REVIEW

Paleontology to policy: the Quaternary history of Southeast Asian tapirs (Tapiridae) in relation to large mammal species turnover, with a proposal for conservation of Malayan tapir by reintroduction to Borneo

Earl of CRANBROOK[1] and Philip J. PIPER[2,3]

[1]Great Glemham House, Saxmundham, UK, [2]School of Archaeology and Anthropology, Australian National University, Canberra, Australia and [3]Archaeological Studies Program, Palma Hall, Diliman 1101, Quezon City, Philippines

Abstract

The Southeast Asian zoogeographical region is divided into Indochinese, Sundaic and Philippine subregions. Two clades of tapirs, *Tapirus* spp., have been recognized in Quaternary Southeast Asia. A review of sites at which they occurred shows that representatives of both clades, one of which was the ancestral Malayan tapir *Tapirus indicus*, co-existed with a diversity of other Pleistocene mammal megafauna. The process of replacement of archaic large mammals was progressive and prolonged through the Quaternary. Zooarcheological investigation has extended knowledge of the former occurrence and distribution of tapirs and other large mammals of the region, with discoveries beyond the outer limits of their previously known ranges. These large mammals were subjected to paleoenvironmental changes as a consequence of the Quaternary cycles of glacial and interglacial periods. Archeological evidence suggests that hunting pressure has intensified the effects of altered environments, leading ultimately to the local disappearance of the Malayan tapir in most of Southeast Asia, including Borneo. The survival of the Malayan tapir through the Quaternary until the present shows that the species is both resilient to environmental change and flexible in its ecological requirements and, given proper protection, could continue to inhabit tropical Southeast Asia. To assist the species' conservation, reintroduction is proposed from the remaining range of Malayan tapir in the wild, to suitable sites of past occurrence in Borneo, where these ancient survivors of the Quaternary megafauna can be accommodated and safeguarded alongside other forms of land usage.

Key words: extinction, large mammals, Pleistocene, reintroduction, tapir

Correspondence: Lord Cranbrook, Great Glemham House, Saxmundham IP17 1LP, UK.
Email: lordcranbrook@greatglemhamfarms.co.uk

CONVENTIONS

The term 'megafauna' is customarily defined as animals exceeding 44 kg weight. In this review, consideration is given to a wider group weighing over 6 kg, col-

lectively referred to as 'large mammals', with members principally among the orders Primates, Carnivora, Proboscidea, Perissodactyla and Artiodactyla. Systematic names are given with vernacular names at first mention, thereafter, if the identity is clear in context, the vernacular name is used alone. In summarizing paleontological and archeological records, apart from updating some generic names in accordance with current opinion, taxonomic identities have not been reassessed and the nomenclature of source references has been followed. To denote an extinct taxon, the symbol † is placed to the left of the genus, species or subspecies name, as applicable. Chinese place names are in Pinyin; however, in some instances, for clarity, the alternative Wade-Giles transcription system is also given. For brevity, the term(s) Southeast Asia(n) and Island Southeast Asia(n) are abbreviated to SEA and ISEA, respectively. ISEA refers to Sumatra, Java, Borneo, Palawan and other islands located on the Sunda shelf and within the Sundaic biogeographic region, to distinguish these from the Wallacean islands to the east. Other conventional abbreviations used are: LGP, last glacial period; LGM, last glacial maximum; kyr, thousand years; Myr, million years; ka, thousand years ago; and Ma, million years ago.

INTRODUCTION

Southeast Asian regional zoogeography

The zoogeographic region of SEA was defined by Corbet and Hill (1992) as the combination of 3 Indomalayan subregions: Indochinese with southern China (C1, C2), Sundaic including Palawan (D1–D5, D6) and Philippines (E) (Fig. 1). In political terms, the region comprises Bangladesh, northeastern India, southern China, Burma (Myanmar), Thailand, Laos, Cambodia, Vietnam, Malaysia, Singapore, Brunei, Indonesia west of Wallace's Line and the Philippines. Among living mammals, the region is characterized by many tropical forest genera and species that do not extend into India, or to temperate China where, since the Early Pleistocene, the Qinling mountain range in Shaanxi province has formed
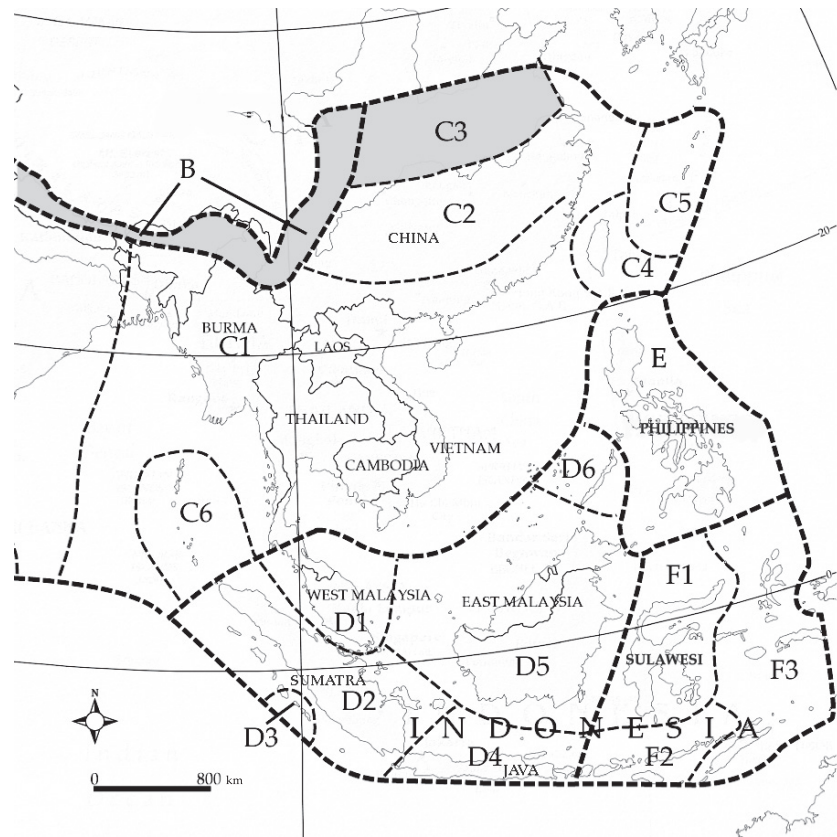

Figure 1 The zoogeographic region of Southeast Asia, subdivided into subregions (C) Indochinese, (D) Sundaic, with Palawan and (E) Philippines; adapted from Corbet and Hill (1992). (F) Wallacea is not treated in this review.

the zoogeographic boundary separating eastern Palearctic and Indomalayan faunas (Rink *et al.* 2008). At the subregional level, there is an important boundary in the Thai–Malay peninsula defining the continental limit of a distinctive Sundaic fauna that includes several endemic genera and many endemic species. Of the 3 Greater Sunda Islands, Sumatra supports the most diverse mammal fauna, with many genus-level taxa shared with Peninsular Malaysia, while that of Java is disproportionately depleted. Borneo has a rich mammal fauna of 239 known species, among which 50 of 136 terrestrial species (i.e. excluding bats) are endemic, including 3 endemic genera. The mammal community of Palawan consists of 62 species, of which 13 are endemic. Although species-poor by comparison with Borneo, this fauna includes characteristic Sundaic mammalian genera which do not occur naturally elsewhere in the Philippines (Heaney 1985; Esselstyn *et al.* 2004).

Origin, distribution and nomenclature of tapirs

The first tapir, family Tapiridae, appeared in the Oligocene, as the extinct genus †*Protapirus*, occurring through North America and Europe. In the Late Pliocene, tapirs extended from South America to eastern Asia (as *Tapirus,* in Romer 1966). Worldwide, there are now 4 living species. Three occur in Central and South America and 1, the Malayan tapir, is the sole representative of the family in SEA. A combination of anatomical features and molecular divergence indicates that the American tapirs form a clade distinct from the Malayan tapir, with the split at about 18 Ma and a further separation among the American species at about 3 Ma. Groves and Grubb (2011) have reflected this evidence in generic nomenclature, with 2 American species in *Tapirus* and the third in *Tapirella*. The available generic-level name for the Asian clade is *Acrocodia*, yielding *Acrocodia indica* (Desmarest, 1819) as the systematic name for the Malayan tapir. While noting this opinion, the present review follows the earlier classification of the late Peter Grubb (2005), who placed all 4 living tapir species in the single genus *Tapirus* with the Malayan tapir *Tapirus indicus* Desmarest, 1819. This generic usage has been current for many years in paleontological literature and, since retrospective amendment of many historical references would be potentially confusing, this terminology has been retained.

The Quaternary period and megafauna extinctions

The Quaternary geological period began with the Pliocene–Pleistocene transition, dated by the International Union of Geological Sciences (IUGS) at 2.588 Ma and is divided into the Early, Middle and Late Pleistocene epochs followed by the present Holocene, beginning about 11 ka. During the Quaternary, global climatic fluctuations had profound environmental impacts, worldwide, as 'glacial' periods of lowered average ambient temperature alternated with briefer, warm 'interglacial' periods. From the mid-Middle Pleistocene (about 500 ka) successive glacial periods each lasted around 100 kyr, separated by interglacials of ~15 kyr. During glacial periods, polar ice sheets enlarged and high altitude glaciers expanded, sequestering large volumes of the world's finite supply of surface water so that global sea-levels fell. Worldwide, fluctuations in climate had the effect of altering the vertical and horizontal distribution of ecological communities, with expansions and contractions dependent on the locally prevailing environmental conditions. Large mammals may be particularly vulnerable to the changing availability of resources, periodically resulting in total or local extinction events, sometimes succeeded by expansion and re-colonization. A widespread loss of large mammal species at the close of the Pleistocene epoch has been termed the 'Quaternary megafauna extinctions' (Martin & Klein 1984). Beginning about 50 ka, by the close of the episode at ~7 ka at least 101 mammalian genera became extinct worldwide. Extinction intensity varied by continent; the hardest hit being Australia losing 88% of megafauna genera, South America 83% and North America 72%. The least affected was Eurasia, which, as a whole, lost only 35% of its megafauna mammal genera: 4 globally extinct, 5 extinct on the continent, 17 surviving (Corlett 2010). Molecular data have provided additional insights into the phylogeny of regional taxa and the timing of past divergences (e.g. Lucchini *et al.* 2005). Authors including Tougard (1998), van den Bergh *et al.* (2001), Louys *et al.* (2007), Corlett (2010) and Louys and Meijaard (2010) have reviewed SEA regional megafauna extinctions and debated the nature and variety of causes.

