

Characteristics of Pleistocene megafauna extinctions in Southeast Asia

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Abstract

The extinction of large-bodied taxa from the Pleistocene in Southeast Asia is examined. Although the chronological resolution of these extinctions is poor, and number of excavations in the region relatively few, broad characteristics of these extinctions can be described. Many taxa which became extinct appear to have been endemic to regions within Southeast Asia, while some taxa which experienced extinction or severe range reduction occurred in several regions. Members of the latter group include proboscideans (*Stegodon* and *Palaeloxodon*), the pygmy hippopotamus (*Hexaprotodon*), the orangutan (*Pongo*), hyenas (*Crocota* and *Hyaena*), the giant panda (*Ailuropoda*), tapirs (*Tapirus* and *Megatapirus*), rhinoceroses (*Rhinoceros*), and the giant Asian ape *Gigantopithecus*. The loss of these species cannot be assigned to a single cause. Rather their disappearance is likely tied to both climatic and human agents. Unlike other regions which experienced megafauna extinctions, eustatic changes in sea level in Southeast Asia seems to have been an important factor.

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1. Introduction

The extinction of large-bodied species in the Late Pleistocene has been observed on every continent save Antarctica. The causes of extinctions have traditionally been divided into two camps—human agents or climatic agents, although increasingly researchers are opting for a multi-agent (including humans and cli-

mate) causative model (e.g. Barnosky et al., 2004; Wroe et al., 2004). Despite an ever growing body of work concerned with megafaunal extinctions in many parts of the world, the history of their disappearances remain virtually unstudied in several geographic regions. In particular, the extinction of megafauna in Southeast Asia and South America has received little scrutiny. In the case of Southeast Asia, this has largely been the result of a poor chronology for these extinctions (Martin, 1984). However, poor chronology does not prevent discussion of the extinction. While several studies have examined extinctions in Southeast Asia (e.g. Medway, 1972, 1977; Sondaar, 1987; Tougaard et al., 1996; Cranbrook, 2000, Cranbrook et

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al., 2000), these have been restricted to particular taxonomic or geographic groups. This region provides an interesting case study whereby several possible mechanisms of extinction can be examined.

It has long been thought that extinctions in Africa were less severe than in other regions of the world due to the long term coevolution of humans and megafauna (Martin, 1966; Barnosky et al., 2004). In Southeast Asia however, this period of coevolution did not occur, although the region has experienced the greatest duration of hominin habitation outside of Africa. If anything, the extinction record of Southeast Asia should parallel Europe, where it is commonly assumed that hunting for over 400,000 years of megafauna was not detrimental to their survival, and that it was only the emergence of behaviourally modern humans which led to acceleration of extinctions (Barnosky et al., 2004). Unlike Europe, but like Africa, Southeast Asia continues to host a number of extremely large-bodied species, including the Asian elephant and the rhinoceros.

Southeast Asia also holds special significance for the extinctions in Greater Australia (Sahul). The hypothesis that extinctions occurred soon after the first arrival of humans in Sahul is commonly accepted (e.g. Miller et al., 1999; Roberts et al., 2001; Miller et al., 2005), and is dependent on the assumption that the first Australians either hunted the megafauna or created significant habitat alteration resulting in their extinction. We argue that in order to understand the role of humans on the Australian ecosystem, it is necessary to also examine the effect and ecology of their ancestors—in this case, Southeast Asians.

2. Methodology

We decided to restrict this analysis to five orders of (mostly) large bodied taxa (Table 1) owing to an often arbitrary and subjective application of the term “megafauna” (see Marshall, 1984; Wroe et al., 2004), combined with a scarcity of papers dealing with body mass estimates for extinct species in Southeast Asia. As mam-

mals within the same order often exhibit a similar range of size variation (Smith et al., 2004), it can be safely assumed that those extinct species examined will not exhibit radically different body proportions to those of their most closely related living forms. The orders studied are Primates, Carnivora, Proboscidea, Artiodactyla and Perissodactyla. Only the latter three orders have a mean body mass greater than the average definition of megafauna (>44 kg as per Martin (1984); Table 1). However, it was felt that an examination of Carnivora would be prudent for two reasons: firstly, any loss of herbivores from the overall biomass would undoubtedly affect carnivores, regardless of body mass. Secondly, it is generally recognised that large body mass in mammals is a response to the need to digest low quality vegetation (Owen-Smith, 1992). It is axiomatic that these principles will not affect the Carnivora (with the notable exception of the giant panda), and that (terrestrial) carnivores are unlikely to achieve the body masses of their herbivorous prey. With respect to the primates, although they generally have a smaller body mass, this is not true of the apes: their mass falls within the common definition of “megafauna”.

Extinction lists were compiled from published literature (Tables 2–11), by comparing Pleistocene faunal assemblages with extant taxa (compiled from Corbet and Hill, 1992; Nowak, 1999). Taxonomic nomenclature follows Nowak (1999) for extant species, McKenna and Bell (1997) for extinct genera and Corbet and Hill (1992) for extant genera but extinct species, except for Proboscidean taxonomy, which follows Shoshani and Tassy (2005). The subdivision of the Pleistocene into Early (2.5 Mya to 780 kya), Middle (780 kya to 128 kya) and Late (128 kya to 11 kya) follows Jablonski and Whitford (1999). Extinction lists are sorted according to country, period and site (Tables 2–11). In the following analysis, any species designated “c.f.” is treated as the conferred species; a species designated “sp.” is ignored if another species of the same genus is present in the site, as these taxa may be conspecific. Our analysis is confined to the species and genus levels, with subspecies ignored. Taxa unassigned above genus level have not been included. Thus, our analysis provides a minimum estimate of extinction.

Southeast Asia as discussed in this paper is defined as the area of land south of the Yangtze river in China, and west of Huxley’s line (which runs between Bali and Lombok in the south, between Borneo and Sulawesi, and west of the Phillipines; Figs. 1–3). Biogeographically, Southeast Asia can be split into two distinct provinces—the Indochinese Province (consisting of southern China, Burma/Myanmar, Laos,

Table 1
Mean body mass of the five orders examined

Order	Mean body mass (grams)
Artiodactyla	47,863
Carnivora	3548
Primates	1778
Perissodactyla	398,107
Proboscidea	5,128,614

Adapted from Smith et al. (2004) and Smith et al. (2003).

Cambodia, Vietnam and northern Thailand) and the Sundaic Province (consisting of southern Thailand, Malaysia, Sumatra, Java and Borneo) on the basis of climatic, botanical and zoological factors (Lekagul and McNeely, 1988; Gray et al., 1994; Tougaard, 2001). Each province was separated into their individual countries (Thailand was grouped within the Indochinese province as all sites examined from this country are situated in northern Thailand) and taxa were examined independently for each. Countries share a number of extinctions or range reductions of the same genera (Table 12). Among these taxa, some are discussed in detail in the text. These include *Stegodon*, *Hexaprotodon*, *Palaeloxodon*, *Pongo*, *Crocota*, *Hyae-na*, *Ailuropoda*, *Rhinoceros*, *Tapirus*, *Megatapirus* and *Gigantopithecus*.

3. Results and discussion

The extinction list for each country is provided in Tables 2–11. Generic-level extinctions for the Early, Middle and Late Pleistocene are shown in Figs. 1, 2 and 3 respectively.

3.1. Indochinese province

3.1.1. Southern China

The extinction list for Southern China (Table 2) is the most extensive for the region, largely because of the larger number of excavations that have taken place there (Han and Xu, 1985). The extinction list and the chronology of the sites are based on Han and Xu (1985) and Kahlke (1961), and as a discussion of each site would unnecessarily encumber this manuscript, the interested reader is directed to these works for more information. The relatively large sample should allow for detection of diachronic trends not discernible within other (smaller) regional samples. It should be noted however that this list is by no means exhaustive.

The southern Chinese and Burmese extinction lists are the only ones to show progressively fewer extinctions through the Pleistocene (Figs. 1–3), suggesting that Early Pleistocene extinctions were more significant for the northern parts of Southeast Asia. Many of the species that became extinct during the Early Pleistocene in southern China appear to be the last surviving members of lineages that had been in decline since the Miocene (e.g. *Hesperotherium*). Of interest during this period is the extinction of *Acinonyx* and *Gazella*, which are currently restricted to Africa (Nowak, 1999). In addition to these, most species of *Stegodon* became extinct during the Early Pleistocene.

The Middle Pleistocene has far fewer generic extinctions. This period saw the extinction of the last members of *Equus* and *Gigantopithecus* in the region. Northern Chinese hominins specialised in predation on *Equus* until at least Middle Pleistocene times (Keates, 2003), and evidence suggests that early settlers roasted horse heads at Zhoukoudian (Binford and Stone, 1986). *Equus* is also one genus thought to have been hunted to extinction by early Clovis hunters in North America (Martin, 1984), as it coincides with the colonisation of the Americas by humans (Barnosky et al., 2004). The colonisation of China by humans may have also affected the horse. Equally the extinction of the horse may mark a change in foraging strategy by humans in the region. This change may also have adversely affected the distribution of *Gigantopithecus* (but see below). The Late Pleistocene saw the disappearance of many species that seem to characterise the Southeast Asian Pleistocene extinctions at an interregional level (see below), however, some species that became extinct in the Late Pleistocene in other regions appear to have survived into the Holocene in China (Ma and Tang, 1992; Tong and Liu, 2004). These include *Crocota ultima*, *Stegodon orientalis* and *Megatapirus augustus* (see Tong and Liu, 2004 for a discussion on sites and dates).

