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Biogeography and migration routes of large mammal faunas in South–East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand

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Abstract

Thailand has long held a key position in South–East Asia because of its location at the boundary of the Indochinese and Sundaic provinces, the major biogeographical regions of South–East Asia. These provinces are distinct climatically, floristically and faunistically. The present-day limit between them is located at the Kra Isthmus, in peninsular Thailand.

Previous studies of the Javanese large mammal fossil faunas and the recent study of fossil large mammal faunas from Thailand strengthen the hypothesis of a “continental” migration route (in contrast with the “insular” hypothesis via Taiwan and the Philippines) during the Late Middle/Late Pleistocene period. Thailand was even part of this migration route. During the glacial periods, the faunal exchanges were favored by the emersion of a huge continental shelf called Sundaland (South–East Asian continental area connected to Borneo and Indonesia islands by land bridges), when the sea level was low. No geological, biogeographical or paleobiogeographical evidence supports the hypothesis of a migration route via Taiwan and the Philippines.

Analysis of the extant and Late Middle Pleistocene large mammal faunas (Carnivora, Primates, Proboscidea and Ungulata) points out the antiquity of the Indochinese and Sundaic provinces. This idea is also supported by the fact that mainland faunas already displayed modern character, whereas the Javanese faunas were mainly composed of endemic forms. However, the occurrence of the extinct species, *Elephas namadicus* found in a Malaysian site (Tambun) indicates that the limit between the two provinces, if not close to the present place, was located more southward than today, possibly in peninsular Malaysia. It is also confirmed by the presence of northern species, such as *Ailuropoda melanoleuca baconi* and *Crocota crocota ultima*, in Late Middle Pleistocene sites of Thailand. In fact, because of climatic cooling that occurred in the northern hemisphere during the Pleistocene, the northern faunas had to move southward. To our knowledge, the hypothesis of the antiquity of the South–East Asian provinces with a boundary south of the present-day one is mentioned here for the first time.

Previous biogeographical studies were based mainly on insular data from the Philippine Archipelago (geological and mainly present-day zoogeographical data) but also from Indonesia and Borneo (paleontological data). However, the recent discovery of Thai large mammal faunas from Late Middle Pleistocene allows to bridge the gap in the fossil record between the northern faunas of South–East Asia and the southern ones. These Thai faunas are characterized mainly by extant forms but some are today absent from the Thai territory (*Ailuropoda melanoleuca*, *Crocota crocota*, *Pongo pygmaeus*, *Sus cf. barbatus*, *Rhinoceros cf. unicornis*, *Cervus eldii*). © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Biogeography; Faunal exchanges; Large mammal; Pleistocene; South–East Asia

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1. Introduction: present biogeographical context of South–East Asia

The world is today divided into six biogeographical regions: Palearctic, Oriental, Ethiopian, Australian, Neartic and Neotropical (Watts, 1984). Within these regions, distinct subregions or provinces have been proposed. For example, the Oriental region clusters the Indochinese, Sundaic, Indian and Wallacean provinces (Lekagul and McNeely, 1988).

Thailand (20–7°N) straddles two distinct biogeographical areas: the Indochinese province (northern), and the Sundaic province (southern) (Lekagul and McNeely, 1988; Gray et al., 1994) (Fig. 1). In addition

to the northern part of Thailand, the former province also includes South China, Myanmar (ex-Burma), Vietnam, Laos and Cambodia. The Sundaic province includes the southern part of Thailand, Malaysia, Sumatra, Java and Borneo (Lekagul and McNeely, 1988). The boundary between the two provinces is presently located at the Kra Isthmus, in peninsular Thailand, north to Tavoy on the Myanmar side (14°N) and the Chumpon-Prachuap border (11°N) on the Thai side (Whitmore, 1984; Lekagul and McNeely, 1988).

The Indochinese and Sundaic provinces display important climatic differences. Indeed, the Indochinese province presents a stronger seasonality with a

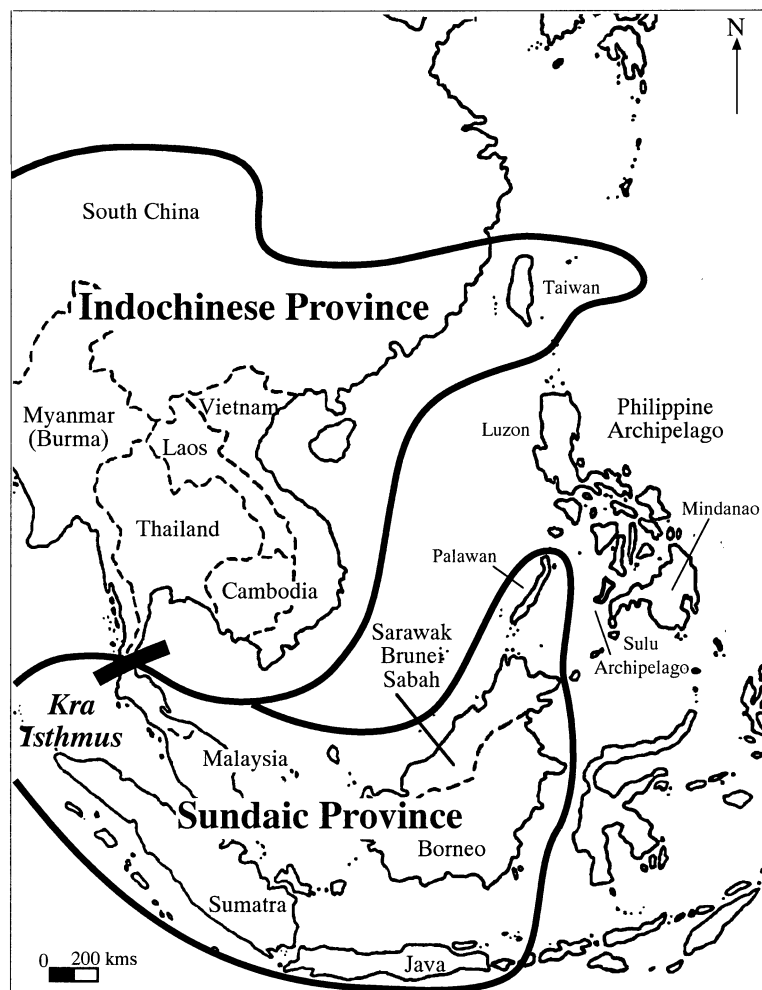


Fig. 1. Map of South–East Asia showing the boundaries of Indochinese and Sundaic provinces (after Lekagul and McNeely, 1988).

Table 1
List of richest large mammal fossil sites taken into consideration in the present study

Country	Faunas ^a	Reference
Middle Pleistocene		
Philippines	Luzon, Mindanao	von Koenigswald, 1956; Bautista, 1991
early Late Middle Pleistocene ^b		
South China	Koloshan, Hoshangtung, Hsingan	Kahlke, 1961
Myanmar	Mogok	Colbert, 1943
Vietnam	Tham Om, Hang Hum, Keo Leng	Olsen and Ciochon, 1990
Laos	Tam Hang	Fromaget, 1936
late Late Middle Pleistocene		
Thailand	Thum Wiman Nakin, Thum Phra Khai Phet	Tougaard et al., 1996; Tougaard, 1998
Cambodia	Phnom Loang	Beden and Guérin, 1973
Malaysia	Tambun	Hooijer, 1962; Medway, 1973
Java	Ngandong	Oppenoorth, 1932; Medway, 1973; van den Bergh et al., 1996; Falguères et al., 1998; de Vos, pers. comm.
Late Pleistocene		
Vietnam	Lang Trang	Vu et al., 1996
Sumatra	Sibrambang, Lida Ajer	de Vos, 1983
Java	Punung	Badoux, 1959; van den Bergh et al., 1996
Borneo (Sarawak)	Niah	Medway, 1964, 1988; Harrison, 1996

^a The faunas are grouped by period (for details of the age, see their bibliographic references), except for the Philippines since the sites are not very well known.

^b The terms used to designate the different period follow Harland et al. (1989); “early” and “late” (without capital letter) defined the beginning and the end of the Late Middle Pleistocene, respectively.

lower rainfall (Whitmore, 1984; Gray et al., 1994). However, the boundary between both provinces is especially valid for plants (limit between rain forest and monsoon forest) (Whitmore, 1984). It is also true for insects, amphibians, birds and mammals (Whitmore, 1984; Lekagul and Round, 1991; Corbet and Hill, 1992; Gray et al., 1994).

However, has Thailand already been a biogeographical privileged place as today? In order to answer this question, we will use data from the Pleistocene geological framework as well as data from the analysis of the extant and fossil large mammal faunas. The present study is only based on the large mammal faunas from South–East Asia and the Philippines, because comparisons are possible only with large mammal fossil faunas. Few small mammal fossil faunas are available in South–East Asia, except in South China (Huang, 1991; Zheng, 1993) and Thailand (Chaimanee, 1998). It is also important to note that the marine mammals are not taken into consideration. The faunal composition of the Indochinese and Sundaic provinces is compared. Moreover, complete faunal lists of extant

species, from Corbet and Hill (1992) and Nowak (1999), are given in Appendix A and those of fossil species in Appendix B (see also Table 1).