The paleogeography and paleoecology of SEA were strongly affected by the glacial cycles, notably in the Sundaic biogeographic subregion. In the shallow seas of the Sunda shelf, Quaternary marine recessions during glacial periods extended shorelines and exposed the seabed, thereby providing links between the present islands and with the continent. At glacial peaks, lowered ambient temperature and decreased rainfall impacted adversely on forest habitat. The last interglacial, ~126–115 ka was followed by the LGP which culminated at the LGM, 23–18 ka, when average global ambient air tem-

peratures fell to around 5 °C lower than present. The sea level dropped by ~120 m below the present datum, exposing the entire Sunda Shelf as a huge terrain of subcontinental dimensions. Following this episode, as global temperatures began to increase, the sea level rose, slowly at first, with a rapid surge about 14 ka and finally severed the land bridge between Sumatra and Borneo ~10 ka (Bird *et al.* 2005; Cannon *et al.* 2009; Cranbrook 2010).

Today's SEA regional geography is therefore untypical, representing an extreme state in the latest of a succession of interglacial episodes that may cumulatively amount to no more than 42 kyr or 2% of the Quaternary period (Woodruff 2010). The depressed sea level that has been the norm throughout most of this period permitted migration, colonization, and exchange of species between the continent and the islands of Southeast Asia. Hence, the majority of plants and animals of the Sundaic subregion have a shared derivation from continental SEA, supplemented by regional radiation (Darlington 1957). Yet, as Darlington (1957) also noted, in their present occurrence some conspicuous members of the widespread SEA regional large mammal fauna are absent from Borneo: dhole or serigala *Cuon alpinus* (Pallas, 1811)*,* tiger *Panthera tigris* (Linnaeus, 1758)*,* leopard *Panthera pardus* (Linnaeus, 1758)*,* Javan rhinoceros *Rhinoceros sondaicus* Desmarest, 1822*,* Malayan tapir and serow *Capricornis sumatraensis* (Bechstein, 1899). It is an achievement of archeology that some of these anomalous distributions have been shown since to be the consequence of Quaternary or recent extinctions.

The Quaternary history of tapirs

Given adequate comparative reference specimens, tapirs are readily recognizable in paleontological or zooarcheological contexts. The dentition is sufficiently distinctive that confident identification can be based on a single tooth or an isolated crown (Fig. 2). The foot skeleton is peculiar, with 4 toes on the fore feet and 3 on the hind feet. Small foot bones survive well as fossils and are therefore useful identifiers of tapir among the skeletal remains of other large mammals (Fig. 3). The identification of tapirs in the paleontological and archeological record in SEA has been fundamental in determining the past presence, timings of appearance and extinction of members of the family in association with diverse faunal communities. The representation of Tapiridae at paleontological sites, summarized below from published sources, identifies 2 clades coexisting at the outset of the Quaternary. By the close of the period, 1 lineage had be-

come extinct while, of the other, 1 representative species survived: the Malayan tapir. In combination, paleontological and zooarcheological records show that the Malayan tapir is an ancient species that has existed within SEA for at least 1 Myr.

There have been a few reports in historic times of Malayan tapir from southern Vietnam, Cambodia and Laos (Grubb 2005). From the mid-20th century, however, its range has been restricted to Sumatra and Peninsular Malaysia (Chasen 1940), southeastern Burma in the "evergreen forests of Tenasserim from 18°N southwards" (Tun Yin 1967, p. 148) and adjacent parts of southwestern and peninsular Thailand (Lekagul & McNeely 1977; Fig. 4). It is therefore evident that the con-
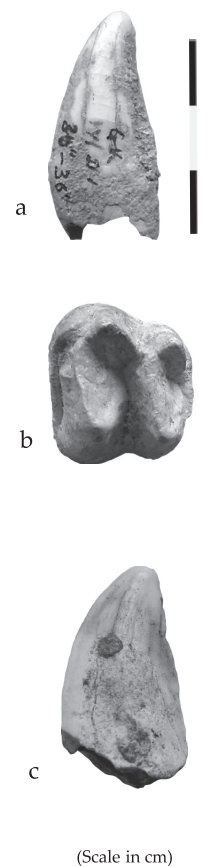
(Scale in cm)

Figure 2 Archeological specimens of Malayan tapir from Sarawak, Malaysian Borneo: a partially erupted left mandibular canine (No. 5 in Table 2), the crown of a, partially erupted left 1st maxillary molar (No. 6 in Table 2); b, both from the Gan Kira mouth of Niah Cave; and c, a partially erupted (right) mandibular canine from Gua Sireh (No. 3 in Table 2).

traction and local extinction of Malayan tapirs within past geographic ranges has been relatively recent, mostly occurring within the last century. The 2012 IUCN Red List places Malayan tapir in the category 'endangered'.

A combination of archeological evidence and eye witness accounts combine to confirm that in Borneo, the disappearance of Malayan tapir is a recent occurrence. Proof of its historic presence in Borneo suggests that this surviving member of the Middle Pleistocene mammal megafauna was adapted to environments that exist on the island. It is therefore concluded that reintroduction of Malayan tapir to selected localities in Borneo by relevant agencies, within the national boundaries of Malaysia or Indonesia, is likely to succeed and may be important to aid the long term conservation and survival of this ancient species.

TAPIRS AND QUATERNARY LARGE MAMMAL SPECIES TURNOVER

Early Pleistocene (2.58 Ma–778 ka)

In southern Asia, a rich array of Neogene (~23–2.59 Ma) and early Quaternary fossil sites occurs along the length of the Siwalik hills, fringing the southern Himalayas from Pakistan through India to Nepal and Burma. The geology is complex and a sequence of biostratigraphic zones is recognized (Nanda 2002). Among others, Hooijer (1952), Medway (1972), de Vos (1984), de Vos and Long (2001) and Patnaik and Nanda (2010) have drawn attention to genera or species common to the Siwalik formations and Early Pleistocene SEA fossil sites. Yet there are also significant differences between assemblages in the 2 regions, notably the absence of any record of tapir from the Siwalik group where other perissodactyls are well represented. Rather than direct contact, it is more likely that, along with genera and species of other origins (including local radiations contained within geographic or climatic barriers), both the Early Pleistocene faunas included members from a shared central Asian source. Such a source may have been the vast grasslands extending from south Asia to north China during this period (Dennell 2009), which facilitated movements of large grazing mammals over the continent. Dennell and Roebroeks (2005) suggested the term 'savannastan' to express the immensity of these grasslands.

In Asia, an Early Pleistocene species *Tapirus* †*sanyauensis* Huang, 1991 occurred in southern Palearctic China. With progressive increase in size and showing some dental modifications, this was succeeded by *Tapirus* †*sinensis* Owen, 1870 of Early to Middle Pleistocene age, which in turn was ancestral to the largest form *Tapirus (Megatapirus)* †*augustus* (Matthew & Granger, 1923) of the Middle to Late Pleistocene (Tong & Xu 2001; Tong *et al.* 2002; Tong & Liu 2004; Tong 2005). South of the Qinling range, a separate clade emerged in SEA identifiable as ancestral *T. indicus*, slightly larg-
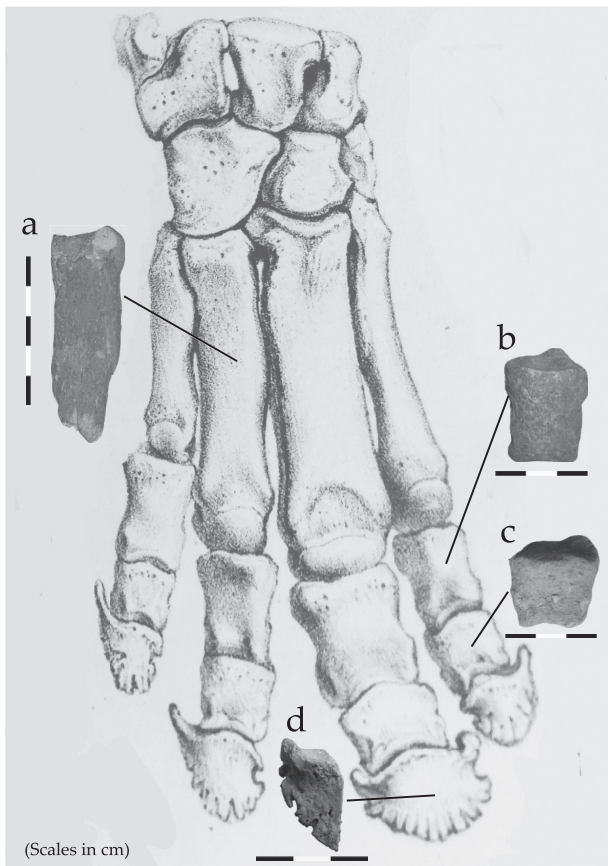