3.1.2. Burma/Myanmar

Deposits in Burma are described in detail by Colbert (1943), and the extinction list provided in Table 3 is drawn from his species lists. Colbert (1943) describes three principal faunas, those being from Terrace deposits, Mogok Caves and the Irrawaddy beds. The Terrace deposits are considered by Colbert (1943) to be Upper Pleistocene in age and consist solely of extant fauna, they are therefore not discussed further here.

The Mogok caves are fissures found in the Mogok district, and are interpreted as Middle Pleistocene by Colbert on the basis of the presence of *Stegodon*, although Hooijer (1950) considers them ‘Lower’ Pleistocene. Colbert provides details of two caves, however of the extinct species listed in Table 3, Colbert mentions finding only the proboscideans *in situ*. The presence of *Ailuropoda* is based on collection by others (notably villagers) not from either cave described, but rather from nearby caves. However given the ubiquitous nature of this species during the Middle Pleistocene in Southeast Asia, its presence in Burma during this time is warranted.

The Irrawaddy beds represent both reworked and *in situ* fossils, which likely span the ages of Late Pliocene to Early Pleistocene (Colbert, 1943). They are

Table 2

Extinct species for Southern China; sites ordered into Early, Middle and Late Pleistocene, listed chronologically (oldest to youngest; for full discussion of chronology see text); * indicates local extinction; † indicates global extinction; bold indicates last appearance

Early Pleistocene

Gigantopithecus cave

†*Gigantopithecus blacki***Pongo* sp.***Cuon fubius******Artonyx fminor******Ailuropoda fmicrota*****Hyaena fbrevirostris****Felis fteilhardi*****Acinonyx fpleistocaenicus*†***Gomphotherium serridentoides***†*Stegodon preorientalis***Equus fyunnanensis*

Yuanmou

Canis fyuanmoensis***Vulpes* cf. †*chikushenensis*****Hyaena fbrevirostris*†***Megantereon meganteron***†***Stegodon elephantoides***†***Stegodon zhaotongensis***†***Stegodon yuanmoensis*****Equus fyunnanensis*†***Hesperotherium* sp.***Rhinoceros fsinensis****Muntiacus flacustris***

Jianshi

†*Gigantopithecus blacki***Hyaena fbrevirostris*†*Stegodon* sp.****Equus fyunnanensis*****Tapirus findicus*

Bijiashan

Hyaena fbrevirostris*†*Gomphotherium serridentoides***†***Stegodon* cf. *preorientalis***†*Stegodon orientalis***Tapirus findicus**Rhinoceros fsinensis****Sus fxiaozhu****Sus fbijashanensis*

Middle Pleistocene

Daxin

†*Gigantopithecus blacki***Pongo* sp.†*Stegodon orientalis**Rhinoceros fsinensis*†*Megatapirus augustus*†***Dicoryphochoerus ultimus***†***Megalovis guangxiensis******Sus fbijashanensis***

Hoshantung

****Pongo pygamaeus*****Crocota crocuta**Felis *lynx*†*Palaeoloxodon namadicus*†*Megatapirus augustus*

Hsingan

Macaca frobustus***Cuon fsimplicidens******Martes fsinensis***†***Melodon simplicidens****Rhinoceros fsinensis*†*Megatapirus augustus****Muntiacus fszechuanensis******Bubalus fbrevicornis*******Tapirus indicus***

Koloshan

****Pongo pygamaeus*****Crocota crocuta*†*Palaeoloxodon* sp.†*Stegodon orientalis**Rhinoceros fsinensis***Tapirus findicus*

Wuming

†*Gigantopithecus blacki***Hyaena* sp.†*Stegodon* sp.

(continued on next page)

Table 2 (continued)

Middle Pleistocene

Wuming

*Rhinoceros †sinensis**Naemorhedos cf. †sumatraensis*

Bama

†Gigantopithecus blacki**Pongo* sp.*Rhinoceros †sinensis***Tapirus* sp.†*Stegodon* sp.

Guanyindong

†Stegodon cf. orientalis**Crocota crocuta*†*Stegodon guizhouensis*†*Megatapirus augustus**Rhinoceros †sinensis****Naemorhedos †sumatraensis******Vulpes cf. †vulgaris*****Equus* sp.

Shilontou

Hyaena †brevirostris*†*Stegodon orientalisRhinoceros †sinensis*

Late Pleistocene

Maba

Hyaena* sp.†*Stegodon* sp.†*Palaeoloxodon namadicus*Tapirus* sp.

Tongzi

Pongo** sp.**Crocota crocuta*†*Megatapirus augustus**Rhinoceros †sinensis*†*Stegodon orientalis*Tapirus** sp.

Changyang

***Hyaena †brevirostris**†*Megatapirus augustus**Rhinoceros †sinensis*†*Stegodon orientalis*

Jiande

Crocota crocuta*^b†*Megatapirus augustusRhinoceros †sinensis*†*Stegodon orientalis***†Palaeoloxodon cf. namadicus*****Ovis** sp.

Liujiang

†*Megatapirus augustus*^b***Rhinoceros †sinensis***†*Stegodon orientalis*^b

For the full list of species from each site see Han and Xu (1985), except Hoshantung, Hsingan and Koloshan see Kahlke (1961).

^a Not formally described.

^b Survived into the Holocene (Tong and Liu, 2004).

Table 3

Extinct species for Burma; sites ordered into Early and Middle Pleistocene, listed chronologically (oldest to youngest; for full discussion of chronology see text); * indicates local extinction; † indicates global extinction

Early Pleistocene
Irrawaddy beds
† <i>Stegodon elephantoides</i>
† <i>Stegalophodon latidens</i>
† <i>Palaeoloxodon namadicus</i>
<i>Rhinoceros †sivalensis</i>
* <i>Equus †yunnanensis</i>
† <i>Hipparion</i> cf. <i>antelopinum</i>
* <i>Potamochoerus</i> sp.
* <i>Hexaprotodon †iravaticus</i>
* <i>Gazella</i> sp.
† <i>Hemibos triquetricornis</i>
† <i>Proleptobos birmanicus</i>
† <i>Merycopotamus dissimilis</i>
Middle Pleistocene
Mogok caves
* <i>Ailuropoda melanoleuca</i>
† <i>Stegodon orientalis</i>
† <i>Palaeoloxodon namadicus</i>

For the full list of species from each site see Colbert (1943).

likely derived from the Upper Irrawadies, and share many species in common with the Siwalik faunas of India (Colbert, 1943). The Mogok faunas represent more eastern Asian characteristics (Colbert, 1943), although Hooijer (1950) argues that the fauna agrees with that of the Tatrot zone of the Siwaliks. If Colbert's hypothesis is borne out, then these two deposits record a faunal turnover between the Lower and Middle Pleistocene.

3.1.3. Laos

The extinction list for Laos (Table 4) comes from deposits found in the “Chaîne Annamitique septentrionale” (northern Annamese Cordillera), described by Fromaget (1936) and Arambourg and Fromaget (1938). Although these authors mention two “sites”, Tam Hang (Fromaget, 1936) and Tam Nang (Arambourg and Fromaget, 1938), the specific locations of these sites are not provided.

The site of Tam Hang as recorded by Fromaget (1936) is presumably the same as that dated to the Late Pleistocene by Shackelford (2003). Fromaget (1936) does not record the specific fauna recovered from this site, remarking only on its similarity to that of other Pleistocene Southeast Asian faunas including those of Trinil and Zhoukoudian. He also records the recovery of further Pleistocene mammals from a silt and gravel layer 12 km to the north of Tam Hang, at 1000 m altitude. It is from this horizon that the faunal list comes (although this is not

entirely clear), and Fromaget notes that the two faunas are the same. To our knowledge, the fauna from Tam Hang has not been further investigated, and among the countries studied here, Laos remains one of the most starved of palaeontological research. Based on the presence of *Pongo* and *Megatapirus* within the faunal list, it is likely that this fauna belongs to the Middle Pleistocene. Tougaard (1998) in her biochronological scheme places Tam Hang in the middle of the Middle Pleistocene, and tentatively dates this period as between 170 ka and 475 ka (however this determination appears to be based on a combined fauna between Tam Hang and Tam Nang, discussed in more detail below). If this is the case, either Fromaget and Shackelford's “Tam Hang” represent separate deposits within the same site, or the two faunas (“Tam Hang” proper, and the site north of Tam Hang) described by Fromaget (1936) are not contemporaneous (unlikely if his contention that the faunas are the same is borne out). The fauna is therefore interpreted here as Middle Pleistocene.

Table 4

Extinct species for Laos; sites listed chronologically (oldest to youngest; for full discussion of chronology see text); bold indicates last appearance; * indicates local extinction; † indicates global extinction

Middle Pleistocene	Tam Hang
Tam Nang, tuff layer, lower horizon	
<i>Sus</i> cf. <i>†brachygnathus</i>	<i>Macca †robustus</i>
<i>Naemorhedus</i> cf. * <i>goral</i>	* <i>Pongo pygmaeus</i>
<i>Cervus</i> cf. <i>†leptodus</i>	<i>Ursus</i> cf. <i>†angustidens</i>
† <i>Proboselaphus</i> sp.	† <i>Megatapirus augustus</i>
<i>Canis</i> cf. <i>†cynooides</i>	<i>Rhinoceros</i> cf. <i>†plicidens</i>
* <i>Crocota crocata</i>	<i>Rhinoceros</i> cf. <i>†sivalensis</i>
<i>Felis †micotis</i>	<i>Sus</i> cf. <i>†lydekkeri</i>
* <i>Pongo pygmaeus</i>	<i>Cervus †grayi</i>
* <i>Ailuropoda melanoleuca</i>	
Tam Nang, tuff layer, upper horizon	
<i>Ursus †premalayanus</i>	
† <i>Stegodon sinensis</i>	
† <i>Palaeoloxodon namadicus</i>	
<i>Rhinoceros †sivalensis</i>	
† <i>Megatapirus augustus</i>	
<i>Sus †lydekkeri</i>	
<i>Arctonyx †rostratus</i>	
<i>Panthera</i> * <i>leo</i>	
<i>Felis</i> aff. <i>†fissidiorensis</i>	
? <i>Bibos †geron</i>	
? <i>Bubalus †teilhardi</i>	
<i>Cervus †orientalis</i>	
<i>Macca</i> cf. <i>†andersonni</i>	
<i>Macaca †robustus</i>	
Tam Nang, red layer	
* <i>Tapirus</i> sp.	
† <i>Spiroceros</i> sp.	
<i>Ursus †premalayanus</i>	
<i>Macaca †robustus</i>	

For the full list of species from: Tam Hang see Fromaget (1936); Tam Nang see Arambourg and Fromaget (1938).