From a paleontological point of view, the Late Middle Pleistocene biogeography of large mammal faunas is less well known than for the extant faunas. The Pleistocene fossil record is more documented in South China, Vietnam and Java, whereas few large mammal fossils were discovered in the other countries of South–East Asia, except in Thailand. Indeed, until the 1980s, no Pleistocene large mammal fauna was known in Thailand. So, there was an important gap between the northern and southern fossil faunas of South–East Asia, and the Thai fossil faunas should link them.

2. Geological context

2.1. Tectonic history

An extensive literature (Molnar and Tapponnier,

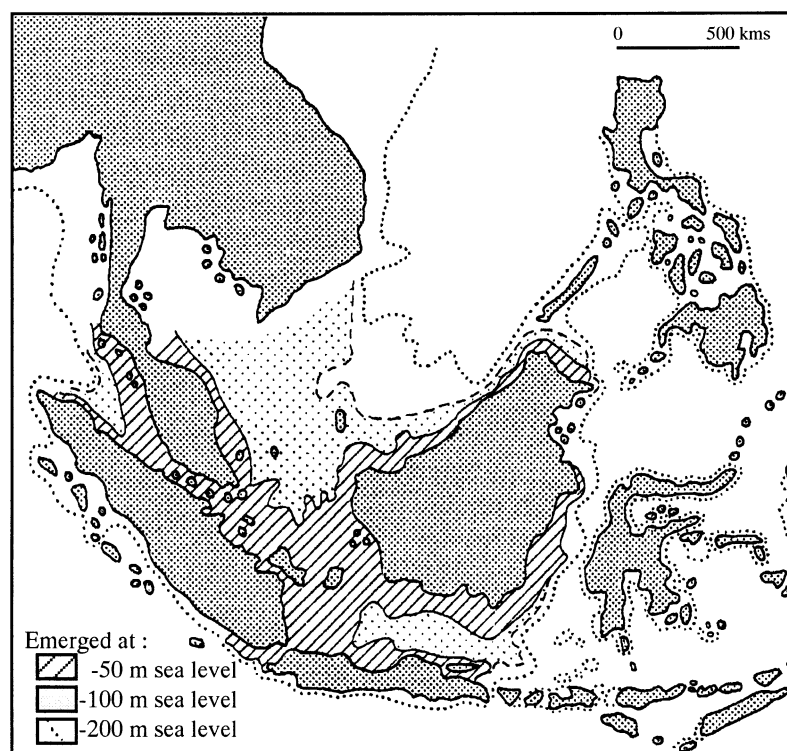


Fig. 2. Bathymetric map of South–East Asia showing the 50, 100 and 200 m isobaths (from van den Bergh et al., 1996).

1975; Tapponnier et al., 1982; Hutchison, 1989; Tapponnier et al., 1990; Dheeradilok, 1992) deals with the geological evolution of South–East Asia in some details, so I will just be focused on some points.

The South–East Asian region is characterized by two major lithospheric continental plates, that of Sundaland (South–East Asia landmass including Sumatra, Java and Borneo) representing a south-eastwards extension of the Eurasian plate, and the northwards extension of the Australian platform, into the south and eastern Indonesian region (Hutchison, 1989). Between Sundaland and the Australian platform, lie a set of small continental lithospheric fragments mixed with island arcs such as the Philippines (Vondra et al., 1981; Hutchison, 1989).

The geological history of South–East Asia is mainly linked to two major plate collisions. The first one was the collision between India, separated from Eastern Gondwanaland (Australia), and Eurasia about 65–55 myr (Courtilot et al., 1986; Beck et al., 1995). This event led to the formation of several faults such

as the Red River (Yunnan province), Sagaing (Myanmar), Mae Ping, Three Pagodas (Thailand) and Sumatran faults for the most important (Hutchison, 1989; Polachan et al., 1991). The southern part of the Sundaland lithospheric continental plate (Malaysia, Sumatra, Java and Borneo) and then the northern part (Southern China, Myanmar, Indochina and Thailand) were pushed away (Tapponnier et al., 1982; Hutchison, 1989; Dheeradilok et al., 1992). The second collision was that between South–East Asia and Australia about 15 myr ago, leading to the formation of the Lesser Sunda islands and parts of Sulawesi and the Philippine Archipelago (Tapponnier et al., 1982; Hutchison, 1989). During the Pleistocene, the South–East Asian volcanic and tectonic events lay in the framework of the collisions of the continental Eurasian and oceanic Indo-Australian tectonic plates. These events had mainly effects in Indonesia located in the southern limit of the Sundaland, and in the Philippine Archipelago located in the area of four major subduction zones (Heaney, 1985; Hutchison,

1989). Especially eastern Indonesian and Philippine islands are subject to uplifts. South–East Asia is currently an aseismic region except the Cenozoic fault zones (Hutchison, 1989).

2.2. Glacio-eustatic events

One of the most important Pleistocene geological events in South–East Asia has been a series of glacio-eustatic sea level fluctuations (Fig. 2). Before 0.8 myr, sea level fluctuations were moderate with a mean of 70 m and lowest sea levels at around 100 m below present-day sea level after the planktonic $\delta^{18}\text{O}$ (Prentice and Denton, 1988). At 0.8 myr, there was a dramatic change with minimum sea levels down to 170 m and an average sea level of around 90 m below present-day sea level. This fluctuation mode continued up to recent times. In details, several less important drops of the sea level seem to have occurred during the Late Middle and Late Pleistocene. It was due to cooler climatic conditions around 0.28 and 0.24 myr and then around 0.18 and 0.125 myr, according to palynological data (van der Kaars, 1991; Zheng and Lei, 1999). The sea levels were respectively between 50 and 130 m for the former coolings and around 150 m for the latter ones (Prentice and Denton, 1988).

During the glacial periods of the Pleistocene, low sea levels led to the emersion of a huge continental shelf extending until the marine areas of 200 m depth (Hutchison, 1989). This shelf was also considered as Sundaland. The Philippine islands were out of this contour line except Palawan, since the depth of water is about 145 m between Borneo and Palawan (Heaney, 1985). In a modern bathymetric setting, a sea level lowering of 50 m would be enough to connect Sumatra, Java and Borneo with Asian mainland (van den Bergh et al., 1996). However, Java would still remain quite isolated as a large elongated bay would have separated Java from Borneo to the north (van den Bergh et al., 1996). Moreover, the minimum sea depth between Borneo and Luzon (Philippine Archipelago) via Palawan is 485 m, and between Borneo and Mindanao via the Sulu archipelago (other Philippine islands) is 290 m (Heaney, 1985). It is worth noting also that there is a small island arc extending north from Luzon toward Taiwan. However, the minimum sea depth between

these latter islands is over 1000 m (Heaney, 1985; Hutchison, 1989).

3. Zoogeography of extant large mammals in South–East Asia and Philippines

3.1. Features of the large mammal faunas

The extant faunas of South–East Asia include 129 species of large mammals (Primates, Carnivora, Proboscidea, Perissodactyla and Artiodactyla) (for details, see Appendix A). Among them, 53 species of large mammals (41%) are of Indochinese affinity whereas 44 species (34%) are of Sundaic affinity. The remaining species are of both affinities (16 species of large mammals; 12.5%) or of other (Palearctic, Indian, ...) affinities (16 species of large mammals; 12.5%). The large mammal faunas of the Indochinese and Sundaic provinces display a greater faunal similarity to each other than to that of the Philippine Archipelago (Wallacean province). Despite their affinities, both provinces have 48 species in common. On the other hand, the whole Philippine Archipelago shares five large mammal species with the Indochinese faunas and nine with the Sundaic ones (see Appendix A). Among the nine species in common, three species are only found in Palawan. This latter island has 58% of its whole mammalian fauna in common with that of Borneo (Heaney, 1985).

3.2. Endemism rate

The number of large mammal endemic species (from islands or small continental area) is 23. Among them, 19 species are found in the Sundaic province, especially Indonesia (Sumatra, Java) and Borneo, and only four are present in the Indochinese province. For the larger Indonesian islands, the large mammal endemism rate is around 9% in Sumatra, 22% in Java and 20% in Borneo. However, if the whole mammalian fauna is considered, this rate is much lower except for Borneo (24%), whereas it is around 3% in peninsular Malaysia, 6.5% on Sumatra and 12% on Java (Heaney, 1985). Moreover, the faunas of the Indonesia and Borneo are balanced faunas, contrary to that of the Philippine Archipelago. An unbalanced fauna is an endemic fauna with very few taxa (de Vos et al., 1999). On the other hand, the

