

Pleistocene paleoenvironmental reconstructions and mammalian evolution in South-East Asia: focus on fossil faunas from Thailand

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Abstract

Mammalian faunal studies have provided various clues for a better reconstruction of hominid Quaternary paleoenvironments. In this work, two methods were used: (1) the cenogram method, based on a graphical representation of the mammalian community structure, and (2) the species richness of murine rodents to estimate climatic parameters. These methods were applied to Middle and Late Pleistocene mammalian faunas of South-East Asia, from South China to Indonesia. Special emphasis was laid on a fauna from north-east Thailand dated back to approximately 170,000 years (i.e. a glacial period). This Thai fauna seems characteristic of a slightly open forested environment intermediate between those of present-day central Myanmar and the northern part of South China. In the Thai fauna, the occurrence of both cool-loving mammalian taxa, currently living further north, and species of larger body size than their living counterparts, indicates cooler and probably drier climatic conditions than present-day climates in Thailand. These results are quite consistent with Middle Pleistocene palynological records from South China and eastern Java. From other less well-documented Pleistocene faunas, taken into account in this work, humid climatic conditions of interglacial periods were revealed from large mammalian taxa.

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1. Introduction

South-East Asia was one of the most important cradles of human history during the Pleistocene. Several paleontological sites from South China to Indonesia (notably, Fromaget and Saurin, 1936; Kahlke, 1961; de Vos, 1985; Olsen and Ciochon, 1990; Harrison, 1996; Tougard et al., 1998; Demeter et al., 2004) yielded human fossil remains. Moreover, during the same period, South-East Asia witnessed active tectonism (continuation of the collision between India and Eurasia; Molnar and Tapponnier, 1975; Lee and Lawver, 1995) and dynamic climate changes (successive warm and cooler periods; Heaney, 1991; van der Kaars and Dam, 1995; Zheng and Lei, 1999; Jian et al., 2003;

Liu et al., 2003). These changes on relatively short time scales (i.e. each Quaternary climate cycle) influenced the environment, and consequently the evolutionary history of mammalian communities.

A paleoecological analysis has been conducted using two methods: (1) the cenogram method (i.e. a graphical representation of mammalian community structure; Legendre, 1986, 1989) and (2) the species richness of murine rodents to estimate temperature and rainfall (Misonne, 1969; Aguilar et al., 1998; Montuire, 1999; Montuire and Marcolini, 2002). This analysis was performed for Middle and Late Pleistocene mammalian faunas found in South-East Asian paleontological and paleoanthropological sites. The mammalian community structure of these faunas was compared with that of South-East Asian extant faunas whose environmental context is known. Unfortunately, most South-East Asian mammalian fossil faunas are poorly documented (i.e. mainly composed of large mammal species) and

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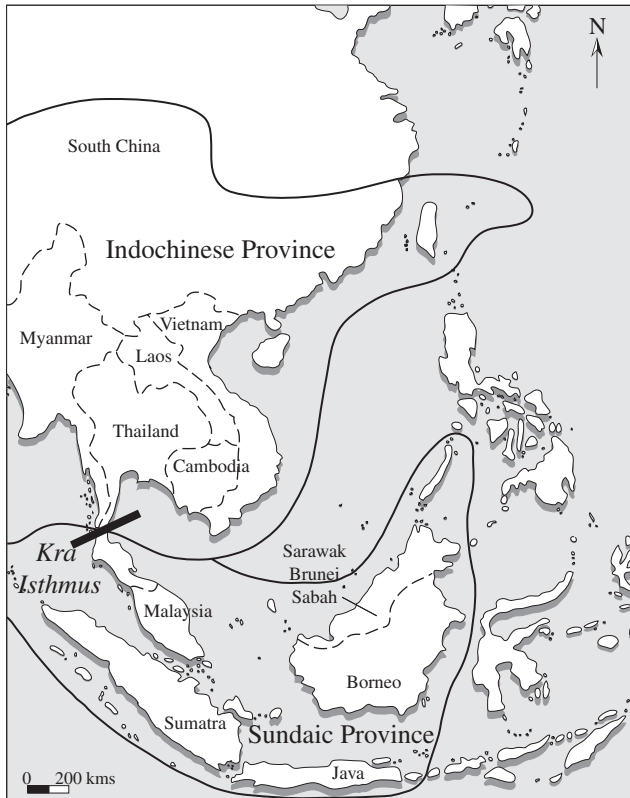


Fig. 1. Map of the South-East Asian biogeographic provinces (after Lekagul and McNeely, 1988).

diversified at the species level. However, some faunas were recently studied or revised, allowing access to faunas with large but also medium and small mammal species.

Special emphasis is on Thailand because of its key biogeographical position in South-East Asia (Fig. 1). Indeed, Thailand is located at the boundary of the major biogeographical regions of South-East Asia: the Indochinese and Sundaic provinces. The present-day limit between them is at the Kra Isthmus level, in peninsular Thailand. However, the origin of these two biogeographical provinces seems old in regard to the large mammal faunas from South-East Asia, notably those of the late Middle Pleistocene (Tougaard, 2001). Moreover, Thailand was certainly the witness of major faunal exchanges between both South-East Asian provinces. It was part of the Sino-Malayan migration route between the continental parts of South-East Asia and the neighbouring Indonesian islands, and probably used by humans during their colonisation of these regions (Tougaard, 2001).

2. Materials and methods

2.1. Materials

Paleontological sites taken into account in the present study are listed in Table 1 and located in Fig. 2, and

Table 1
List of mammalian fossil sites taken into consideration in the present study

Country	Sites	Reference
South China	Yenchingkuo	Colbert and Hooijer, 1953
Vietnam	Tham Khuyen	Olsen and Ciochon, 1990
	Lang Trang	Long et al., 1996
Thailand	Thum Wiman Nakin	Tougaard, 2001
Sumatra	Lida Ajer	de Vos, 1983
Java	Punung	van den Bergh et al., 2001
Borneo	Niah	Harrison, 1996



Fig. 2. Map of the fossil localities taken into account in the present work (●: middle Middle Pleistocene; ★: late Middle Pleistocene; ■: Late Pleistocene). Faunal details of each fossil site are listed in Appendix A.

mammalian faunal lists from these sites are given in Appendix A. In our study, the better-documented and diversified fossil faunas are considered as the best reflection of the mammalian community for a given area and a given period. For example, in Sumatra, two Late Pleistocene sites yielded a large mammal fauna: the Lida Ajer and Sibrambang caves (de Vos, 1983). The faunal composition is the same for both sites, except that 24 species were identified in the Lida Ajer fauna and 16 in the Sibrambang fauna. On the other hand, only one fossil site was studied from the same period in Java

(van den Bergh et al., 2001). For these reasons, one single site is used for each area (country) and period.

The Thum Wiman Nakin (TWN) site in Thailand is dated from about $169,000 \pm 11,000$ yr using the uranium/thorium method (Esposito et al., 1998; Esposito, 2002). In Vietnam, the age of the Tham Khuyen locality is around $475,000 \pm 125,000$ yr using the electron spin resonance method (Ciochon et al., 1996), whereas the age of the Lang Trang locality is estimated to be between 60,000–80,000 yr, based on the faunal composition (Long et al., 1996). In China, the age of the Yenchingkuo locality can be estimated also as around 475,000 yr, considering the faunal similarities between this fauna and the Vietnamese fauna of Tham Khuyen, but also the more archaic character of the Chinese fauna compared with the Thai example. In Sumatra, the Lida Ajer fauna is dated to around 60,000–80,000 yr (de Vos, 1983), whereas the age of the Punung fauna in Java is estimated as around 60,000–125,000 yr, based on its faunal association (van den Bergh et al., 2001). The Niah locality (Borneo) is dated to $40,000 \pm 1000$ yr based on the ^{14}C method (Medway, 1964; Harrison, 1996; Barker, 2002).

