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Late Pleistocene of Southeast Asia

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Introduction

The Late Pleistocene period begins 126 ka with the base of the Eemian interglacial stage, corresponding to the base of marine oxygen isotopic substage 5e. It also includes the last glacial episode of the Pleistocene and ends with the beginning of the Holocene, 11.5 ka. Due to high amplitude climatic fluctuations induced by cyclical glaciations alternating with interstadials, this period represents a key for the understanding of the distribution and composition of extant mammalian communities and for the evolution of modern humans, *Homo sapiens*.

Biogeography of Southeast Asia

Today, two biogeographic provinces are distinguished in Southeast Asia. The Indochinese Province or Northern Province includes many mammals that do not extend west into India or north into temperate China, but some extend southward, as far as Malaysia and the Greater Sunda Islands. The Sundaic or Southern Province contains many endemic genera (Corbet and Hill, 1992). The boundary between these two provinces is located at the Isthmus of Kra in Thailand, at about 10° 30′ N (**Fig. 1**). This Isthmus was initially based upon vegetation changes with evergreen rain forest in the south and more seasonal forest in the north. Most animal species distributions are affected by this boundary, but its importance varies according to the different taxonomic groups. The mammalian boundary is also located slightly north of the Isthmus of Kra (Tougard, 2001; Woodruff, 2003). A cluster analysis by Tougard (2001) indicated that large mammal faunas of Thailand north of Kra Isthmus group with those of the Indochinese Province, whereas faunas south of Kra Isthmus group with those of the Sundaic Province. This was initially demonstrated by Chaimanee (1998) for rodents, which show a more significant change at the Kra Isthmus than large mammals.

Southeast Asia has undergone dramatic climatic and geographic changes during the Pleistocene. It is supposed to have been significantly drier and cooler with more seasonal climates during glacial periods (An, 2000). These climatic oscillations are associated with repeated shrinking and expansion of rain forests and correlative spreading and shrinking of savannas. According to Morley (2000), pine woodlands and savanna grasslands expanded and replaced the rain forest over large areas of Southeast Asia during the glacial periods. Such a change corresponds to a downward shift of vegetation zones, estimated of 600–1,000 m. Simultaneously, glacioeustatic sea fall enlarged the surface of the Thai–Malay Peninsula and connected nearly all the islands together. The sea-level drop is estimated to have been at least 100 m (Voris, 2000) for the Last Glacial Maximum (LGM) (20 ka), causing the Sunda Shelf to emerge and the Andaman Sea to retreat. Such a change is supposed to have had a strong impact on the monsoonal climate which led to the development of a savannah corridor in the central flood plain of the Sunda Shelf. The distribution of teak forest (*Tectona grandis*), which widely occurs today in the Northern Province but with isolated patches in Java, supports this hypothesis. Although most authors agree that during the coldest and driest glacial periods, including the LGM, some rain forest refuges existed, they disagree about their location (Kershaw *et al.*, 2001; Gathorne-Hardy *et al.*, 2002; Meijaard, 2003).

Figure 1 Indochinese and Sundaic Province and the Kra Isthmus.

Surprisingly, the Late Pleistocene period is probably the less well-known period concerning its climate and vegetation, but also concerning its sedimentary deposits, either from caves or from fluvial terraces. In Thailand, among more than 20 investigated fossiliferous caves and fissure fillings, four of them had been assigned to the late Pliocene or the Early Pleistocene and all others to the late Middle Pleistocene (*see* Mid-Pleistocene of Southern Asia) (**Figs. 2** and **3**). Only one archeological site could be assigned to the Late Pleistocene (Chaimanee, 1998). Cave filling is the result of a sedimentary process that occurs during phases of heavy rainfall or of tectonic subsidence. At some other periods, erosion is dominant because of the drop of sea level or tectonic uplift. Therefore, the cave fossiliferous sediments document the most recent episode of infilling. In some rare cases, remnants of older filling events can be found as relictual patches left by erosion on the lateral walls of the caves, but they can only be identified if they yield older fossils. Speleothems calcite deposits are rarely contemporaneous to the fossiliferous sediments and are usually more recent than fossils. As cave fillings, they are polycyclic and their dating is of little use to date the fossiliferous cave deposits unless they clearly cover the sediments like stalagmitic floors. Terrace deposits are also dependent on climate and tectonic activity (**Figs. 4** and **5**). During periods of low sea levels, river

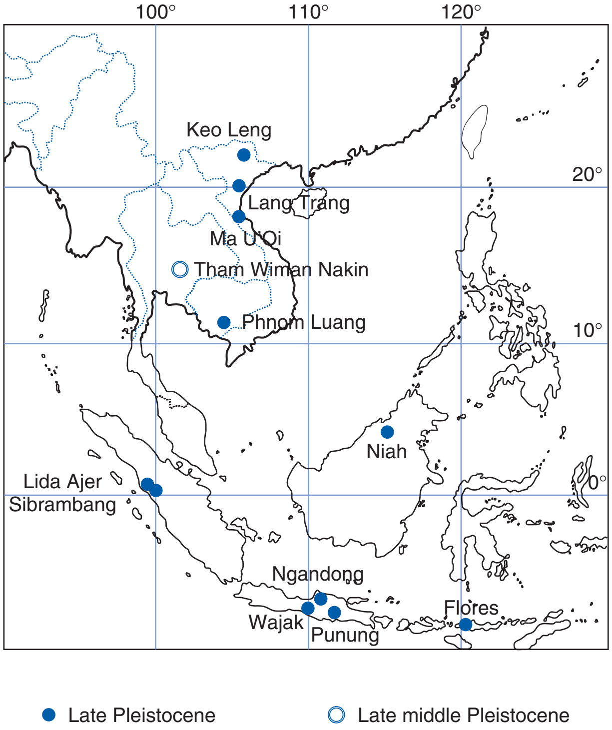

Figure 2 Late Pleistocene and late middle Pleistocene vertebrate localities in Southeast Asia mentioned in the text.