The second site examined, that of Tam Nang (Arambourg and Fromaget, 1938), is often overlooked or combined with that of Tam Hang when faunal lists of Laos are compiled. We have found no evidence to suggest that Tam Hang and Tam Nang are the same site, and proceed on the understanding that they represent separate sites. The fauna recovered from Tam Nang comes from two Quaternary layers, a red silt layer which sits unconformably above a calcareous tuff divided into two “horizons” (an upper and a lower horizon). The extinction list is separated in accordance with these layers and horizons (Table 7). Arambourg and Fromaget (1938) compare the fauna from these deposits with those of Pleistocene sites in Java and China. They assign an

age of “Pleistocene inférieur” to the calcareous layers, and that of “Quaternaire moyen ou supérieur” for the red silt layer. We interpret the calcareous layers and the red silt layers as Middle Pleistocene, due to the presence of typical Middle Pleistocene fauna within the list (such as *Ailuropoda*, *Megatapirus*, *Stegodon*, *Pongo*, *Macaca robustus* and *Palaeoloxodon*) although we acknowledge the tenuousness of such dating. We further interpret the red silt layers as being younger than the calcareous ones based on their relative stratigraphic positions as described by Arambourg and Fromaget (1938).

Of interest in this extinction list is the presence of *Panthera leo*, the Asiatic lion. If the specific diagnosis made by Arambourg and Fromaget is borne out, this

Table 5

Extinct species for Vietnam; sites ordered into Early, Middle and Late Pleistocene, listed chronologically (oldest to youngest; for full discussion of chronology see text); bold indicates last appearance; * indicates local extinction; † indicates global extinction

Middle Pleistocene

Tham Khuyen

†***Gigantopithecus blacki***
 **Pongo pygmaeus*
 †? *Palaeoloxodon namadicus*
 †*Stegodon orientalis*
Rhinoceros †*sinensis*
Sus cf. †*lydekkeri*
 **Ailuropoda melanoleuca*
Ursus* **malayanus
 †*Megatapirus augustus*

Tham Om

†*Palaeoloxodon* cf. *namadicus*
 †*Stegodon orientalis*
Rhinoceros †*sinensis*
 ****Elaphodus* sp.**
 **Ailuropoda melanoleuca*
Bos (*Bibos*) **gaurus*
 †*Megatapirus augustus*
 †*Naemorhedus sumatraensis*

Tham Hai

†? ***Gigantopithecus blacki***
 **Pongo pygmaeus*
 †*Stegodon orientalis*
Rhinoceros †*sinensis*

Late Pleistocene

Hang Hum I

†*Stegodon orientalis*
Rhinoceros †*sinensis*
 †*Megatapirus augustus*
Sus* cf. †*lydekkeri
Sus* cf. ?*officinalis

Keo Leng

****Pongo pygmaeus***^a
 †*Stegodon orientalis*
 **Ailuropoda melanoleuca*
Rhinoceros †*sinensis*
 †*Megatapirus augustus*
Sus cf. †*lydekkeri*
 †*Naemorhedus sumatraensis*

Hang Hum II

**Pongo pygmaeus*
 †***Palaeoloxodon* cf. *namadicus***

Ma U’Oi

Rhinoceros* cf. **unicornis

For the full list of species from: Tham Khuyen, Tham Hai, Tham Om, Hang Hum I, Hang Hum II and Keo Leng see Olsen and Ciochon (1990); Ma U’Oi cave see Bacon et al. (2004).

^a May have survived into the Holocene (Kahlke, 1972).

would represent the most eastern example of this species; its current range in Asia restricted to western India, although subfossil species have been found as far east as Bengal (Corbet and Hill, 1992). In addition to taxa mentioned above, Laos during this time saw the disappearance of two species each of *Rhinoceros*, *Macaca*, *Ursus* and *Sus*.

3.1.4. Vietnam

The extinction list for Vietnam (Table 5) is compiled on the basis of three Middle Pleistocene and four Late Pleistocene sites. Thum Khuyen and Tham Hai were roughly estimated at between 300 ka and 200 ka on the basis of biostratigraphic correlations (Olsen and Ciochon, 1990); however subsequent absolute dating assigned an age of 475 ka for Tham Khuyen on the basis of ESR dating of tooth enamel (Ciochon et al., 1996). Again on the basis of faunal correlations dates of 140–80 ka and 30–20 ka were suggested for Hang Hum and Keo Leng respectively (Olsen and Ciochon, 1990). Dating of Ma U’Oi is even more tenuous, being tentatively assigned to the Late Pleistocene by Bacon et al. (2004) on the basis of its similarity with other Late Pleistocene faunas of Southeast Asia. With regards to palaeoenvironments of the various sites, Bacon et al. (2004) suggest that the absence of *Pongo* from Ma U’Oi indicates an open woodland environment, while the presence of *Niviventer fulvescens* and *Leopoldamys sabinus*, two Murid species, suggests the presence of lowlands and foothills of evergreen forests. The presence of *Gigantopithecus* and *Pongo* in Tham Khuyen and Tham Hai, and the latter also in Hang Hum and Keo Leng suggests the presence of tropical to sub-tropical vegetation, while the presence of *Ailuropoda* suggests temperate bamboo species.

Vietnam and Southern China are, at present, the only two countries where *Gigantopithecus* fossils have been found (Tables 2 and 5). This ape became extinct during the Middle Pleistocene (Fig. 2). As with China, this could mark the time of the first occurrence of *Homo sapiens*, or alternatively, a change in foraging strategies of humans in the region. Apart from *Pongo*, *Ailuropoda*, *Stegodon*, *Palaeoloxodon* and *Megatapirus* (discussed in more detail below), Vietnam saw little in the way of additional generic extinction.

3.1.5. Cambodia

Cambodia shows relatively few extinctions on the basis of the sites examined here. Due to the difficulty in locating references for Cambodia, the list provided by Tougard (2001) is the primary reference used, however this is supplemented by the species list provided by Carbonnel and Guth (1968). Although both sites are from

Table 6

Extinct species for Cambodia; * indicates local extinction; † indicates global extinction

Middle Pleistocene	
Phnom Loang	Préah Vihear
* <i>Pongo pygmaeus</i>	* <i>Crocota crocuta</i>
* <i>Crocota crocuta</i>	<i>Cervus †grayi</i>
* <i>Tapirus indicus</i>	* <i>Dicerorhinus</i>
	† <i>mercki</i>

For the full list of species from: Phnom Loang see Tougard (2001); Préah Vihear see Carbonnel and Guth (1968).

Phnom Loang, it is unlikely (on the basis of the faunas recorded) that these sites are the same. In Table 6, we have followed the naming conventions used by both authors: i.e. Phnom Loang for those species listed by Tougard (2001) and Préah Vihear for those listed by Carbonnel and Guth (1968). Phnom Loang is described as Middle Pleistocene by Tougard (2001), while Carbonnel and Guth (1968) attribute a lower to middle Pleistocene age on the basis of the presence of *Dicerorhinus mercki* and *Crocota crocuta*. The site is interpreted as Middle Pleistocene here. Among the extinction list, Cambodia sees the loss of *Pongo*, *Crocota*, *Tapirus*, *Dicerorhinus mercki* and *Cervus grayi*, disappearances characteristic of Southeast Asia.

3.1.6. Thailand

The extinction lists for Thailand (Table 7) comes from four sites: Kao Pah Nam (Pope et al., 1981), the Cave of the Monk of Ban Fa Suai (Zeiton et al., 2005), Thum Wiman Nakin and Thum Phra Khai Phet (Tougaard, 1998), all being Middle Pleistocene in age. The only site to be given an absolute age is that of Thum Wiman Nakin. Calcified clay sediments from above the fossiliferous layer have been dated to 169 ka ± 11 ka, thereby providing an absolute minimum age to the fossils (Esposito et al., 2002). Thum Phra Khai Phet is thought to be of a comparable age based on taxonomic similarity (Tougaard, 1998). Zeiton et al. (2005) consider the Cave of the Monk to be Middle to late Middle Pleistocene based on the presence of *Stegodon–Ailuropoda* fauna at the site, although they acknowledge the tenuousness of such dating. The Kao Pah Nam site is estimated at 690 ka based on its geological position and fauna (Pope et al., 1981).

