkaus, 2002, Lebel and Trinkaus, 2002, Weidenreich, 1936). This is the most common pattern demonstrated by modern humans, with 56.3% of East Asian early modern humans and a vast majority of western Eurasian early modern humans (71.4%) demonstrating this pattern. In contrast, 57.7% of Neandertals demonstrate a rank of 2 with no projecting *tuber symphyseos* (Table S3).

There is a single mental foramen on each side of the mandible, and each is located below P_4 - M_1 . In early modern humans, the mental foramen tends to have a mesial position (below P_4) relative to a more distal position in archaic humans (below P_4/M_1 or M_1) (Table S3). Although this is the “more archaic” condition, the position of the foramen in TPL2 is the same as that found in the majority of East Asian early modern humans (61.1%) (Table S3) and is most likely a reflection of the very short mandibular length of the individual (Quam and Smith, 1998, Trinkaus, 2006).

In strict *norma lateralis*, the anteroinferior margin of the ramus crosses the alveolar plane at the distal neck of the M_3 on the right side; although the left M_3 crown is missing, the position of the anteroinferior margin of the left ramus is in approximately the same place. The roots of the rami lie above the lateral eminences, adjacent to the mesial M_3 s. A retromolar space is absent on both the right and left sides of TPL2, which is the more frequent condition when the mental foramen is anteriorly located (Table S3).

On the medial side of each ramus, the mandibular foramen is open with its aperture directed posterosuperiorly and there is a small, minimally-projecting lingula. On each side, the opening narrows to a shallow mylohyoid groove with no bridging. This open configuration is seen in the vast majority of western Eurasian and East Asian early modern humans (Table S3), except in one specimen, which has the horizontal-oval form (ZKD UC104), as well as in most recent human populations (Jidoi et al., 2000).

On the right ramus, both the coronoid process and the condyle are missing at the approximate level of the mandibular notch, making an estimate of its position unreliable. The left superior ramus is better preserved with a complete coronoid process but without a condyle. The lowest point of the mandibular notch lacks its posterior end, but its anterior and middle parts are in a position just posterior to the coronoid process; its lowest point is located anterior to the mandibular foramen. A symmetrical notch where the lowest point is approximately midway between the coronoid process and the mandibular condyle is consistent with the majority of early modern humans. In contrast, the lowest point of the notch is shifted

posteriorly to a position just anterior to the neck of the condyle in the majority of archaic humans (Stefan and Trinkaus, 1998).

Archaic human features: lateral corpus. In *norma lateralis*, the corpus is very robust, particularly with respect to its breadth at the position of the mental foramen and M_1/M_2 . Across archaic and early modern humans, there is relatively little difference in corpus height at the mental foramen ($p=0.85$) (Table 3). Corpus breadths, however, are significantly different between comparative samples ($p<0.0001$) (Table 3). At the position of the mental foramen and the M_1/M_2 , a relatively broad corpus distinguishes archaic humans from the western Eurasian and eastern Asian early modern humans (Table 3). In these dimensions, TPL2 is most similar to the archaic humans, demonstrating a significantly broader corpus than the early modern human samples. At the position of the mental foramen, TPL2 has a corpus breadth that is broader than the average breadth of all Late Pleistocene archaic and early modern human samples. It falls within the range of variation of Late Pleistocene archaic humans (13.8-17.4 mm) and above the ranges of variation of East Asian and Western Eurasian early modern humans (11.4-12.8 mm and 11.1-14.1 mm, respectively). At the position of M_1/M_2 , TPL2 falls above the range of variation for Late Pleistocene archaic humans (14.6-17.8 mm), East Asian early modern humans (11.7-14.1 mm) and western Eurasian early modern humans (12.4-16.0 mm) (Table 3, Fig. S6).

Geometric morphometric analysis. A geometric morphometric analysis was performed on a set of 17 landmarks taken on 67 hemi-mandibles of Pleistocene and Holocene humans from across the Old World (Fig. S7, Table S4). A between-group principal component analysis (bgPCA) was performed to identify axes in shape space that best discriminate between *a priori* defined temporal groups: Middle and Late Pleistocene archaic humans; Late Pleistocene early modern humans; and Holocene modern humans (Table S5). The samples were separated by computing a covariance matrix of the group means and projecting all specimens into the space spanned by the first two eigenvectors of this matrix (Mitteroecker and Bookstein, 2011). TPL2 was subsequently projected onto the PCs to identify its closest neighbors.

There is significant overlap of the 95% confidence ellipses (CE) for the early modern human and Holocene human groups, while the archaic human group is clearly separated in the morphospace represented by two non-zero eigenvectors (Fig. 3). Only one early modern human (Qafzeh 9) falls into the archaic human 95% CE. Tam Pa Ling 2 groups well within the archaic human CE, where it is also closely aligned with both the Zhoukoudian UC 104 and Zhoukoudian *Homo erectus* specimens.

Shape differences in bgPC1 are most strongly correlated with gnathion (the most inferior midline point on the mandibular symphysis); the superior transverse torus (the most posterior midline point on the superior transverse torus); mesial M_1 projected onto the inferior border of the corpus and onto the mylohyoid line on the lingual aspect of the corpus; and the point on the alveolar bone at the M_3 . The archaic humans, with positive values on PC1, have relatively thick midline symphyses and pronounced mylohyoid lines that approach shelf-like configurations. In this way, TPL2 is more similar to the archaic humans, particularly in the expanded mylohyoid region. Another archaic feature, inherited from large anthropoids, which symphysis were buttressed to withstand the chewing and biting, TPL2 that was rejoined at the symphysis, has a relatively thick superior transverse torus.

Discussion and Conclusions

The TPL1 cranium and TPL2 mandible were found in the same stratigraphic unit. Although direct dating of both specimens cannot confirm a strict contemporaneity, they belong to the same chronological frame of 63-44 ka. The TPL2 mandible demonstrates clear affinities with modern humans based on the presence of a chin with a protruding *tuber symphyseos* and

lateral tubercles as well as other discrete traits of the mandible (Table S3). This derived morphology is juxtaposed, however, with archaic features such as the robusticity of the mandibular corpus – particularly at the M₁-M₃ level – and the relatively thick superior transverse torus, which more closely aligns TPL2 with the most robust archaic humans (Table 3, Fig. S6). Geometric morphometric analyses also classify TPL2 as an archaic human, due in large part to the morphology and robusticity of its corpus and maintenance of shelf-like tori combined with the shortness of the mandible.

Within the genus *Homo*, linear dimensions of the mandible - particularly those related to the lateral corpus - have been identified as taxonomically informative (Lague et al., 2008, de Ruiter et al., 2013). In the western Old World, mandibular traits vary in frequency between Neandertals and early modern humans (Trinkaus, 2006, Stefan and Trinkaus, 1998, Rosas, 2001). Lateral corpus breadth, however, consistently separates these groups with the archaic humans having significantly larger breadths than the early modern humans (Walker et al., 2010). A similar pattern of mosaic morphology has been noted in sub-Saharan African fossils dated to MIS 6-5 (White et al., 2003a, Rightmire and Deacon, 1991, Day, 1969, Lam et al., 1996).

A lack of fossil material from Eastern Eurasia has prevented a thorough understanding of the variation of mandibular trait frequencies in archaic and early modern human samples more globally. A recent analysis of the Xujiayao 14 mandibular remains from northern China, dated to the early Late Pleistocene (MIS 4-3), demonstrates a difference in mandibular traits and/or trait frequencies between archaic and early modern humans in the eastern Old World as well, at least in ramus morphology (Wu and Trinkaus, 2013). Similarly, the Zhirendong mandible from southern China exhibits a modern human-like anterior symphysis and mental foramen position but maintains corporal robusticity similar to archaic humans (Liu et al., 2010b). As with mosaic morphology in fossils from southern Africa (White et al., 2003a, Rightmire and Deacon, 1991, Day, 1969, Lam et al., 1996), the early presence of this derived morphology at Zhiren cave has been explained as the result of early modern human gene flow out of Africa and into East Asia with substantial admixture between dispersing populations and regional populations (Liu et al., 2010b).

Similarly, the retention of lateral corporal robusticity in TPL2 has implications for morphological variation and population dynamics in the region. Fossil evidence at Tam Pa Ling supports an early dispersal out of Africa and into Southeast Asia by the middle Late Pleistocene (Demeter et al., 2012b). Archaic traits of TPL2 and the fully modern human morphology of TPL1 (with no archaic features) suggest that a large range of morphological variation was present in early modern human populations residing in the region.

As such, it raises the question of whether those first early modern humans replaced archaic humans already residing in Southeast Asia or interbred with them as has been suggested by fossil evidence from other Eastern Eurasian sites (Liu et al., 2010b, Shang and Trinkaus, 2010). While these fossils may be further evidence of the overlap in traits and varying trait frequencies between archaic and early modern humans (Trinkaus, 2006, Stefan and Trinkaus, 1998, Rosas, 2001), the morphology of the TPL fossils provide the first occurrence of early modern human biology and its co-existence with archaic morphology in eastern Eurasia by MIS 3.

Materials and methods

A comparative assessment of TPL2 was performed using discrete traits, linear and angular morphometrics following (Brauer, 1988) and geometric morphometrics (Nicholson and Harvati, 2006, Viterbo et al., 2012) (Figs. 3, S7; Tables 3, S3, S7). Late Pleistocene samples were evaluated for differences in linear dimensions and discrete traits using model II analysis of variance (ANOVA) with post-hoc Bonferroni tests for multiple comparisons. Due to the mixed archaic and modern human features of TPL2 and its geologic age, comparative samples

included the following: 1) Late Pleistocene archaic humans (i.e. Neandertals); 2) Late Pleistocene early modern humans (EMH) from Western Eurasia and Africa; 3) Late Pleistocene EMH from East Asia (Table S5).

The geometric morphometric analysis was performed using 67 hemi-mandibles. Data were collected in the form of 51 3-D coordinates representing 17 landmarks (Fig S8, Table S4). Cross-sectional imaging of TPL2 was generated using the microfocus tube of the micro-CT scanner “v|tome|x L 240” (GE Sensing & Inspection Technologies Phoenix X|ray) and the AST-RX platform (*Accès Scientifique à la Tomographie à Rayons X*). The complete TPL2 specimen was numerized at a resolution of 60 μm .

Sample composition for this analysis was expanded to include both Middle Pleistocene and Holocene data, but was limited to specimens for which comparable 3-D data were available (Table S5). Comparative samples included 1) Middle and Late Pleistocene archaic humans; 2) Late Pleistocene EMH from all geographic regions; and 3) Holocene humans from China.