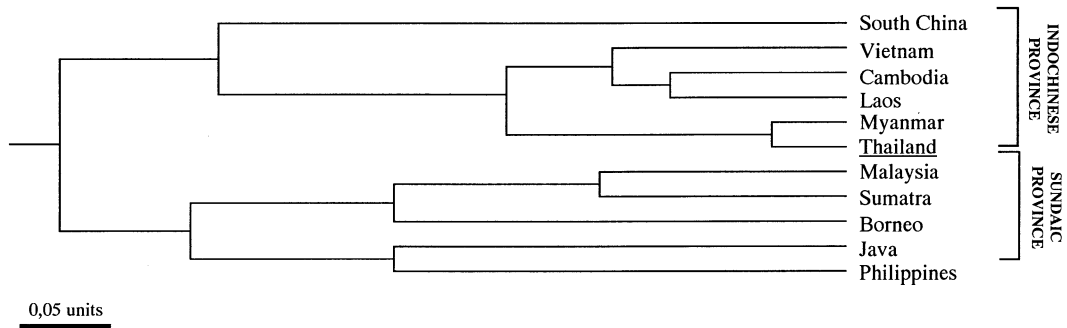


Fig. 3. Dendrogram based on the occurrence of large mammal species found in South–East Asian countries showing the affinities of the extant Thai large mammal fauna with those of the Indochinese province. The fauna of Thailand is here considered as a unit. The informative species (species found at least in two faunas) are considered to elaborate a matrix of appearance/disappearance, coded in 1/0, respectively. With the program “S. A. H. N. Clustering” (Sequential Agglomerative, Hierarchical and Nested Clustering, version 1.80; Rolf, 1993) from the software NTSYS-pc, this matrix was transformed in a distance matrix. The dendrogram is obtained with the method U. P. G. M. A. (Unweighted Pair Group Method, Arithmetic average; Sneath and Sokal, 1973). This analysis was based on the species listed in Appendix A without distinction between the Thai large mammal faunas found north and south of the Kra Isthmus, cross being replaced by the number 1.

endemism rate is 85% for the whole mammalian fauna of the Philippine islands: 42% on Palawan and between 55 and 87% on the other Philippine islands (Heaney, 1985; van Oosterzee, 1997).

3.3. Zoogeographical affinities of the Thai faunas

Concerning the Thai large mammal fauna, it appears that this fauna, considered as a unit, is more similar to the Indochinese province fauna as shown by the dendrogram (Fig. 3) based on the occurrence of the species found in each country of South–East Asia. On the other hand, if the Thai fauna is decomposed in large mammal fauna found

north and south of the Kra Isthmus, the dendrogram (Fig. 4) shows that the northern Thai fauna is related to the Indochinese fauna and the southern Thai fauna is closer to the Sundaic one. In fact, 31% of the Thai large mammals (20 of 64 large mammal species) are of Indochinese affinity and 20% (13 of 64 species) are of Sundaic affinity. It is worth noting that, in both dendrograms, Java and the whole Philippine Archipelago seem to be closely related. It is maybe due to the UPGMA method (distances considered of equal length) or to high endemism rate on the Philippine Archipelago and to the impoverishment of the Javanese fauna since the island isolation more than a strong faunal affinity.

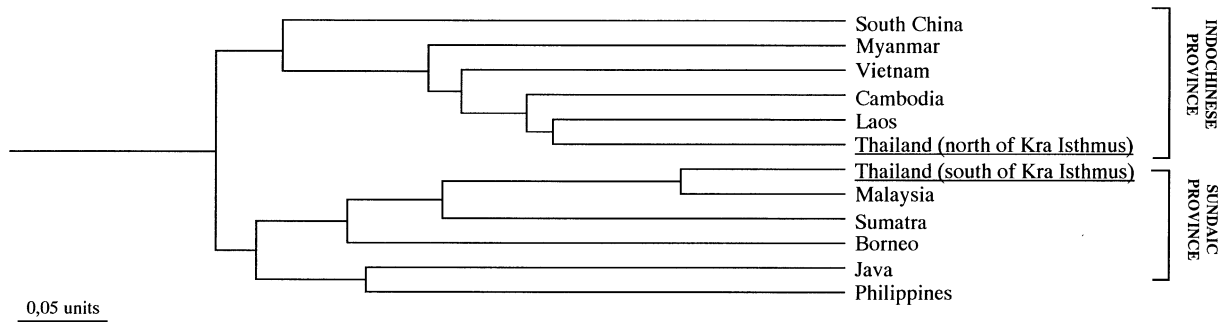


Fig. 4. Dendrogram based on the occurrence of South–East Asian large mammal species showing the division of the Thai extant faunas into two groups: one with Indochinese similarities and the other with Sundaic similarities. This dendrogram was elaborated like that of Fig. 3. However, the Thai fauna was decomposed in large mammal faunas found north and south of the Kra Isthmus (see Appendix A for the detailed north and south Thai large mammals).

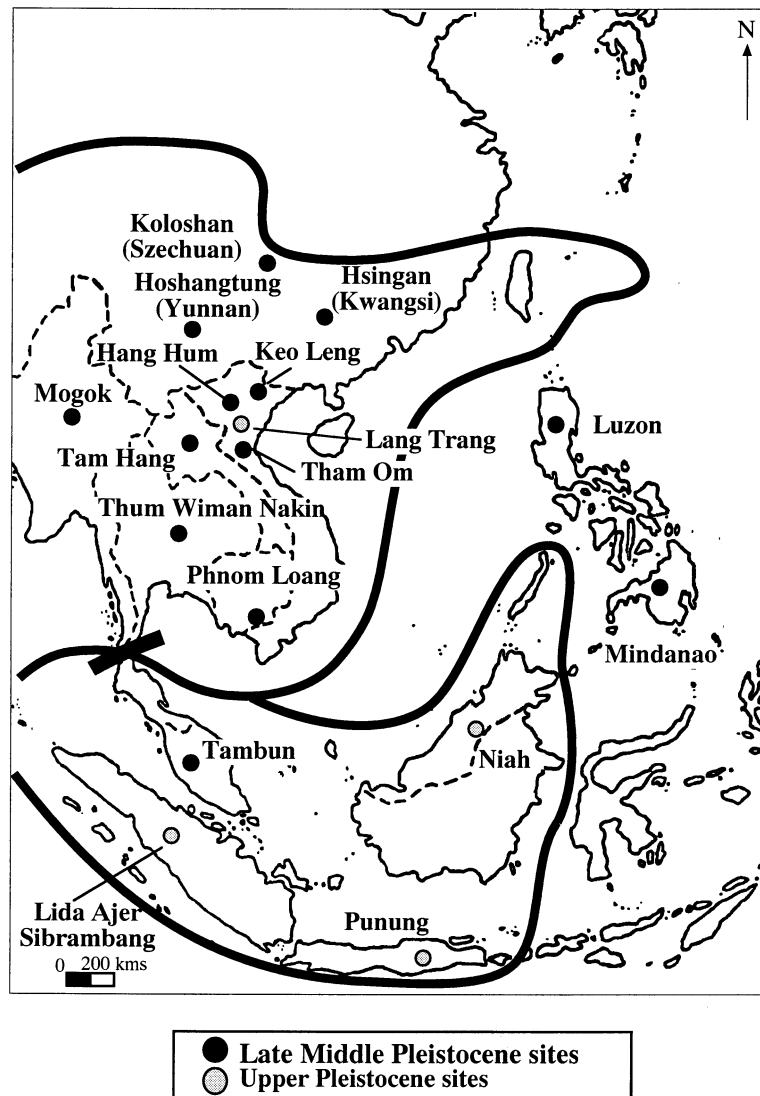


Fig. 5. Location map of the late Late Middle and Late Pleistocene richest large mammal sites in South–East Asia (for references, see Table 1).

4. Late Middle and Late Pleistocene fossils

4.1. General context

In South–East Asia, the fossil record is unequally documented for the Middle and Late Pleistocene periods. Numerous localities are known for the Middle Pleistocene of the Indochinese province but few, related to this period, have been found in the Sundaic one. As for the Late Pleistocene, several fossiliferous sites are known in the Sundaic province, contrary to the Indochinese one. It

is worse for the Philippine fossil record. Few sites have been found (Luzon, Mindanao) and poorly studied (von Koenigswald, 1956; Shutler and Mathisen, 1979; Bautista, 1991). For that study, sites specifically diversified and found in the Indochinese and Sundaic provinces are taken into account (Fig. 5, Table 1, Appendix B). Studies of fossil faunas from South China, Laos, Myanmar, Cambodia, Malaysia and Philippines, are old and often limited to the genus determination, whereas recent taxonomic reviews were done for the fossil faunas found in Vietnam, Sumatra, Java and Borneo.