Thailand saw the disappearance of *Ailuropoda melanoleuca*, *C. crocuta*, *Pongo pygmaeus*, *Sus* cf. *barbatus*, *Rhinoceros* cf. *unicornis*, *Cervus eldii*, *Nemorhaedus* c.f. *goral*, *Nemorhaedus* c.f. *caudatus*, *Tapirus* sp. and *Stegodon* sp. during the Middle Pleistocene (Table 7). Tougaard (1998) briefly addressed the extinction question for Thailand however her examination was restricted to only four species—*A. melanoleuca*, *C. crocuta*, *P. pygmaeus* and *R. cf. unicornis*. She advocated a

Table 7

Extinct species for Thailand; sites listed chronologically (oldest to youngest; for full discussion of chronology see text); bold indicates last appearance; * indicates local extinction; † indicates global extinction

Middle Pleistocene		
Kao Pah Nam		Cave of the Monk (Ban Fa Suai)
* ? <i>Pongo</i> sp.		* <i>Pongo</i> cf. <i>pygmaeus</i>
* <i>Crocota</i> sp.		* <i>Ailuropoda</i> cf. <i>melanoleuca</i>
<i>Cervus feldii</i>		<i>Cervus</i> cf. <i>feldii</i>
Thum Wiman Nakin	Thum Phra Khai Phet	? <i>Nemorhaedus</i> c.f. * <i>goral</i>
* <i>Pongo pygmaeus</i>	* <i>Ailuropoda melanoleuca</i>	<i>Nemorhaedus</i> c.f. * <i>caudatus</i>
* <i>Ailuropoda melanoleuca</i>	* <i>Crocota crocuta</i>	† <i>Stegodon</i> sp.
* <i>Crocota crocuta</i>	<i>Sus</i> * <i>barbatus</i>	
<i>Rhinoceros</i> * <i>unicornis</i>		
<i>Sus</i> * <i>barbatus</i>		
<i>Cervus</i> * <i>eldii</i>		

For the full list of species from: Thum Wiman Nakin and Thum Phra Khai Phet see Tougard (1998); Kao Pah Nam see Pope et al. (1981) Cave of the Monk see Zeiton et al. (2005).

multi-causal mode of extinction, with *Ailropoda* and *Crocota* affected by changes in climate and vegetation, while *Pongo* and *Rhinoceros* were argued to have been adversely affected by the negative ecological influence of humans. Palaeoenvironmental analysis of the region based on the mammals from Thum Wiman Nakin suggest that the region was composed of slightly open forested landscape with relatively humid conditions, representing a more temperate and open environment than presently found (Tougaard and Montuire, 2006).

3.2. Sundaic province

3.2.1. Malaysia

The Malaysian fossil record is poorly known for the Pleistocene and the extinction list provided (Table 8) is based on only one site, Tambun, being Middle Pleistocene in age (Medway, 1972). Besides *Palaeoloxodon*, Malaysia saw the local extinction of *Hexaprotodon* and *Duboisia* during this time.

3.2.2. Borneo/Kalimantan

The late Pleistocene of Borneo saw the local extinction of four genera, *Cuon*, *Panthera*, *Tapirus* and *Rhinoceros*,

Table 8

Extinct species for Malaysia; * indicates local extinction; † indicates global extinction

Middle Pleistocene
Tambun
† <i>Palaeoloxodon namadicus</i>
* <i>Hexaprotodon</i> sp.
* <i>Duboisia santeng</i>

For the full list of species see Medway (1972).

based on the faunal records of Niah Caves (Table 9), dated on the basis of ^{14}C at 40 ka±1 ka (Medway, 1964; Harrison, 1996; Barker, 2002). Cranbrook addressed the question of megafauna extinctions in Borneo in a number of publications (Medway, 1972, 1977; Cranbrook, 2000, Cranbrook et al., 2000). He noted that the only animal to become extinct from the Niah caves faunas was the giant pangolin, *Manis gigantea*. He also noted the disappearance of *Hexaprotodon* and proboscideans from Borneo (Cranbrook, 2000, Cranbrook et al., 2000), however their specific provenance could not be determined (and hence they are not listed in Table 9). Given that the majority of these were grazers or browsers dependent on short vegetation, he concluded their extinctions were largely the result of changes in the vegetative mosaic of the region. Medway (1972) postulated that the loss of most grazing animals by the close of the Late Pleistocene were tied to the loss of large tracts of grasslands, while Holocene changes in vegetation were detrimental to forest dwelling species such as *Tapirus* and *Pongo*. These floristic changes are thought to result from global climatic changes

Table 9

Extinct species for Borneo; * indicates local extinction

Late Pleistocene
Niah Caves
* <i>Cuon alpinus</i> ^a
* <i>Panthera tigris</i>
* <i>Tapirus indicus</i> ^b
* <i>Rhinoceros sondaicus</i> ^b

For the full list of species see Medway (1960).

^a May in fact be *Canis familiaris* (Cranbrook, 2000, Cranbrook et al., 2000).

^b May have survived until Holocene (Medway, 1960; Cranbrook, 2000, Cranbrook et al., 2000).

acting regionally (Medway, 1972, 1977; Cranbrook, 2000, Cranbrook et al., 2000), in particular the rising mean ambient temperatures and an increasing, less seasonal rainfall (Medway, 1972). The change from a more complex and heterogenous vegetation structure present in the Pleistocene to a more uniform rainforest environment today may have resulted in many taxa becoming extinct. This is likely to have happened during the transition to the last glacial (see below). Interestingly, this causative model is also posited for a number of other megafauna extinctions in both North America and Australia (e.g. Guthrie, 1984; Lundelius, 1989; Graham et al., 1996; Price and Sobbe, 2005).

3.2.3. Sumatra

The extinction list for Sumatra (Table 10) comes from one site, Lida Ajer, being Late Pleistocene in age (de Vos, 1983). All but one species (*Panthera pardus*) are currently extant on the island. Meijaard (2004) suggested that *P. pardus* could not have survived on Sumatra due to the limited ungulate biomass and carnivore competition once Sumatra became isolated from other Southeast Asian islands from the last glacial maximum onwards.

3.2.4. Java

The palaeontological record for Java is, along with that of Southern China, the best known for the region. Extinction lists (Table 11) were compiled from the following faunal units (listed in chronological order): Satir, Ci Saat, Trinil H.K., Kedung Brubus, Ngangdong, Punung and Wajak (Leinders et al., 1985; Theunissen et al., 1990; van den Bergh et al., 2001). The oldest faunas, those of Satir and Ci Saat, have been dated to 1.5 and 1.2 Ma respectively (de Vos et al., 1994; de Vos and Long, 2001). The Satir fauna is thought to represent a swampy environment based on pollen records, while that of Ci Saat represents a drier environment with more grasses (Sémah, 1984; de Vos and Long, 2001). A faunal turnover is evident from these sites, with the more primitive *Hexaprotodon simplex* and *Tetralophodon bumiajuensis* replaced by the more derived *Hexaprotodon sivalensis* and *Stegodon trigonocephalus* respectively (de Vos et al., 1994). These replacements are likely tied to the environmental change recorded by the pollen records,

Table 10
Extinct species for Sumatra; * indicates local extinction

Late Pleistocene
Lida Ajer
<i>Panthera</i> * <i>pardus</i>

For the full list of species see de Vos (1983).

Table 11

Extinct species for Java; sites ordered into Early, Middle and Late Pleistocene, listed chronologically (oldest to youngest; for full discussion of chronology see text); bold indicates last appearance; * indicates local extinction; † indicates global extinction

Early Pleistocene
Satir
† <i>Sinomastodon bumiajuensis</i>
* <i>Hexaprotodon</i> † <i>sivalensis</i>
Ci Saat
† <i>Stegodon trigonocephalus</i>
* <i>Hexaprotodon</i> † <i>sivalensis</i>
<i>Axis</i> † <i>hydekkeri</i>
† <i>Duboisia santeng</i>
<i>Bubalus</i> † <i>palaeokerabau</i>
<i>Bos</i> (<i>Bibos</i>) † <i>palaesondaicus</i>
Trinil H.K.
† <i>Stegodon trigonocephalus</i>
<i>Axis</i> † <i>hydekkeri</i>
† <i>Duboisia santeng</i>
<i>Bubalus</i> † <i>palaeokerabau</i>
<i>Bos</i> (<i>Bibos</i>) † <i>palaesondaicus</i>
<i>Sus</i> † <i>brachgnathus</i>
<i>Cuon</i> †(<i>Mececyon</i>) <i>trinilensis</i>
Middle Pleistocene
Kedung Brubus
* <i>Hyaena</i> † <i>brevirostris</i>
† <i>Stegodon trigonocephalus</i>
† <i>Stegodon?</i> <i>Hypsilophus</i>
<i>Elephas</i> † <i>hysudrindicus</i>
<i>Rhinoceros</i> *<i>unicornis</i>
* <i>Hexaprotodon</i> † <i>sivalensis</i>
<i>Axis</i> † <i>hydekkeri</i>
† <i>Duboisia santeng</i>
† <i>Epileptobos groeneveldtii</i>
<i>Bubalus</i> † <i>palaeokerabau</i>
<i>Bos</i> (<i>Bibos</i>) † <i>palaesondaicus</i>
<i>Sus</i> † <i>macrognathus</i>
Late Pleistocene
Ngangdong
† <i>Stegodon trigonocephalus</i>
<i>Elephas</i> † <i>hysudrindicus</i>
* <i>Hexaprotodon</i> † <i>sivalensis</i>
<i>Bubalus</i> † <i>palaeokerabau</i>
<i>Bos</i> (<i>Bibos</i>) † <i>palaesondaicus</i>
? <i>Sus</i> † <i>brachgnathus</i>
<i>Sus</i> † <i>macrognathus</i>
Punung
<i>Macaca</i> * <i>nemestrina</i>
<i>Hylobates</i> * <i>syndactylus</i>
* <i>Pongo pygmaeus</i>
* <i>Ursus malayanus</i>
* <i>Helarctos malayanus</i>
<i>Sus</i> * <i>barbatus</i>
* <i>Naemorhedus</i> (<i>Capricornis</i>) <i>sumatraensis</i>

For the full list of species from: Satir, Ci Saat, Trinil H.K., Kedung Brubus and Ngangdong see van den Bergh et al. (2001); Punung see de Vos (1983).