Unfortunately, except for the Thai fossil fauna, the others are composed mainly of large mammalian taxa. The absence of teeth and bones of medium- and small-sized mammal species is undoubtedly due to factors of preservation and recovery related to their relatively small size. In the present work, the faunal composition has been taken from literature which does not really deal with taphonomic issues. However, van Kolfshoten (1995) considered that fossil faunas cannot be the exact reflection of original faunas, but can help to understand the changes in paleoenvironments. For these reasons, the better-documented and diversified faunas have been selected for the paleoecological analysis.

In order to replace the reconstruction of the South-East Asian paleoenvironments in a geographical context, we took a transect for the present-day mammalian faunas from South China to Borneo (Fig. 3). Their faunal lists are compiled from the following atlases of mammalian distribution: Lekagul and McNeely (1988), Corbet and Hill (1992) and Nowak (1999). The list of present-day mammalian faunas is given in Appendix B.

2.2. Methods

2.2.1. Cenogram method

The cenogram method was developed by Legendre (1986, 1989). This method describes the weight distribution of herbivorous and insectivorous species in a mammalian community. Investigations of recent faunas have demonstrated that this distribution is closely related to the environment (Legendre, 1986, 1989). A cenogram (Fig. 4A) is built by putting the logarithm of

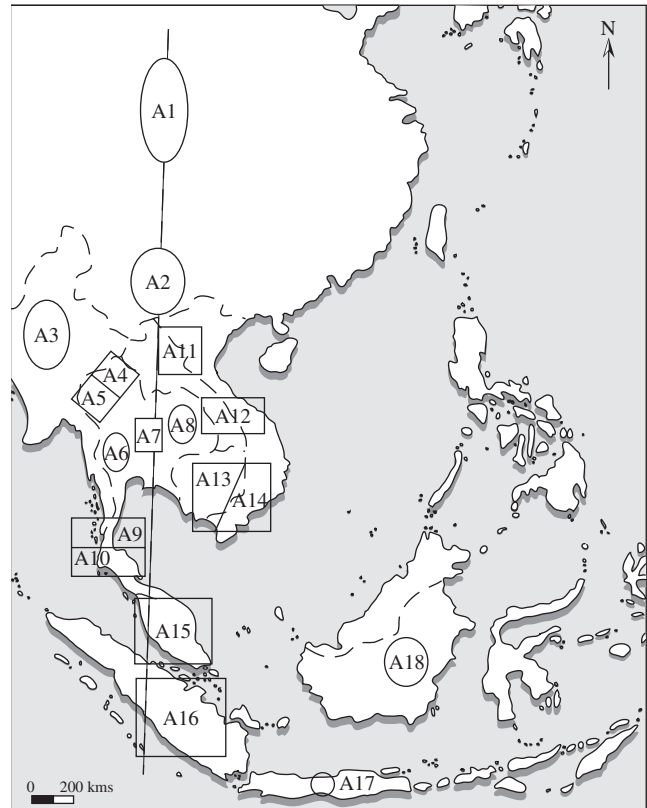


Fig. 3. Map showing the South-East Asian present-day faunas taken into account in the present work along a geographical transect from the North (South of China) to the South (Borneo). Faunal details of each area (A1–A18) are listed in Appendix B.

the mean body weight of each species of the community on the Y -axis, and the species rank in a decreasing order of size on the X -axis. The body weight of the fossil species is estimated using the allometric relationship of the occlusal surface mean of first lower molars ($M/1$) and body weight (after Gingerich, 1977; Creighton, 1980; Legendre, 1989). In our study, for the extinct species, the weight has been estimated by direct use of the surface of $M/1$. For one particular species *Gigantopithecus*, the weight was found in the literature (Ciochon et al., 1990) and for the other species, in the case of a missing $M/1$, the weight has been estimated using $M/1$ from other fossil sites, or the present-day species, or the closest relative in present-day species. Even if a difference exists between the weight of fossil and present-day individuals, it is minimised by the use of a naperian logarithm, and does not affect the slope of the cenogram, but only inverts the order of species rank. Carnivora and chiropteres are excluded from this analysis because they are generally poorly represented in the fossil faunas.

The analysis of a very large number of present-day faunas (Legendre, 1989) allowed definition of four main categories of cenograms (Fig. 4B), characterising certain types of environment (open or closed) as well as climatic

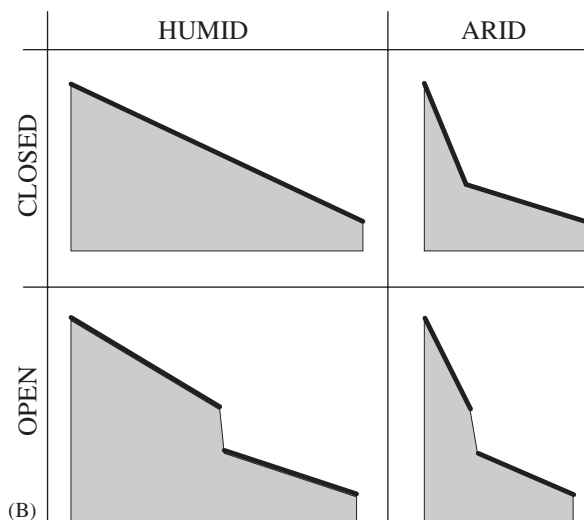
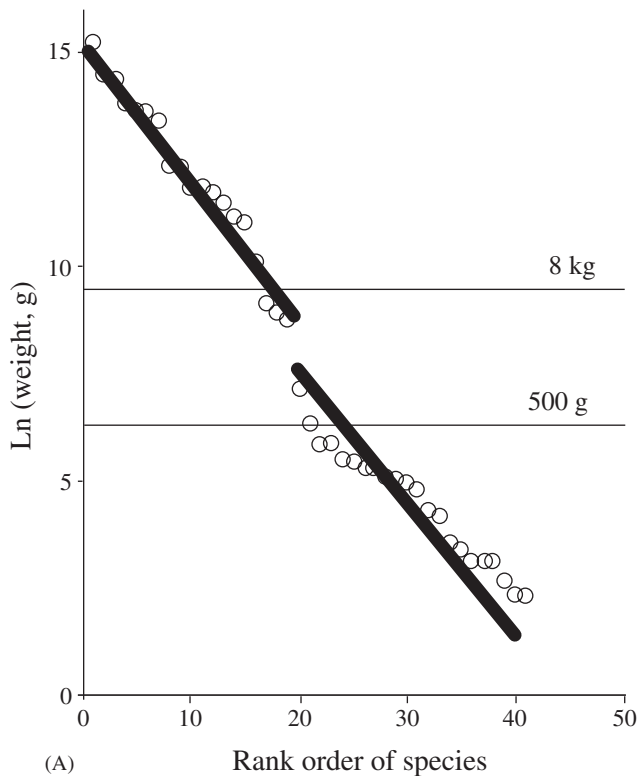


Fig. 4. Cenogram method. (A) Illustration of the cenogram construction with the Thum Wiman Nakin fauna (Thailand). Each point corresponds with the mean body weight (on Y-axis) of a mammalian species in a community (except carnivores and bats) classified on the X-axis by a decreasing order of size. (B) Schematic representation of categories of cenograms (after Legendre, 1989). A continuous distribution of weight is characteristic of closed habitats (above), whereas the medium weight species (between 500 g and 8 kg) are rare or absent in open environments (below). An abundance of large species (weight over 8 kg) is seen in humid conditions (left), whereas they are rare in arid conditions (right).

conditions (arid or humid). It was demonstrated that a continuous distribution of body weight is characteristic of a forested habitat. On the other hand, a lack of

medium weight species (with a body weight between 500 g and 8 kg) is seen in faunas from open landscapes. An abundance of large species (body weight over 8 kg) characterises humid conditions, whereas a deep slope is associated with arid environments. In tropical zones, the slope for the small mammals (body weight under 500 g) reflects the temperatures. The higher the number, the warmer the temperature.