4.2. Temporal comparison (Late Middle Pleistocene/Late Pleistocene)

If the Late Middle Pleistocene faunas are compared with those of the Late Pleistocene, a faunal turnover can be observed. It is more marked on Indonesian islands, mainly on Java (de Vos et al., 1999; Sondaar et al., 1999). Indeed, the Punung fauna, also called *Pongo-Homo sapiens* fauna, is completely different from the archaic Ngandong fauna, also called *Stegodon-Homo erectus* fauna (Aziz et al., 1999). In the Punung fauna, genera and species are still living on the Asian continent or in Indonesia. Eight out of 11 taxa defined at the species level were and are still widely widespread in South–East Asia. One species (*Elephas maximus*) of the Punung fauna is of Indochinese affinity. Three species, *Pongo pygmaeus*, *Tapirus indicus* and *Sus barbatus*, were found first in Middle Pleistocene sites of the Indochinese province. Later, when the land bridges were submerged by the sea during interglacial periods, some specimens of these species were probably trapped on islands, whereas they became extinct on the mainland. Probably all new Javanese faunal elements are the result of a novel migration wave (Aziz et al., 1999). On the mainland, the early Late Middle Pleistocene was characterized by the *Ailuropoda-Stegodon* fauna, mainly defined by the occurrence of *Ailuropoda melanoleuca baconi* and *Stegodon orientalis* but also *Ursus thibetanus kokeni*, *Arctonyx collaris rostratus*, *Elephas namadicus*, *Megatapirus augustus* and *P. pygmaeus* (Kahlke, 1961; Aigner, 1978; Huang, 1979; Li, 1981). However, archaic forms such as *S. orientalis*, *E. namadicus*, *M. augustus* or *Rhinoceros sinensis* were not found in the late Late Middle Pleistocene localities from Thailand and Cambodia (Beden and Guérin, 1973; Tougard et al., 1996; Tougard, 1998), whereas *S. orientalis*, and perhaps, *E. namadicus* were discovered in the Late Pleistocene site of Lang Trang, Vietnam (Vu et al., 1996). The Thai and Cambodian faunas are modern in their composition because they do not contain extinct species. On the other hand, some extinct subspecies occurred (*Crocota crocota ultima*, *A. collaris rostratus*, *Rhinoceros sondaicus guthi* and others; for more details, see Appendix B). In general, subspecies are larger than their homologous Holocene or recent species (Hooijer, 1949; Tougard, 1998; de Vos et al., 1999). It was probably

due to a body mass adaptation in order to better resist to cooler climatic conditions to avoid important body heat wastes (Bergmann, 1847; James, 1968; Fooden and Albrecht, 1993), as recorded during the late Late Middle Pleistocene (van der Kaars, 1991; Zheng and Lei, 1999). The Late Pleistocene fauna is composed of extant species, except *S. orientalis* and *E. namadicus*, even if some species (*P. pygmaeus*, *A. melanoleuca*, *T. indicus* and *Cervus unicolor*) are not living today in Vietnam (Vu et al., 1996).

4.3. Geographical comparison (mainland/islands)

According to Vu et al. (1996) and de Vos et al. (1999), the Lang Trang fauna is similar to the Indonesian Late Pleistocene faunas, especially those of Sumatra (Lida Ajer and Sibrambang), Java (Punung) and Borneo (Niah). However, the extinct *S. orientalis* as well as *Ursus thibetanus* and *A. melanoleuca* are absent from the Indonesian sites. On the other hand, *S. barbatus* and *Bos javanicus* do not occur in the Lang Trang fauna. For the late Late Middle Pleistocene faunas, the difference of faunal composition between the Indochinese and Sundaic provinces is strongly marked. Indeed, in the mainland, the faunas have a recent character since all species found in the Thai and Cambodian sites are extant. The Tambun (peninsular Malaysia) and Ngandong (Java) sites still have archaic forms (*Stegodon trigonocephalus*, *Hexaprotodon sivalensis*, *S. macrognathus*, *Homo erectus*, *E. namadicus*, *Duboisia santeng* and others; see Appendix B for the complete faunal lists). These forms, related to the Siwalik faunas, are from an earlier migration route (Early to Middle Pleistocene), the so-called “Siva-Malayan” route (from the continent to the Sunda shelf; von Koenigswald, 1935).

4.4. Zoogeographical affinities of the fossil faunas

Studies of the Late Middle and Late Pleistocene South–East Asian faunas reveal that some large mammals which today characterize either the Indochinese province or the Sundaic province have been discovered in several localities (Table 1, Appendix B). In fact some living species such as *Macaca assamensis*, *U. thibetanus*, *A. melanoleuca*, but also *Elaphodus cephalophus* were present in fossil faunas of South China, Vietnam, Myanmar and/or Thailand, whereas *Hylobates syndactylus* or *S. barbatus* have only been

found in Sumatra, Java and/or Borneo. These species occur today exclusively in the same provinces in which they occurred during the Late Middle and Late Pleistocene. The number of species is probably not exhaustive, but all the present-day large mammal species have not been found in fossiliferous deposits. Some were and are also too widespread in South–East Asia (for more details about the geographical affinity of species, see Appendices A and B).

Except these extant species, some other extinct or missing species are also known exclusively in the northern part of South–East Asia or in the southern part. It is notably the case for *S. orientalis*, *E. namadicus* and *M. augustus* in the northern part, and *S. trigonocephalus* and *D. santeng* in the southern one (for more details about the province affinity of each fossil species, see Appendix B). It is difficult to consider some species as endemic, for example *Szechuanopithecus yangtsensis* or *Parameles simplicidens*, because it may be a taphonomic bias or a wrong determination of a taxa due to the preservation state or the paucity of the fossil material.

As for the faunas of the Philippine Archipelago (Luzon and Mindanao), they were characterized mainly by endemic species (von Koenigswald, 1956; Bautista, 1991; Appendix B). Only one species, *S. cf. trigonocephalus*, was found in common with the Ngandong fauna (Late Middle Pleistocene, Java). However, elephants are generally considered as good swimmers (Heaney, 1985; van Oosterzee, 1997). This form can not strongly testify to a land connection between Java and Luzon, probably via Borneo.

4.5. Zoogeographical affinities of the Thai fossil faunas

The recent study of the Late Middle Pleistocene fauna from northeastern Thailand (Tougaard, 1998) shows that this fauna is characterized by a more important number of Indochinese large mammal species (40% of the 27 Thai large mammal defined at the species level) compared to the Sundaic ones (15%). Moreover, this fauna is characterized notably by the occurrence of the hyena *C. crocuta ultima*, the panda *A. melanoleuca baconi* and the orang-utan *P. pygmaeus*. These species were widespread during the Late Middle Pleistocene in the northern part of South–East Asia. On the other hand, they do not live in Thailand any more. Their geographical distri-

bution is today restricted to small continental areas, islands or other world region. The spotted hyena, *Crocuta crocuta*, is only found in Africa, south of the Sahara (Nowak, 1999). The habitat of the giant panda, *A. melanoleuca*, is restricted to some South China mountains, whereas the orang-utan lives only in Sumatra and Borneo (Nowak, 1999). Three situations are thus presented. According to Kurten (1956), *C. crocuta ultima* took over from *Hyaena brevirostris sinensis* first in South China. Indeed, this latter species became extinct at the same time a cooling event occurred. On the other hand, the cooling caused an altitudinal drop of the mountain vegetation zones, as those of the bamboo species (Zheng and Lei, 1999). In this way, this kind of plants could have covered some lowland areas perhaps in contact with each other. This could have allowed the southward migration of *A. melanoleuca baconi*, that subsists on this plant (Tougaard et al., 1996). According to Heaney (1985), most of the species that are endemic to a single island are restricted to mountain habitats. However, because of the altitudinal depression of mountain forests during the glacial periods, most mountain mammal species were widespread in appropriate habitats. This indicates that immigration across the Sundaland took place in the recent past. Concerning *P. pygmaeus*, fossil remains from the Late Middle Pleistocene and the Late Pleistocene were found in South China, Vietnam, Laos, Cambodia and Thailand. On the other hand, some fossil remains were also discovered in Late Pleistocene sites of Indonesia and Borneo. The migration of *Pongo* from mainland to Indonesia and Borneo was probably due to the sea level lowering (40–65 m below present-day sea level) before 70,000 yr, but after the glacial maximum at about 135,000 yr (van den Bergh et al., 1996). These three examples show how the late Late Middle Pleistocene cooling might have had an influence on the southward extension of the northern faunas.

Unfortunately, it is currently not possible to know whether the extension of the Indochinese species, except *P. pygmaeus*, was limited southward to Thailand or to peninsular Malaysia, because of the nearly complete lack of Pleistocene fossiliferous sites in the latter area. However, the discovery of the extinct species, *D. santeng* and especially *E. namadicus*, in the Tambun site (Hooijer, 1962; Medway, 1973) is a valuable evidence. Indeed, *E. namadicus* was found