Figure 3 Skeleton of the right forefoot of Malayan tapir, adapted from de Blainville (1839–64), plate G. *Tapirus* IV, showing whole or partial elements that have been identified among zooarcheological specimens from cave sites in northwest and northern Borneo; a, proximal end of a metacarpal II or IV from Niah Cave West mouth (No. 6 in Table 3); b, basal phalanx II from Niah Cave West mouth (No. 13 in Table 3); c, right subterminal phalanx II of the manus from Cave V, Jambusan (No. 15 in Table 3); d, fragment of a terminal (ungual) phalanx digit III from Cave V, Jambusan (No. 17 in Table 3).
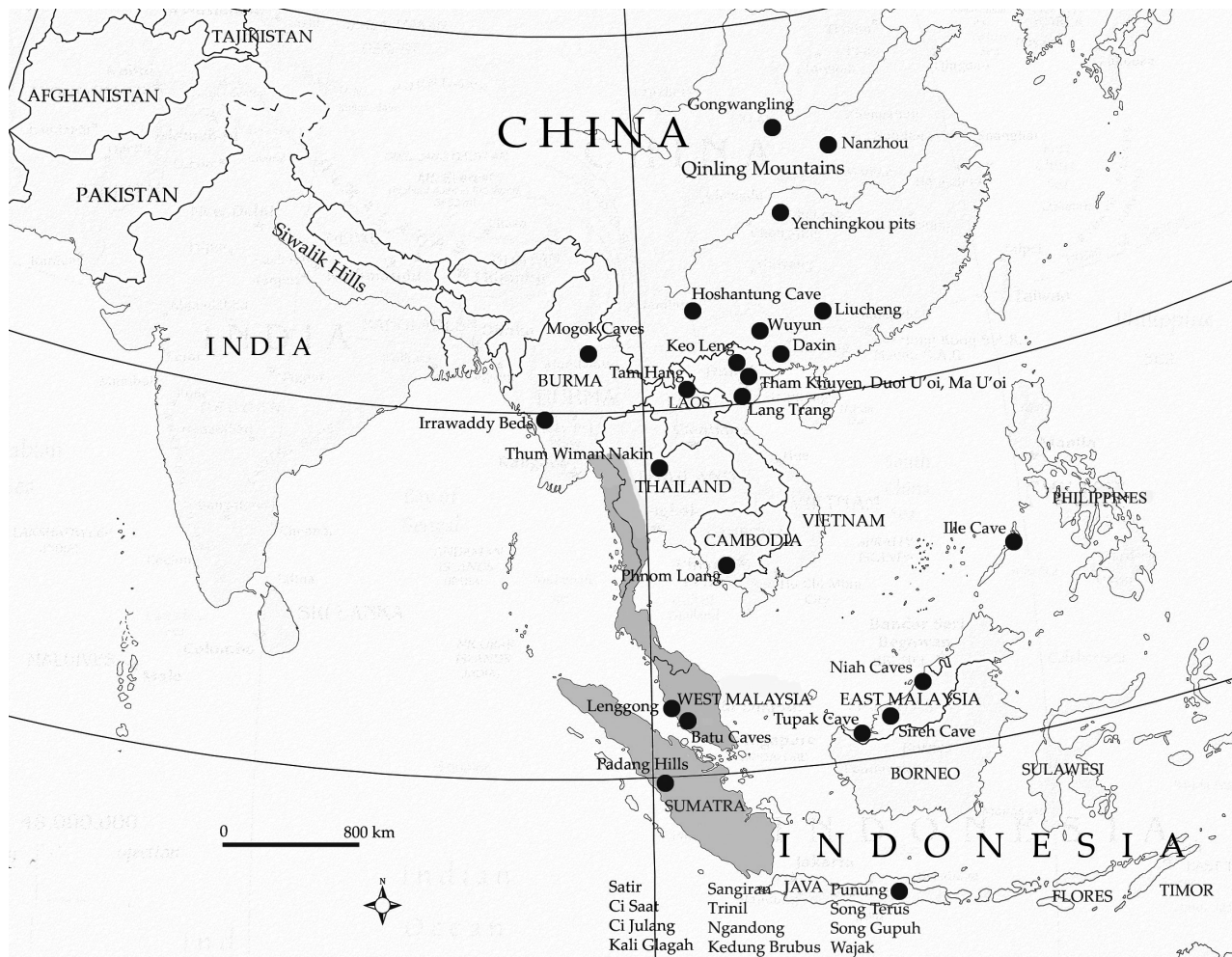
Figure 4 A map of South and Southeast Asia, showing locations (filled circles) mentioned in the text and (shaded area) the present distribution of the Malayan tapir (illustration by Piper & Cranbrook). See text for full details.

er than *Tapirus* †*sanyuanensis* (Tong *et al.* 2002). Porosity of the Palaearctic/SEA zoogeographical boundary (Norton *et al.* 2010) is exemplified by the expansion of *T.* †*sinensis* into the Indochinese subregion, identified in Middle Pleistocene cave sites in Guangxi and Guangdong (Kahlke 1961).

Early Pleistocene tapirs co-existed in SEA with a mix of Tertiary genera or archaic species of modern genera of primates, carnivores, proboscideans, perissodactyls and artiodactyls. Notably, the fauna of southern China included some large mammals with Siwalik or Palearctic affinity atypical of SEA: wolf *Canis*, horse *Equus* and gazelle *Gazella* (Table 1). Early Pleistocene Ir-

rawaddy beds of Burma also yielded horse and gazelle, with a mix of megafauna allied to the Siwalik mammals and an early appearance of modern SEA rhinoceros species (Table 1; Colbert 1943; Thien *et al.* 2006, 2010). The absence of tapirs at Irrawaddy sites sets a western limit to their Quaternary SEA distribution.

In the Sundaic subregion in the Early Pleistocene, some large mammals of Siwalik affinity were present in Java as components of a fauna termed 'Siva–Malayan' (Hooijer 1952) found at Satir, Ci Saat, Ci Julang and Kali Glagah. Tapirs were not among this fauna, of which indicators were the widespread Quaternary hyena *Hyaena (Pachycrocuta)* †*brevirostris* Aymard,

Table 1 Characteristic large mammals of selected Southeast Asian sites, by subregion and country locations

Location	Age (ka)	Primates	Carnivora	Proboscidea	Perissodactyla	Artiodactyla
Early Pleistocene						
Yuanmou, Jianshi, Bijiashan, southern China		†*Gigantopithecus blacki*	*Canis* †*yuanmoensis* *Cuon* †*dubius* †*Meganterion* *Panthera* †*teilhardii* *Hyaena* †*brevirostris*	†*Gomphotherium* †*Stegodon elephantoides* †*Stegodon preorientalis* †*Stegodon orientalis* †*Stegodon haoangensis* †*Stegodon yuanmoensis* †*Stegodon zhaotongensis*	*Equus* †*yunnanensis* *Rhinoceros* †*sinensis* *Tapirus* †*peii* *Tapirus indicus*	*Sus* †*xiaozhu* *Sus* †*peii* *Sus* †*bijashanensis* †*Cervavitus* spp. †*Metacervulus* †*Paracervulus* *Cervus* †*yunnanensis* †*Megalovis guangxiensis* *Gazella* sp.
Irrawaddy beds, Myanmar				†*Stegodon elephantoides* †*Stegodon insignis* †*Stegolophodon latidens* *Elephas* †*hysudricus*	†*Hipparion* sp. *Equus* †*yunnanensis* *Rhinoceros* †*sivalensis* *Rhinoceros sondaicus* *Dicerorhinus* †*gwebinensis* *Dicerorhinus sumatrensis*	*Hexaprotodon* †sp. †*Merycopotamus* †*Potamochoerus* Caprinae †*Hemibos trietricornis* †*Proleptobos birmanicus* *Bos sondaicus* Hippotraginae *Gazella* Boselaphinae
Cu Julang, Satir, Ci Saat, Kali Glagah, Java			*Panthera* †sp. (large)	†*Mastodon bumiajuensis* †*Stegodon trigonocephalus* *Elaphas* †*planifrons*		*Hexaprotodon* †*sivalensis* *Sus* †*brachygnathus* *Axis* †*lydekkeri* *Bubalus* †*palaeokerabau* *Bos* †*palaeosondaicus* †*Duboisia santeng*
Middle Pleistocene						
Liucheng, southern China	1206–940	†*Gigantopithecus blacki* *Pongo* sp.	*Cuon* (*Sinicuon*) †*dubius* *Ailuropoda* †*microta* *Ursus thibetanus* †*kokeni* *Arctonyx* †*minor* *Hyaena* †*brevirostris* *Acinonyx* †*pleistocaenicus* *Panthera* †*teilhardii* *Panthera pardus*	†*Gomphotherium serridentoides* †*Stegodon preorientalis*	*Equus* †*yunnanensis* †*Nestoritherium* *Rhinoceros* †*chiai* *Dicerorhinus sumatrensis* *Tapirus* †*peii*	†*Dicoryphochoerus* †*Potamochoerus* *Sus* †*xiaozhu* *Sus* †*peii* †*Dorcabune liuchengensis* *Muntiacus* †*lacustris* *Cervus* †*fenqii* *Cervus* †*yunnanensis* †*Megalovis guangxiensis*

Table 1 Continued

Location	Age (ka)	Primates	Carnivora	Proboscidea	Perissodactyla	Artiodactyla
Yenchingkuo, China		Rhinopithecus roxellanae tingianus Hylobates (†sericus)	Ailuropoda melanoleuca Ursus thibetanus †kokeni Hyaena †brevirostris sinensis Arctonyx collaris †rostratus Cuon alpinus †antiquus	†Stegodon orientalis Elephas †namadicus	Tapirus †augustus	Capricornis sumatraensis †kamjercus Muntiacus muntjak †margae
Daxin, southern China	380–308	†Gigantopithecus blacki Pongo sp. Hylobates Macaca	Cuon alpinus Ailuropoda melaleuca †fovealis Arctonyx collaris Ursus thibetanus	†Stegodon orientalis	Rhinoceros †sinensis Tapirus †augustus	†Dicoryphochoerus Sus †bijiashanensis Sus sp. Muntiacus Cervus sp. Bos (Bibos) sp. Caprinae indet. †Megalovis
Wuyun, southern China	275–175	Pongo †weidenreichi. Macaca sp. Presbytis spp. (2)	Cuon †antiquus Ailuropoda melanoleuca †baconi Ursus thibetanus Arctonyx collaris Panthera †teilhardii Panthera tigris Panthera pardus	†Stegodon orientalis Elaphas maximus	Rhinoceros †sinensis Tapirus †augustus	Sus scrofa Muntiacus Cervus spp. (2) Bovinae Capricornis sumatraensis
Tham Khuyen Cave, Vietnam	475 ± 125	†Gigantopithecus blacki †Langsonia liquidens Pongo †hooijeri Pongo †kahlkei	Cuon sp. Ailuropoda melanoleuca Ursus thibetanus Ursus malayanus Arctonyx	†Stegodon oreorientalis Elephas †namadicus	Rhinoceros †sinensis Tapirus †augustus	Sus †lydekkeri Sus scrofa Muntiacus muntjak Rusa unicolor Bos sp. Bubalus †sp.
Phnom Loang, Cambodia		Pongo pygmaeus	Crocuta crocuta Panthera tigris	Elephas sp.	Rhinoceros sondaicus †guthi Tapirus indicus †intermedius	Muntiacus sp. Rusa unicolor Cervus cf. leptodus Bubalus bubalis Capricornis sp.