Even if this method is still under discussion (Rodriguez, 1999; Alroy, 2000; Montuire, 2000), cenograms have now been widely applied on several fossil faunas from the Paleogene, Neogene and Quaternary from different continents (e.g. Legendre and Sudre, 1984; Ducrocq et al., 1994; Gibernau and Montuire, 1996, 1999; Montuire and Desclaux, 1997; Montuire et al., 1997; Croft, 2001; Montuire and Marcolini, 2002; Flynn et al., 2003; Storer, 2003; Valensi and Psathi, 2004).

2.2.2. Quantification of climatic parameters

The geographical distribution of the species and the species richness are at present closely related to climate and environmental factors for both continent and ocean (e.g. Jeffree and Jeffree, 1994; Brown, 1995; MacPherson, 2002, 2003; Willig, 2003; Willig et al., 2003) (Fig. 5). This observation has led to recently developed methods of quantifying climatic parameters using the species richness of several rodent subfamilies, Arvicolinae, Murinae and Sigmodontinae (Montuire, 1994, 1996; Michaux et al., 1997; Montuire et al., 1997; Aguilar et al., 1998; Montuire et al., in press).

These methods are based on the relationships between climatic parameters (temperature and rainfall) and species richness by using simple linear regressions. Some other authors correlate the species richness in bats (Patten, 2004; Stevens, 2004) or in mammalian species in South America (Tognelli and Kelt, 2004) also using regression techniques. The correlation between parameters is relatively high, with the determination coefficient (R^2) for temperatures greater than 0.8 for arvicolines, 0.5 for murines and 0.88 for sigmodontines. The determination coefficient for rainfall is about 0.5 using murines. The method based on arvicoline species richness has recently been validated using oxygen isotope compositions of tooth phosphate (Navarro et al., 2004).

For South-East Asia, the murine species are very well diversified (see Misonne, 1969; Montuire, 1994; Aguilar et al., 1998), whereas the other two sub-families are absent. Murines have therefore been used to estimate the climatic parameters. Based on Fig. 5, the number of murine species is the highest in warm and humid conditions. The number of species is compiled for about 150 murine faunas (Montuire, 1994), and the associated climatic parameters are taken from Wernstedt (1972). R^2 means that around 50% of the variation in the species

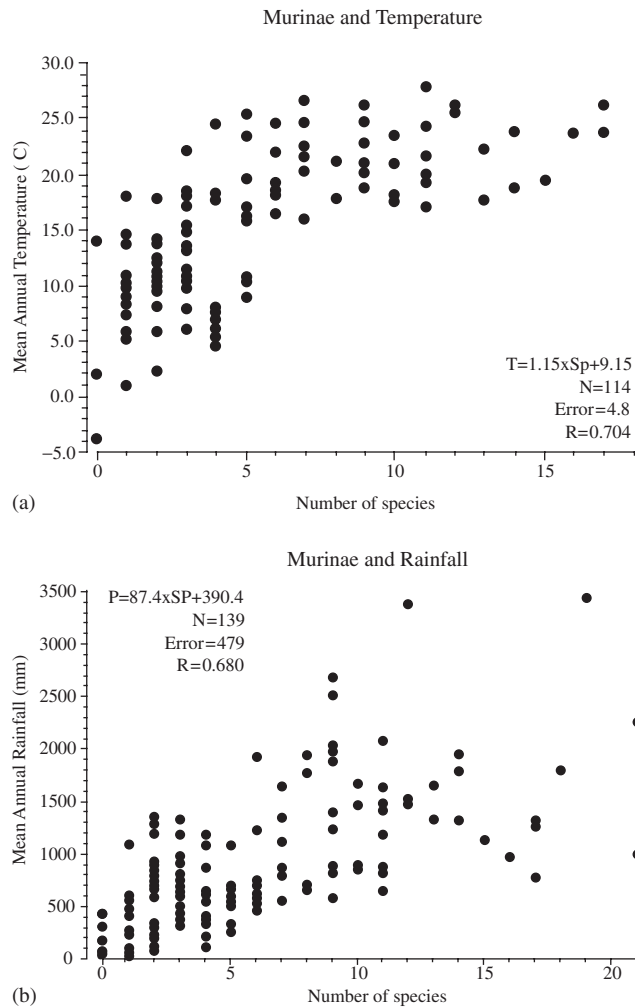


Fig. 5. Scatter diagram of the number of species and mean annual temperatures and rainfall for murine rodents (after Montuire, 1994; Aguilar et al., 1998).

richness can be explained by temperature and rainfall variations. The relatively good correlations between climatic parameters and species diversity mean that this method can be applied to fossil faunas to quantify past climates.

3. Results

3.1. Cenogram method

3.1.1. Present-day faunas

In the Indochinese Province, the present-day faunas from South China (A1 and A2) have no very large mammal species, but a relatively high number of small ones (Fig. 6). Indeed, the distribution of these species is characteristic of a temperate environment with a slightly

less closed forested landscape in the northern part of South China (A1).

In Thailand (A4–A9), the cenograms characterise tropical environments with numerous mammal species, especially of medium and small sizes. However, these Thai environments are not homogeneous. Indeed, the tropical character is lessened in east (A8) and central (A7) Thailand, with fewer species of medium and small sizes. In south Thailand/north of Kra Isthmus (A9), the landscape is again more closed and more humid.

Present-day faunas of Laos and Vietnam (All, A12 and A14) are similar to those of west (A6) and south Thailand (A9) with numerous species, whereas the present-day fauna of Cambodia (A13) is close to those of east and central Thailand, with fewer species, especially of medium and small sizes. On the other hand, the Myanmar (A3) cenogram is intermediate between those of South China and Thailand, with more large mammal species than in South China and fewer species of medium and small sizes than in Thailand. This species distribution is characteristic of a subtropical environment, with a slightly open landscape.

Concerning the Sundaic Province, both south Thailand/south of Kra Isthmus (A10) and Malaysia (A15) present typical tropical rainforest environments. In Sumatra (A16), the same tropical conditions are present with numerous medium and small species. However, compared with the faunas of South Thailand (A10) and Malaysia (A15), there are fewer large species (7 versus 9). For the fauna from Borneo (A18), there are very few large and small species, but the distribution of weight is continuous. This character is more accentuated for Java (A17). This fact is probably related to the biogeographical history and the insular status of most Sundaic areas (MacArthur and Wilson, 1967; Heaney, 1985; van den Bergh et al., 1996; Tougard, 2001).