Between-group principal component analysis (bgPCA), the projection of data onto the principal components of the group means (Mitteroecker and Bookstein, 2011), was used to identify axes in shape space that best discriminate between the three *a priori* defined comparative groups described above (performed using R free software; see <http://www.r-project.org>). The advantage of this method relative to canonical variates analysis is that the axes remain orthogonal and data do not have to be of full rank. Tam Pa Ling 2 was not included in the calculations of the PCs, and this fossil was subsequently projected onto the PCs to identify its closest neighbors. This step is critical to the statistical analysis because its removal from the database enables one to build a model that is free of the parameter to be judged and to avoid bias in assigning group membership.

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Author contributions:

F.D., L.S., A-M.B., T.S. directed the project. F.D. and L.S. were responsible for analysis and interpretation of the hominid remains. F.D. and J.B. performed 3D reconstructions, J.B. was responsible for 3D morphometrics analysis. Ph.D., J.L.P., K.W., A-M.K. and M.B. were responsible for all sedimentology and mineralogy. F.S. was responsible for analysis of rodents. K.W., L.B., provided OSL and TL ages. J.X.Z. provided U/Th dating of the mandible. F.D., L.S., A-M.B., J.B., X.W., P.S., E.P-E., Ph.D, Y.C. were responsible for theoretical work.

Table 1. OSL single-grain dating of sediments from Tam Pa Ling: dose rate data, equivalent doses and ages.

Sample code	Depth (m)	Grain size (μm)	Beta dose rate ^a (Gy ka ⁻¹)	Field gamma dose rate ^b (Gy ka ⁻¹)	Cosmic-ray dose rate ^c (Gy ka ⁻¹)	Water content ^d (%)	Total dose rate ^e (Gy ka ⁻¹)	Stat. model ^f	Equiv. dose ^{g,h} (Gy)
TPL4-OSL	2.10	180-212	1.513 ± 0.067	1.108 ± 0.04	0.015	30 / 25 ± 5	2.67 ± 0.16	MAM	86 ± 5
TPL5-OSL	1.85	180-212	1.393 ± 0.063	1.008 ± 0.04	0.015	31 / 25 ± 5 47 / 30 ±	2.45 ± 0.13	MAM	54 ± 4
TPL6-OSL	1.60	180-212	1.295 ± 0.062	0.844 ± 0.05	0.014	10	2.19 ± 0.22	MAM	29 ± 3
TPL7-OSL	1.20	180-212	1.143 ± 0.057	0.436 ± 0.05	0.014	38 / 30 ± 5	1.63 ± 0.10	MAM	20 ± 1
TPL8-OSL	0.60	180-212	1.295 ± 0.064	0.852 ± 0.04	0.015	28 / 20 ± 5	2.51 ± 0.14	MAM	6 ± 1

^a 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 rates and OSL ages

^e Mean ± total (1σ) uncertainty, calculated as the quadratic sum of the random and systematic uncertainties. An internal dose rate of 0.03 included

^f Statistical model used to determine the dose distribution between grains -MAM - Minimum Age Model

^g Equivalent doses include a ± 2% systematic uncertainty associated with laboratory beta-source calibrations

^h OSL signal measured using single-grains of quartz - between 800-1800 grains were run for each sample with between 6-20% of the grains emitting an acceptable luminescence signal, with the De derived from a MAM.

ⁱ Uncertainties at 68% confidence interval

Table 2. Uranium-series dating of Tam Pa Ling stalactite and TPL2 bone: ages and supporting data.

Sample Name	Sample depth (m) ^{a,b}	U (ppm)	²³² Th (ppb)	(²³⁰ Th/ ²³² Th) ratio ^c	(²³⁰ Th/ ²³⁸ U) ratio	(²³⁴ U/ ²³⁸ U) ratio ^c	Uncorr. Age (ka) ^c	Corr. Age (ka) ^c
LS12-F3	2.8	0.24	5.13	128.69	0.908 ± 0.002	1.96	64.2 ± 0.2	64.0 ± 0.2
LS12-B1	2.6	67.20	6932	12.19	0.414 ± 0.002	1.38	38.4 ± 0.2	36.2 ± 1.0
LS12-B2	2.6	55.42	1196	66.02	0.469 ± 0.002	1.39	44.1 ± 0.2	43.7 ± 0.3
LS12-B3	2.6	68.21	3942	21.84	0.416 ± 0.001	1.39	38.2 ± 0.1	37.0 ± 0.5
LS12-B4	2.6	61.26	3591	21.22	0.410 ± 0.001	1.38	37.7 ± 0.1	36.5 ± 0.5
LS12-B5	2.6	57.19	3147	25.37	0.460 ± 0.002	1.39	43.0 ± 0.2	41.8 ± 0.5

^a Measured from base of the cave floor to sampling height

^b Depth of the bone in the sediment column

^c Uncertainties at 95% confidence interval.

Table 3. Overall mandibular and corpus dimensions of the TPL2 mandible and Late Pleistocene comparative samples (mean, standard deviation, N). See SI for fossils included in analyses. Parentheses indicate an estimated measurement.

	TPL 2	Archaic humans	East Asian modern humans	Western Eurasian modern humans
Superior length (mm) ^a	(87.0)	109.5* 6.5 16	98.7 2.2 4	102.2* 5.7 14
Arcade breadth at M ₂ (mm)	48.3	67.5* 3.4 16	66.4* 2.2 5	64.7* 3.6 12
Corpus height at mental foramen (M-69(1)) (mm) ^b	30.5 (R)/ 31.1 (L)	32.0 3.6 32	30.4 1.5 6	31.5 4.2 16
Corpus breadth at mental foramen (M-69(3)) (mm) ^b	16.2 (R)/ 16.1 (L)	15.6 1.8 32	12.1* 0.73 6	12.6* 1.5 15
Robusticity index at MF ^c	1023.0	745.6* 133.9 16	543.0* 34.7 5	638.2* 128.0 9
Corpus breadth at M ₁ /M ₂ (mm)	18.3 (R)/ 18.6 (L)	16.2 1.6 24	12.9* 1.2 5	14.2* 1.8 15

^a Midsagittal distance from the mid-condyles to infradentale.

^b M-#: Measurement definition in (Brauer, 1988).

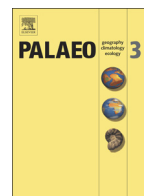
^c Corpus robusticity index at mental foramen = [(corpus height*corpus breadth)/arcade breadth at M₂] *100 (Brown and Maeda, 2009).

* Sample mean significantly different from TPL2 ($\alpha=0.05$ with multiple comparisons corrections).

Fig. 1. Site of TPL, Laos. TPL is located on the upper plateau of the Pa Hang Mountain with the Tam Hang rock shelter at the mountain's base. The 4.5 m stratigraphic section shows the accumulation of sandy and silty clay layers punctuated by seven powdery, calcitic precipitates from the TPL trench. Provenance of the charcoals sampled for ^{14}C dating and soil sampled for OSL and TL dating is identified on the stratigraphy. TPL1 was recovered at a depth of 2.35 m; TPL2 was found at a depth of 2.65 m. Inset: Location of TPL in Huà Pan Province, Laos.

Fig. 2. Human fossil remains designated as TPL2. (A) Mandible in *norma verticalis*; (B) mandible in *norma lateralis*, right side; (C) mandible in *norma latelaris*, left side; (D) mandible in *norma facialis* external; (E) mandible in *norma facialis* internal (F) mandible in *norma basilaris*; (G) occlusal view of the right M_3 .

Fig. 3. Between group principal component analysis (bgPCA) plot of first two eigenvectors that separates three *a priori* defined groups: blue circles: Middle and Late Pleistocene archaic humans; green circles: Late Pleistocene early modern humans; red circles: Holocene humans. Fossils of particular interest are specified by name. Specimens included in the analysis are listed in Table S5



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 paleoecology and paleoclimatology of the region. We analyzed the assemblages recovered in three mainland and two insular karstic sites: Tam Hang South and Nam Lot in northern Laos, Duoi U'Oï 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'Oï) allows us to emphasize different interactions with large carnivores (felids, hyaenids, canids).

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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,b), 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

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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 analyze 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,b, 2011, 2012; Düringer 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 paleoecology (de Vos, 1983, 1995; Sondaar, 1984; Leinders et al., 1985; van den Bergh et al., 1996, 2001; Tougaard, 1998; Storm et al., 2005; Tougaard and Montuire, 2006; Bacon et al., 2008a,b, 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 ± 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 ± 15 ka/ 118 ± 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; Antoine, 2012; Düringer et al., 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 analyzed 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 *H. sapiens*”) and the arrival of anatomically modern *H. sapiens*.

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 m 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



Fig. 1. Location of Pleistocene sites (stars).

Table 1

Location, estimated ages^(e), and numerical age estimates (OSL, U-series, AAR) of the five fossil mammalian faunas considered in the study. Main corresponding references are noted.

Sites	Location	Age	References
Duoi U'Oi	Northern Vietnam Hoà Binh province	66 ± 3 ka (U-series) Late Pleistocene	Bacon et al. (2008b) Antoine (2012)
Nam Lot	North East Laos Huà Pan province	Late Middle Pleistocene/Late Pleistocene ^(e)	Duringer et al. (2012), Bacon et al. (2012)
Tam Hang South	North East Laos Huà Pan province	Late Middle Pleistocene ^(e)	Bacon et al. (2008a), Bacon et al. (2011), Duringer et al. (2012), Antoine (2012), Bacon et al. (2012)
Sibrambang	West Sumatra Padang Highlands	80–60 ka ^(e) >70 ka (AAR, Djamboe site) >81 ka (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 ^(e) 110–70 ka ^(e) ca. 125–60 ka ^(e) 128 ± 15 ka/118 ± 3 ka (OSL, U-series)	de Vos (1995) van den Bergh et al. (1996) van den Bergh et al. (2001) Westaway et al. (2007)

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 (among them *Pongo pygmaeus*, *Hyllobates syndactylus*, or *Helarctos malayanus*) (de Vos, 1983). The age of the Punung III “yellow” breccia has been estimated between 128 ± 15 ka and 118 ± 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 (1983) to *H. 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 *H. 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 *H. erectus* by *H. 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 archeological and human remains from the Paleolithic to the Neolithic (Fromaget, 1936, 1937, 1940a,b; Fromaget and Saurin, 1936; Saurin, 1951; Demeter, 2000; Shackelford, 2007; Shackelford and Demeter, 2012).

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, 1940a,b; 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 paleoecological 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 Fig. 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 fluvialite. 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 carnivorans 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).