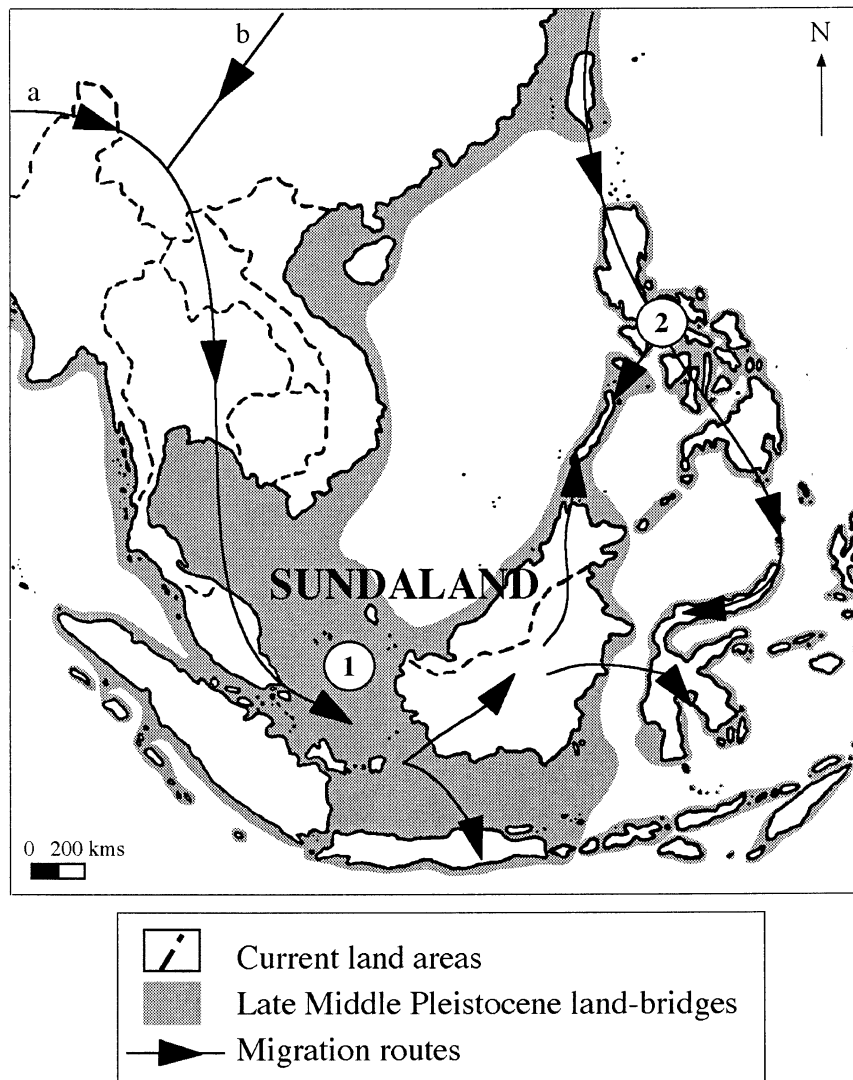


Fig. 6. Map of South–East Asia showing the Sundaland boundary during the Late Middle Pleistocene (adapted from Hutchison, 1989; Heaney, 1991). The migration route hypothesis (by ① continental or ② insular ways) are illustrated by the arrows. The Early and Middle Pleistocene Siva-Malayan route (a) and the Late Pleistocene Sino-Malayan one (b) are considered here as part of the continental way.

mainly in South China and Vietnam (Kahlke, 1961; Olsen and Ciochon, 1990). Therefore, it was a characteristic of the Indochinese province. Concerning *D. santeng*, this species was also found in Lower Pleistocene localities of Java. It seems that it was characteristic of the Sundaic province. However, the attribution of the fossil remains to this species has to be considered carefully. The remains, especially the teeth, could belong to *Boselaphus*.

5. Discussion

5.1. Late Middle and Late Pleistocene migration routes

5.1.1. Historical review of previous works

In South–East Asia, numerous important faunal exchanges occurred, notably between the Late Middle Pleistocene and the Late Pleistocene. This is testified

by the large mammal turnover in the Punung site (Java) of Late Pleistocene age. However, the way used by faunas to migrate from mainland to Indonesian islands and inversely was long debated. Two migration routes were considered: a “continental” way via Myanmar, Thailand or Indochina (Laos, Vietnam and Cambodia) and then peninsular Malaysia, or an “insular” way via Taiwan and the Philippine Archipelago (Fig. 6).

von Koenigswald (1935, 1939) supposed that the mammals migrated during the Pleistocene to Java via the Philippines on the base of elements identified as of Chinese affinities in Javanese Pleistocene faunas, the occurrence of a Pleistocene fauna in the Philippines, and the lack of fossil evidence from the Sundaland area. This author called this way, the “Sino-Malayan” migration route. On the other hand, de Terra (1943) and Colbert (1943) suggested that Javanese faunas could have originated from Myanmar as the Javanese faunas of Lower Pleistocene age seems to have. These authors are followed by Shutler and Braches (1985), who considered the island status of Luzon as reflected in the fossil fauna from Pleistocene. De Vos et al. (1999) agreed with a continental migration route from China, Vietnam, and Cambodia to Indonesia.

5.1.2. Geological evidences

In South–East Asia, the Pleistocene geological events indicate that there have been important glacio-eustatic sea level fluctuations, especially during the Middle and Late Pleistocene. A sea level lowering between 50 and 150 m could have occurred several times (Prentice and Denton, 1988). Land bridges within the mainland and Indonesian islands such as Sumatra, Java and Borneo could exist because of the emersion of a huge continental shelf called Sundaland (Heaney, 1985; Lekagul and McNeely, 1988). Palawan could have been the only Philippine island connected to Asian mainland via Borneo. Indeed, the sea is about 145 m deep between Palawan and Borneo, whereas it is much deeper compared to the other Philippine islands (Heaney, 1985; van Oosterzee, 1997). On the other hand, there is no proof of land bridge connection between mainland and the Philippine Archipelago via Taiwan because of the sea depth.

5.1.3. Evidences from extant large mammals and other vertebrates

The analysis of the present-day Indochinese and Sundaic large mammal faunas compared to those of the Philippine Archipelago (Wallacean province) (Corbet and Hill, 1992) can provide information on the most plausible migration route. The Indochinese and Sundaic faunas are more similar to each other than to that of the Philippines. After the dendrograms (Figs. 3 and 4), the large mammal fauna from all the Philippine islands displays greater affinities with faunas from the Sundaic province (than with those of the Indochinese one; nine and five large mammal species in common, respectively). If the Philippine islands had been directly connected with the Asian mainland and a possible passage way between north and south of South–East Asia, the Philippine fauna should also include elements from the Indochinese province (Heaney, 1985; Corbet and Hill, 1992), which is not the case. This fact is reflected by both large and small mammal faunas (Rodentia, Insectivora, Scandentia, Dermoptera, Pholidota) except bats (*Cynopterus brachyotis*, *Eonycteris spelaea*, *Myotis formosus*, *Tylonycteris pachypus*, *Murina cyclotis* and others; Corbet and Hill, 1992). However, the Palawan mammal fauna displays 58% of similarity with that of Borneo (Heaney, 1985; van Oosterzee, 1997).

There are also data pertaining to freshwater fishes (Kornfield and Carpenter, 1984). Rivers and lakes of Philippines currently support depauperate fish faunas. Cyprinid fishes are the most widespread, and current evidence indicates that they are descendant of a single species that dispersed from Borneo to Mindanao probably during the Pliocene. The cyprinids of Palawan also originated on Borneo and could have arrived probably prior to the Middle Pleistocene (Kornfield and Carpenter, 1984). The results of studies about amphibians and reptiles closely parallel those of the studies on mammals (Brown and Alcala, 1970). Palawan supports a significant number of endemic species, but its faunal relationships lie strongly with Borneo.

5.1.4. Evidences from fossil large mammal faunas

The analysis of the fossil large mammal faunas shows that faunas with modern character were already present in mainland in the late Late

Middle Pleistocene, whereas the Javanese faunas still contained archaic forms. As shown by three forms (*P. pygmaeus*, *A. melanoleuca baconi* and *C. crocuta ultima*) from the Thai localities, the late Late Middle Pleistocene cooling has certainly modified the geographical distribution of the South–East Asian faunas, notably in shifting northern faunas even further southwards, i.e. to the Indonesian islands. This hypothesis is supported by the occurrence of *P. pygmaeus*, *S. barbatus*, *Naemorhedus sumatraensis*, *E. maximus* or *Ursus malayanus* in the Late Pleistocene Punung (Java) site. These species were first found in Late Middle Pleistocene continental localities, and then in Late Pleistocene sites from Indonesia. According to Aziz et al. (1999), a marked faunal turnover happened in Indonesia and mainly in Java with the arrival of new immigrants from the Asian mainland. Indeed, these new immigrants were mainly of Indochinese affinities, or widespread through South–East Asian mainland. It is worth noting that *S. barbatus*, *T. indicus* and *P. pygmaeus* have currently only habitats in Indonesia and Borneo, whereas they were found in mainland sites older than those of Indonesia (Punung, Lida Ajer, Sibrambang) and Borneo (Niah).

Moreover, the Late Middle Pleistocene faunas from Vietnam (Olsen and Ciochon, 1990; Vu et al., 1996), Cambodia (Beden and Guérin, 1973) and mainly from Thailand (Tougaard et al., 1996; Tougaard, 1998) share numerous species with countries located at the northern and southern ends of the South–East Asian provinces, namely South China, Sumatra, Java, and Borneo.

Unfortunately, no evidence of faunal exchanges from Indonesia to the South–East Asian mainland was found, except the possible presence of *D. santeng* in the Tambun site, peninsular Malaysia. However, this species could have migrated via the Siva-Malayan migration route, probably by 0.8 myr during the dramatic sea level lowering, because it was found only in Lower Pleistocene Javanese sites.

5.1.5. Conclusion

A low endemism rate and a balanced fauna as the extant and fossil Indonesian faunas indicate that a

connection had existed between the Asian mainland and the Indonesian islands in the recent past (Heaney, 1985; de Vos et al., 1999). On the contrary, a high endemism rate and an unbalanced fauna as the extant and fossil faunas testify to a significant isolation as for the Philippines, except Palawan (Heaney, 1985; de Vos et al., 1999).

From the geological point of view as well as the extant and fossil large mammal fauna studies, it clearly appears that the emersion of the Sundaland allowed faunal exchanges from continental South–East Asia to the Indonesian islands, and probably inversely, between the late Late Middle Pleistocene and the Late Pleistocene. It was the consequence of land bridge connections between landmasses when the sea level was low, because of the continental glacier formation during glacial periods.