Table 1 Continued

Location	Age (ka)	Primates	Carnivora	Proboscidea	Perissodactyla	Artiodactyla
Thum Wiman Nakim, Thailand	169 ± 15	*Pongo (pygmaeus)* *Macaca nemestrina* *Trachypithecus* sp.	*Ailuropoda melanoleuca* †*baconi* *Ursus thibetanus* *Arctonyx collaris* †*rostratus* *Crocuta* cf. *crocuta*	*Elephas maximus*	*Rhinoceros unicornis* *Rhinoceros sondaicus* *Tapirus indicus* †*intermedius*	*Sus scrofa* *Sus barbatus* *Muntiacus muntjak* *Rusa unicolor* *Rucervus eldi* *Axis porcinus* *Capricornis sumatraensis* †*kanjereus* *Bubalus bubalis* *Bos javanicus* *Bos frontalis* *Bos sauveli*
Tam Hang South, Laos	Late Middle Pleistocene	*Macaca* sp. *Hylobates* sp. *Pongo pygmaeus*	*Ursus thibetanus* cf. †*kokeni* *Ursus malayanus* *Arctonyx collaris* cf. †*rostratus* *Cuon alpinus* cf. †*antiquus* *Panthera tigris*	*Elephas* sp. †*Stegodon orientalis*	*Rhinoceros unicornis* *Rhinoceros sondaicus* *Tapirus* †*augustus* *Tapirus indicus* †*intermedius*	*Sus scrofa* *Sus barbatus* *Capricornis* *Rusa unicolor* ?*Cervus eldii* ?*Axis porcinus* *Bos sauveli* *Bubalus bubalis*
Trinil H. K., Java	~900	*Macaca fascicularis* *Trachypithecus* sp.	*Panthera tigris* †*Mececyon trinilensis*	†*Stegodon trigonocephalus*	*Rhinoceros sondaicus*	*Hexaprotodon* †*sivalensis* *Axis* †*lydekkeri* †*Duboisia santeng* †*Epileptobos groeneveldtii* *Bubalus* †*palaeokerabau* *Bibos* †*palaeosondaicus* *Sus* †*brachgnathus*
Kedung Brubus, Java	800–700		*Hyaena* †*brevirostris* *Panthera* †*oxygnatha*	†*Stegodon trigonocephalus* *Elephas* †*hysudrindicus*	*Rhinoceros* †*kendengindicus* *Rhinoceros sondaicus* *Tapirus indicus*	*Hexaprotodon* †*sivalensis* *Sus* †*macrognathus* *Axis* †*lydekkeri* *Bubalus* †*palaeokerabau* †*Epileptobos groenveldtii* *Bos* †*palaeosondaicus*

Table 1 Continued

Location	Age (ka)	Primates	Carnivora	Proboscidea	Perissodactyla	Artiodactyla
Late Pleistocene						
Keo Leng, Vietnam	30–20	*Pongo †weidenreichi* *Hylobates* *Macaca assamensis* *Macaca mulatta* *Semnopithecus*	*Ailuropoda melanoleuca* *Ursus thibetanus* *Arctonyx collaris*	*†Stegodon orientalis* *Elephas †namadicus*	*Rhinoceros †sinensis* *Rhinoceros unicornis* *Tapirus †augustus*	*Sus †lydekkeri* *Sus scrofa* *Muntiacus muntjak* *Rusa unicolor* *Bubalus bubalis* *Capricornis sumatraensis*
Duoi U'Oi, Vietnam	66 ± 3	*Macaca* sp. *Hylobates* sp. *Pongo pygmaeus*	*Ursus thibetanus* *Ursus malayanus* *Arctonyx collaris* *Cuon alpinus* *Neofelis nebulosa* *Panthera pardus* *Panthera tigris*		*Rhinoceros unicornis* *Rhinoceros sondaicus* *Dicerorhinus sumatrensis* *Tapirus indicus*	*Sus scrofa* *Sus barbatus* *Muntiacus muntjak* *Rusa unicolor* *Bubalus bubalis*
Ma U'Oi, Vietnam	>44 ± 4	*Macaca* sp.	*Cuon* sp.	*Elephas* sp.	*Rhinoceros* cf. *sondaicus* *Rhinoceros* cf. *unicornis*	*Sus scrofa* *Muntiacus muntjak* *Rusa* cf. *unicolor*
Punung, Java	128–118	*Pongo* *Hylobates moloch* *Symphalangus syndactylus* *Macaca* *Trachypithecus*	*Ursus malayanus* *Panthera tigris* *Panthera pardus*	*Elephas maximus*	*Rhinoceros sondaicus* *Tapirus indicus*	*Sus scrofa.* *Sus barbatus/verrucosus* *Muntiacus muntjak* *Rusa unicolor* *Axis* *Capricornis sumatraensis* *Bubalus †palaeokerabau* *Bos javanicus*
Song Terus, Java	120–80	*Symphalangus syndactylus*				*Sus verrucosus* *Muntiacus muntjak* *Cervus* sp. *Axis* sp.
Song Gupuh, Java	70–1	*Macaca fascicularis*	*Ursus malayanus*	*Elephas maximus*	*Rhinoceros sondaicus* *Tapirus indicus*	*Sus scrofa* *Sus indet* *Muntiacus* *Cervus (Rusa)* sp. *Bos* sp. & *Bubalus* sp.

Table 1 Continued

Location	Age (ka)	Primates	Carnivora	Proboscidea	Perissodactyla	Artiodactyla
Ngandong, Java	53–27 or c.125		Panthera †paleojavanica †soloensis, Panthera tigris, Panthera pardus	†Stegodon trigonocephalus, Elephas †hysudrindicus	Rhinoceros sondaicus, Tapirus indicus	Hexaprotodon †sivalensis, Sus †namadicus, Sus †brachygnathus, Sus †macrognathus, Rusa timorensis, Axis, Bubalus †palaeokerabau, Bos †palaeosondaicus
Wajak, Java	10.5	Presbytis sp.	Panthera tigris		Rhinoceros sondaicus, Tapirus indicus	Sus scrofa, Rusa timorensis, Bubalus bubalis, Bos javanicus
Lida Air & Sibrambang caves, Sumatra	80–60	Pongo (abelii), †palaeosumatrensis, Symphalangus syndactylus, Hylobates sp., Macaca fascicularis, Macaca nemestrina, Presbytis sp., Trachypithecus sp.	Ursus malayanus, Panthera tigris	Elaphas maximus	Rhinoceros sondaicus, Dicerorhinus sumatrensis, Tapirus indicus †intermedius	Sus scrofa, Sus barbatus, Muntiacus muntjak, Cervus (Rusa) sp., Capriconis sumatraensis, Bubalus bubalis, Bos javanicus
Niah Cave, West mouth, Borneo	50–2	Pongo pygmaeus, Hylobates muelleri, Macaca fascicularis, Macaca nemestrina, Presbytis (rubicunda), Trachypithecus cristatus	Ursus malayanus, Panthera tigris, Neofelis		Rhinoceros sondaicus, Dicerorhinus sumatrensis, Tapirus indicus	Sus barbatus, Muntiacus, Rusa unicolor, Bos javanicus
Ille Cave, Palawan	14 to recent	Macaca fascicularis philippinensis	cf. Cuon alpinus, Panthera tigris			Sus ahoenobarbus, Axis calamianensis, Rusa †sp.

See Fig. 4 for locations and main text for source references. Identifications follow original publications.

1846, the endemic stegodont †*Stegodon trigonocephalus* Martin, 1887, primitive elephant *Elephas* †*planifrons* Falconer & Cautley, 1845, Siwalik rhinoceros *Rhinoceros* †*sivalensis* Koken, 1885 and Siwalik hippopotamus *Hexaprotodon* †*sivalensis* Falconer & Cautley, 1836 (Table 1; Medway 1972; Hooijer 1982; Louys *et al.* 2007). Mammal fossils of Early Pleistocene age are unknown elsewhere in the Sundaic subregion, but a single tooth of †*Stegolophodon lydekkeri* Osborn, 1936 obtained in northwestern Borneo in enigmatic circumstances would, if authentic, suggest connection with Plio-Pleistocene Burma where †*Stegolophodon latidens* (Lydekker, 1880) occurred (Cranbrook *et al.* 2007).

Middle Pleistocene (778–126 ka)

In the Middle Pleistocene a distinctive assemblage, termed the *Stegodon–Ailuropoda* fauna, expanded in the Indochinese subregion of SEA (Dennell 2009). Diagnostic members were an extinct large ape †*Gigantopithecus blacki* von Koenigswald, 1935, orangutans *Pongo*, giant pandas *Ailuropoda* and stegodonts †*Stegodon* spp. Associated faunas varied in composition and diversity, some containing archaic proboscidean genera such as †*Mastodon* and others recent genera such as *Elephas*. Bovine genera included archaic and modern cattle and buffalo and caprines were represented by the extant serow. Tapirs occurred at several sites, at different times and in different places in association with different communities of other large mammals (Table 1).

A transitional Early/Middle Pleistocene assemblage at Liucheng *Gigantopithecus* Cave in southern China (Fig. 4) included an archaic tapir *Tapirus* †*peii* Li, 1979 with †*Gigantopithecus*, orangutan, an archaic giant panda *Ailuropoda* †*microta* Pei, 1963, †*Stegodon preorientalis* Young, 1938, an extinct cheetah *Acinonyx*, dhole, hyena *H.* †*brevirostris*, Asiatic black bear *Ursus thibetanus* Cuvier, 1823, hog badger *Arctonyx* †*minor* Pei, 1987, large felids, a pachyderm †*Gomphotherium*, horse, Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814) and a variety of pigs, barking deer, deer and a sheep †*Megalovis* (Table 1; Louys *et al.* 2007; Rink *et al.* 2008; Tong & Guérin 2009). Dates derived by Rink *et al.* (2008) indicate an absolute age at Liucheng of about 1000 ka (1206–940 ka, including uncertainties).

At Xinghau Shan, Nanzhau county, an enigmatic Middle Pleistocene record of 'giant' tapir *T.* †(*M.*) *augustus* was associated with grey wolf *Canis lupus* Linnaeus, 1758, tiger, Asiatic black bear, a horse *Equus*

†*sanmeniensis* Tielhard & Piveteau, 1930, rhino *Rhinoceros* †*sinensis* and giant deer †*Megaloceros* (Dennell 2009). At other sites in southern China, dated biostratigraphically as Middle Pleistocene listed by Kahlke (1961), in Yunnan at Heshangdong (Hoshantung) Cave, at 3 sites in Sichuan, in Guangxi, Hubei and Guizhou, giant tapir occurred in association with †*Stegodon-Ailuropoda* fauna. The Malayan tapir co-occurred with giant tapir at 1 site, confirming the separate identity of the 2 species. In Burma, at Mogok caves, giant panda *Ailuropoda melanoleuca* (David, 1869) was recorded, but not tapir, indicating the persistence of a western limit to the SEA distribution of the genus despite evident environmental change (Table 1).