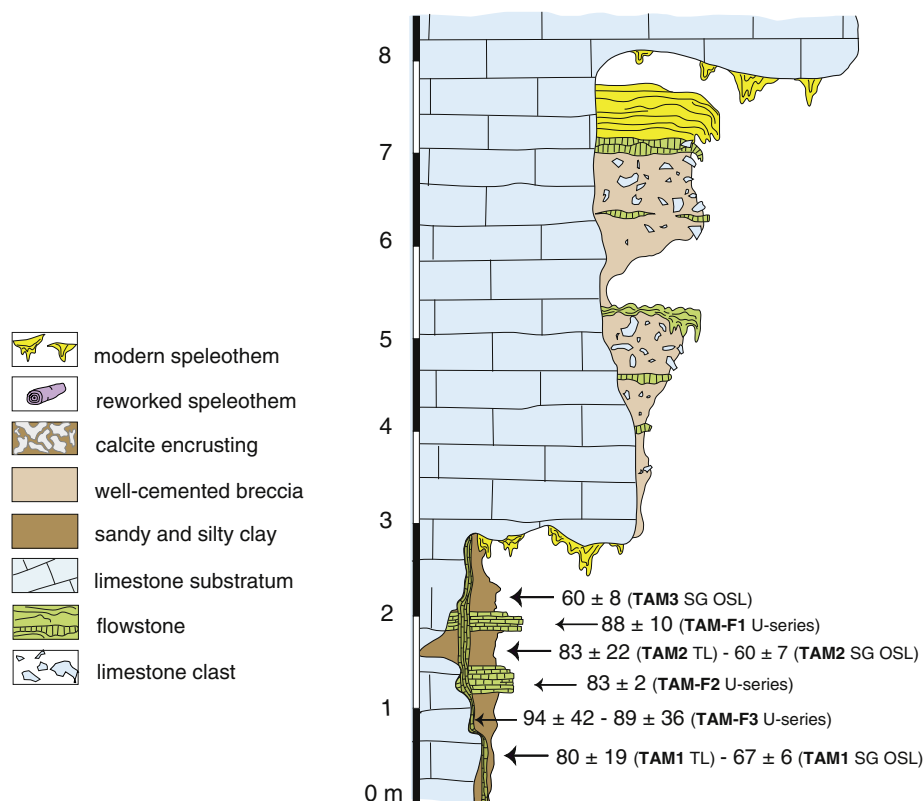


Fig. 2. Stratigraphy of the Tam Hang South locality (see Tables 2 and 3 for dating results).

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 (Bacon et al., 2012; Durringer et al., 2012). The cave is a network of superimposed and interconnected galleries and chambers on four levels. The main chamber is about 60 m long and contains a complicated depositional history due to several filling/reworking processes (Durringer 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) (Durringer 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.

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

25 m 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'Oï 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 ± 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.

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'Oï, 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.

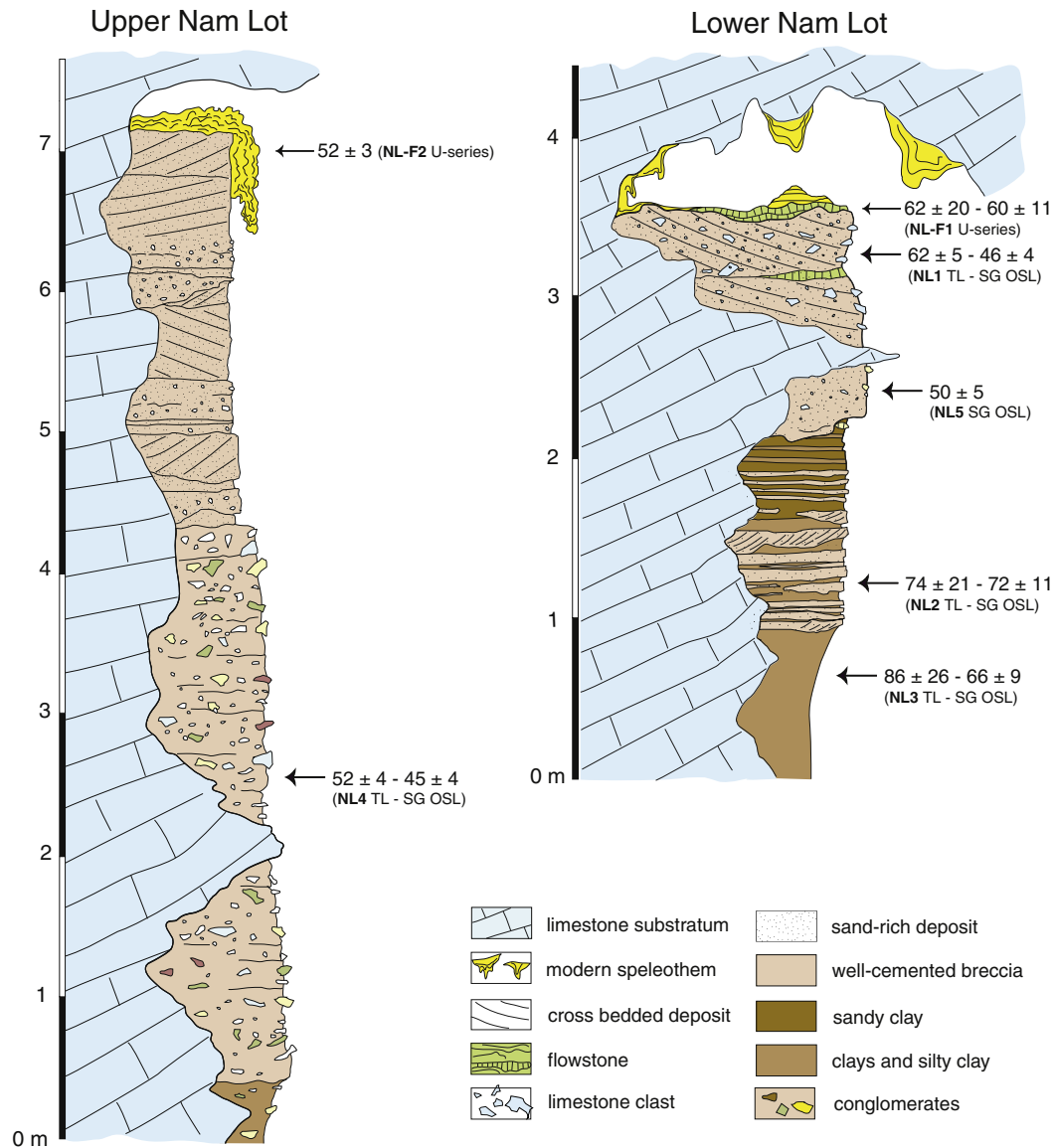


Fig. 3. Stratigraphy of the Nam Lot locality, Upper and Lower sections (see Tables 2 and 3 for dating results).

3.1.1. Luminescence dating

Bulk breccia matrix was sampled from cleaned exposures in the stratigraphy using only red-filtered torch light. Quartz grains of 90–125 μm and 180–212 μm 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 paleodoses 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 and 10.38 Gy/min for the aluminium single-rain disks and 7.41 Gy/min for the stainless steel single-aliquot and red TL disks. Total dose rates were measured by in situ gamma spectrometry and laboratory beta counting, while concentrations of ^{238}U , ^{235}U , ^{232}Th

and ^{40}K were measured by high-resolution gamma-ray spectrometry. We used an effective internal alpha dose rate of 0.03 Gy ka^{-1} and a long-term water content of between 3 and 19 $\pm 5\%$.

3.1.2. 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}Th ages were calculated using Isoplot/EX 3.0 (Ludwig, 2003) and half-lives of $75,690 \pm 230$ years (^{230}Th) and 245,250 years (^{234}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}Th concentrations and low U/Th ratios), all ^{230}Th ages must be corrected for non-radiogenic ^{230}Th , that contributes to an age excess, making the ^{230}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}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}U , ^{234}U , ^{232}Th and ^{230}Th in the detrital

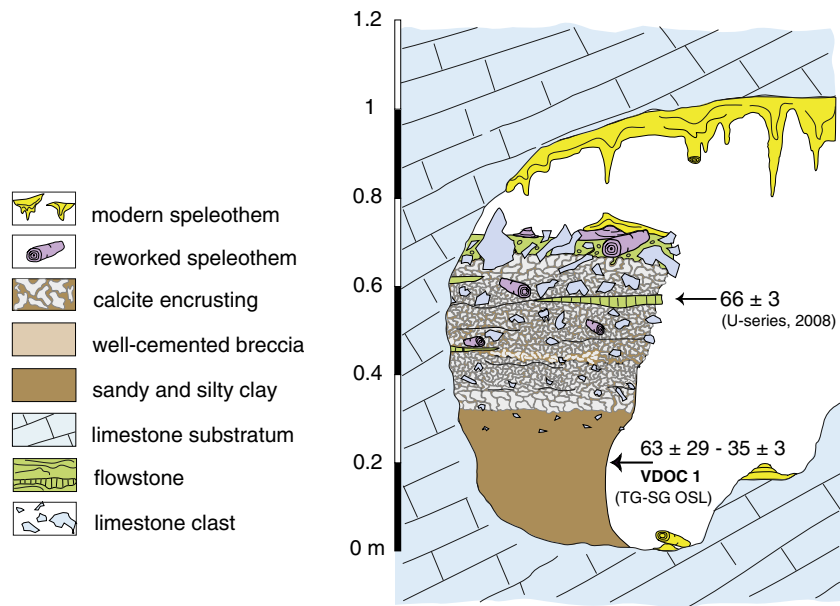


Fig. 4. Stratigraphy of the Duoi U'O'i locality (see Tables 2 and 3 for dating results). The results of the U-series datings are from Bacon et al. (2008b).