3.1.2. Fossil faunas

The South-East Asian fossil faunas from late Middle and Late Pleistocene contain more large mammal species than the present-day ones, even the South Chinese and Bornean faunas (Fig. 7). Unfortunately, the fossil faunas taken into account in this study are incomplete. Most of the medium-sized and small species are missing, except for the TWN fauna from Thailand. However, based on these faunas, the occurrence of numerous large mammal species is characteristic of humid conditions, as well as for the older and younger faunas.

In Thailand, the cenogram for the TWN fauna is characteristic of a slightly open forested environment and humid conditions. This is shown by the infrequency of medium body weight species and the relative abundance of large mammals. Moreover, the humid conditions of the environment are strengthened by the

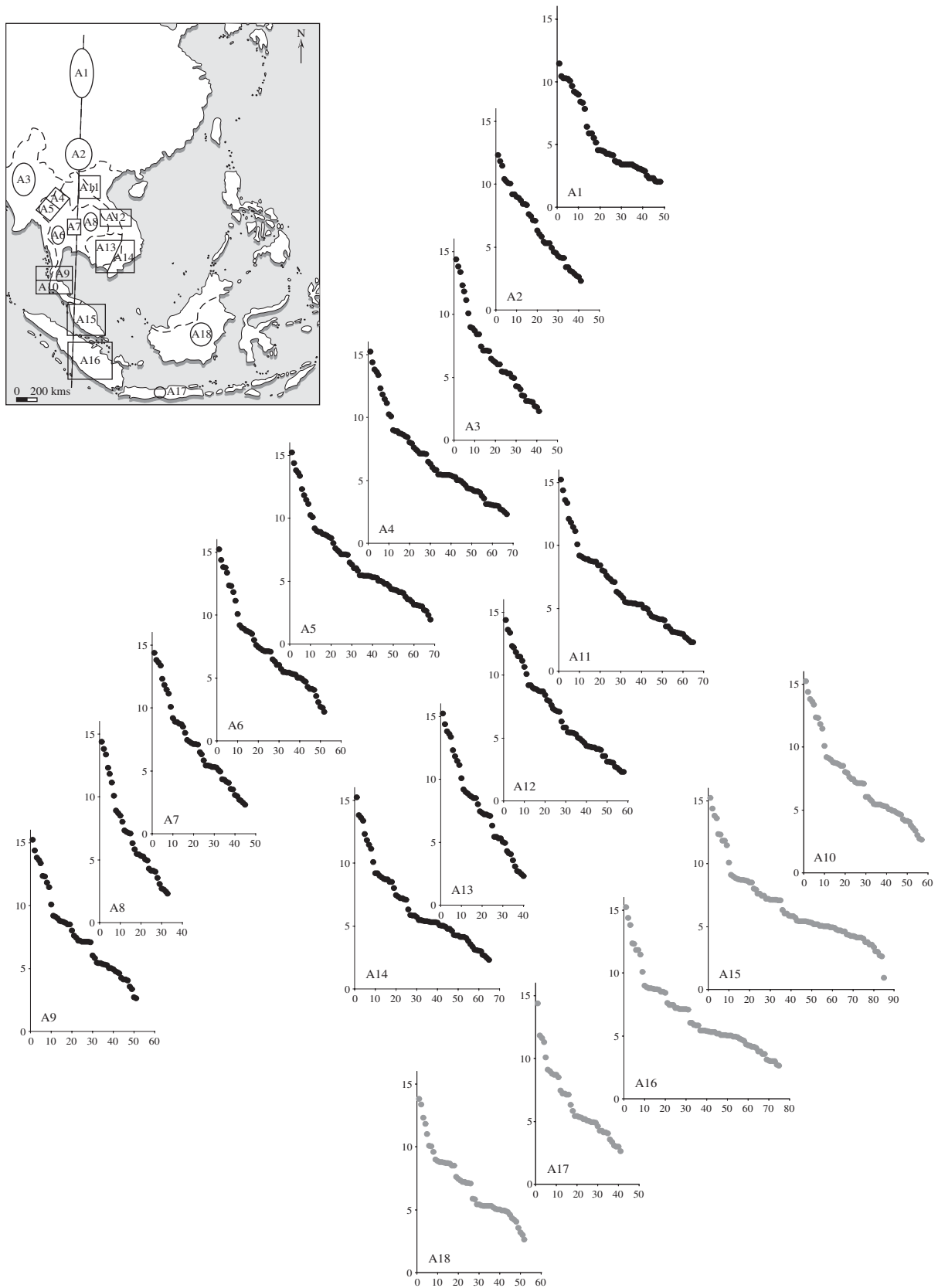


Fig. 6. Cenograms for the present-day faunas of South-East Asia. Cenograms for the Indochinese provinces have black dots (upper part), whereas those of the Sundaic province are represented by grey dots (lower part).