A succession of chronometrically dated Middle Pleistocene sites in the Indochinese subregion shows progressive turnover in the large mammal faunas with which tapirs were associated (Fig. 4). At Tham Khuyen cave, Vietnam, 475 ± 125 ka, the giant tapir occurred with a fauna including †*Gigantopithecus,* an enigmatic large hominoid known only from this cave †*Langsonia liquidens* Schwartz *et al.*, 1995, 2 orangutans *Pongo* †*hooijeri* Schwartz *et al.*, 1995 and *Pongo* †*kahlkei* Schwartz *et al.*, 1995, a gibbon *Hylobates,* macaques, Asiatic black bear, sun bear *Ursus* (*Helarctos*) *malayanus* Raffles, 1821, giant panda, †*Stegodon orientalis* Owen, 1870, archaic forms of elephant, rhinoceros and pig (Table 1; Schwartz *et al.* 1995; Tougard 1998; Louys *et al.* 2007; Rink *et al.* 2008). At Daxin, southern China, 380–308 ka, the giant tapir was associated with †*Gigantopithecus,* orangutan, macaque, dhole, Asian black bear, giant panda, hog badger, †*S. orientaliis*, pigs †*Dicoryphochoerus* and *Sus* and modern genera and species of deer, cattle and an extinct sheep †*Megalovis* (Table 1; Tougard 1998; Rink *et al.* 2008). At Wuyun, southern China, 275–175 ka, tapirs were present with archaic subspecies of orangutan and giant panda, †*S. orientalis* and a mix of modern genera (Table 1; Schwartz *et al.* 1995; Rink *et al.* 2008). At Thum Wiman Nakim (Cave of the Sacred Serpent), Thailand, calcified clay sediments dated at 169 ± 11 ka immediately above the fossiliferous stratum set a minimum age for the assemblage (Bacon *et al.* 2011). Malayan tapir was present, with orangutan and giant panda and a near-modern fauna represented in some instances by extinct chrono-subspecies: pig-tailed macaque *Macaca nemestrina* (Linnaeus, 1766), langur, hyena, Asian black bear, hog-badger, Asian elephant, Indian rhinoceros *Rhinoceros unicornis* Linnaeus, 1758 and Javan rhinoceros *Rhinoceros sondaicus* Desmarest, 1822, Eurasian wild pig *Sus scro-*

fa Linnaeus, 1758 and bearded pig *Sus barbatus* Müller, 1838, 3 cattle, buffalo, serow, muntjac *Muntiacus* and 3 deer (Table 1; Tougard 1998). At Tam Hang S. cave, Laos, giant tapir and Malayan tapir co-occured (Bacon *et al.* 2011).

Neither †*Gigantopithecus* nor giant panda reached the Sundaic subregion, where the equivalent Middle Pleistocene fauna of Java, termed 'Sino-Malayan' (Hooijer 1952), was indicated by orangutan *Pongo* and additional immigrants from the SEA continental mainland supplementing the more ancient Siva–Malayan fauna, plus the products of local radiation, notably †*S. trigonocephalus,* archaic bovids and Dubois's antelope †*Duboisia santeng* (Dubois, 1891) (Dubois 1908). Among chronometrically dated faunas, at ~900 ka the transitional early Middle Pleistocene assemblage at Trinil H. K. lacked tapir, but included modern primate genera, with an archaic tiger, archaic dog, †*S. trigonocephalus,* Javan rhino, archaic pigs, chital, cattle and buffalo. Tapir remains were found in the later Kedung Brubus site, 800–700 ka. The Kedung Brubus specimens were described by Dubois (1908) as *Tapirus* †*pandanicus* (Dubois, 1908), but this name has been synonymized with *T. indicus* (Hooijer 1947; Storm 2001). The associated fauna of large mammals comprised a rich mix of extinct genera and archaic forms of extant genera (Table 1.) In all Javan sites, Malayan tapir remains were disproportionately scarce by comparison with other large mammal species, being represented by only 6 teeth from Kedung Brubus, Kedung Lumbu and Kebun Duren in the Kendeng hills (Hooijer 1947; Storm 2001).

In Peninsular Malaysia, cave washings in Perak yielding *Elephas* †*namadicus* Falconer & Cautley, 1846, *Rhinoceros, Hexaprotodon* and †*Duboisia* (Andrews 1905; Hooijer 1962a) have confirmed that a Sino-Malayan fauna, presumed to be of Middle Pleistocene age, extended to the continental part of the Sundaic subregion. Dated finds of mid-Middle Pleistocene age (~600 ka) in the Lenggong Valley, Perak, include Malayan tapir with an assemblage of other extant large mammal genera with Middle Pleistocene origins that have, like Malayan tapir, survived into modern times (Yasamin *et al.* 2010).

Late Pleistocene (126–10 ka)

The ape †*Gigantopithecus* was absent from Late Pleistocene SEA, its last dated occurrence being 380–310 ka (Rink *et al.* 2008). In the Indochinese subregion other archaic Middle Pleistocene megafauna genera and species did survive for many millennia through the LGP. In southern China, for example, giant tapir and Malayan

tapir were both present during the LGP, with orangutan, 2 hyenas *H.* †*brevirostris* and *Crocuta crocuta* (Erxleben, 1777), †*S. orientalis*, *E.* †*namadicus* and *R.* †*sinensis.* There is evidence that hyena *Crocuta*, †*Stegodon* and giant tapir even persisted into the Holocene (Louys *et al.* 2007). If correctly dated, the Keo Leng site in Vietnam shows that giant tapir was certainly present up to the LGM, with orangutan and giant panda and a transitional fauna in which †*S. orientalis*, *E.* †*namadicus*, *R.* †*sinensis* and *Sus* †*lydekkeri* Zdansky, 1923 occurred alongside an essentially modern assemblage of smaller primates, Indian rhinoceros, Eurasian wild pig, deer, wild buffalo and serow (Table 1; Tougard 1998; Louys *et al.* 2007).

In the Sundaic subregion there was greater variability, both geographical and temporal, during the Late Pleistocene. In Java, at Punung near the south coast, a combination of caves and open breccias of Last Interglacial age, dated at 128 ± 15 to 118 ± 3 ka (Westaway *et al.* 2007), yielded a fully modern fauna that included Malayan tapir with rainforest-dependent species, orangutan, siamang, gibbon and sun bear (also a rainforest indicator) as well as macaque and langur, Asian elephant, Javan rhinoceros, pigs indentified as Eurasian wild pig, bearded pig and Javan warty pig *Sus verrucosus* Boie, 1832, muntjac and other deer, banteng *Bos javanicus* D'Alton, 1923, buffalo and serow. The mammal community at Song Terus, dated 120–80 ka, has also been judged to represent a modern tropical rainforest fauna (Anysori 2010), denoted by the presence of moonrat *Echinosorex* sp., siamang, Javan warty pig and Indian muntjac *Muntiacus muntjak* (Zimmermann, 1780). In the Late Pleistocene sites at Punung and Song Terus, the absence of archaic large mammals recorded at sites such as Ci Saat, Trinil and Kedung Brubus suggests an extinction event in Java associated with the environmental upheavals at the beginning of the penultimate interglacial period around 120 ka, when open woodland and grassland landscapes were replaced by the dense tropical rainforests (van den Bergh *et al.* 2001). †*S. trigonocephalus, Elephas* †*hysudrindicus* Dubois, 1908, *Hexaprotodon* †*sivalensis* Falconer and Cautley, 1836, *Axis* †*lydekkeri* Martin, 1886, *Bubalis* †*palaeokerabau* Dubois, 1908 and †*D. santeng* all disappeared along with other archaic bovids and suids. Large mammals that appear to have had the ecological flexibility to endure through this transition include tiger, Javan rhinoceros, Malayan tapir, with modern forms of pigs and other cervids and bovids.

Tropical rainforest environments then seem to have persisted in Java until c. 80 ka when there was once again a climatic reversal towards drier and more open

conditions (van der Kaars & Dam 1995). This transition is recorded in the fauna of the partially collapsed cave Song Gupuh, where over 16 m of deposits yielded a rich sequence dated by mixed methods from about 70 ka to 1 ka, i.e. mid-LGP to first millennium AD. Malayan tapir was present, but orangutan and other obligatory rainforest primates of the Punung assemblage were lacking. The remaining species were entirely modern: long-tailed macaque *Macaca fascicularis* (Raffles, 1821)*,* sun bear*,* Asian elephant, Javan rhinoceros, Eurasian wild pig and *Sus* indet., deer *Cervus* sp., muntjac and bovines *Bos* sp. and *Bubalus* sp. (Table 1; Morwood *et al.* 2008).

The controversial Ngandong site, Central Java, was dated at 53–27 ka, i.e. mid to late LGP, by Swisher *et al.* (1996). The large mammals included Malayan tapir*,* with genera and species of Middle Pleistocene affinity such as *H.* †*brevirostris, Rhinoceros unicornis* †*kendengindicus* Dubois, 1908, bovid †*Epileptobos groeneveldtii* Dubois, 1908 and pig *Sus* †*macrognathus* Dubois 1908 (Table 1; Storm 2001; van den Bergh *et al.* 2001). On biostratigraphic grounds, de Vos and Sondaar (1994) considered that the Ngandong fauna was older than Punung. Although Curtis *et al.* (2002) reiterated confidence in the terminal Pleistocene date, an alternative redating of the Ngandong stratigraphy suggested that the site and the fossils it contained were no younger than Oxygen Isotope Stage 5 (Westaway *et al.* 2002, 2007).

At the inception of the Holocene epoch in Java, Malayan tapir was present at Wajak, ^{14}C dated at 10 560 ± 65 BP. The associated mammals consisted of modern species but included only a langur among primates, with tiger, Javan rhinoceros*,* Eurasian wild pig*,* banteng*,* modern buffalo and Javan deer *Rusa timorensis* (Blainville, 1822) suggesting the persistence, at least in this part of Java, of relatively open, lightly wooded environments (Table 1; Storm 2001).

In Sumatra, collections made by Dubois in 1888–1890 in limestone caves near Padang have an estimated age of 80–60 ka (de Vos 1983; Drawhorn 1995). Tapir remains (exclusively teeth) were described as a large chrono-subspecies of Malayan tapir *Tapirus indicus* †*intermedius* Hooijer, 1948. The distinction was challenged by Badoux (1959), but the subspecies name has been used by others to identify large-toothed Middle or Late Pleistocene Malayan tapirs elsewhere (see Table 1). The orangutan of these caves was also described as an extinct chrono-subspecies *Pongo* (*abelii*) †*palaeosumatrensis* Hooijer, 1948*,* averaging larger in dental measurements than modern comparatives. Other remains were extant forms (Table 1; Hooijer 1948; de Vos 1983).

In Peninsular Malaysia, Malayan tapir has been identified in Late Pleistocene sites at Batu caves, Selangor, associated with an assemblage of extant mammal genera or species of Middle Pleistocene origin, including orangutan, long-tailed macaque, canid*,* sun bear, tiger, rhinoceros sp. indet., Eurasian wild pig and bearded pig, sambar, muntjac and serow (Yasamin *et al.* 2010, 2013).