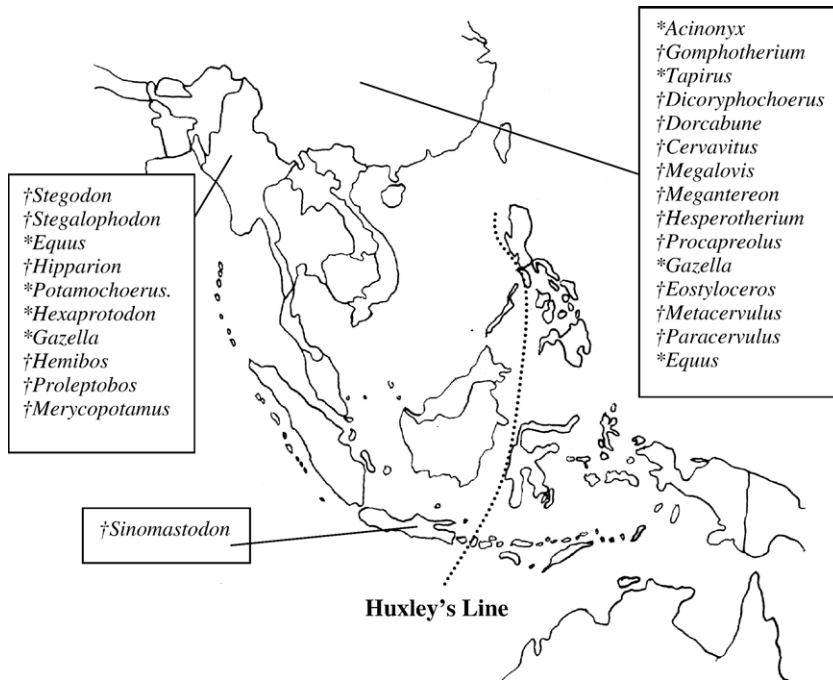


Fig. 1. Generic level extinctions in the Early Pleistocene. †—complete extinction; *—local extinction. For complete extinction list and a break down of sites refer to [Tables 2–11](#).

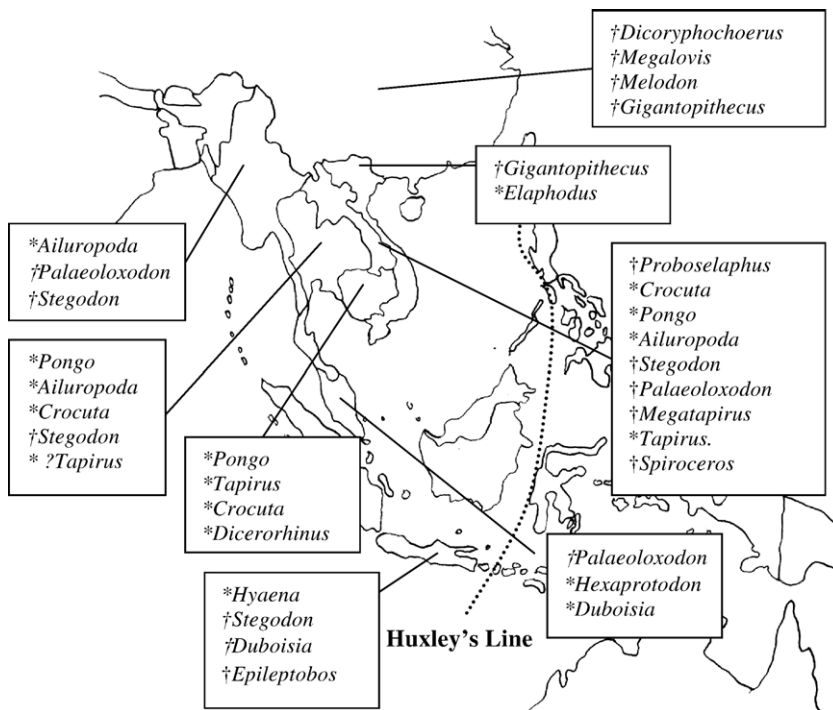


Fig. 2. Generic level extinctions in the Middle Pleistocene. †—complete extinction; *—local extinction. For complete extinction list and a break down of sites refer to [Tables 2–11](#).

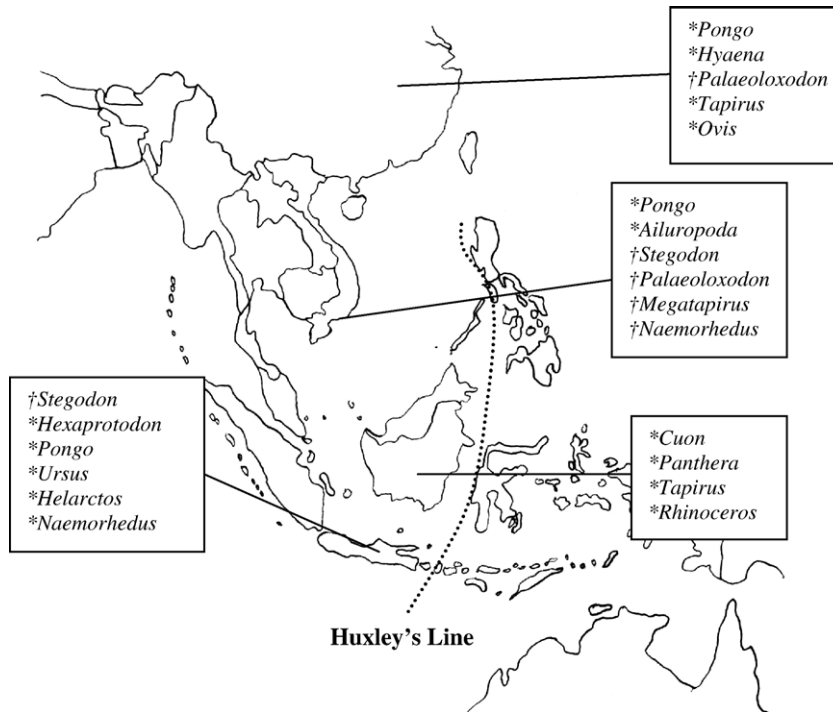


Fig. 3. Generic level extinctions in the Late Pleistocene. †—complete extinction; *—local extinction. For complete extinction list and a break down of sites refer to Tables 2–11.

and/or through competition with invading species (de Vos et al., 1994). Satir and Ci Saat are relatively poor in species, which indicates predominately isolated island conditions for Java during this time period (de Vos et al.,

1994; de Vos and Long, 2001; van den Bergh et al., 2001). This relative isolation is thought to prevail until 0.8 Ma, where a large immigration event is evident in the Kedung Brubus fauna (van den Bergh et al., 2001).

Table 12

List of species where extinctions range over more than one country; * indicates taxa discussed in detail in the text

Species	Number of countries	South China	Burma	Laos	Cambodia	Vietnam	Thailand	Malaysia	Java	Borneo
<i>Duboisia santeng</i>	2							×	×	
<i>Equus yunnanensis</i>	2	×	×							
<i>Gazella</i> sp.	2	×	×							
<i>Gigantopithecus blacki</i> *	2	×				×				
<i>Macaca robustus</i>	2	×		×						
<i>Hyaena brevirostris</i> *	2	×							×	
<i>Rhinoceros sinensis</i> *	2	×				×				
<i>Rhinoceros sivalensis</i> *	2		×	×						
<i>Sus barbatus</i>	2						×		×	
<i>Sus lydekkeri</i>	2			×		×				
<i>Stegodon elephantoides</i> *	2	×	×							
<i>Megatapirus augustus</i> *	3	×		×		×				
<i>Rhinoceros unicornis</i> *	3					×	×		×	
<i>Stegodon orientalis</i> *	3	×	×			×				
<i>Tapirus indicus</i> *	3	×			×					×
<i>Naemorhedus sumatraensis</i>	3	×				×			×	
<i>Ailuropoda melanoleuca</i> *	4		×	×		×	×			
<i>Crocota crocuta</i> *	4	×		×	×		×			
<i>Palaeoloxodon namadicus</i> *	5	×	×	×		×		×		
<i>Pongo pygmaeus</i> *	6	×		×	×	×	×		×	

Trinil H.K., Kedung Brubus and Ngandong are thought to represent an open woodland habitat (de Vos, 1983; Sondaar, 1984; de Vos, 1995; van den Bergh et al., 2001), as indicated by the large number of bovids present, as well as the lack of typically tropical rainforest species such as *Pongo*, *Hylobates* and *Helacrtos* (van den Bergh et al., 2001; Storm, 2001). The later Punung fauna, however, presents more modern, humid rainforest characteristics. The faunal turnover recorded between Kedung Brubus and Punung indicates the disappearance of 17 taxa, and the appearance of 10 new species (van den Bergh et al., 2001). This turnover is thought to have occurred between 110 ka and 70 ka, when the sea levels were sufficiently low enough to allow passage of fauna from the mainland (van den Bergh et al., 2001). Among those disappearing during this time are *S. trigonocephalus*, *H. sivalensis*, *Elephas hysudrindus* and *Sus macrognathus*; disappearances which are likely tied to both environmental changes as well as competition with new taxa which had migrated southwards. The extinction of *Pongo* and other species such as *Hylobates syndactylus*, *Macaca nemestrina* and *S. barbatus* from Java most likely occurred during the Late Pleistocene, as these species are absent in the Wajak fauna (10,560 ka) (Storm et al., 2005). These local extinctions may be a result of the drier and cooler climate in Java present after 81 ka (van der Kaars and Dam, 1995), and the resultant loss of rainforest habitat (Storm et al., 2005).