The recent discovery of Late Middle Pleistocene faunas in Thailand brings new information about the migration routes, strengthening the continental hypothesis. This route could be also called the Sino-Malayan route, though it referred first to a migration route from mainland to Java via the Philippines (von Koenigswald, 1935, 1939). Whereas Sundaland offered more possibilities to move for the mammalian faunas because of its large surface, Thailand was even part of this migration route. The fossil large mammal Thai faunas allow to link and compare those found from South China to Indonesia. The study of the fossil large mammal faunas from the Philippines (Luzon and Mindanao) do not give strong information to deny this idea.

5.2. Late Middle Pleistocene biogeography of large mammal faunas

South–East Asia is currently divided into two distinct biogeographical provinces: the Indochinese province and the Sundaic province. The boundary between these provinces is presently located at the Kra Isthmus, in peninsular Thailand (Whitmore, 1984; Lekagul and McNeely, 1988). As seen earlier, faunal exchanges happened on the Sundaland between the Late Middle Pleistocene and the Late Pleistocene. It is also confirmed by the presence of extant species characteristic of the Sundaic province in Indochinese

faunas and inversely (Appendix A). However, the boundary between the northern and southern faunas of South–East Asia had to move because several climatic changes occurred during the Pleistocene succession of glacial and interglacial periods (van der Kaars, 1991; Zheng and Lei, 1999). This event is clearly illustrated by the Thai occurrence of the three species mentioned earlier (*P. pygmaeus*, *C. crocuta ultima* and *A. melanoleuca baconi*), but also by the northward shift of the panda (*A. melanoleuca*) distribution to some mountains of South China during the Late Pleistocene and the Holocene (Tougaard et al., 1996).

As seen previously, the continental faunas presented already a modern character, whereas the Javanese ones were mainly characterized by archaic forms. This fact allows to suppose that two distinct faunas were present in South–East Asia in the late Late Middle Pleistocene. Moreover, 40% (of 27 taxa defined at the species level) of the fossil Thai faunas and 75% (of eight species) of the fossil Cambodian fauna are of Indochinese affinity, whereas 60% of the fossil Ngandong faunas (Java) was of Sundaic affinity. The Tambun fauna is not considered here because three species only were determined. Among them, *Rhinoceros sondai-cus* was widespread in South–East Asia. *E. namadicus* was characteristic of the northern part of South–East Asia, whereas *D. santeng* was only present in the southern part. So, it seems that there was a northern fauna biogeographically distinct from the southern one in South–East Asia during the Late Middle Pleistocene.

Unfortunately, it is currently difficult to specify where the boundary between the northern and southern fossil faunas could be located, because of the nearly complete lack of Middle Pleistocene sites in Indonesia and peninsular Malaysia. The lack of data relative to the peninsular Malaysia Pleistocene fauna (Tambun) and of those relative to Sumatra (Sibram-bang and Lida Ajer) and Borneo (Niah) does not allow to know if the species found in Java were distributed throughout the Indonesian islands and the mainland or if they were endemic to Java. Only the presence of *E. namadicus* in the Tambun site is a valuable clue. It allows to suppose that the boundary between the Indochinese and Sundaic provinces, if not close to the present place, was located further south, possibly in

the northern part of peninsular Malaysia in the late Late Middle Pleistocene.

6. Conclusions

With its privileged geographical situation, Thailand is located at the crossroads of the South–East Asian northern (the Indochinese province) and southern (the Sundaic province) parts. These provinces are distinct from the climatic (seasonality and rainfall differences) as well as from the floristic and faunistic points of view. Their origin seems old in regard to the large mammal faunas (carnivores, primates, proboscideans and ungulates) from South–East Asia, notably those of the Late Middle Pleistocene. And because a cooling occurred during this period, the biogeographical boundary between these two provinces seemed to have been located further south than the present one, i.e. south of the Kra Isthmus in peninsular Thailand and probably in northern peninsular Malaysia.

Moreover, Thailand was certainly the witness of faunal exchanges between the both South–East Asian provinces. It was part of the Sino-Malayan migration route between the continental parts of South–East Asia and the neighboring Indonesian islands, notably for the human colonization. It is especially true since a tooth attributed to *Homo* sp. was found in a late Late Middle Pleistocene site of Thailand (Tougaard et al., 1998). It is worth noting that this is the only human fossil remain found for this period, hence its importance.

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Appendix A

Faunal lists of the large mammal species found in South China (SC), Myanmar (MY), Laos (LA), Cambodia (CA), Vietnam (VI), Thailand (with a distinction between the faunas found north and south of the Kra Isthmus, NK and SK, respectively), peninsular Malaysia (MA), Sumatra (SU), Java (JA) and Borneo (BO). The species in common with the Philippines (PH) of the Wallacean province (WP) are also indicated, especially those found in Palawan (P). For each species, the biogeographical affinity is given in parentheses: Indochinese (I), Sundaic (S) and other (O) affinities (Palearctic, Indian, ...) or widespread (W) species. The asterisk (*) indicates that the species has currently a Sundaic habitat but it was exclusively found in the Indochinese province before the Late Pleistocene. Faunal lists and geographical distribution are from Corbet and Hill (1992) and Nowak (1999). Taxonomic names follow Wilson and Reeder (1993).

	Indochinese province					Thailand		Sundaic province				WP
	SC	MY	LA	CA	VI	NK	SK	MA	SU	JA	BO	PH
PRIMATES												
<i>Nycticebus coucang</i> (I, S)	×	×	×	×	×	×	×	×	×	×	×	
<i>Nycticebus pygmaeus</i> (I)	×		×	×	×							
<i>Tarsius bancanus</i> (S)									×		×	
<i>Macaca arctoides</i> (I)	×	×	×	×	×	×	×					
<i>Macaca assamensis</i> (I, O)	×	×	×	×	×	×						
<i>Macaca fascicularis</i> (S)		×	×	×	×	×	×	×	×	×	×	×
<i>Macaca mulatta</i> (I, O)	×	×	×		×		×					
<i>Macaca nemestrina</i> (I, S)		×	×	×	×	×	×	×	×		×	
<i>Macaca thibetana</i> (I)	×											
<i>Presbytis comata</i> (S)										×		
<i>Presbytis femoralis</i> (S)		×				×	×	×	×			
<i>Presbytis frontana</i> (S)												×
<i>Presbytis hosei</i> (S)												×
<i>Presbytis melalophos</i> (S)									×			
<i>Presbytis potenziani</i> (S)									×			
<i>Presbytis rubicunda</i> (S)												×
<i>Presbytis thomasi</i> (S)									×			
<i>Trachypithecus auratus</i> (S)											×	
<i>Trachypithecus cristatus</i> (S)		×	×	×	×	×	×	×	×			×
<i>Trachypithecus francoisi</i> (I)	×		×		×							
<i>Trachypithecus obscurus</i> (S)		×				×	×	×				
<i>Trachypithecus phayrei</i> (I)	×	×	×		×	×						
<i>Trachypithecus pileatus</i> (I)		×										
<i>Pygathrix avunculus</i> (I)					×							
<i>Pygathrix bieti</i> (I)	×											
<i>Pygathrix brelichii</i> (I)	×											
<i>Pygathrix nemausus</i> (I)			×	×	×							
<i>Pygathrix roxellana</i> (I)	×											
<i>Nasalis larvatus</i> (S)												×
<i>Nasalis concolor</i> (S)									×			
<i>Hylobates agilis</i> (S)							×		×	×	×	
<i>Hylobates concolor</i> (I)	×		×		×							
<i>Hylobates gabriellae</i> (I)				×	×							
<i>Hylobates hoolock</i> (I)	×	×										
<i>Hylobates klossi</i> (S)										×		
<i>Hylobates lar</i> (I, S)	×	×				×	×	×	×			
<i>Hylobates leucogenys</i> (I)	×		×		×							
<i>Hylobates moloch</i> (S)										×		
<i>Hylobates muelleri</i> (S)												×
<i>Hylobates pileatus</i> (I)			×	×		×						
<i>Hylobates syndactylus</i> (S)								×	×			
<i>Pongo pygmaeus</i> (S*)									×		×	

(continued)