In northwestern and northern Borneo, Late Pleistocene sites overlapping chronologically with Song Gupuh and Wajak show the presence of a richer assemblage of large mammals of forms associated with tropical rainforest, with Malayan tapir also present. At the West mouth, Niah caves, Sarawak, securely dated from about 50 ka through the Holocene (Barker *et al.* 2007), among a very large collection of mammalian remains, only 1 extinct taxon was represented: giant pangolin *Manis* cf. †*palaeojavanica* Dubois, 1907, a single individual in a context datable to 45 ka (Piper *et al.* 2007a). The remainder included a diverse sample of modern mammal fauna with the addition of tiger (Piper *et al.* 2007b), Javan rhinoceros (Cranbrook & Piper 2007) and Malayan tapir (Cranbrook & Piper 2009), 3 species no longer extant in Borneo. Others included orangutan *Pongo pygmaeus* (Linnaeus, 1760), extending throughout the profile, gibbon *Hylobates muelleri* Martin, 1841*,* long-tailed and pig-tail macaques*,* maroon ?langur *Presbytis ?rubicunda* (Müller, 1838) and silvered langur *Trachypithecus cristatus* (Raffles, 1821)*,* sun bear*,* Sumatran rhinoceros, bearded pig*,* muntjac, sambar *Rusa unicolor* (Kerr, 1792) and banteng (Table 1; Hooijer 1961, 1962b,c; Cranbrook 2010).

Although occurring widely in terminal Pleistocene and Holocene sites of northwest Borneo, Malayan tapir was again represented in very small numbers. The sum of items identified from all sites amounts to 6 teeth and 19 foot bones (Tables 2 and 3). From 2 major mouths of Niah caves (West mouth and Gan Kira combined) P. J. Piper and associates (Piper & Rabett 2013) assessed a total of 10 683 identifiable whole or fragmentary bones and teeth of large or medium-sized mammals, of which only 19 items (0.18%) represented the Malayan tapir.

Superficial finds in an archeological context indicate a recent date. Juvenile canines found at 0–6 inches (0–15 cm) depth at the Gan Kira mouth of Niah caves and also on the surface of the cave soil in Sireh cave (Table 2; Cranbrook 2013a) were potentially deposited not long ago. Four foot-bones of tapir in the A. H. Everett Collection in the Paleontology Department of the Natural History Museum, London (reg. nos. M83323-

4, M83782-3) were recovered from Everett's Excavation B, Cave V, Jambusan, Sarawak (Table 3; Cranbrook 2004; Cranbrook & Piper 2009; Cranbrook 2013b). In a subsequent excavation of an adjoining cave, No. XIII, known as Tupak, by Gani *et al.* (2009), charcoal samples from Trench A, 30–40 cm, gave ^{14}C ages of Cal-BP 470-270, i.e. AD 1480–1680 and other samples were more recent. Everett's excavations in Cave V extend-

ed deeper, to 90 cm. The depth at which the Malayan tapir foot-bones were found was not recorded but, by inference, it is possible that they too dated from no more than a few centuries ago.

Although situated on the northeastern fringes of the Sunda Shelf and intermittently connected to Borneo during the Middle Pleistocene (Heaney 1985, 1986), Palawan is the only large island in the Sundaic subregion

Table 2 Teeth of Malayan tapir from Sarawak, Borneo, recorded by the trench and depth from which they were recovered in each of their respective sites and the approximate age of the bones (modified from Cranbrook & Piper 2009). A left lower mandibular canine in Y/D1 24–30 ins (No. 5) and a 1st left maxillary molar in Y/A1 0–6 ins (No. 6) from the Gan Kira entrance to the Niah caves have been added to the list (Fig. 2a,b). Note: the 2 deciduous upper canines from L3 15–20 cm and the lower deciduous premolar (exact provenance unknown) from Madai Cave, Sabah, illustrated in Cranbrook and Piper (2009), were misidentified as tapir and have consequently been omitted from this list

#	Cave site	Element	Trench	Depth (inches)	Period
1	Niah, West mouth[1]	R maxillary canine	E/G 1	30–36	?
2	Niah, West mouth[1]	L maxillary canine (split)*	E/G 1	42–48	?
3	Sireh Cave[2]	R mandibular canine (juvenile)	Surface	0	Sub-recent
4	Niah, West mouth[2]	L mandibular canine (adult)	NCP 01	(2044)	?
5	Niah, Gan Kira	L mandibular canine (sub-adult)	Y/D1	24–30	Early Holocene?
6	Niah, Gan Kira	L maxillary M1 (sub-adult)	Y/A1	0–6	Sub-recent?

*Damaged or fragmentary specimen; [1]Medway (1961); [2]Cranbrook and Piper (2009).

Table 3 Post cranial skeletal elements of Malayan tapir from cave sites in Sarawak, Borneo, recorded by the trench and depth from which they were recovered in each of their respective sites and the approximate age of the bones (modified from Cranbrook & Piper 2009)

#	Cave site	Item	Trench or BM reg. no	Depth (inches)	Period
1	Niah, West mouth[2]	L magnum, lateral portion *	HQ 5	84–87	Late Pleistocene
2	Niah, West mouth[1]	Metatarsal III R (proximal)*	W/E 1	24–36	Early Holocene
3	Niah, West mouth[1]	Metapodial III (distal)*	W/E 1	24–36	Early Holocene
4	Niah, West mouth[1]	Metapodial III (distal)*	X/W 1	48–60	Terminal Pleistocene
5	Sireh Cave[1]	Metatarsal IV R (proximal)*	B/10	24–30	Mid/Late Holocene
6	Niah, West mouth[3]	Metacarpal II or IV (proximal)*	X/2	24–48	Mid/Late Holocene
7	Niah, West mouth[1]	Cf. metatarsal II R (distal)*	Y/1 (A)	54–60	Terminal Pleistocene
8	Niah, West mouth[1]	Lateral metapodial (distal)*	X/2	24–36	Mid/Late Holocene
9	Niah, West mouth[3]	Cf. metatarsal II L (proximal)*	E/W 5	33–36	Early Holocene
10	Niah, West mouth[1]	Lateral basal phalanx	E/C1	24–48	Early Holocene?
11	Niah, West mouth[1]	Lateral basal phalanx	E/B2	48–60	Terminal Pleistocene?
12	Cave V, Jambusan[3]	Lateral basal phalanx, cf. II (pes)	M83324	Exc. B	Late Holocene/recent
13	Niah, West mouth[3]	Basal phalanx II	X/V 1	60–72	Late Pleistocene
14	Niah, West mouth[2]	Subterminal phalanx I or IV (manus)	HQ9 (B)	78–81	Late Pleistocene
15	Cave V, Jambusan[3]	Subterminal phalanx II (manus) R	M83323	Exc. B	Late Holocene/recent
16	Niah, Gan Kira[1]	Lateral subterminal phalanx	Y/A 21	30–36	Early Holocene?
17	Cave V, Jambusan[3]	Terminal (ungual) phalanx digit III*	M83782	Exc. B	Late Holocene/recent
18	Niah, West mouth[1]	Ungual phalanx digit III*	E/C1	0–24	Late Holocene
19	Cave V, Jambusan[3]	Proximal metapodial (indet)*	M83783	Exc. B	Late Holocene/recent

*Damaged or fragmentary specimen; [1]Medway (1961); [2]Hooijer (1962b); [3]Cranbrook (2012b); and this paper.

where tapirs have yet to be recorded. Currently the oldest well-studied vertebrate assemblage, from Ille Cave in the north of the island, dates from c. 14 ka through the terminal Pleistocene and Holocene (Lewis *et al.* 2008; Ochoa 2008; Piper *et al.* 2008, 2011). Primarily hunted by humans, but also likely including a component of a natural death assemblage, 27 different extant and locally extinct mammal taxa were identified, including Philippine long-tailed macaque *Macaca fascicularis philippinensis* Geoffroy, 1843, Palawan pangolin *Manis culionensis* Elera, 1915, arrow-tailed flying squirrel *Hylopetes nigripes* Thomas, 1893, Palawan spiny rat *Maxomys panglima* Robinson, 1921, Palawan porcupine *Hystrix pumila* Günther, 1879 and Palawan stink badger *Mydaus marchei* Huet, 1887 (Piper & Ochoa 2007; Ochoa 2008; Piper *et al.* 2008, 2011). Most significantly, the Ille Cave bone assemblages produced the first records of 2 species of deer *Rusa* sp. and Calamian hog deer *Axis calamianensis* Heude, 1888, possibly dhole and the former presence of tiger.

Reconstructions of Palawan paleogeography and past environment suggests that the island then covered almost 80 000 km^2 (>80% larger than its current Holocene landmass) and was joined with Busuanga and Culion to the north and Balabac to the south (Piper *et al.* 2011). The climate was cooler and drier than at present and the vegetation probably consisted of open woodland and savanna rather than the tropical rainforests that characterize the island today (Bird *et al.* 2007; Wurster *et al.* 2010). The Pleistocene landscapes of Palawan with their more open environments and large deer populations must have been sufficient to support tiger and dhole populations. There is, however, no evidence that Malayan tapir reached Palawan, possibly testifying to a limited capacity to cross maritime barriers that did not prevent the invasion of other large mammal species.

DISCUSSION

Local radiation and size changes within Quaternary SEA

Of 2 clades of tapirs of Early and early Middle Pleistocene SEA, one lineage *T.* †*sanyuanensis* > *T.* †*sinensis* > giant tapir *T.* (*M.*) †*augustus* trended towards larger size. Around the Early–Middle Pleistocene transition, *T.* †*sinensis* occurred on both sides of the eastern Palearctic/Indomalayan faunistic boundary and at some sites both this species and its apparent descendant giant tapir were sympatric with forms of Malayan tapir, represent-

ing the smaller, strictly SEA clade. Comparable Quaternary sympatries included, among Primates, the large ape †*Gigantopithecus* found with smaller orangutans *Pongo*. If the taxonomy of Schwartz *et al.* (1995) is valid, radiation of hominoids in Middle Pleistocene north Vietnam produced an additional genus †*Langsonia,* a large orangutan *P.* †*hooijeri* and a diversity of distinctive local clades of *Pongo* described as chrono-subspecies, all larger than ancestral *P. pygmaeus*. Among Carnivora, a large extinct dog †*Megacyon* co-occurred with precursors of the dhole. The Neogene bear *Ursus* †*minimus* Linnaeus, 1758 was ancestral both to Asian black bear and the smaller sun bear. Archaic forms of both bears occurred in Middle Pleistocene SEA sites (Table 1). Asian black bear also ranged into Europe in the Pleistocene. Competition with the largely herbivorous cave bears *Ursus* †*speleus* Rosenmüller, 1794 may have been a factor in its extirpation from its west Eurasian range (McLellan & Reiner 1994). The range of Asian black bear extended to Peninsular Malaysia (Yasamin *et al.* 2013) but did not reach Sumatra, Java or Borneo.