Of the countries studied here, only Sumatra, Borneo and Java are islands. Humans have been implicated in the extinctions of island endemics in Southeast Asia (Sondaar, 1987). However, the factors involving extinctions on continents are unlikely to be as simple as extinctions occurring on islands (Wroe et al., 2004), and as such are unlikely to apply for much of the region. Furthermore, only one island within this study (Java) is smaller than the largest island where overkill has been relatively universally accepted, the south island of New Zealand (Wroe et al., 2004) (Table 13). Java was connected to Sumatra and Borneo during periods of low sea level (Voris, 2000), making it easier for human settlement. If overkill did

Table 13
Landmass areas for islands within the range of this study

Island	Landmass (km ²)
Borneo	744,000
Sumatra	474,000
Java	132,000
South Island, New Zealand	150,000

Only Java is smaller than the largest island where overkill is generally accepted, the South Island of New Zealand (Wroe et al., 2004). However, during the periods of low sea levels, these islands were joined (see text for discussion).

occur on these islands, then it is more likely to have taken place when island extinction dynamics, as opposed to continental factors, were in play—the period when sea levels were high. If this was the situation, then humans could be a causative agent in extinctions there. However, extinctions would not ensue without being preceded by sea level changes, which also brought about changes in vegetation, as well as allowing the immigration of new species in the region.

3.3. Taxa

3.3.1. *Stegodon* and *Palaeoloxodon*

Stegodon remains are found in Late Pleistocene deposits in Burma, Laos, Borneo and Java, and survived into the Holocene in Southern China (Tong and Patou-Mathis, 2003; Tong and Liu, 2004; Ma and Tang, 1992) (Figs. 1 and 2). Although absent from other faunal lists, given the wide chronological and geographical distribution of *Stegodon*, it is reasonable to assume that this is a result of limited field work as opposed to real absence. This abundance and distribution has led to the “*Stegodon–Ailuropoda* faunas”, which are often cited as characteristic of the Middle Pleistocene of Southeast Asia. However, no study has thus far examined the extinction of this genus across its entire range. Sondaar (1987) postulated that the arrival of early humans on islands in Southeast Asia (specifically Flores) led to the extinction of the pygmy stegodon, *Stegodon sondaari*. *Stegodon florensis*, however, appears to have had a long-term coexistence with *Homo* in Flores (Morwood et al., 2004). The more likely explanation is that *Stegodon* was adversely affected by the southward latitudinal shifts of the tropical and subtropical zones, decreases in the areal extent of these zones (Jablonski and Whitford, 1999) and the corresponding reduction in heterogeneity of vegetation during the Pleistocene. This corresponds to the gradual reduction in the number of species of *Stegodon* evident from the Early through to Late Pleistocene, especially when the southern Chinese data are examined. Although the impact of humans on these taxa cannot be discounted, this would probably have been more pronounced on islands rather than on the continent.

Palaeoloxodon is likely to have shared a similar fate to that of *Stegodon*. Much more closely related to *Elephas* than *Stegodon*, during the Pleistocene (in China at least) *Palaeoloxodon* exhibited a similar distribution to that of *Elephas*, but became extinct before the Holocene (Tong and Patou-Mathis, 2003). It is found until the Middle Pleistocene in Burma, Laos and Malaysia (Fig. 2), and until the Late Pleistocene in Southern China and Vietnam (Fig. 3). Why these two proboscideans became extinct in

the region, while *Elephas* continued to survive to today, is not satisfactorily explained by human- or climate-mediated models of extinction; it may perhaps be tied to subtle differences in ecology and body size. *Stegodon* abundances appear to be greater than for those of *Elephas* in Late Pleistocene Southern China, providing some support to a generalist vs. specialist hypothesis (Saegusa, 2001). Without an in-depth study of the ecology and behaviour of these extinct taxa, however, it would be unwise to pronounce anything more than tentative suggestions.

3.3.2. *Pongo* and *Gigantopithecus*

Pongo is currently confined to Sumatra and Borneo, however, Pleistocene fossil specimens are known from Southern China, Cambodia, Thailand, Vietnam, Laos and Java (Table 12, Figs. 2 and 3). It is known only from Middle Pleistocene deposits of Laos and Cambodia (Fig. 2), but this is likely to be a reflection of the small number of excavations rather than actual absence. It is also possible that *Pongo* survived into the Holocene in Vietnam (Kahlke, 1972). Pleistocene *Pongo* was larger than the modern orangutan (Nowak, 1999), a similar condition to that in a number of other Pleistocene Southeast Asian taxa (Medway, 1972; Pope, 1995; Tougard, 2001; Brown et al., 2004). A reduction in body size is another characteristic of the megafauna extinctions on other continents (e.g. North America, Guthrie, 2003). It has been suggested that during the Pleistocene, the orangutan was group living and terrestrial, rather than solitary and arboreal, as seen today (MacKinnon, 1971). The hypothetical change from terrestriality to arboreality has been linked to competition with an invading terrestrial ape, humans, and thought to include hunting pressure for at least 35,000 years (MacKinnon, 1971). However, it is more likely that the orangutan's solitary and arboreal habitats were present from before the incursion of humans, given its arboreal limb adaptations and frugivorous diet (Galdikas, 1988). The negative influence of humans, through hunting pressure or habitat alteration, which has been observed in historical times (Rijksen, 1978), should not be discounted when looking at the Pleistocene range reduction of this species.

Gigantopithecus is the only extinct primate genus known from the Pleistocene in Southeast Asia, known only from teeth and mandibular fragments. Based on comparisons of these with those of *Gorilla*, its hypothesised long bones would be 20–25% longer and more robust than the extant ape's (Johnson, 1979). It shows a general increase in size throughout the Pleistocene (Ciochon et al., 1996). Although it is currently known only from deposits in China and Vietnam (Fig. 2), the limited number of excavations for the region in general suggest that it may have had a much wider geographical

distribution. Faunas associated with *Gigantopithecus* suggest it inhabited a tropical or subtropical forest environment (Kahlke, 1984; Ciochon et al., 1990), and it has been reconstructed as subsisting on a variety of grasses and fruits (Ciochon et al., 1990).

Both *Pongo* and *Gigantopithecus* exhibit range reductions, and extinction in the case of the latter, throughout the Pleistocene (Jablonski and Whitford, 1999; Jablonski et al., 2000). The southward latitudinal shifts of the tropical and subtropical vegetation zones coupled with a decrease in area of these zones are the likely causes of these reductions (Jablonski and Whitford, 1999; Jablonski et al., 2000). Other catarrhine species with different life history parameters were less adversely affected (Jablonski et al., 2000). Although the influence of hunting and possible competition with humans is not discounted, these factors are, we suggest, unlikely to have been the sole contributing factor to the range reductions or extinctions experienced by these apes.

3.3.3. *Crocota* and *Hyaena*

While we understand that taxonomically, *Hyaena* from Southern China has recently been replaced by *Pachycrocota*, and *C. crocuta* with *C. ultima*, for the sake of consistency with older works the older names are utilised here. *Crocota* is known until the Middle Pleistocene in Cambodia, Thailand and Laos (Fig. 2), and survived into the Holocene in China (Tong and Liu, 2004). *Hyaena* is known until the Middle Pleistocene in Java and Late Pleistocene in Southern China (Figs. 2 and 3). Kurtén (1956) suggested the extinction of *Hyaena brevirostris* in China was the result of competition with the better adapted *C. crocuta*, a point based on their respective stratigraphic positions. This hypothesis is supported by Tougard (1998), who noted that *Crocota* was found in more recent deposits in Southern China, Laos and Cambodia, and tied its dominance over *Hyaena* to climatic cooling which occurred during the middle Pleistocene (480–440 ka). What caused the eventual extinction of *Crocota*? Perhaps the introduction of the domestic dog commensurate with modern humans led to competitive exclusion. Or, perhaps the increase in rainforest during the Late Pleistocene adversely affected *Crocota*, as its preferred habitat of open areas (Nowak, 1999) gave way to more enclosed forest. The possibility also exists that a combination of these two factors ultimately led to the disappearance of *Crocota* from Southeast Asia.

3.3.4. *Ailuropoda*

The widespread distribution of *Ailuropoda* during the Pleistocene is well documented, exemplified by its pairing to *Stegodon* to form the characteristic elements of Middle

Pleistocene fauna in Southeast Asia. Tougaard et al. (1996) specifically examined the disappearance of the giant panda from Southeast Asia. They attribute reduction in range of *Ailuropoda* to changes in bamboo distribution during the Pleistocene, a phenomenon intrinsically tied to changes in climate. They postulated that during the Pleistocene, temperate bamboo species, the food of *Ailuropoda*, were widespread in Thailand, and presumably wherever else *Ailuropoda* occurred. However, climatic conditions became unfavourable for temperate bamboo in the latest Middle Pleistocene and it subsequently retreated northwards, with *Ailuropoda* following its food until it reached its present range, restricted to the Southwest of China (Nowak, 1999). *Ailuropoda* is known until the Middle Pleistocene in Burma, Thailand and Laos, and Late Pleistocene in Vietnam (Table 12; Figs. 2 and 3).