	Indochinese province					Thailand		Sundaic province				WP
	SC	MY	LA	CA	VI	NK	SK	MA	SU	JA	BO	PH
CARNIVORA												
<i>Canis aureus</i> (I, O)		×	×			×						
<i>Canis lupus</i> (W)	×											
<i>Vulpes vulpes</i> (I, O)	×				×							
<i>Nyctereutes procyonoides</i> (I, O)	×				×							
<i>Cuon alpinus</i> (W)	×	×	×	×	×	×	×	×	×	×		
<i>Ursus thibetanus</i> (I)	×	×	×		×	×						
<i>Helarctos malayanus</i> (I, S)	×	×	×	×	×	×	×	×	×		×	
<i>Ailuropoda melanoleuca</i> (I)	×											
<i>Ailurus fulgens</i> (I)	×	×										
<i>Mustela kathiah</i> (I, O)	×	×	×		×							
<i>Mustela lutreolina</i> (S)									×	×		
<i>Mustela nivalis</i> (I, O)	×				×							
<i>Mustela nudipes</i> (S)							×	×	×		×	
<i>Mustela sibirica</i> (I, O)	×	×	×		×	×						
<i>Mustela strigidorsa</i> (I)	×	×	×		×	×						
<i>Martes flavigula</i> (I, S, O)	×	×	×	×	×	×	×	×	×	×	×	
<i>Meles meles</i> (I, O)	×		×		×							
<i>Arctonyx collaris</i> (I, O)	×	×	×	×	×	×	×		×			
<i>Melogale everetti</i> (S)											×	
<i>Melogale moschata</i> (I)	×	×			×							
<i>Melogale orientalis</i> (S)										×		
<i>Melogale personata</i> (I)		×			×	×						
<i>Mydaus javanensis</i> (S)									×	×	×	
<i>Lutra lutra</i> (W)	×	×	×	×	×	×			×			
<i>Lutra sumatrana</i> (S)				×	×		×	×	×		×	
<i>Lutrogale perspicillata</i> (W)	×	×	×	×	×	×	×	×	×	×	×	
<i>Amblonyx cinereus</i> (W)	×	×	×	×	×	×	×	×	×	×	×	×
<i>Viverra megaspila</i> (I)	×	×	×	×	×	×	×	×	×	×	×	×
<i>Viverra tangalunga</i> (S)								×	×		×	×
<i>Viverra zibetha</i> (I)	×	×	×	×	×	×	×	×				
<i>Viverricula indica</i> (W)	×	×	×	×	×	×	×	×	×	×		
<i>Prionodon linsang</i> (S)		×				×	×	×	×	×	×	
<i>Prionodon pardicolor</i> (I)	×	×	×		×	×						
<i>Paradoxurus hermaphroditus</i> (W)	×	×	×	×	×	×	×	×	×	×	×	×
<i>Paguma larvata</i> (I, S, O)	×	×	×	×	×	×	×	×	×		×	
<i>Arctictis binturong</i> (I, S)	×	×	×	×	×	×	×	×	×	×	×	×
<i>Arctogalidia trivirgata</i> (I, S)	×	×	×	×	×	×	×	×	×	×	×	
<i>Hemigalus derbyanus</i> (S)		×					×	×	×		×	
<i>Chrotogale owstoni</i> (I)	×		×		×							
<i>Diplogale hosei</i> (S)											×	
<i>Cynogale bennettii</i> (S)								×	×		×	
<i>Herpestes brachyurus</i> (S)								×	×		×	×
<i>Herpestes javanicus</i> (I, S, O)	×	×	×	×	×	×	×	×		×		×
<i>Herpestes semitorquatus</i> (S)									×		×	
<i>Herpestes urva</i> (I)	×	×	×	×	×	×	×	×				
<i>Felis chaus</i> (W)	×	×	×	×	×	×						
<i>Prionailurus bengalensis</i> (W)	×	×	×	×	×	×	×	×	×	×	×	×
<i>Prionailurus planiceps</i> (S)							×	×	×		×	
<i>Prionailurus viverrinus</i> (W)	×	×	×	×	×	×			×	×		
<i>Catopuma badia</i> (S)											×	
<i>Catopuma temminckii</i> (I, S)	×	×	×	×	×	×	×	×	×			

(continued)

	Indochinese province					Thailand		Sundaic province				WP
	SC	MY	LA	CA	VI	NK	SK	MA	SU	JA	BO	PH
<i>Pardofelis marmorata</i> (I, S)	×	×			×		×	×	×		×	
<i>Neofelis nebulosa</i> (I, S)	×	×	×	×	×	×	×	×	×		×	
<i>Panthera pardus</i> (W)	×	×	×	×	×	×	×	×		×		
<i>Panthera tigris</i> (W)	×	×	×	×	×	×	×	×	×	×		
PROBOSCIDEA												
<i>Elephas maximus</i> (I, O)	×	×	×	×	×	×	×	×	×		×	
PERISSODACTYLA												
<i>Tapirus indicus</i> (S ⁺)		×	×			×	×	×	×			
<i>Rhinoceros sondaicus</i> (I, S)	×	×	×	×	×	×	×	×	×	×		
<i>Dicerorhinus sumatrensis</i> (I, S)	×	×	×	×	×	×	×	×	×		×	
ARTIODACTYLA												
<i>Sus barbatus</i> (S ⁺)								×	×		×	×
<i>Sus scrofa</i> (W)	×	×	×	×	×	×	×	×	×	×		
<i>Sus verrucosus</i> (S)										×		
<i>Tragulus javanicus</i> (S)		×	×	×	×	×	×	×	×	×	×	
<i>Tragulus napu</i> (S)		×	×		×	×	×	×	×		×	
<i>Moschus berezovskii</i> (I)	×				×							
<i>Cervus eldii</i> (I)			×	×								
<i>Cervus nippon</i> (I)	×											
<i>Cervus timorensis</i> (S, O)										×		
<i>Cervus unicolor</i> (W)	×	×	×	×	×	×	×	×	×		×	
<i>Axis kuhlii</i> (S)										×		
<i>Axis porcinus</i> (I, O)	×	×	×	×	×	×						
<i>Muntiacus atherodes</i> (S)											×	
<i>Muntiacus feae</i> (I)		×				×						
<i>Muntiacus gongshanensis</i> (I)	×	×										
<i>Muntiacus muntjak</i> (W)	×	×	×	×	×	×	×	×	×	×	×	
<i>Muntiacus reevesi</i> (I)	×				×							
<i>Muntiacus rooseveltorum</i> (I)			×									
<i>Elaphodus cephalophus</i> (I)	×	×										
<i>Hydropotes inermis</i> (I)	×											
<i>Bos frontalis</i> (I)	×	×	×	×	×	×	×	×				
<i>Bos javanicus</i> (I, S)		×	×	×	×	×	×			×	×	
<i>Bos sauveli</i> (I)			×	×	×	×						
<i>Bubalus bubalis</i> (W)			×	×	×	×					×	
<i>Budorcas taxicolor</i> (I)	×	×										
<i>Naemorhedus baileyi</i> (I)	×	×										
<i>Naemorhedus caudatus</i> (I)	×	×				×						
<i>Naemorhedus sumatraensis</i> (I, S, O)	×	×	×	×	×	×	×	×	×			

Appendix B

Faunal lists of fossil large mammal species of South China (Hoshangtung, Koloshan, Hsingan), Laos (Tam Hang), Vietnam (Tham Om, Hang Hum, Keo Leng, Lang Trang), Cambodia (Phnom Loang), Myanmar (Mogok), Thailand (Thum Wiman Nakin, Thum Phra Khai Phet), peninsular Malaysia (Tambun), Sumatra (Lida Ajer, Sibrambang), Java (Ngandong, Punung) and Borneo (Niah) (for site references, see Table 1). The large mammal faunas from the Philippine sites are listed apart because of their high endemism. The biogeographical affinity is given in parentheses: Indochinese (I), Sundaic (S) and other (O) affinities (Palearctic, Indian, ...) or widespread (W) species. The asterisk (*) indicates that the species has currently a Sundaic habitat but it was exclusively found in the Indochinese province before the Late Pleistocene.

Late Middle Pleistocene faunas from South–East Asian sites

	Hoshangtung	Koloshan	Hsingan	Tam Hang	Tham Om	Hang Hum	Keo Leng	Phnom Loang	Thum Wiman Nakin	Ngandong		
PRIMATES												
<i>Macaca</i> sp.	×				×	×						
<i>Macaca assamensis</i> (I)							×					
<i>Macaca fascicularis</i> (S)										×		
<i>Macaca mulatta</i> (I)							×					
<i>Macaca</i> cf. <i>nemestrina</i> (I)									×			
<i>Macaca robustus</i> (I)		×		×								
<i>Semnopithecus</i> sp.							×					
<i>Trachypithecus</i> sp.									×			
<i>Hylobates</i> sp.						×	×					
<i>Szechuanopithecus yangtsensis</i> (I)		×										
<i>Pongo pygmaeus</i> (*)	×		×	×		×	×	×	×			
<i>Homo</i> sp.									×			
<i>Homo</i> cf. <i>erectus</i> (W)				×								
<i>Homo erectus</i> (W)										×		
<i>Homo sapiens</i> (W)					×	×	×					
	Holoshan	Koloshan	Hsingan	Mogok	Tam Hang	Tham Om	Hang Hum	Keo Leng	Phnom Loang	Thum Wiman Nakin	Thum Phra Khai Phet	Ngandong
CARNIVORA												
<i>Canidae</i> indet.	×	×										
<i>Nyctereutes</i> sp.							×					
<i>Cuon</i> sp.						×	×					
<i>Cuon alpinus</i> (W)							×					
<i>Cuon simplicidens</i> (I, O)		×										
<i>Ursus</i> cf. <i>angustidens</i> (I, O)					×							
<i>Ursus angustidens</i> (I, O)	×											
<i>Ursus thibetanus</i> (I)											×	
<i>Ursus thibetanus kokeni</i> (I)		×	×			×	×	×				
<i>Ailuropoda melanoleuca baconi</i> (I, O)	×	×	×	×	×	×		×		×		
<i>Ailurus fulgens</i> (I)	×											
<i>Mustela sibirica</i> (I)		×										
<i>Martes</i> sp.									×			
<i>Martes flavigula</i> (I, S)											×	
<i>Martes sinensis</i> (I, O)		×										
<i>Parameles simplicidens</i> (I)		×										
<i>Arctonyx</i> sp.	×											
<i>Arctonyx collaris</i> cf. <i>rostratus</i> (I)						×	×	×				
<i>Arctonyx collaris rostratus</i> (I)			×								×	
<i>Viverra</i> cf. <i>zibetha</i> (I)								×				
<i>Paradoxurus</i> sp.							×					
<i>Paradoxurus</i> cf. <i>hermaphroditus</i> (W)							×	×				
<i>Paradoxurus hermaphroditus</i> (W)										×		
<i>Paguma</i> cf. <i>larvata</i> (I, S)						×						
<i>Paguma larvata</i> (I, S)							×			×		
<i>Crocuta crocuta ultima</i> (I, O)	×		×		×				×	×	×	