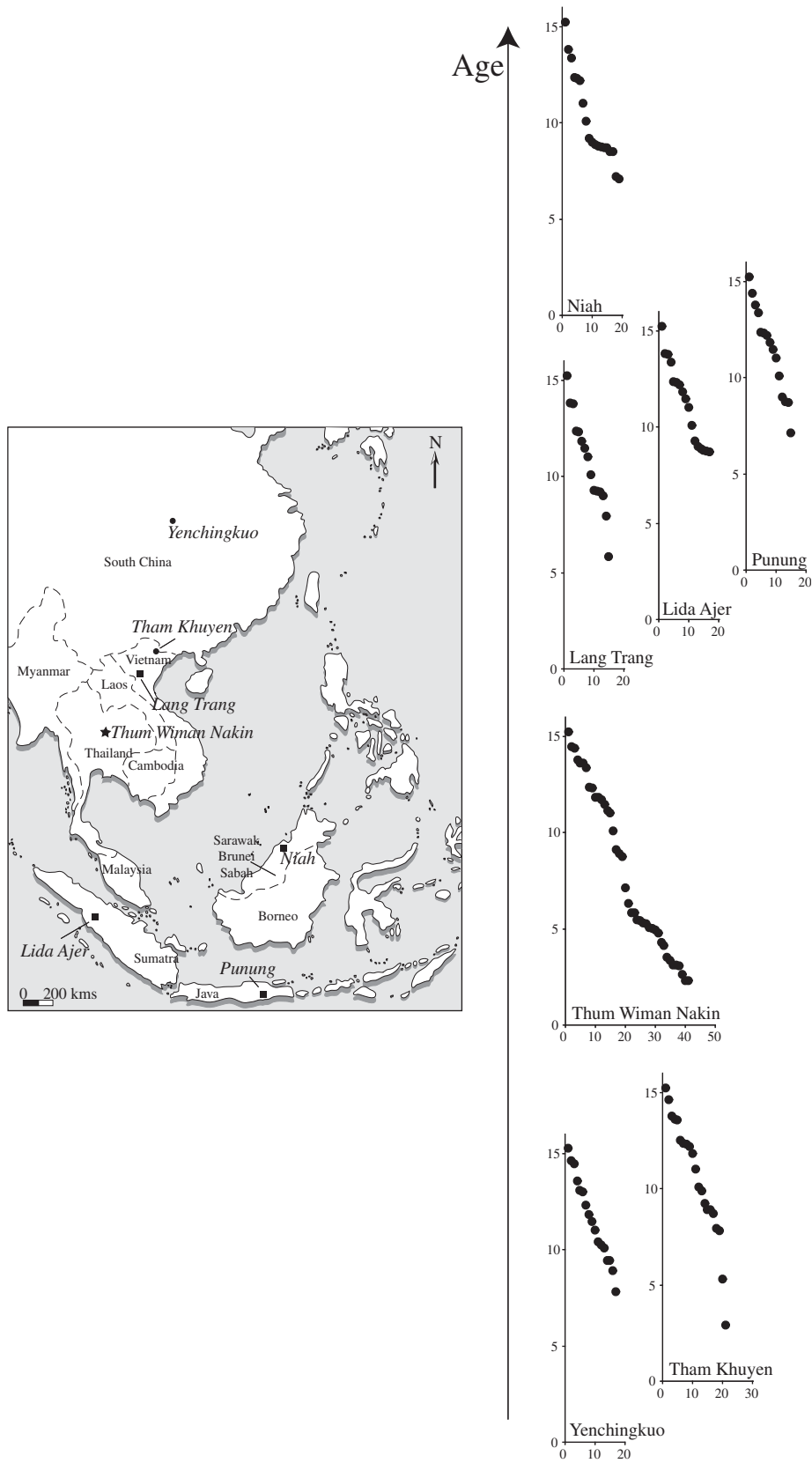


Fig. 7. Cenograms for Middle and Late Pleistocene faunas in South-East Asia. The cenograms are arranged following their age, i.e. from the oldest (lower part) to the younger (upper part) fossil sites. See the text for the age details.

fact that this Thai fossil cenogram displays the same slopes for both large and small species.

3.2. Quantification of climatic parameters

Table 2 displays the results of estimated mean annual temperatures and rainfall from the murines of present-day and Thum Wiman Nakin faunas. Present-day temperatures and rainfall have been also estimated using murine species richness as reference and standard for the fossil faunas. Temperatures are estimated as approximately between 18 and 34.5 °C in the Indochinese Province and between 19.5 and 35.5 °C in the Sundaic Province; rainfall estimates are from 1090 to 2313 mm, and from 1177 to 2400 mm, respectively.

In the TWN fauna, the number of murine species is 14. For this reason, the estimation of the temperature is about 25 °C, and the rainfall about 1614 mm.

4. Discussion

4.1. Comparison between present-day and fossil faunas

Thailand currently enjoys a subtropical climate. According to Gray et al. (1994), the mean annual rainfall is about 1550 mm, but it is not evenly distributed throughout the country. The mean annual temperature is between 25.8 and 29 °C depending on the region (Lekagul and McNeely, 1988). These variations in rainfall and temperature are due to a reversal of wind

direction between summer and winter (Lekagul and McNeely, 1988). The south-west monsoon carries moisture from the Indian Ocean from May to mid-October, whereas the north-east monsoon brings in dry, cold air from China from mid-October to mid-February (Gray et al., 1994). These climate conditions allowed the development of a tropical rainforest in Asia (Whitmore, 2003). In Thailand, 70% of the country was under forest cover in the 1930s, compared with 20% in 1994 (Gray et al., 1994). About 65% of Thai forests can be classed as deciduous (i.e. marked seasons, with most trees shedding their leaves in the dry season), whereas the remaining 35% are evergreen forests with minimal seasonal changes. There is important inter-mingling of the deciduous and evergreen forests, and a number of subcategories of each type exists (Lekagul and McNeely, 1988; Gray et al., 1994). The various cenograms of the present-day Thai faunas reflect the heterogeneous tropical climate conditions and the mosaic of forested landscape.

The Thum Wiman Nakin site is located close to the Nam Nao National Park, among the mountains of the Chaiyaphum and Phetchabun provinces, in north-eastern Thailand. The area is set in rolling Permian sandstone hills and covered by semi-evergreen forests with dense bamboo groves, dry dipterocarp stands and pines (Gray et al., 1994). The mean annual temperature is 27 °C, and the mean annual rainfall is 1180 mm (Gray et al., 1994; National Climatic Data Center database, i.e. NCDC database from <http://ingrid.ideo.columbia.edu/SOURCES/.NOAA/.NCDC/>). A7 (central Thailand) includes the Nam Nao National Park, and the TWN site. The cenogram for this area reflects a subtropical and relatively closed environment. Estimations of mean annual temperatures and rainfall are, respectively, 24.1 °C and 1526 mm. On the other hand, the fossil fauna from TWN seems characteristic of a slightly open forested environment with humid conditions. However, the estimated mean annual temperature and rainfall are 25.25 °C and 1614 mm, respectively. Despite the more open features of the landscape, these temperature and rainfall estimates fall into the range of the Thai present-day faunas (Table 2).

Compared with the cenograms of the present-day faunas from the South-East Asian transect, the TWN cenogram displays an outline intermediate between those of the northern part of South China corresponding to the Sichuan province (A1), and central Myanmar (A3). Although reflecting a slightly open forested environment, the Chinese fauna has fewer large mammal species, especially very large ones (*Elephas maximus*, the Asian rhinoceroses and some large bovids), and more small mammal species than the TWN fauna. The Myanmar fauna and the TWN fauna contain the same number of species. However, for Myanmar, *Elephas maximus* is missing, and more mammal species of

Table 2
Species richness of murine rodents and estimated mean annual temperatures and rainfall for the present-day faunas of South-East Asia and the fossil fauna of Thum Wiman Nakin (TWN, Thailand)

Site/area	Number of murine species	Temperature (°C)	Rainfall (mm)
TWN	14	25.25	1614
A1	8	18.35	1089.6
A2	11	21.8	1351.18
A3	15	26.4	1701.4
A4	20	32.15	2138.4
A5	21	33.3	2225.8
A6	13	24.1	1526.6
A7	13	24.1	1526.6
A8	10	20.65	1264.4
A9	10	20.65	1264.4
A10	13	24.1	1526.6
A11	20	32.15	2138.4
A12	18	29.85	1963.6
A13	9	19.5	1177
A14	22	34.45	2313.2
A15	23	35.6	2400.6
A16	18	29.85	1963.6
A17	13	24.1	1526.6
A18	9	19.5	1177

medium size are present. For these reasons, its environment appears slightly more closed than that of TWN. The mean annual temperature and rainfall estimated for the TWN fauna are close to those estimated for the A1 and A3 faunas (Table 2). While these estimates are close to observed mean annual temperature (27.21 °C) and rainfall (853 mm) in Myanmar (Mandalay weather station, NCDC database), this is not the case for South China. Indeed, the mean annual temperature varies between 9.41 °C (Lanzhou station) and 16.39 °C (Chengdu station), whereas the mean annual rainfall is from 319 mm in the North to 958 mm in the South of A1 (NCDC database). As in Thailand, the monsoons alternately blow in a south-westerly and northerly/north-easterly direction over South China and Myanmar. The climate of the Sichuan province can be classified as wet subtropical. However, Lanzhou (north) has the distinct features of a semi-arid climate, whereas Chengdu (south) enjoys a subtropical monsoon climate (<http://www.muztagh.com/china-weather/>). The Sichuan basin is an expanse of low hills and plains completely encircled by mountains. The typical vegetation comprises subtropical evergreen broad-leaf forests (Fagaceae, Lauraceae, Magnoliaceae and so on), subtropical coniferous woods (Pinaceae, Taxodiaceae, Cupressaceae), and bamboo stands (<http://www.blasum.net/holger/wri/biol/sichuanp.html>). In Myanmar, the central part of the country is relatively dry, unlike the coastlines, which are exposed to heavy rainfall. For this reason, the forest cover in the centre of the area is dominated by dry forests with thorny trees and dry dipterocarps, as well as upper mixed deciduous forests with teak and bamboos (<http://www.forest-treasure.com/>; <http://www.worldwildlife.org/>). In contrast, only mixed deciduous forest is found nearer the coast.