3.3.5. *Tapirus* and *Megatapirus*

Tapirus is currently restricted to Burma, Thailand, Malaysia, Sumatra and possibly Laos. It is adapted for locomotion in thick undergrowth, with its habitat in nearly any wooded or grassed area near water (Nowak, 1999). It is known until the Middle Pleistocene in Cambodia (Fig. 2), and until the Late Pleistocene in Southern China and Borneo (Fig. 3), where it could have survived until at least 8 ka (Medway, 1960). *Megatapirus* is much larger than the current tapir—its teeth and skull are one-quarter larger than *Tapirus indicus* (Tong, 2005). *Megatapirus* derived in the later part of the Early Pleistocene, and is known from Middle and Late Pleistocene deposits in Laos and Vietnam, respectively, as well as from two Holocene sites in China, Chongqing (4235 ybp) and Zhejiang (7815±385 ybp) (Tong and Liu, 2004).

3.3.6. *Hexaprotodon*

The hippopotamus is known until the Early Pleistocene in Burma, Middle Pleistocene in Malaysia and Late Pleistocene in Java (Figs. 1, 2 and 3). It is also represented by a single fragment from Borneo (Cranbrook, 2000, Cranbrook et al., 2000), however the provenance of this find (and hence its age) has not been determined. Due to its critical dependence on open water sources, Jablonski (2004) has tied the extinction of *Hexaprotodon* in Southeast Asia to a drying up of river and lake systems, a result of increasing seasonality of rainfall and river flow. These changes are also associated with the intensification of summer and winter monsoons. It is highly likely that the isolation of many islands, and the ensuing disruption to river systems resulting from changes in sea level (Vorisi, 2000), contributed equally to the extinction of this genus.

3.3.7. *Rhinoceros* and *Dicerorhinus*

Rhinoceros is represented by at least five species during the Pleistocene: *R. sondaicus*, *R. sivalensis*, *R. unicornis*, *R. plicideus*, *R. sinensis*, as well as a sixth (referred to as “*R. chaili*”, though yet to be formally described). *Dicerorhinus* is represented by two species: *D. sumatrensis* and *D. merki*. Of all these rhinocerotids, only *R. sondaicus*, *R. unicornis* and *D. sumatrensis* are not extinct, although all three are highly endangered. *R. unicornis* still survives in Assam and Nepal, while *R. sondaicus* can be found in Java, Borneo, Malaysia, Burma and Indochina (Groves and Guérin, 1980). *Dicerorhinus* survives today in Sumatra, Borneo, Malaysia, Burma and Indochina (Nowak, 1999). *R. unicornis* is able to graze, while *R. sondaicus* and *D. sumatrensis* are browsers, inhabiting swamps and dense forests (Prothero et al., 1989).

R. sondaicus probably became extinct in Borneo in the Late Pleistocene (however it may have survived into the Holocene; see Medway, 1960; Cranbrook, 2000, Cranbrook et al., 2000); *R. sivalensis* became extinct in the Early Pleistocene in Burma and Middle Pleistocene in Laos; *R. unicornis* disappeared from Java and Thailand in the Middle Pleistocene, as well as the Late Pleistocene of Vietnam; *R. plicideus* became extinct in the Middle Pleistocene of Laos; and *R. sinensis* disappeared in the Late Pleistocene of Southern China and Vietnam. *D. merki* is last recorded from the Middle Pleistocene of Cambodia.

Along with *Stegodon*, *Palaeoloxodon*, *Tapirus*, *Megatapirus* and *Hexaprotodon*, rhinocerotids constitute a likely food source for hunting or scavenging hominids. In China, rhinoceros remains are found in 78% of anthropogenic sites (Tong, 2000). Most sites in China contain only fragmentary remains of *Rhinoceros*, with complete postcranial and cranial remains rare (Tong, 2000). However, this is not the case in at least one Indonesian site, Trinil, where numerous complete and almost complete postcranial elements were observed (Louys, personal observation). At the Middle Pleistocene site of Nanjing, just south of the Yangtze River and west of Shanghai, *Dicerorhinus* material is found alongside human remains. Age profile analysis indicates that the majority (74%) of the individuals represented are juvenile (Tong, 2001). A predominantly juvenile profile is also observed at Guanyindong, a lower Palaeolithic site in the Guizhou province, China (Li and Wen, 1986). Tong (2000, 2001) suggests that human hunting rather than carnivore activity accounts for these distributions; however as in other regions a lack of direct evidence of hunting renders this evidence circumstantial. That early humans in Asia utilized rhinocerotids is however not debated. Examples include Zhoukoudian and Yanjiagang in North China (Chow, 1978; Jiang, 1990). As with other

taxa however, questions remain as to whether these animals were hunted, or their remains scavenged (Binford and Ho, 1985; Binford and Stone, 1986; Boaz et al., 2000, 2004).

3.4. Influence of humans in the region

The human colonisation of Southeast Asia most probably occurred during the Early Pleistocene. Evidence from southern China and Indonesia in the form of human fossils suggest colonisation before 1.5 Ma (Sémah et al., 2000; Larick et al., 2001). Precisely which hominin species settled the region is a matter of debate. The earliest East Asians are argued to be of the general grade of either early *Homo* (i.e. *H. habilis*: Huang et al., 1995, but see Wu (2000)) or early *H. sapiens sensu lato* [= *H. erectus*/*H. ergaster*: Huang et al., 1995; Antón and Swisher, 2004; for a discussion of taxonomic issues see Curnoe and Tobias, 2006]. However, evidence for colonisation by early *Homo* relies heavily on limited dental evidence, making it controversial. In this discussion, we assume that early *H. sapiens sensu lato* was the first hominin to have colonised East Asia, including Southeast Asia.

Fossils from the Middle Pleistocene continue to sample early *H. sapiens sensu lato*, the youngest dated to greater than 400 ka in southern China (Chen et al., 1998; Zhou et al., 1999; Zhao et al., 2001). In Indonesia, stone-tools associated with early hominins have been recovered from Flores and dated to about 800 ka (Morwood et al., 1998). Uranium-series dating of fossil humans from Ngandong in Indonesia have provided contradictory ages—mid-Middle Pleistocene (Yokoyama et al., 1998) and late Upper Pleistocene (Yokoyama and Falgueres, 2002; Falgueres, personal communication). While electron spin resonance dating of associated fauna is also consistent with a late Upper Pleistocene age (Swisher et al., 1996), these dates have been challenged on several grounds (Grün and Thorne, 1997). Most recently, a new species of hominin (*H. floresiensis*) has been described for Flores and dated to the late Upper Pleistocene (Brown et al., 2004; Morwood et al., 2004; Morwood et al., 2005). This taxon is claimed to have descended from early *H. sapiens sensu lato* or even an australopithecine (Morwood et al., 2005) in isolation on Flores. It should be noted, however, that this research is controversial (see Henneberg and Thorne, 2004; Weber et al., 2005). *Homo* is represented in Thailand by a single tooth from the late Middle Pleistocene (Tougaard et al., 1998). In Vietnam, *H. sapiens sensu lato* is associated with *Gigantopithecus* in deposits dated to around 475 ka (Ciochon et al., 1996).

Earliest so-called archaic *H. sapiens* is less than 400 ka in China (Chen et al., 1994; Wu and Poirier, 1995; Rink et

al., 2003), being unknown from other sites in East Asia and Southeast Asia. Oldest so-called modern *H. sapiens* in the region could be up to 220 ka, but an estimate of less than 200 ka for this group is probably more realistic (Wu and Poirier, 1995; Shen et al., 1997, 2002). Apart from southern China, direct evidence for earliest modern *H. sapiens* is absent from Southeast Asia until the Holocene. However, the earliest Aboriginal Australians must have colonised Sahul via Southeast Asia, and Australian fossils demonstrate their presence in the region by at least 70 ka (Thorne et al., 1999; Thorne and Curnoe, 2000; however some authors advocate human presence no earlier than c 50 ka [e.g. Bowler et al., 2003]).

Both early *Homo* and early *H. sapiens sensu lato* produced sophisticated stone tools and exploited animal matter, and there is a strong case for them having hunted to acquire meat and intramuscular fat (see Domínguez-Rodrigo and Pickering, 2003). However, the small (australopith-size) body of early *Homo* suggests important ecological and behavioural differences to early *H. sapiens sensu lato*, with its modern human-size body. While the cause of this change remains unknown, it has been associated with a greater commitment to a terrestrial lifestyle, inhabitation of more open environments, increased foraging distances and/or dietary shifts (Foley, 1987; Wheeler, 1992; McHenry, 1994; Leonard and Robertson, 1997; Klein, 1999). Increased body size is also associated with higher mobility, larger territory size and increased meat eating (Foley, 1987), and linked by some workers with the emergence of a modern human-like hunting and gathering lifestyle (Leonard and Robertson, 1997). Larger body size has also been suggested as a major factor in the successful colonisation of the non-African Old World by hominins (Foley, 1987).

Earliest direct evidence for animal exploitation by humans in Southeast Asia is indicated by fossils associated with early *H. sapiens sensu lato* in southern China. As discussed above, mortality profile analysis of rhinoceros remains have been used to suggest human exploitation more than 500 ka (Tong, 2001). At the Chinese mid-late Pleistocene site of Panxian Dadong (Shen et al., 1997; Rink et al., 2003), Schepartz et al. (2005) found that early humans at least scavenged *Stegodon* carcasses and are likely to have played an important role in the formation of the faunal assemblage at this site. Despite this level of interaction the continuation of this species does not seem to have been adversely affected; *Stegodon* in China survived into the Holocene (Tong and Patou-Mathis, 2003). The site of Tongzi in China dates to around 111–180 ka and also has stone tools and evidence for fire in association with the remains of *Stegodon* and *Rhinoceros* (Wu et al., 1975; Wu and Lin, 1985; Wu and Wu, 1985; Yuan et al., 1986).