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}Th correction often results in large age error magnifications in the corrected ^{230}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}Th ages). Nevertheless, two significantly purer samples, TAM-F2 from Tam Hang, and NL-F2 from Nam Lot, return precise and robust corrected ^{230}Th ages of 83 ± 2 and 52 ± 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}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'O'i 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 (MNic = 1). When one right d4 and one left d4 corresponded to different age classes, we counted two individuals (MNic = 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 MNic was calculated with all of the dentition in combining incompatible left/right and wear stage. This index is cited in the text as MNic (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 analyzed for four assemblages (Tam Hang, Nam Lot, Duoi U'O'i, 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 *C. 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 (*S. scrofa*, *S. 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'O'i, Tam Hang and Nam Lot have been presented in Table 2 (luminescence) and

Table 2

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

Sample code	Depth (from surface) (m)	Grain size (μm)	Beta dose rate ^a (Gy ka ⁻¹)	Field gamma dose rate ^b (Gy ka ⁻¹)	Cosmic-ray dose rate ^c (Gy ka ⁻¹)	Water content ^d (%)	Total dose rate ^e (Gy ka ⁻¹)	Technique ^f	Statistical model ^g	Equivalent dose ^{h,i} (Gy)	Age ^j (ka)
<i>Tam Hang</i>											
TAM1	8.05	180–212	1.336 \pm 0.059	1.029 \pm 0.002	0.016	13/5 \pm 2	2.41 \pm 0.08	UV _{SG}	MAM	162 \pm 14	67 \pm 6
	8.05	90–125	1.413 \pm 0.061	1.029 \pm 0.002	0.016	14/5 \pm 2	2.49 \pm 0.09	Red TL	DAP UNBL	428 \pm 4	172 \pm 7
TAM2	7.00	180–212	1.261 \pm 0.064	1.140 \pm 0.002	0.015	15/10 \pm 5	2.45 \pm 0.15	UV _{SG}	MAM	199 \pm 46	80 \pm 19
	7.00	90–125	1.334 \pm 0.066	1.140 \pm 0.003	0.015	16/5 \pm 2	2.52 \pm 0.15	Red TL	DAP UNBL	146 \pm 14	60 \pm 7
TAM3	6.20	180–212	1.294 \pm 0.064	1.029 \pm 0.002	0.016	7/5 \pm 2	2.37 \pm 0.09	UV _{SG}	MAM	463 \pm 4	184 \pm 12
	6.20	90–125	1.368 \pm 0.065	1.029 \pm 0.002	0.016	7/5 \pm 2	2.44 \pm 0.09	Red TL	DAP UNBL	210 \pm 54	83 \pm 22
									MAM	142 \pm 11	60 \pm 8
									DAP UNBL	808 \pm 4	331 \pm 14
									DAP BL	/	/
<i>Nam Lot</i>											
NL1	0.14	180–212	2.420 \pm 0.086	2.420 \pm 0.004	0.015	15/15 \pm 5	4.201 \pm 0.231	UV _{SG}	MAM	192 \pm 10	46 \pm 4
	0.14	90–125	2.559 \pm 0.091	1.8862 \pm 0.004	0.015	15/15 \pm 5	4.331 \pm 0.239	UV _{SA}	MAM	231 \pm 8	53 \pm 4
	0.14	90–125	2.559 \pm 0.091	1.8862 \pm 0.004	0.015	15/15 \pm 5	4.331 \pm 0.239	Red TL	DAP UNBL	267 \pm 15	62 \pm 5
NL2	2.60	180–212	1.433 \pm 0.047	1.353 \pm 0.004	0.017	6/5 \pm 2	2.834 \pm 0.082	UV _{SG}	MAM	204 \pm 31	72 \pm 11
	2.60	90–125	1.515 \pm 0.050	1.353 \pm 0.004	0.017	6/5 \pm 2	2.915 \pm 0.085	Red TL	DAP UNBL	297 \pm 13	102 \pm 6
NL3	2.90	180–212	1.390 \pm 0.067	1.525 \pm 0.004	0.015	22/20 \pm 5	2.961 \pm 0.158	UV _{SG}	DAP BL	217 \pm 61	74 \pm 21
	2.90	90–125	1.470 \pm 0.069	1.525 \pm 0.004	0.015	22/20 \pm 5	3.040 \pm 0.163	Red TL	MAM	196 \pm 25	66 \pm 9
NL4	2.00	180–212	2.224 \pm 0.071	2.155 \pm 0.004	0.016	3/2 \pm 5	4.427 \pm 0.080	UV _{SG}	DAP UNBL	325 \pm 16	107 \pm 8
	2.00	90–125	2.352 \pm 0.075	2.155 \pm 0.004	0.016	3/2 \pm 5	4.554 \pm 0.084	UV _{SA}	DAP BL	263 \pm 78	86 \pm 26
	2.00	90–125	2.352 \pm 0.075	2.155 \pm 0.004	0.016	3/2 \pm 5	4.554 \pm 0.084	Red TL	MAM	197 \pm 17	45 \pm 4
									MAM	238 \pm 17	52 \pm 4
									DAP UNBL	554 \pm 30	122 \pm 7
									DAP BL	238 \pm 24	52 \pm 5
<i>Duoi U'O'i</i>											
VDOC 1	2.00	180–212	3.121 \pm 0.113	2.633 \pm 0.003	0.023	19/15 \pm 5	5.809 \pm 0.317	UV _{SG}	MAM	150 \pm 11	35 \pm 3
	0.60	90–125	3.301 \pm 0.119	2.633 \pm 0.004	0.023	19/15 \pm 5	5.987 \pm 0.328	Red TL	DAP UNBL	515 \pm 25	101 \pm 7
									DAP BL	318 \pm 147	63 \pm 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 $\pm 10\%$.^d Field/time-averaged water contents, expressed as (mass of water/mass of dry sample) $\times 100$. The latter values were used to calculate the total dose rates and OSL/TL ages.^e Mean \pm total (1 σ) uncertainty, calculated as the quadratic sum of the random and systematic uncertainties. An internal dose rate of 0.03 Gy ka⁻¹ is also included.^f Three luminescence techniques were applied to these samples; UV_{SG} = 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 Paleodoses include a $\pm 2\%$ systematic uncertainty associated with laboratory beta-source calibrations.ⁱ UV_{SG} 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 (U-series). The chronology of the Duoi U'O'i site (66 ± 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 ± 15 ka and 118 ± 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 ($128\text{--}71$ ka), whereas the age ranges place the Duoi U'O'i fauna in the relatively cooler period of MIS4 ($71\text{--}59$ ka) (Imbrie et al., 1984) (Fig. 5).

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 (<1 kg) (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,b, 2011, 2012). 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'O'i and Sibrambang (Table 4), considering the 21 to 29 species inventoried in the living faunas at the North latitudes ($0^\circ\text{--}25^\circ$) (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

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. ^{230}Th ages are calculated using Isoplot/Ex 3.0 (Ludwig, 2003). Non-radiogenic ^{230}Th correction was applied assuming non-radiogenic $^{230}\text{Th}/^{232}\text{Th}$ atomic ratio = $4.4 \pm 2.2 \times 10^{-6}$ (bulk-earth value), and ^{238}U , ^{234}U , ^{232}Th and ^{230}Th are in secular equilibrium. Non-radiogenic ^{230}Th correction results in large age error magnifications in the corrected ^{230}Th ages for samples with low $^{230}\text{Th}/^{232}\text{Th}$ ratios.

Sample name	Sample depth ^a	U (ppm)	^{232}Th (ppb)	$(^{230}\text{Th}/^{232}\text{Th})^b$	$(^{230}\text{Th}/^{238}\text{U})$	$(^{234}\text{U}/^{238}\text{U})^b$	Uncorr. ^{230}Th Age (ka) ^b	Corr. ^{230}Th Age (ka) ^b	Corr. initial ($^{234}\text{U}/^{238}\text{U}$)
<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

^a Measured from base of the cave floor to sampling height.

^b Uncertainties at 95% confidence interval.

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 *Panthera pardus*, is well represented).

For our excavations at Tam Hang, Nam Lot and Duoi U'O'i, 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).

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'O'i, 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.

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-Tables 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'O'i 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'O'i;

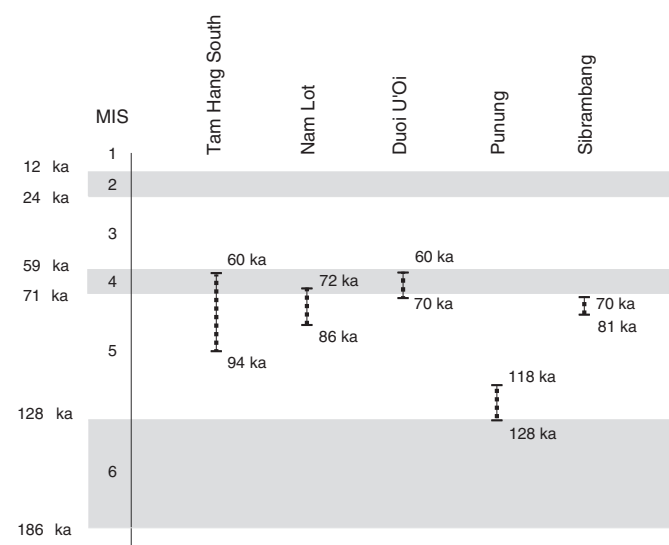


Fig. 5. New chronological framework based on numerical ages for quartz grains (luminescence) and flowstones (U-series) for Tam Hang, Nam Lot and Duoi U'O'i sites. The chronology for Punung has been previously established by Westaway et al. (2007) and that for Sibrambang by de Vos (1983), Skelton (1985),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

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. *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: ⁽¹⁾*Cervus* sp., ⁽²⁾*Naemorhedus sumatrensis*, ⁽³⁾*Bos javanicus*, ⁽⁴⁾*Felis temminckii*, ⁽⁵⁾*Helarctos malayanus*, ⁽⁶⁾*Hystrix brachyura*, ⁽⁷⁾now assigned to *Pliocrocota perrieri* (Werdlin and Lewis, 2012).

	Tam Hang	Nam Lot	Duoi U'Oi	Punung	Sibrambang
Artiodactyla	<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> <i>Bovidae</i> 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> <i>Bovidae</i> indet. <i>Capricornis sumatrensis</i> ⁽²⁾ <i>Sus</i> sp.	<i>Rusa</i> sp. ⁽¹⁾ <i>Muntiacus muntjak</i> <i>Bibos javanicus</i> ⁽³⁾ <i>Bubalus bubalis</i> <i>Capricornis sumatrensis</i> ⁽²⁾ <i>Sus vittatus</i> <i>Sus barbatus</i>
Perissodactyla	<i>Rhinoceros unicornis</i> <i>Rhinoceros sondaicus</i> <i>Rhinoceros</i> sp. <i>Rhinocerotina</i> 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. <i>Rhinocerotidae</i> indet. <i>Tapirus</i> sp.	<i>Rhinoceros unicornis</i> <i>Rhinoceros sondaicus</i> <i>Dicerorhinus sumatrensis</i> <i>Rhinoceros</i> sp. <i>Rhinocerotina</i> indet. <i>Tapirus indicus</i>	<i>Dicerorhinus sumatrensis</i> ^a <i>Rhinoceros sondaicus</i> ^a <i>Tapirus indicus</i> ^a	<i>Rhinoceros sondaicus</i> ^a <i>?Dicerorhinus sumatrensis</i> ^a <i>Tapirus indicus</i> ^a
Proboscidea	<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>
Carnivora	<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 crocota ultima</i> ⁽⁷⁾ cf. <i>Felis temminckii</i>	<i>Arctonyx collaris</i> <i>Meles meles</i> <i>Cuon alpinus</i> <i>Viverra zibetha</i> <i>Viverra</i> cf. <i>megaspila</i> <i>Viverridae</i> 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 temminckii</i> ⁽⁴⁾ <i>Ursus malayanus</i> ⁽⁵⁾ <i>Carnivora</i> indet. <i>Paguma</i> sp.
Primates	<i>Macaca</i> sp <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. <i>Colobinae</i> 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> <i>Acanthion brachiurus</i> ⁽⁶⁾
Rodentia	<i>Hystrix brachyura</i> <i>Leopoldamys sabanus</i>	<i>Hystrix brachyura</i>	<i>Hystrix brachyura</i>	<i>Hystrix brachyura</i>	

^a The Perissodactyls of Punung and Sibrambang have been revised by POA.