4.2. Geological events, palynological records and climatic changes

The geological history of South-East Asia is mainly linked to two major plate collisions: the first one between India and Eurasia about 55–65 Ma ago (Courtilot et al., 1986; Beck et al., 1995); the second one between South-East Asia and Australia about 15 Ma ago (Tapponnier et al., 1982; Hutchison, 1989). The Indo-Eurasian collision was the cause of the elevation of the Himalayas and the Tibetan Plateau. This later was widely involved in the establishment of the modern pattern of monsoonal circulation (Ruddiman and Kutzbach, 1989; Raymo and Ruddiman, 1992; Kutzbach et al., 1993; Jablonski, 1997; Ruddiman, 1998; Zhisheng et al., 2001), i.e. seasonally reversing summer- and winter-monsoon winds mentioned previously. However, the emergence of a huge continental shelf, the so-called Sundaland (South-East Asia landmass including Sumatra, Java,

Borneo and Palawan), due to the growth of continental glaciers during Pleistocene glacial periods, had widely influenced the intensity of these monsoonal winds (Hutchison, 1989; Heaney, 1991). In some regions of South-East Asia, the increased land area would have lessened the surface area of adjacent shallow seas and sea size, thereby decreasing evaporation and the moisture content of the monsoonal winds (Heaney, 1991). As a consequence, interglacials were characterised by strengthened summer-monsoon winds and weakened winter-monsoon winds, as reflected by higher ratios of some minerals (smectites, illite and chlorite) from clay mineral assemblages at the Ocean Drilling Program (ODP) site 1146 in the northern South China Sea (Liu et al., 2003). In contrast, lower ratios indicate a strongly intensified winter monsoon and weakened summer monsoon during glacials. Similar indications are also given by a planktonic foraminifera, *Globigerinoides ruber*, from ODP Core 1148 from the northern South China Sea (Jian et al., 2003). Several large decreases of *G. ruber* $\delta^{13}\text{C}$ suggest that the winter monsoon became episodically stronger about every 400,000 yr during the Pleistocene. One of the most important effects would have been a corridor of low rainfall passing through the centre of the Sundaland, extending in an arc from southern Thailand to eastern Java (Heaney, 1991). Seasonal forest and savannah would perhaps have been the main type of vegetation in this corridor. However, according to Heaney (1991), high-canopy forest habitat probably persisted in a mosaic of forest and savannah along the large rivers that flowed across this relatively dry region. In fact, rainforest could have repeatedly fragmented to become refuge zones for some animals and plants in savannah, and then expanded again (Whitmore, 2003).

Few paleoenvironmental data from South-East Asia document environmental and climatic conditions during the Pleistocene. Moreover, they are mainly related to paleoenvironments of South China and Indonesia (van der Kaars, 1991; van der Kaars and Dam, 1995; Wang et al., 1999; Zheng and Lei, 1999; van der Kaars et al., 2000, 2001; Anshari et al., 2001; Suparan et al., 2001), most of them covering either a short lapse of time such as the Last Glacial Maximum (15,000–29,000 yr) to the present, or a poorly detailed great lapse of time (more than 2 Ma). However, the Chinese and Indonesian paleoenvironmental records are quite consistent, the most relevant being a continuous lacustrine sequence from Tianyang Basin (Leizhou Peninsula, southeastern China) covering 400,000 yr (Zheng and Lei, 1999) and eastern Indonesian marine piston cores extended to 300,000 yr (van der Kaars, 1991; Wang et al., 1999; van der Kaars et al., 2000). During most of the glacial periods, palynological records indicate drier and cooler climatic conditions by the occurrence of montane forest pollens (*Pinus*, *Altingia*, *Dacrydium*) in China (Zheng

and Lei, 1999), grassland vegetation (Cyperaceae, Chenopodiaceae and Gramineae), and lower montane forests dominated by Fagaceae (*Lithocarpus*) in south-eastern Indonesia (van der Kaars, 1991; Wang et al., 1999; van der Kaars et al., 2000). Expansion of monsoon evergreen forest of Fagaceae (*Quercus*) in South China and mangrove, fern and rainforest in eastern Java occurred in interglacial periods, indicating warm and humid conditions (Zheng and Lei, 1999; van der Kaars et al., 2000). From altitudinal shifts in montane forest vegetation boundaries, estimated temperatures indicate that glacial temperatures were 2–6 and 4–7 °C lower than today, in South China and eastern Java, respectively (Zheng and Lei, 1999; van der Kaars et al., 2000). During Oxygen Isotope Stage 6 (OIS 6; 125,000–180,000 yr) and after approximately 81,000 yr, dry conditions and increased seasonality prevailed in western Java with rainfall estimated, respectively, to 750–1000 and 1000–1200 mm. Between these two periods, annual rainfall was higher and estimated as ca. 2000 mm (van der Kaars and Dam, 1995).

In Thailand, a palynological record from a small peat swamp in the Khorat Plateau (north-east Thailand) has provided interesting information on Late Quaternary paleoenvironmental conditions (Penny, 2001). The regional plant cover is currently almost the same as the present-day environment of the Thum Wiman Nakin fossil site with dry Dipterocarpaceae, such as *Dipterocarpus* and *Shorea*, but also conifers such as *Pinus*. Moreover, climatic conditions are relatively close: mean annual rainfall and temperature, respectively, about 1182 mm and 27 °C (Khon Kaen station; NCDC database). Unfortunately, the period covered by the spore and pollen record from the peat swamp is only 40,000 yr. Its study indicates that the region supported a Fagaceae-Coniferous forest, similar to contemporary vegetation described from south-west China during the Late Pleistocene (Penny, 2001). In this way, climatic conditions were cooler and probably drier than present-day climates in Thailand. However, the pollen data give a picture of environmental stability through the Late Pleistocene, contrasting the paleobiogeographic records from high-altitude sites in South-East Asia. This stability seems to be the reflection of the wide ecological tolerance for the relatively dry and cool climatic conditions of the two dominant pollen taxa (*Pinus* and *Quercus*). Moreover, the regional dryland flora of north-east Thailand appears to be a mixture of true tropical taxa, dry deciduous and savannah elements, as well as temperate, tropical-montane or Eurasian taxa. Tropical broad-leaf deciduous forest becomes dominant at the Pleistocene/Holocene boundary and through the early Holocene, with the fragmentation of Fagaceae-Coniferous forest in response to the development of relatively humid and warm climatic conditions (Penny, 2001).