(continued)

	Holoshan	Koloshan	Hsingan	Mogok	Tam Hang	Tham Om	Hang Hum	Keo Leng	Phnom Loang	Thum Wiman Nakin	Thum Phra Khai Phet	Ngandong
<i>Felis</i> sp.			×			×						
<i>Felis lynx</i> (W)	×											
<i>Neofelis nebulosa</i> (I, S)							×					
<i>Neofelis nebulosa</i> cf. <i>primigenia</i> (I, S)							×					
<i>Panthera</i> cf. <i>pardus</i> (W)					×							
<i>Panthera pardus</i> (W)	×						×					
<i>Panthera</i> cf. <i>tigris</i> (W)					×							
<i>Panthera tigris</i> (W)	×	×	×			×	×		×			×

	Hoshangtung	Koloshan	Hsingan	Mogok	Tam Hang	Tham Om	Hang Hum	Keo Leng	Phnom Loang	Thum Wiman Nakin	Thum Phra Khai Phet	Tambun	Ngandong
PROBOSCIDEA													
<i>Stegodon</i> sp.	×												
<i>Stegodon orientalis</i> (I)			×	×	×	×	×						
<i>Stegodon trigonocephalus</i> (S)													×
<i>Palaeoloxodon</i> sp.			×										
<i>Elephas</i> sp.									×				
<i>Elephas hysudrindicus</i> (S)													×
<i>Elephas</i> cf. <i>maximus</i> (I)										×			
<i>Elephas</i> cf. <i>namadicus</i> (I)						×	×						
<i>Elephas namadicus</i> (I)	×			×	×		×					×	
PERISSODACTYLA													
<i>Tapirus</i> sp.						×							
<i>Tapirus indicus</i> (*)			×				×						×
<i>Tapirus indicus</i> cf. <i>intermedius</i> (I)										×			
<i>Tapirus indicus intermedius</i> (I)									×				
<i>Megatapirus augustus</i> (I)	×	×			×	×	×	×					
<i>Rhinoceros</i> sp.	×			×									
<i>Rhinoceros</i> cf. <i>plicideus</i> (I)					×								
<i>Rhinoceros sinensis</i> (I)		×	×			×	×	×					
<i>Rhinoceros</i> cf. <i>sivalensis</i> (I)					×								
<i>Rhinoceros sondaicus</i> (I, S)										×	×	×	
<i>Rhinoceros sondaicus guthi</i> (I)									×				
<i>Rhinoceros</i> cf. <i>unicornis</i> (I)										×			
<i>Dicerorhinus sumatrensis</i> (I, S)													
ARTIODACTYLA													
<i>Sus</i> sp.	×	×	×	×		×		×				×	
<i>Sus</i> cf. <i>barbatus</i> (*)													
<i>Sus</i> cf. <i>lydekkeri</i> (I)					×		×	×		×	×		
<i>Sus macrognathus</i> (S)													×
<i>Sus</i> cf. <i>officinalis</i> (I)							×						
<i>Sus scrofa</i> (W)						×	×	×		×			
<i>Hexaprotodon</i> sp.												×	
<i>Hexaprotodon sivalensis</i> (I)													×
Cervidae indet.	×	×	×	×		×	×	×		×	×	×	×
<i>Cervus eldii</i> (I)										×			
<i>Cervus unicolor</i> (W)						×	×	×	×	×			
<i>Rusa</i> cf. <i>leptodus</i> (I)									×				
<i>Axis porcinus</i> (I)										×	×		
<i>Pseudaxis</i> cf. <i>grayi</i> (I)					×								
<i>Muntiacus</i> sp.	×		×			×		×					
<i>Muntiacus muntjak</i> (I)								×		×	×		
<i>Muntiacus muntjak margae</i> (I)						×							
<i>Muntiacus szechuanensis</i> (I)		×											
<i>Elaphodus</i> sp.						×							
Bovinae indet.	×		×	×								×	
<i>Bos frontalis</i> (I)						×				×			
<i>Bos frontalis</i> cf. <i>grangeri</i> (I)							×						
<i>Bos javanicus</i> (I, S)										×			

(continued)

	Hoshangtung	Koloshan	Hsingan Mogok	Tam Hang	Tham Om	Hang Hum	Keo Leng	Phnom Loang	Thum Wiman Nakin	Thum Khai Phet	Phra Tambun	Ngandong
<i>Bos javanicus palaesondaicus</i> (S)												×
<i>Bos sauveli</i> (I)									×	×		
<i>Bubalus brevirostris</i> (I)		×										
<i>Bubalus cf. bubalis</i> (W)								×				
<i>Bubalus bubalis</i> (W)					×	×	×		×			
<i>Bubalus bubalis palaekerabau</i> (S)												×
<i>Duboisia santeng</i> (S)											×	
Caprinae indet.	×	×				×						
<i>Naemorhedus</i> sp.								×				
<i>Naemorhedus sumatraensis</i> (I, S)					×		×			×		
<i>Naemorhedus sumatraensis</i> cf. <i>kanjereus</i> (I)									×			

Late Pleistocene faunas from South–East Asian sites

	Lang Trang	Sibrambang	Lida Ajer	Punung	Niah
PRIMATES					
<i>Nycticebus coucang</i> (I, S)					×
<i>Macaca</i> sp.	×	×			
<i>Macaca fascicularis</i> (S)					×
<i>Macaca nemestrina</i> (I, S)			×	×	×
<i>Presbytis</i> sp.		×	×		
<i>Presbytis</i> cf. <i>rubicunda</i> (S)					×
<i>Trachypithecus</i> sp.	×				
<i>Trachypithecus cristatus</i> (S)		×	×		×
<i>Hylobates</i> sp.	×	×	×		
<i>Hylobates muelleri</i> (S)					×
<i>Hylobates syndactylus</i> (S)		×	×	×	
<i>Pongo pygmaeus</i> (*)	×	×	×	×	×
<i>Homo sapiens</i> (W)			×	×	×
CARNIVORA					
<i>Cuon alpinus</i> (W)	×		×		×
<i>Ursus thibetanus</i> (I)	×				
<i>Helarctos malayanus</i> (I, S)	×	×	×	×	×
<i>Ailuropoda melanoleuca baconi</i> (I)	×				
<i>Mustela nudipes</i> (S)					
<i>Arctonyx collaris</i> (I)	×		×		
<i>Melogale everetti</i> (S)					
<i>Lutra perspicillata</i> (W)	×				
<i>Lutra sumatrana</i> (S)					
<i>Viverra tangalunga</i> (S)					
<i>Paradoxurus hermaphroditus</i> (W)	×		×		
<i>Arctictis binturong</i> (I, S)					
<i>Hemigalus derbyanus</i> (S)					
<i>Herpestes</i> sp.					
<i>Catopuma temminckii</i> (I, S)	×		×		
<i>Neofelis nebulosa</i> (I, S)					
<i>Panthera pardus</i> (W)	×		×		
<i>Panthera tigris</i> (W)	×		×	×	×
PROBOSCIDEA					
<i>Stegodon orientalis</i> (I)	×				
<i>Elephas namadicus</i> (I)	×				

(continued)

	Lang Trang	Sibrambang	Lida Ajer	Punung	Niah
<i>Elephas maximus</i> (I)		×	×	×	×
PERISSODACTYLA					
<i>Tapirus indicus</i> (*)	×	×	×	×	×
<i>Rhinoceros sondaicus</i> (I, S)				×	×
<i>Dicerorhinus sumatrensis</i> (I, S)	×	×	×		×
ARTIODACTYLA					
<i>Sus barbatus</i> (*)		×	×	×	×
<i>Sus scrofa</i> (W)	×		×		
<i>Sus scrofa vittatus</i> (S)		×		×	
<i>Tragulus javanicus</i> (S)					×
<i>Tragulus napu</i> (S)					×
<i>Cervus</i> sp.		×		×	
<i>Cervus unicolor</i> (W)	×		×		×
<i>Muntiacus muntjak</i> (W)	×	×	×	×	×
<i>Bos</i> sp.				×	
<i>Bos javanicus</i> (I, S)		×	×		×
<i>Bubalus bubalis</i> (W)	×		×	×	
<i>Naemorhedus sumatraensis</i> (I, S)	×	×	×	×	

Pleistocene fossils from the Philippines

Luzon:

- *Stegodon* cf. *trigonocephalus*
- *S. luzonensis*
- *Elephas beyeri*
- *Rhinoceros philippensis*
- *Antelope* sp.
- cf. *Bubalus*
- cf. *Cervus*

Mindanao:

- *Stegodon* cf. *mindanensis*
- *S. mindanensis*

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