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).

4.3.3. Frequency of teeth

4.3.3.1. 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

Table 5

Number of Specimens (NSP) and Number of Identified Specimens (NISF) 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; Bacon et al., 2011; 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).

	Tam Hang	Nam Lot	Duoi U'Oi	Punung	Sibrambang
	NSP	NSP	NSP	NSP	NSP
	979	434	1189	>613	~10,000
	NISF	NISF	NISF	NISF	NISF
Artiodactyla	379	233	386	169	4305
Perissodactyla	30	21	69	48	>171
Proboscidea	7	8	10	4	17
Carnivora	53	34	76	26	139
Primates	117	45	235	257	>2078
Rodentia	87	44	95	>100	>380
Total	673	385	871	>604	>7090

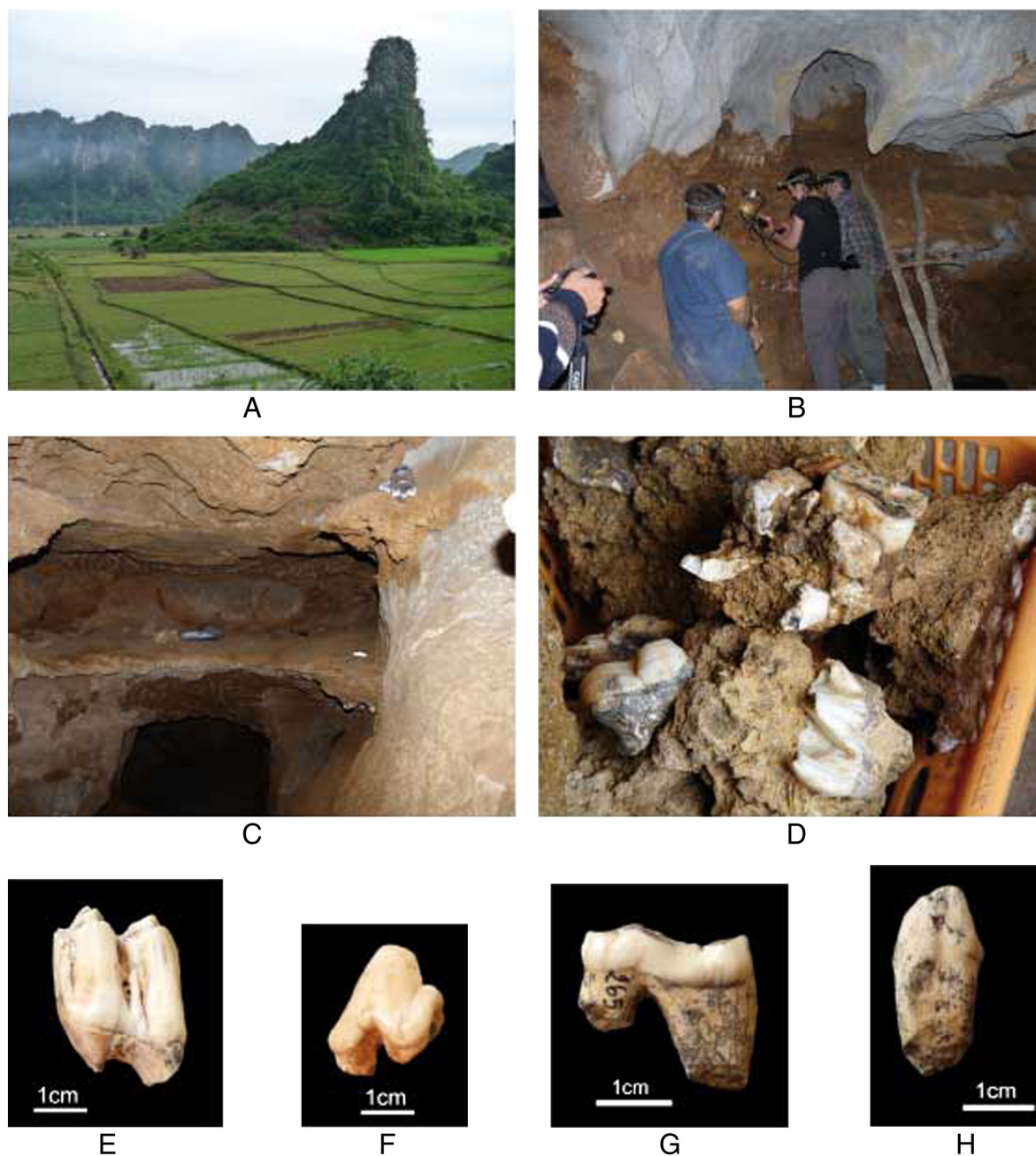


Fig. 6. A. General view of tower karst morphology in the mainland of Southeast Asia; B. Endokarstic breccias that plastered the walls of a cave (Nam Lot, northern Laos), with geochronologists measuring the radioactivity; C. Example of deposits with argillaceous sandy breccias interrupted by horizontal flowstones; D. Fossiliferous karstic breccias with isolated teeth of rhinoceroses; E–G. 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 *Pliocrocuta perrieri*; G. right m1 of *Ursus thibetanus*; H. left I3 of *Ursus thibetanus* partially gnawed (1/4 of the root).

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 (<30 kg) 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 6Percentages of teeth with ungnawed and gnawed roots in some taxa of the five faunas. Germs which only consist of crowns are not considered. ⁽¹⁾number of teeth ≤ 3 ; ⁽²⁾data not observed.

		Ungulates							Carnivora				Primates		
		Rhinocerotidae	Tapiridae	Suidae	<i>Cervus unicolor</i>	<i>Muntiacus muntjak</i>	<i>Bos/Bubalus</i>	<i>Naemorhedus sumatrensis</i>	small Carnivora	large Felidae	Ursidae	<i>Cuon alpinus</i>	<i>Macaca</i> sp.	<i>Pongo pygmaeus</i>	<i>Homo</i> sp.
Duoi U'Oi	ungnawed	61.0	9.1	1.2 ⁽¹⁾	–	1.8 ⁽¹⁾	–	–	50	13.3	16.6	42.8	34.8	12	–
	gnawed	39.0	90.9	98.8	100	98.2	100 ⁽¹⁾	100	50	86.7	83.4	57.2	65.2	88	100 ⁽¹⁾
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 ⁽¹⁾	–
Nam Lot	ungnawed	88.2	75 ⁽¹⁾	–	–	–	–	–	–	–	–	–	–	–	–
	gnawed	11.8	25 ⁽¹⁾	100	100	100	100	100	100	100	100	100	100	100 ⁽¹⁾	100 ⁽¹⁾
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 ⁽¹⁾	26.7	2.6	–	⁽²⁾	2.6 ⁽¹⁾	–	–	–	–	–	⁽²⁾	⁽²⁾	–
	gnawed	10.7 ⁽¹⁾	73.3	97.4	100	⁽²⁾	97.4	100	–	100	100	–	⁽²⁾	⁽²⁾	100 ⁽¹⁾

4.3.3.2. 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 *C. 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). With regard 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). With regard 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., 2015; Fourvel et al., in press). 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

With regard 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.

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-Urbe, 1984; Lyman, 2008). Carnivora and humans have been excluded due to their relatively low abundance (Fig. 7).

Fig. 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

Table 7

Frequency of teeth by species, family or Order in the fossil assemblages. U: upper; L: lower; P: permanent; D: deciduous, when identified. 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); see the text for results.

	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	58	51	19	14	26	23	17	39	60	88	11	5	7	11	1	25	85	110	6
<i>M. muntjak</i>	49	36	70	16	23	13	36	-	81	33	99	15	30	18	43	6	54	184	236	2
Suidae	82	90	136	15	40	60	90	11	>81	>80	146	10	>63	>50	>113	?	1977	1770	3741	6
<i>N. sumatrensis</i>	5	3	8	0	6	8	14	0	5	5	10	0	5	26	31	0	7	5	12	0
Large Bovidae	15	28	41	2	12	37	47	4	-	2	2	0	?	?	?	?	30	76	109	5
Rhinocerotidae	8	17	6	19	1	9	2	15	18	41	34	25	7	20	18	9	68	84	73	79
Tapiridae	1	4	5	0	0	4	4	0	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	0	11	6	12	5
Small Carnivora	14	15	29	0	9	4	13	0	16	12	28	0	-	-	-	-	38	12	50	0
Ursidae	7	7	14	0	7	7	14	0	18	6	24	0	3	8	11	0	45	21	64	2
Felidae/Hyaenidae	6	3	9	0	1	>1	2	frgt	4	11	15	0	2	9	11	0	9	12	21	0
Small primates	>69	>36	102	4	18	21	38	1	147	51	198	?	34	19	52	1	>325	>194	>607	?
<i>P. pygmaeus</i>	2	-	2	0	2	1	3	0	12	19	30	2	112	71	183	?	781	677	1443	28

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.

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, Fig. 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. The Tam Hang and Duoi U'O'i 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'O'i. 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.

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 *C. alpinus*) and hyaenids (the hyena *P. perrieri*) at Nam Lot; canids (*C. alpinus*) and felids (the tiger *P. tigris* and the leopard *P. pardus*) at Duoi U'O'i 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'O'i, 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'O'i (one m1), and a range of 121.6–168.6 kg (mean = 152 kg, 3 m1) at Punung (see

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; Bacon et al., 2011); Nam Lot (Bacon et al., 2012); Duoi U'O'i (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'O'i (*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*).