From the cenogram point of view, the Thum Wiman Nakin fauna, dated back to $169,000 \pm 11,000$ yr (OIS 6), characterises a slightly open forested environment and humid conditions in north-east Thailand. This result is almost consistent with Heaney's idea of a mosaic of high-canopy forest habitat and savannah along the large rivers of the Sundaland during glacial periods. Unfortunately, annual rainfall and temperature estimated for this Thai fossil fauna on the base of the murine species richness do not reflect drier and/or cooler climatic conditions as mentioned previously from the palynological records of South China and eastern Java (van der Kaars, 1991; van der Kaars and Dam, 1995; Wang et al., 1999; Zheng and Lei, 1999). The most likely explanation is that less than 50% of the variation in murine diversity can be explained by temperature and rainfall variations. Concerning the other South-East Asian fossil sites mentioned in this paleoenvironmental study, no conclusion can be really drawn about climatic conditions from either the cenogram results or the climatic parameter estimation. Since most medium- and small-sized mammals are missing, the occurrence of numerous large mammals is characteristic of humid conditions. According to the literature, the Vietnamese (Lang Trang; Long et al., 1996), Sumatran and Javanese (respectively, Lida Ajer and Punung; de Vos, 1983) faunas are characteristic of humid environments, mostly forests. These faunas are related to OIS 5 (between 60,000 and 125,000 yr; de Vos, 1983; Long et al., 1996; van den Bergh et al., 2001). Palynological records covering OIS 5 indicate warm and humid conditions (rainfall ca. 2000 mm) with the expansion of tropical lowland rainforests, humid mid and upper montane forests, fern and woodland cover in eastern Java (van der Kaars and Dam, 1995; van der Kaars et al., 2000) and the dominance of fagaceous monsoon evergreen forest in southern China (Zheng and Lei, 1999). On the other hand, the fauna, especially the large herbivorous mammals, from the Niah locality (Borneo), dated from $40,000 \pm 1000$ yr (OIS 4), is characteristic of drier and more seasonal forests (Medway, 1964; Harrison, 1996). Palynological records suggest montane conifers and then temperate forest elements increased in southern China during this glacial period with a strong depression of the tree line, by as much as 800–1000 m (Zheng and Lei, 1999), whereas in eastern Java, lower montane forests of Fagaceae dominated (van der Kaars et al., 2000). Data from north-east Thailand are in accordance with those previously mentioned for China and Java, since the region supported a Fagaceae-Coniferous forest, indicating cooler and probably drier climatic conditions (Penny, 2001). Neither the paleoenvironmental information from literature nor the palynological record are readily available for the oldest sites used in this study (i.e. Yenchingkuo in South China and Tham Khuyen in Vietnam). According to Matthew and

Granger (1923), the Yenchingkuo fauna characterises heavily forested conditions. Moreover, according to Colbert and Hooijer (1953), this fauna is most closely related to the recent fauna of the Western Highlands of Sichuan. On this basis, these authors estimated that the climate was similar to the present-day temperate climate of this region. However, several authors (Matsumoto, 1915; Kahlke, 1961) considered the Yenchingkuo fossil remains as belonging to two distinct faunas: an older one (Yenchingkuo I) with the remaining Tertiary elements and a younger one (Yenchingkuo II). Unfortunately, the most complete papers dealing with this fauna present the Yenchingkuo fauna in a single faunal list (Matthew and Granger, 1923; Colbert and Hooijer, 1953; Kahlke, 1961).

4.3. Biodiversity and faunal composition

Since most of the Pleistocene faunas from South-East Asia lack documented small mammal fossil remains, it seems from the large mammal data that biodiversity was greater in the Middle and Late Pleistocene than currently: between 7 and 14 large mammal species for present-day faunas (i.e. a mean of less than 11 species by area) and between 10 and 17 large mammal species for fossil faunas (i.e. a mean of more than 13 species by fossil site). The environmental changes of the Pleistocene are correlated with a series of profound changes in the diversity and distribution of mammals in South-East Asia. Indeed, the first consequence of the geological and climatic changes was the size reduction of the subtropical and tropical zones. These zones had extended across East Asia during the Tertiary, but by the late Tertiary and Pleistocene, they had shifted south-eastward (Jablonski, 1997; Jablonski and Whitfort, 1999). Then, the emergence of the Sundaland during glacial periods led to the opening up of new pathways for the dissemination of species (Tougaard, 2001). As a consequence, gene flow was alternately reduced and facilitated through the isolation and rejoining of populations, thus making easier the speciation from refuge zones (Lekagul and McNeely, 1988; Jablonski and Whitfort, 1999; van der Hammen and Hooghiemstra, 2000). Moreover, human influence has always been regarded as a major factor of plant and animal diversity variation, which proceeded in two ways, according to Flerow (1971): first, human influence acted in a passive way, determined by the development of territories in the expansion of agriculture, felling of forests and ploughing. This resulted mainly in a displacement of large species, a destruction of harmful animals, a transformation of the fauna by domestication, and the development of animal breeding. Second, humans acted on fauna by the active extermination of animals, which became especially effective with the invention of firearms and the development of hunting techniques (Flerow, 1971).

However, the human influence on environment seems relatively recent. For example, evidence for human impact (burning and crop cultivation) on the vegetation development in eastern Java and Kalimantan is restricted to the last few hundred years (Anshari et al. 2001; van der Kaars et al, 2001).

The evolution of larger body sizes has occurred in many lineages of mammals. It was one of the commonest strategies employed by mammals to adapt to Pleistocene climatic fluctuations. Indeed, a larger body is more efficient in its utilisation of food energy because its smaller surface area relative to volume makes possible less loss of energy through dissipation of heat at the body's surface (Bergmann, 1847; James, 1968; Jablonski and Whitfort, 1999). This phenomenon is particularly well known in South-East Asian fossil faunas of the Pleistocene (Hooijer, 1949; Colbert and Hooijer, 1953; Harrison, 1996; Tougaard, pers. obs. on Thai fossil faunas). All large mammal orders are concerned: for example, Primates (*Pongo*, *Macaca*), Carnivora (*Ailuropoda*, *Arctonyx*, *Panthera*), Artiodactyla (*Sus*, *Naemorhedus*), as well as Perissodactyla (*Tapirus*, *Rhinoceros*). However, some exceptions to this rule indicate that the general decrease in size over the course of time is not exclusively controlled by environmental factors. According to Jablonski and Whitfort (1999), various primate genera are of great interest in the study of response patterns to environmental changes. Climatic seasonality has a considerable effect on apes with long generation times, but also energy- and time-intensive modes of raising offspring. Moreover, apes possess very large brains relative to their body size, and such metabolically costly organs require nutrient- and energy-rich diets in order to develop and be maintained. For these reasons, evolution of larger body sizes for apes was not a key to evolutionary success as it was for many other mammalian lineages. *Gigantopithecus* was widely affected and, to a lesser extent, the orang-utan *Pongo pygmaeus*. The latter managed to escape extinction, maintaining its distribution in relatively seasonless equatorial tropical forests of the Sundaic province (Jablonski and Whitfort, 1999). On the other hand, monkeys with their abilities to exploit a wide variety of plant foods and to produce offspring more quickly (shorter gestation times and interbirth intervals) were more successful (Jablonski, 1997; Jablonski and Whitfort, 1999).