Only the sun bear has survived to the present in the Sundaic subregion. Comparison of faunal lists (Table 1) shows that, similarly, the larger member of the pair has become globally extinct or locally absent from SEA, suggesting selective pressures favouring smaller size. By the Holocene, if not before, giant tapir was extinct while Malayan tapir survives until today in SEA, albeit in a restricted range, low numbers and threatened circumstances. Among such long-enduring mammal species, ancient forms also tend to be larger than modern representatives. In some instances, size differences have been recognised by description of the archaic form as chrono-subspecies including Malayan tapir *T. indicus* †*intermedius* and orangutan *P.* (*abelii*) †*palaeosumatrensis* of Late Pleistocene Sumatra (Hooijer 1947, 1948).

The paleoenvironment

Perceptions of paleohabitats can be deduced from faunistic evidence, by reference to the known habits of modern mammal genera and species (Louys *et al.* 2007). The earliest Quaternary mammal megafauna of SEA included large proboscideans with comparatively low-crowned molars implying a browsing habit, rhinoceroses (again browsers), hippopotamus that must have required large water-bodies and riparian grazing, with pigs, deer and cattle of genera represented in modern tropical wooded habitats. A mix of large carnivores re-

flected diversity in prey. Horses and gazelle, which require extensive grazing lands, penetrated only to peripheral sites in southern China and central Burma (Table 1). Here, the indicated paleoenvironment was subtropical savannah or semi-open woodland, probably with areas of swamp vegetation surrounding large water bodies and abundant glades or grassland gaps.

Evidence of Middle Pleistocene forested paleoenvironments in SEA is derived from a variety of sources, including palynology and paleophytogeography (Wong 2011). Zoological indications include the presence of giant panda which (in its present ecology) is dependent on sub-temperate bamboos. The range of giant panda did not extend into the Sundaic subregion, presumably marking the distribution of prevailing environments supporting these bamboos. A second Middle Pleistocene indicator species in SEA was the ape †*Gigantopithecus*, which was distributed over a similar range. The association of this large ape (and †*Langsonia*) with a third Middle Pleistocene hominoid genus, orangutans *Pongo* spp., suggests that their ecological requirements overlapped. Yet †*Gigantopithecus* disappeared from the paleontological record after about 300 ka while *Pongo* continued to expand and diversify throughout SEA. The 2 living orangutans, *Pongo abelii* Lesson, 1827 and *P. pygmaeus,* are the most arboreal of the great apes. Even though their ecological versatility and adaptability are demonstrated by the survival, in present times, of individuals or small breeding populations in degraded forests (Payne & Prudente 2008; Wich *et al.* 2008), in their respective ranges both species are none the less good indicators of forested environments of some form.

Bacon *et al.* (2008) noted the strong similarity between the composition of the completely modern Late Pleistocene fauna at Duoi U'Oi Cave in northern Vietnam (c. 66 ± 3 ka) and those of the Sundaic subregion and, specifically, the Padang sites in Sumatra which included orangutan, siamang, sun bear, elephant, Eurasian wild boar and bearded pig (see also Long *et al.* 1996). They concluded that similar ecological conditions, consisting of tropical forests, are likely to have existed across much of mainland and island SEA. However, analysis of the distributions of extant Thai mammals emphasizes the significance of the transition zone around 10°N between the present distinctive Indochinese and Sundaic subregional faunas (Lekagul & McNeely 1977). That a barrier to genetic exchange has existed for a long time is confirmed, for instance, by molecular evidence of separate evolutionary histories of Indochinese and Sundaic gibbons, *Hylobates* spp. (Thinh

et al. 2010). At Pleistocene high sea levels (i.e. interglacials) the narrow Thai-Malay peninsula could have impeded the migration of large mammals. However, mid or low sea levels prevailed for most of the Quaternary, providing a broader land corridor between the Indochinese and Sundaic subregions of SEA (Cannon *et al.* 2009). The existence of an Early Pleistocene connection is confirmed by Sundaic megafauna assemblages in Java that showed affinity with Siwalik and contemporary Indochinese subregional faunas, including browsing proboscideans, hippopotamus, deer, cattle and an antelope, indicative of an open woodland or savannah habitat, with large surface water-bodies. Although there is no evidence that the Early Pleistocene immigration included Malayan tapir, at its first appearance in Middle Pleistocene Java (at Kedung Brubus, 800–700 ka) the species was associated, albeit sparsely, with a faunal assemblage indicating comparable habitat.

At low sea levels, huge northward draining rivers may have impeded the movement of some terrestrial mammals across the exposed bed of the South China Sea (Verstappen 1975), but environmental conditions appear to have provided a more decisive barrier. Expansion and retreat of zonal and altitudinal forest types must have followed the glacial cycles. Genetic divergence between the 2 living species of *Pongo* points to separation since around 400 ka (Locke *et al.* 2011) thereby setting a Middle Pleistocene date after which no further gene exchange occurred between antecedents of *P. pygmaeus* in Borneo and *P. abelii* in Sumatra, as a consequence of the severance of connected habitat suitable for orangutans. From the collective distributions of recent primates, Brandon-Jones (1998) inferred that SEA rainforest was subsequently fragmented by glacial drought around 190 ka and again at about 80 ka, leaving only refugial remnants in Sumatra and Borneo.

That paleoenvironmental factors prevented genetic exchange between eastern and western Sundaic forest refugia is supported by evidence of a corridor of savannah habitat, from which obligate forest-dwelling mammals would have been excluded, extending from Java to the Thai-Malay peninsula at the LGM and, by inference, also during previous Pleistocene glaciations (Bird *et al.* 2005; Wurster *et al.* 2010). Of 4 scenarios for terminal Pleistocene environments modelled by Cannon *et al.* (2009), 2 simulate the separation of eastern (Bornean) and western (central Sumatran) lowland evergreen rainforest blocks, while 2 simulate a narrow corridor from central Sumatra, Bangka and Belitung across the Karimata Strait to western Borneo. If such a corridor existed,

it might have facilitated the migration of some forest-adapted mammals, but evidently did not permit genetic exchange between the 2 *Pongo* species.

Although these climatic events affected the later Quaternary history of forest-dwelling mammals of the Sundaic subregion, Malayan tapir was probably protected by its ecological versatility. During the last interglacial, Malayan tapir was present at Punung, Java, associated with orangutan, gibbon and other large mammals ecologically confined to forest habitat. During the LGP, on the evidence of the faunas of Song Gupuh and Wajak (van den Bergh *et al.* 2009; Storm *et al.* 2005; Table 1), by 70 ka these forest indicator species were no longer present, while Malayan tapir remained among a surviving large mammal fauna denoting open woodland habitat. If the chronological date of Ngandong is correct (rather than biostratigraphical indications), conditions in mid-Late Pleistocene in Java also permitted the retention (or return) of a more archaic megafauna, indicative of well-watered, savannah-like habitat where, again, Malayan tapir was present.

Within Borneo, there is additional evidence of local Middle Pleistocene constriction of forest habitat. Among Borneo orangutans, phylogenetic reconstruction based on mtDNA sequences from 211 wild individuals from all parts of the island have determined time to the most recent common ancestor (TMRCA) at 322–71 ka (Arora *et al.* 2010). It appears that the population has passed through a bottleneck, expanding since late Middle or Late Pleistocene from a restricted area, i.e. a forest refugium. Among gibbons, smaller but more strictly arboreal and forest-adapted primates, a TMRCA of 1.78 Ma for Borneo gibbon indicates a long period of differentiation within the island, consistent with the confinement of the population within Middle to Late Pleistocene forest refugia (Thinh *et al.* 2010). Northwest Borneo has been identified as the location of such a refugium during the Late Pleistocene, supported by the confirmed presence at Niah caves of arboreal primates including orangutan, gibbon, macaques *Macaca* and langurs *Presbytis* and *Trachypithecus*, with sun bear and Malayan tapir in contexts dated from c. 50 ka, through the terminal Pleistocene and Holocene (Table 1).

The mix of rat species at Niah in the Late Pleistocene provides further insight into the prevailing environment. The murine species identified include long-tailed giant rat *Leopoldamys sabanus* (Jentink, 1879), a good climber and normal denizen of closed tall forest, with 2 species that in their present ecology frequent forest fringe and disturbed or secondary woodland vegetation: Mül-

ler's rat *Sundamys muelleri* (Jentink, 1880) and field rat *Rattus* sp. cf. *tiomanicus* (Miller, 1900). While supporting other evidence of a forest refugium in northwestern Borneo, the presence of *Rattus* sp., in particular, indicates that the physiognomy of the vegetation more likely resembled that of present heath forests, secondary forests and other disturbed forest habitats, rather than the tall, closed rainforest that is the normal climax vegetation today at lowland elevations (Cranbrook & Piper 2008).

Tapirs and Quaternary megafauna extinctions in SEA

Although technology has provided some chronometric dates to supplement biostratigraphy, certainty limits are wide and it is not possible to correlate faunal assemblages with recognized Pleistocene glacial cycles prior to the last interglacial. It is clear, however, that in the Early Pleistocene, a combination of climatic and geographical opportunities permitted some members of a late Neogene mammal fauna of central and south Asia with compatible ecology to expand into SEA. Faunal lists (Table 1) show that, subsequently, rather than one or more major episodes of extinction, throughout the Quaternary of SEA there has been progressive replacement of members of this archaic large mammal fauna with modern genera and species (cf. Corlett 2010).

For example, Bacon *et al.* (2008, 2011) proposed a biochronological sequence for well-documented faunas of the Indochinese subregion, from the cave sites of Yenchingkuo (Middle Pleistocene, China), Thum Wiman Nakin (late Middle Pleistocene, Thailand), Tham Hang South (late Middle Pleistocene–Late Pleistocene, northern Laos), Phnom Loang (Middle Pleistocene, Cambodia) and Duoi U'Oi, Ma U'Oi and Lang Trang (Late Pleistocene, northern Vietnam). They proposed that the earliest faunal community in the middle-late Middle Pleistocene consisted of extinct species such as †*S. orientalis, E.* †*namadicus, H.* †*brevirostris* (Yenchingkuo only) and giant tapir, associated with modern species/chrono-subspecies showing few advanced evolutionary stages like *Arctonyx collaris* cf. †*rostrastus* Matthew & Granger, 1923, *T. indicus* cf. †*intermedius, Ursus thibetanus* cf. †*kokeni* Matthew & Granger, 1923 and *Cuon alpinus* cf. †*antiquus* (Matthew & Granger, 1923). The early Late Pleistocene assemblage from Lang Trang (100–80 ka) is distinguished from preceding and succeeding communities by its relative modernity, including the Asiatic black bear, giant panda and Sumatran rhinoceros, but with some archaic

elements such as †*S. orientalis* and probable records of *E.* †*namadicus* and the extinct giant tapir and *T. indicus* †*intermedius*. The Late Pleistocene sites of Duoi U'Oi (66 ± 3 ka) and Ma U'Oi (47 ± 4 ka) contain a fully modern faunal community including pigs, dhole, Asiatic black bear, Sumatran and Javan rhinoceros and Malayan tapir.