Order	Subfamily/family	Tam Hang		Nam Lot		Duoi U'O'i		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	31	7	204	9
	Suidae	172	15	101	11	161	18	>100	25	3747	244
Perissodactyla	Rhinocerotidae	25	13	17	8	59	25	27	10	152	21
	Tapiridae	5	3	4	2	11		21	5	19	4
Proboscidea	Elephantidae	4	2	3	1	10	3	4	2	17	6
	Stegodontidae	3	1	5	2	-	-	-	-	-	-
	Felidae/Hyaenidae	9	2	6	1	15	3	15	3	21	6
Carnivora	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	-	-	50	16
	Cercopithecidae	108	10	41	5	198	18	16	4	209	17
Primates	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	-

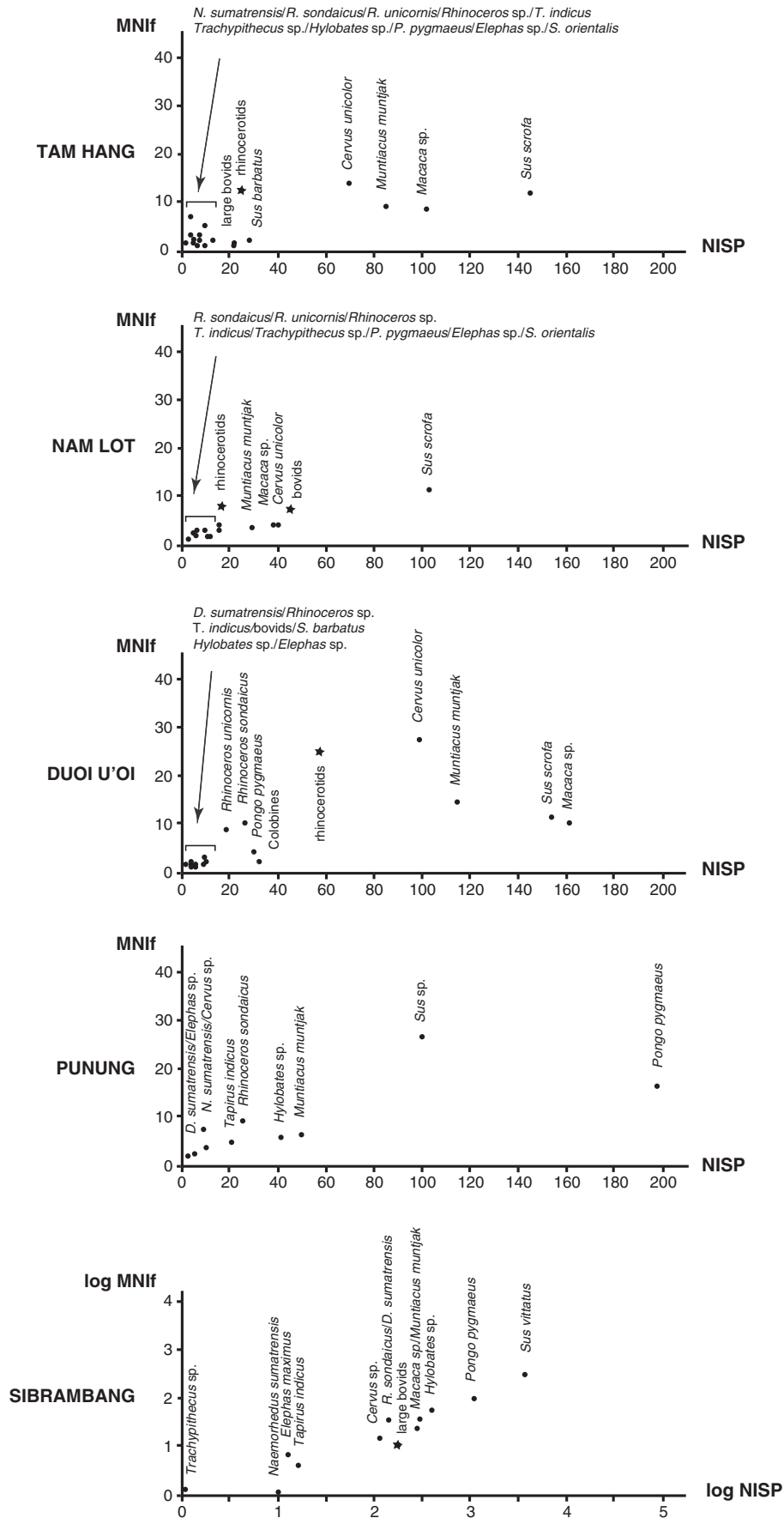


Fig. 7. Two-dimensional diagrams with NISP on abscissa and MNIF on ordinate by species (circles) or family (stars) of ungulates and Primates in the five samples. In order to correct the sampling effect between the Sibrambang assemblage and the other assemblages, we used the logNISP/logMNIF.

also Hertler and Volmer, 2008). Contrary to modern populations, differences in body mass estimates between the Late Pleistocene tigers, from northern Vietnam (Duoi U'O'i) 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'O'i (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).

4.6. Mortality profiles of species

4.6.1. *C. unicolor*/*Rusa* sp.

The MNIC calculated on the basis of d4 and m1 or m3 are: 15 for Tam Hang, 25 for Duoi U'O'i, 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 sambar 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'O'i, is not due to 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.

In the Tam Hang profile, the first age class (juveniles, <1.6 yr) is predominant, and adult cohorts [3–8] contain both prime-aged (3 yrs–9 yrs) and old-aged individuals (>9 yrs up to ~13 yrs 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'O'i profile displays differently a bias towards cohorts [3–6] that contain abundant

prime-adult individuals (3 yrs–9 yrs), 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 sambar 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'O'i mortality profile illustrates a pattern of possible human selective hunting. Fig. 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'O'i 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 archeological 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 Cruz-Urbe, 1984; Stiner, 1990; Steele, 2003, 2004).

4.6.2. *S. scrofa*/*S. vittatus*

We calculated the MNIC on the basis of lower molars (m1/m2/m3): 23 for Tam Hang, 21 for Duoi U'O'i, 15 for Nam Lot (*S. scrofa*), and 164 for Sibrambang (*S. 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

Category	Age class by species	TAM HANG	NAM LOT	DUO U'O'I	PUNUNG	SIBRAMBANG
		MNif	MNif	MNif	MNif	MNif
small size <30 kg	<i>Muntiacus</i>	10 20 30	10 20 30	10 20 30	10 20 30	10 20 30 40
	juvenile <i>Sus</i>	9 5 23%	3 2 12.2%	14 4 19.2%	7 12.1%	20 6 8.1%
medium size 30–175 kg	juvenile <i>Cervus</i>	8	3	3	1	2
	adult <i>Sus</i>	10	9	14	25	238
	juvenile <i>Bos/Bubalus</i>	1	2	2	7	2
	adult <i>Naemorhedus</i>	2	3	2	1	1
	new born rhinocerotine			1	2	5
large size >176 kg	juvenile <i>Tapirus/Megatapirus</i>	34.4%	41.5%	21.5%	60.3%	78.3%
	adult <i>Cervus</i>	5	1	24	1	12
	<i>Rhinoceros/Dicerorhinus</i>	13	8	25	10	16
	adult <i>Bos/Bubalus</i>	2	5	1	2	6
	<i>Elephas/Stegodon</i>	3	3	3	2	6
	adult <i>Tapirus/Megatapirus</i>	3	2	2	3	3
		42.6%	46.3%	59.1%	27.6%	13.5%

Fig. 8. Percentage of individuals by body-size category for the species of Artiodactyla, Perissodactyla and Proboscidea in the fossil faunas studied here: small size (SS: <30 kg), medium size (MS: 31–175 kg), large size (LS: >176 kg). 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'O'i (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).

Table 9

Body mass estimates of predators based on family regression of body mass (BM) against length of first lower molar (m1) of felids and canids (van Valkenburgh, 1990). Equations used: $\log_{10}(\text{BM}) = 3.05\log_{10}(\text{m1}) - 2.15$ for felids ($n = 3$, prediction error = 28%); $\log_{10}(\text{BM}) = 1.82\log_{10}(\text{m1}) - 1.22$ for canids ($n = 27$, prediction error = 27%). ⁽¹⁾Francis (2008), ⁽²⁾Smith and Xie (2008), ⁽³⁾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).

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

those of Tam Hang, Nam Lot and Duoi U'Oi (Kolmogorov–Smirnov test, each $p < 0.001$).

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.

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 *S. 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 200 kg (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 ~30–60 kg 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 (<50 kg) or medium-sized prey (100–200 kg) (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,b). 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

4.6.3.1. Rhinoceroses. In relation to rhinoceroses (Table 10), we calculated the MNIc 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

Table 10

Taxa used for reconstructing mortality profiles within fossil faunas.

Tam Hang South	Nam Lot	Duoi U'Oi	Sibrambang
<i>Cervus unicolor</i>	–	<i>Cervus unicolor</i>	<i>Rusa</i> sp.
<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</i> sp.	<i>Rhinoceros</i> sp.	<i>Rhinoceros</i> sp.	–
–	–	<i>Dicerorhinus sumatrensis</i>	<i>Dicerorhinus sumatrensis</i>
<i>Rhinocerotina</i> indet.	<i>Rhinocerotidae</i> indet.	<i>Rhinocerotina</i> indet.	–
–	–	–	<i>Tapirus indicus</i>

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 = 13.9–15.1 mm, m2 = 16.1–18 mm); Sibrambang (m1 = 10.8–14 mm, m2 = 14.7–16.2 mm).

Sites	Number of teeth	MNIc (m1/m3, cohort)	MNIc (d4, cohort)
Tam Hang	N = 18 9 m1, 9 d4	N = 9 4 lm1, 5 rm1	N = 6 4 ld4, 2 rd4
Duoi U'Oi	N = 41 37 m3, 4 d4	N = 22 22 lm3	N = 3 3 ld4
Sibrambang	N = 19 17 m1, 2 d4	N = 14 12 lm1, 2 rm1	N = 1 1 ld4

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 *S. vittatus*).

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. 11d).