Other examples of interaction between humans and megafauna in Southeast Asia have not produced immediate extinctions. It is suggested that *Homo* selectively hunted juvenile *Stegodon* on Flores (Morwood et al., 2004). However, it appears that hunting was sustained over thousands of years without causing its extinction, which has instead been attributed to volcanic eruptions on the island (Morwood et al., 2004).

The megafaunal losses on Borneo were likewise unlikely to have been a result of human over-hunting (Medway, 1977). Based on the excavations at Niah, Medway (1977) concluded that the effects of prehistoric humans on the mammalian fauna were minimal at best. He based this on two main lines of evidence. Firstly, based on the level of faunal accumulation in the site, he postulated that the density of pre-historic humans in the region was too low to impact greatly on either the fauna or the environment. His second line of evidence is based on faunal distributions. Medway observed that the abundance of the mammal most hunted, the Bearded Pig (*S. barbatus*), shows little change over the depositional history of the site. By contrast the abundance of two rat species (*Rattus muelleri* and *R. sabanus*) changes significantly, even though he suggests they were not significant food sources.

As discussed above, the hunting of the orangutan is known from the historical record (see also Rijksen, 1978). In Southeast Asia, the hunting of this species has been associated with both subsistence and trophy hunting (Rijksen, 1978). While there is no direct evidence that Pleistocene Southeast Asians hunted *P. pygmaeus*, indirect evidence exists. It has been suggested that fossil *Pongo*, which is often associated with human remains, is indicative of their being hunted (MacKinnon, 1971; Rijksen, 1978). If that is the case then it is possible they have been hunted for as long as 500,000 years (Rijksen, 1978). However, this line of argument is based only on association, and more direct evidence is necessary if it is to be tested and substantiated.

What of the subsistence ecology of early humans in the region? It has been suggested that Pleistocene southern Chinese diets were orientated to small animals including invertebrates, while large animal consumption was restricted to the more open north (Keates, 2003). Observations by Watanabe (1985) suggest that rainforest hunter–gatherers are almost exclusively vegetarian, and when hunting are more likely to prey on small mammals, despite the presence large mammals in the area. In addition, stone tools in Southeast Asian are notoriously scarce, and Southeast Asia does not have a clear handaxe-cleaver tradition, unlike Europe and Africa (Corvinus, 2004). The choice of material for tool manufacture

appears to have been largely opportunistic rather than considered (Schepartz et al., 2000; Yamei et al., 2000; Keates, 2004). In China the only tools associated with *H. sapiens* sensu lato are a cobble industry associated with small flake tool assemblages (Corvinus, 2004). No direct association of stone tools with *H. sapiens* sensu lato exists for the rest of Southeast Asia; however, a small flake industry has been provisionally associated with hominins from Sangiran and Ngandong (Corvinus, 2004). More sophisticated stone tool technologies seem only to be associated with so-called modern humans of uppermost Pleistocene age (Corvinus, 2004). This does not mean that early *H. sapiens* sensu lato lacked big game hunting technologies; however, due to evidence of a scavenging behaviour (e.g. Boaz et al., 2004), a case could be made that this hominin in Asia practiced a predominantly scavenging rather than hunting existence.

Finally, environmental cores from the Southeast Asian region show increasing amounts of charcoal from 225 ka onwards that could be associated with burning in southern Indonesia (Kershaw et al., 2006). Thus, human modification of the environment, a possible catalyst of megafauna extinction (e.g. Miller et al., 2005), could have been part of the ecology of Southeast Asia since the Middle Pleistocene. However, processes other than human burning might also explain the presence of charcoal increases (Kershaw et al., 2006), making such inferences uncertain.

Can the timing of the extinctions in Southeast Asia be associated with human migrations, as it has in North America? The current state of the evidence is too incomplete for such an assessment. The dearth of excavations in the region coupled with poor existing chronologies makes it premature for such an analysis to be completed. Perhaps the disappearance of megafauna can be tied to a cultural revolution, where the unsophisticated tool technology of *H. sapiens* sensu lato is replaced by a more sophisticated, and hunting orientated technology. Evidence of this change may be discernable in the anatomical record of hominins, the archaeological record and also the faunal (extinction) record. However, more evidence of all three from Southeast Asia is necessary before such a conclusion can be reached. While these results are preliminary, we conclude by suggesting that human over-hunting in Southeast Asia, while possibly contributing to extinctions of certain taxa in the region, could not be solely responsible. It is at least clear from this analysis that a blitzkrieg model is not applicable for Southeast Asia. Rather, gradual over-exploitation of faunal resources and ecological changes brought about by human settlement might be more appropriate factors contributing to extinctions for this region. The need for more research in Southeast Asia is again demonstrated.

3.5. Climate and vegetation

A detailed review of climatic changes in Southeast Asia is outside the scope of this paper, and as such only the major points are covered below. The region has experienced a long-term trend towards more variable and/or drier climatic conditions over last 200,000 years, accompanied by major changes in the intensity of the monsoon and the El Niño–Southern oscillation (Hope et al., 2004). Due to the growth of continental glaciers, sea level reductions of up to 160 m were experienced during the Middle Pleistocene, and 120 m during the last glacial maximum (Heaney, 1991). Temperatures were also cooler than today, perhaps by around 2–6 °C (Heaney, 1991).

Changes in vegetation are linked to glacial cycles, and Southeast Asia is no exception. The region exhibits vegetational changes in glacial cycles of a similar scale to those of North America (Hope et al., 2004). Southeast Asia is characterised by a number of native vegetation types, the major elements of which are evergreen tropical rainforest, seasonal or monsoon forest, montane forest and natural (as opposed to human-induced) savannah (Heaney, 1991). The extent of these zones is controlled by a number of factors: temperature and rainfall, and in particular for Southeast Asia (but unlike Africa or America), sea level changes (Heaney, 1991; Gathorne-Hardy et al., 2002). This last factor is the result of a reduction in the extent of shallow seas during periods of high sea level, reducing evaporation and therefore moisture in the area (Heaney, 1991). Heaney (1991) hypothesised the existence of a corridor of low rainfall running through the centre of the Sunda shelf during periods of lower sea level. He further postulated that this area would be home to a mosaic of vegetation types. This is supported by research by Hope et al. (2004), who noted that the “greatest variation in vegetation is shown both within and between interglacial periods, while glacial periods (apart from interstadials) have been characterized by greater vegetation homogeneity” (Hope et al., 2004, p. 120). It has also been pointed out that the assemblage of mammals present throughout Southeast Asia could only exist in a mosaic of closed forest with alternating areas of scrub, bush or parkland (Medway, 1972, 1977; Cranbrook, 2000, Cranbrook et al., 2000). As discussed above, this is a characteristic of many late Pleistocene communities that suffered extinctions (Guthrie, 1984; Lundelius, 1989; Graham et al., 1996; Price and Sobbe, 2005). Continued alternation between savannah and rainforest, as well as the fragmentation of the landmass through rises in sea level, may have been a major contributing factor to range reduction and/or extinction of fauna in Southeast Asia, in a self-organising, threshold model of the type envisaged for North America

(Graham, 2005). Although the Pleistocene ended with an extremely cold phase (Ferguson, 1993), an expansion of humid vegetation is recorded at the Pleistocene–Holocene boundary (Hope et al., 2004).

4. Conclusions

The Southeast Asian megafauna extinctions share certain characteristics with megafauna extinctions recorded in other parts of the world, including the presence of disharmonious assemblages, surviving megafauna exhibiting larger body size in the Pleistocene compared with modern forms, and a dearth of kill sites. The Southeast Asian megafauna extinctions are further characterised by the extinction or reduction in range over at least two countries of a number of genera, among them *Stegodon*, *Hexaprotodon*, *Pongo*, *Crocota*, *Hyaena*, *Palaeoloxodon*, *Ailuropoda*, *Tapirus*, *Rhinoceros* and *Megatapirus*. Other generic extinctions seem to be more restricted, although in general this observation is more likely to result from an incomplete/poorly sampled fossil record rather than actual absence or disappearance of taxa. The chronological resolution of the assemblages is still too coarse for us to make more than preliminary predictions about causes of extinction in the region. However, given the complexity of this extinction event, it is likely that the extinctions were not the result of a single cause but more likely a combination of human induced and climatic factors. This contrasts with the extinctions on small Southeast Asian islands where humans are likely to have had a more direct and disastrous impact (Sondaar, 1987).

Another equally important factor in these extinctions is likely to have come from eustatic changes in sea level. These changes in sea level may have allowed easier routes for early colonising mammals, humans among them. It also brought about changes in the structure of the vegetation, disrupted river systems, and isolated islands like Java and Sumatra. This aspect of extinctions is unique to Southeast Asia—it is unlikely that changes in sea level affected the Americas, Europe or Australia in quite the same way.

The lists provided herein are at times based on a single site which was excavated before modern palaeontological techniques were developed. In many cases there exists limited information on taphonomic and palaeoecological factors affecting deposition and preservation. If nothing else, this study highlights the extremely limited number of excavations of Quaternary sites that have been carried out in Southeast Asia. Although a smaller number of genera became extinct in Southeast Asia relative to other continents, examinations of these extinctions will undoubtedly shed new light and,

it is hoped, stimulate new avenues of research in this debate.

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