It is obvious that most of the Pleistocene South-East Asian faunas used in this study are characterised by genera and/or species as similar to their modern counterparts living in the same region or nearby areas. However, some large mammals in these faunas are no longer found in the same region but occur in more distant areas of South-East Asia, or, in few cases, in other parts of the world. Finally, a few genera, species or subspecies are completely extinct. For example, in the

TWN fauna, 18 of the 24 taxa identified are currently known in the Thai fauna, the remaining six (for example: *Ailuropoda*, *Crocuta* or *Pongo*) living in other parts of South-East Asia or elsewhere. Among these 24 taxa, four subspecies are today extinct. Some striking cases can be mentioned to illustrate this fact. The case of *Pongo* was previously broached and is widely debated in Jablonski and Whitfort (1999). This genus has currently a Sundaic habitat (Sumatra and Borneo) and appears to be well adapted to several different types of primary forests, ranging from swamps and other areas near sea level to mountainous forests (Nowak, 1999). It was more widespread in South-East Asia from the Middle Pleistocene as testified by the *Pongo* fossil remains found in South China, Vietnam, Laos, Cambodia, Thailand, and obviously Indonesia, including Java (see notably: Fromaget and Saurin, 1936; Kahlke, 1961, 1972; Beden and Guérin, 1973; de Vos, 1983; Olsen and Ciochon, 1990; Harrison, 1996; Long et al., 1996; Tougaard and Ducrocq, 1999; van den Bergh et al., 2001). According to de Vos (1984), the expansion of its distribution area would have been from South China to Indonesian islands. Moreover, its extinction on the South-East Asian mainland is quite recent, since *Pongo* remains were excavated from Vietnamese sites of Late Pleistocene age (Olsen and Ciochon, 1990). Among the hypotheses about this extinction, some authors suggest this is largely because of excessive hunting and environmental disruption by humans. This extinction would have been accompanied by a behavioural change, i.e. from a terrestrial to arboreal mode of life, in order to escape from the pressure of hunting by humans (MacKinnon, 1971; Rijksen, 1978). However, the hypothesis of Jablonski and Whitfort (1999) remains more plausible. Because of the reliance of *Pongo* on regular supplies of high-energy tropical food sources, its decline in the Pleistocene seems due to its inability to adjust its life history parameters to a more highly seasonal environment.

Ailuropoda melanoleuca, the giant panda, was also widespread in the South-East Asian mainland in past times. Pleistocene remains were found in South China, Myanmar, Vietnam, Laos and Thailand (Fromaget and Saurin, 1936; Colbert, 1943; Kahlke, 1961; Olsen and Ciochon, 1990; Long et al., 1996; Tougaard et al., 1996). *Ailuropoda* reached its peak in the Middle Pleistocene. Since approximately the middle of this period, it has declined to reach the current situation (Huang, 1993). The habitat of the giant panda is currently restricted to some mountainous areas in central China provinces, and is located between 2700 m (800 m in winter) and 3900 m (Nowak, 1999). This habitat is composed of mixed forests, conifers and broad-leaved trees, the undergrowth being covered with temperate bamboos. These bamboos require cool temperatures and humidity in contrast to the tropical bamboos found today, notably

in Thailand and Malaysia (Farrelly, 1984; Reid et al., 1989). The studies conducted on two temperate bamboo species displayed the reliance of *Ailuropoda* on this kind of food (Reid et al., 1989). It seems that this animal can adapt its diet only to other temperate bamboos as the captive giant pandas do in zoos. For this reason, the interglacial climatic conditions led to a northward movement of the temperate bamboo area, and consequently of the giant pandas (Tougaard et al., 1996). Human expansion probably had an influence on *Ailuropoda* decline only in the recent past.

5. Conclusion

Reconstructions of paleoenvironments, in which mammals and hominids evolved during Quaternary cycles in South-East Asia, can be approached from different points of view (pollen records, isotope analyses, fossil mammalian communities, and so on). In the present work, the paleoenvironmental study has been conducted using the cenogram method and the species richness of some rodents in order to estimate climatic parameters. First, for South-East Asian present-day faunas, cenograms were constructed and climatic parameters estimated, along a north–south transect used as reference. The same procedure was then followed for South-East Asian fossil faunas of Middle and Late Pleistocene age. Unfortunately, Pleistocene mammalian faunas found in South-East Asia are incomplete, mostly composed of large mammal species. This is the reason why this work is mainly focused on the Thum Wiman Nakin fauna ($169,000 \pm 11,000$ yr; OIS 6) from north-east Thailand.

The TWN cenogram is characteristic of a slightly open forested landscape with relatively humid conditions. Compared with the South-East Asian present-day faunas, it displays an outline intermediate between those of the northern part of South China (temperate climate and relatively open environment) and central Myanmar (subtropical environment with a slightly open landscape). For this reason, the TWN fauna reflects a slightly more temperate climate and open environment than currently found in Thailand (subtropical climate and mosaic of forested landscape). From palynological records from South China and Indonesia, OIS 6 was a glacial period with drier and cooler climatic conditions than those of the present day, and with increased seasonality (Wang et al., 1999; Zheng and Lei, 1999; van der Kaars et al., 2000). Unfortunately, estimates of temperature and rainfall from murine species richness are not consistent with these expected drier and cooler climatic conditions (probably because of inadequate variation in murine diversity). During this glacial period, the winter monsoon was intensified, whereas the summer monsoon was lessened (Jian et al., 2003).

Besides, some mammal taxa occurring currently in cooler regions such as *Ailuropoda* and *Hapalomys* (Nowak, 1999) were found in TWN. Moreover, most of the large mammal orders are affected by a size increase when compared with their living counterparts. After the corridor hypothesis of Heaney (1991) and various palynological records (Wang et al., 1999; Zheng and Lei, 1999; van der Kaars et al., 2000; Penny, 2001), the following paleoenvironment could be imagined for north-east Thailand from rivers to limestone hill and mountain tops: along the rivers, freshwater swamp forests (*Mallotus* and *Shorea*) with some Ungulates (*Rhinoceros sondaicus*, *Bubalus bubalis*, *Cervus eldi*), rodents (*Berylmys berdmorei*) and perhaps *Pongo pygmaeus* as in Borneo; in the lowlands, a mixture of true tropical taxa (palm trees, *Lagerstroemia*), dry deciduous forest and savannah elements (Gramineae, *Acacia* and dry dipterocarps), as well as temperate or tropical-montane taxa (*Alnus*, *Betula*, *Carpinus*, *Dacrydium*, *Rhododendron*, *Ulmus*, *Artemisia*) sheltering nearly all the mammals found in the TWN fauna, such as *Elephas*, *Macaca*, *Crocuta* and other small carnivores, *Rhinoceros unicornis*, some cervids and bovids, *Crocidura* and various rodents; on hill and mountain slopes, dominance of Fagaceae-Coniferous forests (respectively, *Quercus* and *Pinus*) with temperate bamboo undergrowth where *Ailuropoda*, *Ursus thibetanus*, *Naemorhedus*, *Bos sauveli*, *Petaurista* and *Hylomys* were living.

Combined with other data sources, the cenogram method was shown to be useful, whereas the model (Murinae) used in the climatic parameter estimation method is not as well-adapted for South-East Asian paleoenvironments, as Arvicolinae are for European ones (Montuire, 1999; Montuire and Marcolini, 2002). One of the reasons for this unsupported result is the lack of Asian faunas in the model. Indeed, around 150 present-day faunas have been used to build the equation of temperature and rainfall estimation, but most of these faunas are from Europe and Africa. This model is now in revision and is completed by using more Asian faunas. The other Pleistocene faunas mentioned in this work lack medium- and small-sized mammals, which is why a complete paleoenvironmental reconstruction of these faunas was not possible. Therefore, it appears important to revise and better document the South-East Asian mammalian fossil sites in order to improve understanding of the environmental and climatic parameters that have influenced the evolutionary history of hominids in South-East Asia.

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Appendix A. Supplementary Materials

Appendices A and B are available in the online version of this article doi:10.1016/j.quascirev.2005.04.010.

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