We compared the profiles with that of the natural demographic composition observed in a modern population of *Rhinoceros unicornis*

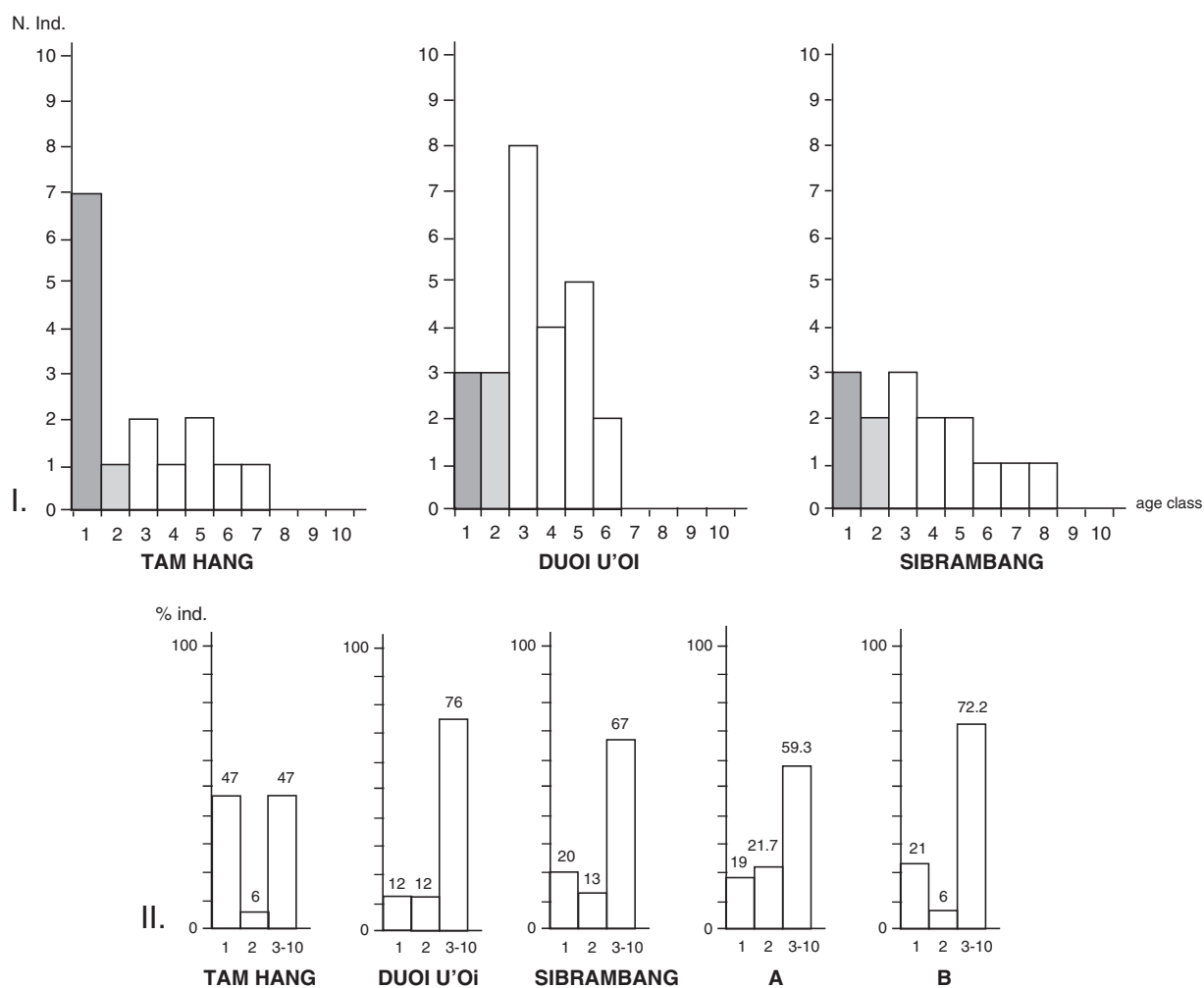


Fig. 9. I. Mortality profiles of *Cervus unicolor* from Tam Hang and Duoi U'Oi and *Rusa* sp. from Sibrambang. Age classes [1–10] are defined by Klein et al. (1981): [1] young (<1.6 year), [2] yearling (<3.2 years), [3–6] prime-adult, and [6–10] old adult individuals (up to 16 years). II. The three-cohort 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).

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'O'i samples, and for the Punung and Sibrambang samples when necessary. Tam Hang and Duoi U'O'i ($m1 = 10\text{--}13\text{ mm}$) and ($m2 = 14\text{--}17\text{ mm}$); Sibrambang ($m1 = 8\text{--}12.50\text{ mm}$) and ($m2 = 12.50\text{--}17\text{ mm}$).

Sites	Number of teeth	MNIc type (m1/m2/m3), side (left/right) of tooth
Tam Hang	$N = 39$	$N = 23$
	16 m1, 7 m2, 16 m3	3 lm1, 13 rm1, 2 rm2, 5 rm3
Duoi U'O'i	$N = 45$	$N = 21$
	7 m1, 14 m2, 24 m3	3 lm1, 8 lm2, 10 lm3
Nam Lot	$N = 25$	$N = 15$
	6 m1, 6 m2, 13 m3	2 lm1, 2 rm1, 5 lm2, 5 lm3, 1 rm3
Sibrambang	$N = 1581$	$N = 164$
	1154 m1/m2, 427 m3	27 lm1, 45 lm2, 92 lm3

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'O'i population to 87.6% in that of Nam Lot (Fig. 12). Taking this into account, the Duoi U'O'i 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,b). 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'O'i (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'O'i 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, <12 yrs], 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 carnivorous 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 a 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 (200–400 kg – up to 13%) and even elands (>400 kg – 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.

4.6.3.2. Tapirs. A sample of nineteen teeth of the Malayan tapir *T. 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'O'i 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,b, 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).

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'O'i (70–60 ka) agrees with the previously obtained age for the overlying breccias (66 ± 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

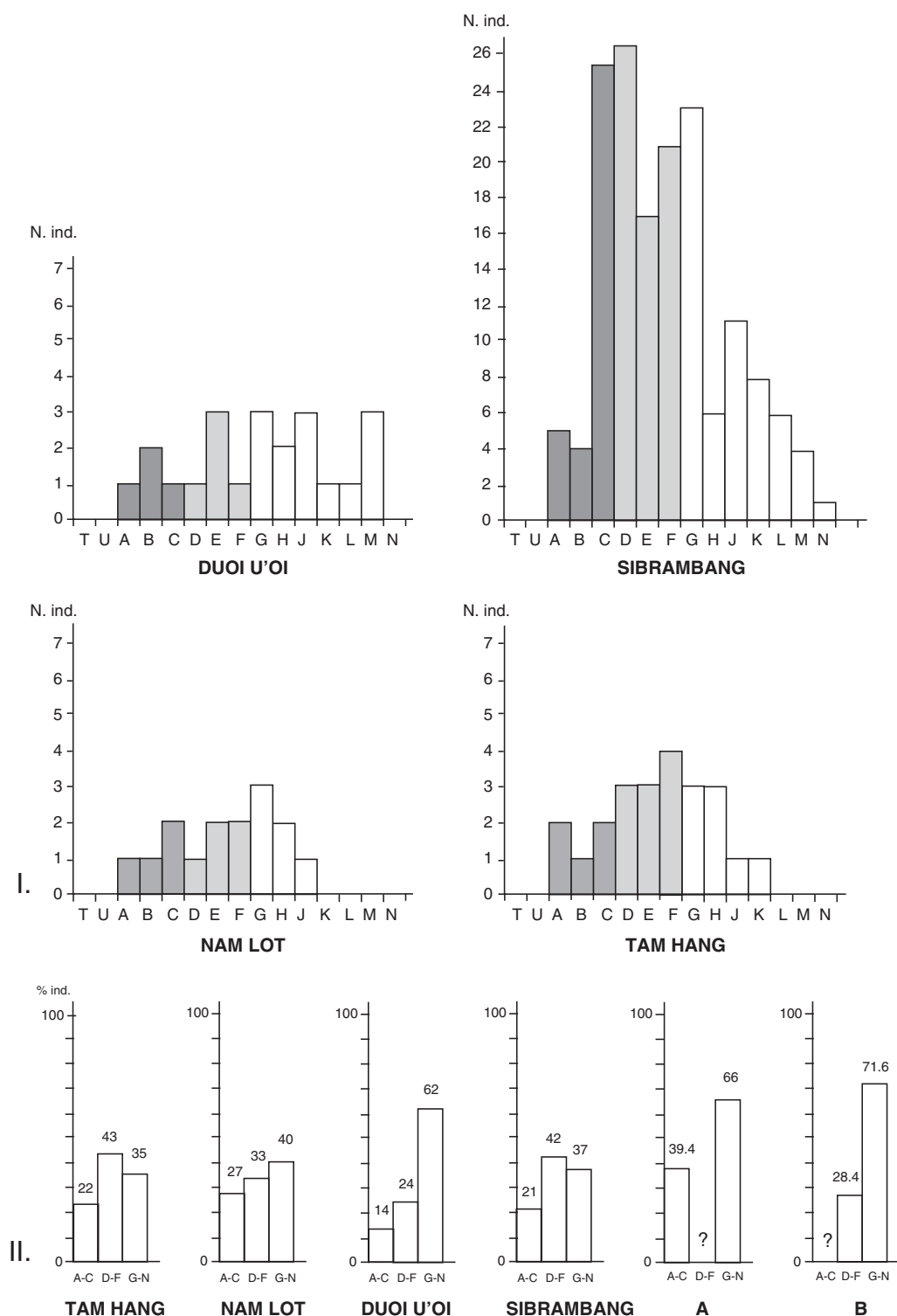


Fig. 10. I. Mortality profiles of *Sus scrofa* from Tam Hang, Nam Lot, and Duoi U'O'i, and *Sus vittatus* from Sibrambang. Age classes [T–U, A–N] are defined by Grant (1982) and Rolett and Chiu (1994): [T–U] piglets <5–8 months and [A–C] piglets <10–14 months, [D–F] young adult (<18–26 months), [G–L] 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).

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 ka; Wang et al., 2007; 279–76 ka; Rink et al., 2008) and Upper Pubu cave (280–88 ka; Rink et al., 2008), Ma U'O'i 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 paleoecological changes on the basis of faunal composition poses a real challenge. We propose that the application on the multi-

Table 13

MNIc calculated on permanent and deciduous teeth in rhinocerotids for the analysis of mortality profiles.

Sites	Number of teeth	MNIc (permanent teeth)	MNIc (deciduous teeth)
Tam Hang	N = 19	N = 4 4 lower m1-m3	N = 15 3 upper; 12 lower D2-D3; d1-d4
Duoi U'Oi	N = 51	N = 30 9 upper; 21 lower M1, M3; p2-p4/m1-m3	N = 21 7 upper; 14 lower D1-D4; d1, d3-d4
Nam Lot	N = 8	-	N = 8 1 upper; 7 lower D2; d1-d4
Sibrambang	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

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 *S. 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) (Figs. 1 and 5).

Both Punung and Sibrambang faunas are exclusively composed of modern species. The age estimate of the Punung fauna, between 128 ± 15 ka and 118 ± 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 demonstrated by 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., 2008b; Antoine, 2012). The solid chronology of the fauna (66 ± 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 (Figs. 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 southernmost 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).

In the sites we studied, Tam Hang, Nam Lot, and Duoi U'Oi, the lack of very small and light teeth of microvertebrates (<3 mm) is striking. The sedimentological analysis shows that the sites are not formed in situ (Bacon et al., 2008a,b; 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).