In the Middle Pleistocene, as some members of the early megafauna became extinct and others evolved into descendent forms, tapirs, evidently at home in an open wooded paleoenvironment, diversified and spread through the Indochinese region. The generic tolerance of varied habitat is shown by the appearance of giant tapir at sites dated between 475 ka and 20 ka in southern China and Vietnam. Giant tapir and Malayan tapir were sympatric at a site in southern China and at Tam Hang S., Laos. However, ancestral Malayan tapirs spread further into the Sundaic subregion, reaching Java from at least 800–700 ka in association with other large ungulates whose presence indicates an open wooded and well-watered landscape. The very low representation of tapirs compared with other large ungulates suggests that they were rare, probably occupying marginal habitats in the prevailing environment.

Cyclic post-glacial restoration of warm climate and high rainfall across the region would have prompted the periodic expansion of closed forest from refugia. Such an ecological change, operating at a Middle Pleistocene interglacial cycle, could therefore account for the disappearances of early savannah-adapted megafauna mammals. In the Sundaic subregion, periodic high sea levels at interglacials caused fragmentation of exposed land area, thereby intensifying evolutionary processes among isolated populations. In the Late Pleistocene, these same cyclic changes from cool to warm climate continued to favour smaller against larger members of related taxa and, when there was no interspecific competition, progressive reduction in size. The process is reflected in the disappearance of the giant tapir and survival of Malayan tapir.

Large mammals themselves impact on their environment. In suitable climates and soil conditions, mammals such as proboscideans or rhinoceroses, by trampling and browsing, can maintain shrubby habitat and foster ruderal softwood species characteristic of disturbed forests. Such conditions match the feeding requirements of Malayan tapirs. The zooarcheological evidence, including identification of field rats at deep levels in Niah caves, Sarawak, supports the conclusion that the vegetation cover of lowland northwest Borneo during the ter-

minal Late Pleistocene had the character of disturbed forests, rather than the tall 'cathedrals' popularly visualized as pristine tropical evergreen rain forest. Without humans, the large browsing mammals themselves could have maintained sub-climax forest vegetation, while the grazing community of cattle, buffalo and others, could have kept open unforested gaps and glades.

In the Sundaic subregion at the LGM, as at previous glacial maxima, a comparatively cool, arid and more seasonal climate would have reduced the extent of tall, closed tropical rainforest, which retreated to constrained refugia. The subsequent return to interglacial conditions of warmth and high, non-seasonal rainfall favored the resurgence of rainforest vegetation. Once the regrowth of tall trees outstripped the physical capacity of the large mammals to maintain the habitat structure necessary for their sustenance, megafuana species including Malayan tapir would have suffered from diminished resources. In Borneo, in addition to botanical evidence of floristic sequences in the terminal Pleistocene (Bird *et al.* 2005), dramatic changes in the representation of cavernicolous bats at Niah and Jambusan, Sarawak, have been interpreted as consequences of environmental change (Cranbrook 2010). Although probably skewed by the preponderance of hunted quarry among mammal remains (see below), the low representation of remains of Malayan tapir at Niah again indicates that, in the terminal Pleistocene and early Holocene environments, the species continued to be rare. It is likely that the ecological versatility of Malayan tapir permitted it to survive through successive climatic transitions, occupying a range of habitats that appear to have varied from dense tropical rainforest to open woodland.

The presence in Borneo and Palawan of dhole and tiger, characteristic mammals of Middle and Late Pleistocene SEA, demonstrates that in the past both species had a wider Sundaic distribution than historically recorded. However, there is as yet no evidence that Malayan tapirs crossed the intervening geographic or ecological barrier.

Human impact

The Quaternary megafauna extinctions of Late Pleistocene Australia and North America have been linked with the arrival of modern humans in these continents (Flannery 1994, 2001). The longer existence of *Homo* spp. in SEA makes it more difficult to assess the relative impact of humans on the regional megafauna. The general conclusion of SEA regional reviews is that human interventions, including habitat modification and hunt-

ing, are likely to have intensified the effects of climatic and environmental change, to the detriment of megafauna mammals in particular (Louys *et al.* 2007; Corlett 2010).

In Java, a forest-adapted mammal fauna flourished at Punung during the last interglacial but, at nearby Song Gupuh, during the LGP from 70 ka indicator species of closed forest had been lost, as progressive cooling and desiccation took hold. The disappearance of those mammals most dependent on closed forest was attributed to ecological factors by van den Berg *et al.* (2001) and Storm *et al.* (2005), although the later identification of a possible modern human tooth has raised a question mark (Morwood *et al.* 2008). In Borneo, at Niah caves, modern humans were associated throughout the zooarcheological sequence, which has been dated from about 50 ka to near recent (Barker *et al.* 2007).

It has been argued that the local extinction of several large mammals on Palawan was, at least in part, due to human hunting pressure. From the Late Pleistocene, sea levels rose to a height estimated to have been between 0.3–1.5 m higher than at present. At the same time, the environment of the island reverted from open woodland and grassland to the now dominant evergreen tropical rainforests. The animal bone assemblage of Ille Cave, derived primarily from human hunting, chronicles the disappearance of the tiger, deer and dhole, probably as the combined result of changing environment, habitat loss and human predation–the last almost certainly intensified for deer. As deer numbers diminished, the human populations inhabiting the cave switched their main prey resource to the more forest adapted endemic wild pig *Sus ahoenobarbus* Huet, 1888 (Ochoa 2008; Piper *et al.* 2011; Ochoa & Piper 2013).

Did hunting by humans similarly exacerbate the environmental changes faced by Malayan tapirs throughout their Quaternary range? The species has a potentially long life-span, with a record (in captivity) of 31 years. Reflecting this long life expectation, recruitment is slow: after 13 months gestation normally one young is born, which then accompanies its dam for several years (biodata from Medway 1983). Johnson (2006) has modelled different levels of off-take applied to any large mammal with these characteristics and shown that a small increase in the mortality of juveniles can hold recruitment rate below levels needed to replace natural mortality of breeding adults. It is notable that in all sites in Borneo, the majority of dental remains of Malayan tapir represent juveniles (Table 2; Cranbrook & Piper 2009). At Niah, pigs were the principal ground quarry, accounting for 90–95% of all ungulate bones recovered from the excavations; by comparison, remains of tapir were trivial in number (Piper & Rabett 2009, 2013). In a post glacial environment which had become suboptimal for the survival of Malayan tapir, hunting strategies that were targeted at pigs, but unintentionally or deliberately also trapped juvenile tapirs, could tip the balance and precipitate extinction. This impact would have been intensified when Iron Age weaponry arrived and, ultimately, shotguns were introduced.

FROM PALEONTOLOGY TO POLICY: A PROPOSAL FOR THE REINTRODUCTION OF THE MALAY TAPIR TO BORNEO

The Malayan tapir has been shown to be the last remaining Old World species within the ancient family Tapiridae, with a known history that extends back some 1.5 Myr in SEA. Although primitive in form among Perissodactyla, this member of the ancient Quaternary megafuana has proved remarkably adaptable and durable, throughout its long history co-existing with many different mammalian communities and apparently thriving in many different climatic and ecological regimes. As shown above, there is zooarcheological evidence in Borneo that Malayan tapir has been a member of faunal communities on the island from at least ~50 ka to within the last few hundred years (see also Cranbrook & Piper 2009). Although there are no authenticated specimens in Museum collections, it has been claimed that Pierre Diard, who toured what is now West Kalimantan in 1826, obtained a specimen in the interior of Pontianak (Smythies 1960). Eye-witness reports of Malayan tapirs in Sarawak, Brunei and Sabah, as late as 1931, have been summarized elsewhere (Piper & Cranbrook 2007; Cranbrook & Piper 2009). It is probable that Malayan tapirs, although extremely rare, were still fairly widespread across northwest and northern Borneo up to that time. Medway (1977) conjectured that during the global economic depression of the 1930s, when the remaining rhinoceroses in Borneo were almost exterminated by trophy hunters, the last Malayan tapirs, not much smaller in size and with similar habits, may have suffered with them and finally been exterminated.

Although shy and secretive, Malayan tapirs tolerate contact with people and disturbance by human activity in rural areas. In Peninsular Malaysia, unmolested ta-

pirs have survived for long periods in secondary habitat close to settlements (Mohd Khan 1997). Trial trapping and immobilisation of wild animals has been successful (Williams 1978a,b). Malayan tapirs in zoos take almost any vegetable food and some captive pairs have proved fecund, e.g. 10 births at San Diego were reported by Ryder (in Medway 1983).

These characteristics have been emphasised in the IUCN/SSG Tapir Specialist Group guidelines on reintroduction and translocation, noting that tapirs are highly adaptable to changes in diet, environmental conditions and habitat use and, hence, have the potential to successfully overcome some of the greatest challenges presented to relocated animals. Moreover, tapirs live in ecosystems where biological diversity is maintained, in part, by the tapirs' key ecological roles, including seed predation and dispersal (especially of large seeds), selective sapling browsing in tree fall gaps and nutrient recycling. The guidelines conclude that these important roles make tapirs fundamental components of the restoration of ecosystems and ecological processes (Medici *et al.* 2008).

Given its recent extermination in Borneo, there appears to be no cultural, environmental, or ecological reason why Malayan tapir could not be reintroduced into suitable protected areas. Translocation could be entirely within national limits and under national legislative control, moving animals within Indonesia from Sumatra to Kalimantan or within Malaysia from a peninsular state to Sarawak or Sabah. The proposal by Piper and Cranbrook (2007) for reintroduction into Borneo under carefully supervised conditions and into 1 or more well-protected areas of suitable habitat of reasonable extent, is therefore a sound, exciting and feasible prospect. If achieved, such action could be of singular benefit to the conservation of this endangered and vulnerable survivor of the Quaternary megafauna of Southeast Asia.

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