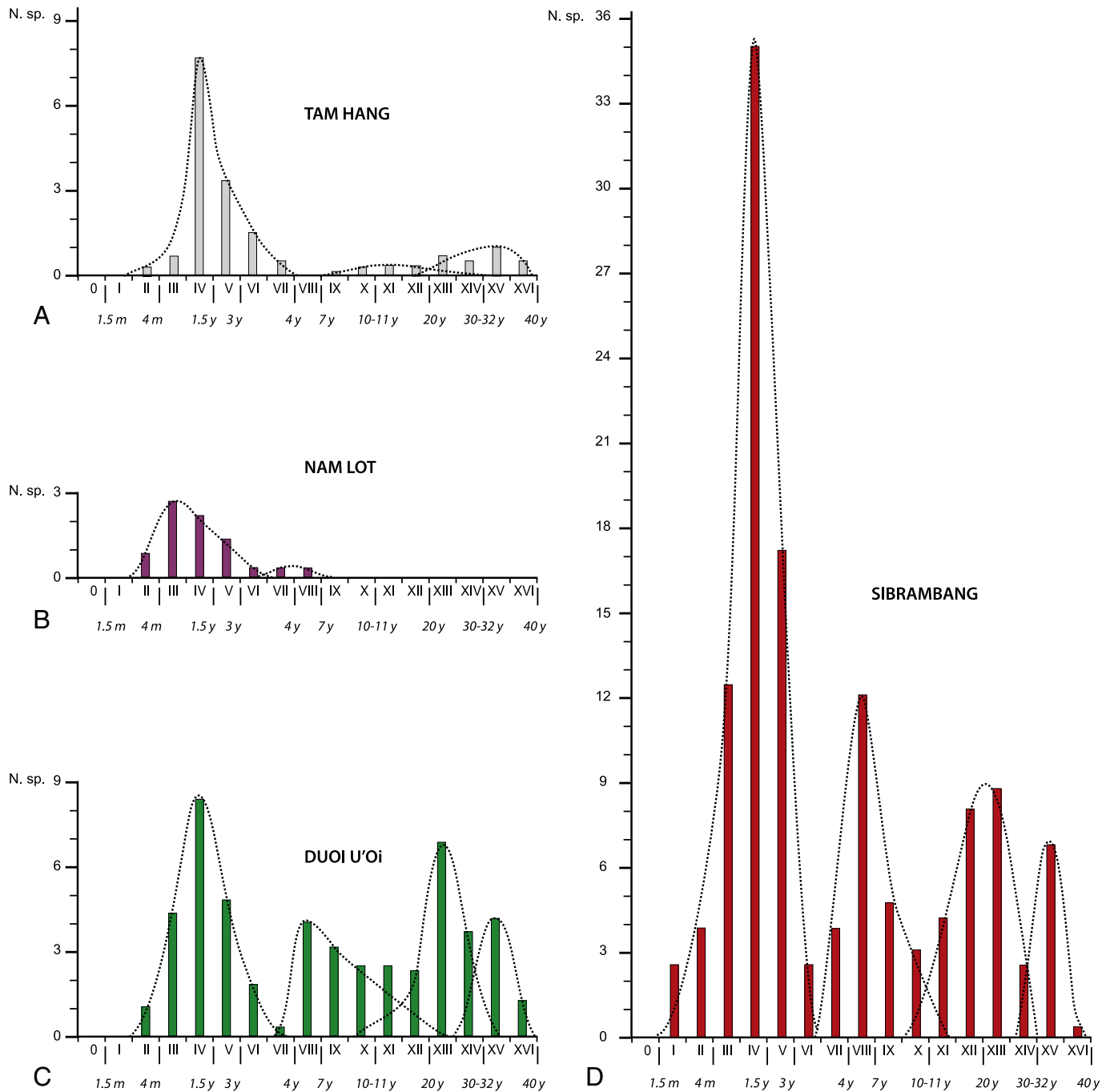


Fig. 11. Mortality profiles of rhinocerotids from (A) Tam Hang, (B) Nam Lot, (C) Duoi U'O'i, and (D) Sibrambang based on dental remains (at family level) and following a protocol modified from Hillman-Smith et al. (1986) by one of the author POA (Bacon et al., 2008a). Age classes [I–XVI] and corresponding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

It is clear that porcupines (*H. 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'O'i 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'O'i, 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'O'i 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,

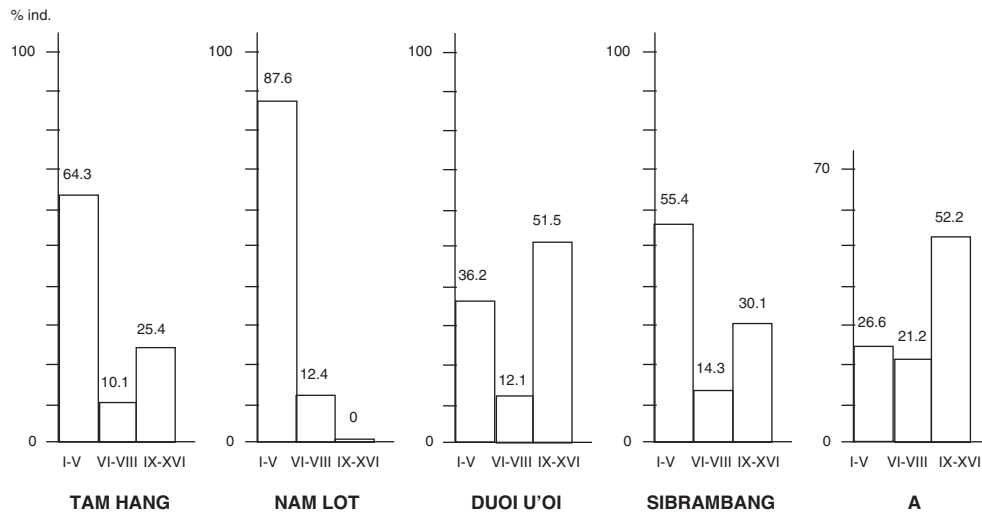


Fig. 12. Three-cohort profiles of rhinocerotids from Tam Hang, Nam Lot, Duoi U'Oi, and Sibrambang compared with (A) the natural demographic composition observed in one modern population of *Rhinoceros unicornis* from Chitawan Valley, Nepal (Laurie, 1982). Calves are less than 3 years-old [0–V], subadults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

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).

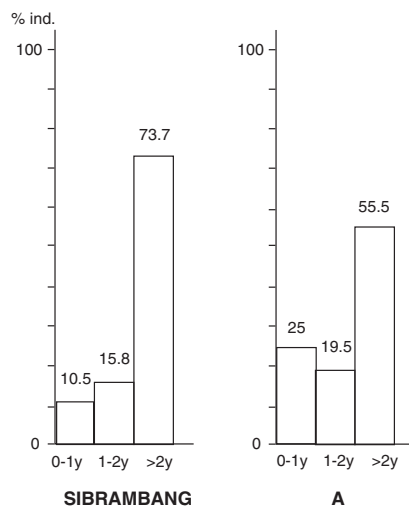


Fig. 13. Three-cohort profiles of *Tapirus indicus* from Sibrambang compared with (A) the natural demographic composition observed in one modern natural population of *Tapirus terrestris* at Chaco, Bolivia (Maffei, 2003). Calves are less than 1 year-old, subadults between 1 and 2 years-old, and adults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

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 et al. (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 paleoecological data (van der Kaars and Dam, 1995, 1997; van den Bergh et al., 1996, 2001; Wang et al., 1999; Tougaard and Montuire, 2006; Louys and Meijaard, 2010). The

Table 14

Summary table of pre- and post-depositional factors assessed in the present analysis for the five assemblages.

		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
Action of excavators	Selection of teeth	present	absent	absent	present	absent
Action of floods	Selection of large mammals vs microvertebrates	large-sized mammals	large-sized mammals	large-sized mammals	large-sized mammals	large-sized mammals
Action of porcupines	Gnawing intensity by porcupines	High (moderate in rhinocerotids) ^a	high (moderate in rhinocerotids)	high (moderate in Perissodactyla) ^a	moderate (high in ungulates)	moderate (high in tapirs + Artiodactyla)
Action of predators	Primary agent of prey selection	-	dhole (<i>Cuon alpinus</i>)	hyena (<i>Pliocrocota perrieri</i>) ^d	? tiger (<i>Panthera tigris</i>)	humans (<i>Homo</i> sp.)
	Predation pressure on <i>Muntiacus muntjak</i> ^b	-	dhole (<i>Cuon alpinus</i>)	-	-	leopard (<i>Panthera pardus</i>) dhole (<i>Cuon alpinus</i>)
	Predation pressure on large bovids ^b	-	-	hyena (<i>Pliocrocota perrieri</i>)	-	-
	Predation pressure on <i>Cervus unicolor</i> ^{b + c}	-	dhole (<i>Cuon alpinus</i>)	-	-	humans (<i>Homo</i> sp.)
	Predation pressure on suids ^c	-	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 ^{b + c}	-	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> ^c	-	-	-	tiger (<i>Panthera tigris</i>)	-

^a Results based on few observations.^b Based on bi-dimensional diagrams (large MNIF for NISP).^c Based on mortality profiles.^d Defined as *Crocota crocata* in the original description (Bacon et al., 2012).

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 paleocological 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 (*T. 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 ± 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 paleofaunas 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 (~200 kg). 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 (250–350 kg) and young rhinoceroses (~400 kg), 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,b), 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 packs from 5 to 11 individuals usually at night, early in the morning, or in the daytime (Johnsingh, 1982; Selvan et al., 2013b). With regard 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., 2015; Fourvel et al., in press). 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, 1972; 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; Blumenshine 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 (60–80 kg), 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; Cooper et al., 1999; Nowak, 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* (~110 kg; 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 cannot 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 cannot assume that humans (*H. 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 Cruz-Urbe, 1996;

Bar-Yosef, 1998; Marean, 1998; Marean and Assefa, 1999; McBrearty and Brooks, 2000).

The behavior of people present at Duoi U'O'i (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 *H. 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,b) 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 *H. sapiens* vs early modern *H. sapiens*) present at Duoi U'O'i, 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 *H. 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 analyzed 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 cannot assume that the selective hunting of sambar by humans from Duoi U'O'i originated from that of early modern *H. sapiens* present in Asia since around 100 ka, or from that of new migrants represented by anatomically modern *H. sapiens*, arriving from Africa at ca. 70–60 ka (Stringer and Andrews, 1988; Wu, 2004; Macaulay et al., 2005; Mellars, 2006a,b; 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 *H. sapiens* in northern China, at Tianyuan cave (42–39 ka) (Shang et al., 2007) and later fully modern *H. 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'O'i (~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'O'i site is all the more important since Southeast Asia lacks evidence on this pre-Upper Paleolithic 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 at Duoi U'O'i 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'O'i site (Düringer et al., 2012), which is 2 to 10 times lower than the

estimated rate in China, around 0.1 m per ka and 0.5 m 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 m 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., 2008a,b; 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'O'i assemblage, with most of the elements probably destroyed by intrakarstic mechanisms, uncertainties surround most of the possible skills by humans at this site. We cannot 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 paleoecology and paleoclimatology 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 zooarcheological data are needed to refine the knowledge of human subsistence behavior, especially that related to the emergence of modern *H. sapiens* in Southeast Asia around ~70–60 ka.

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Appendix A. Supplementary data

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