Figure 3 Mammalian community of the middle and late Pleistocene in Thailand.

channels cut the former terraces deposits and develop new terraces of minimal width which may be easily eroded during later Holocene flooding. Therefore, the scarcity of Late Pleistocene deposits in Southeast Asia can be explained by a peculiar climatic setting. The climate was colder and drier, and these characteristics have been confirmed by the fossil pollen record in Java and Thailand and by the larger than average size of mammals that have extant representatives in the same area. Palynological data are extremely scarce, and most authors refer to the study of Van de Kaars and Dam (1995) in Java where a core documenting the vegetation of the last 135 kyr has been investigated. Nevertheless, despite its great interest, it cannot be simply extrapolated to other areas. Recently, however, new data have been provided concerning Thailand, which confirm the extension of a temperate forest during the cooler and drier LGM (Penny *et al.*, 2001; White *et al.*, 2004).

Figure 4 Cave deposits in limestone are source of Pleistocene fossils in Southeast Asia.

Figure 5 Another important source for Pleistocene mammalian fossils is terrace deposits.

In the light of these considerations, the Late Pleistocene mammalian fossil records of Southeast Asia will be reviewed.

Late Pleistocene Mammals in Southeast Asia

Sundaic Province

Java The rich *Homo erectus* record in Java has stimulated much paleontological and biochronological research. However, a fluctuating sea level has caused island isolation and led to a high endemicity, making it difficult to develop a biochronological timescale. Nevertheless, a consensus exists currently that the Kedung Brubus faunal stratum corresponds to a Middle Pleistocene faunal assemblage. It is followed by the highly controversial Ngandong fauna, then by Punung and finally by Wajak, which represents the last faunal assemblage before the extant fauna comes into existance.

The Punung fauna, Wajak fauna, and perhaps also the older Ngandong fauna are considered to be of Late Pleistocene age.

Punung faunal assemblage De Vos (1983) and Sondaar (1984) defined the Punung faunal strata on the first appearance datum (FAD) of the extant Asian elephant (*Elephas maximus*) and the extant pig species (*Sus vittatus*). The Punung Caves fauna has yielded 18 mammalian species including *H. sapiens*. The composite faunal list, from at least two separate caves, I and II, contains no extinct species. The occurrence of orangutans (*Pongo pygmaeus*), siamang (*Hylobates syndactylus*), and sun bear (*Ursus malayanus*), taxa not known to cross water barriers, suggests that a land connection existed at that time with mainland Southeast Asia and that the community lived in a rain forest environment. As orangutans and modern humans are unrecorded from older faunal strata, one can therefore conclude that they are immigrants from the mainland (Van den Bergh *et al.*, 2001). Therefore, this rain forest faunal association probably corresponds to the end of the last interglacial or the beginning of the last glacial.

According to this interpretation, one could also add orangutans and modern humans to the previous list of Late Pleistocene FAD on Java. Another interesting point is that if this fauna is really from the terminal part of the last interglacial, it supports the argument that the sea level was, at that time, at least 60–80 m lower than at present day, to permit land mammal exchanges with the Indochinese Province, where some of these taxa (Asian elephant and orangutans) have been documented from older localities. Tham Wiman Nakin Cave in Thailand, for example, which is older than 169 ka, has yielded Asian elephant. It is unfortunate that no absolute ages are available for Punung I and II localities, which have yielded early *H. sapiens*. The presumed age of the Punung fauna is 80–60 kyr. Van den Bergh *et al* (2001) also mention the discovery of Asian elephant from the Cipeundeuy sand pit in Java, located next to Bandung, dated between 35.5 and 29.6 kyr by ^{14}C (Van den Bergh, 1999). The site has also yielded a few modern taxa that are still present on that island.

Wajak faunal assemblage The Wajak fauna is of early Holocene age and has been dated to about 10.56 ± .075 kyr BP (Storm, 1995). The fauna is modern with 10 large mammal species including *H. sapiens* and four rodent species. *Elephas* is absent and tapir (*Tapirus indicus*) has its last appearance datum (LAD) on the island. According to De Vos (1983) the fauna indicates an open woodland environment and shows that rain forest must therefore have disappeared before 10 kyr BP from that area because it lacks the species most strongly adapted to the humid forest.

Ngandong faunal assemblage The Ngandong faunal composition appears largely similar to the Kedung Brubus fauna. Of the 15 species of large mammals, 9 are extinct and shared with Kedung Brubus (Sondaar, 1984). However, several species, including *H. erectus*, differ at the subspecific level, suggesting a younger age. Van den Bergh *et al.* (2001) therefore propose an intermediate age of about 135 kyr for that faunal assemblage. In contrast, Swisher *et al.* (1996) U/Th series dating on Ngandong fossil teeth gave an age between 53 and 27 kyr. One dramatic consequence of that absolute age is the putative contemporanity and sympatry of late *H. erectus* (Ngandong man) with early *H. sapiens,* which has so far never been observed elsewhere in Asia, with the possible exception of Flores Island (Morwood *et al.*, 2004). However, the U/Th series dating method is not accurate in tropical regions where the weathering of dentine and enamel is significant and diagenesis is considerable (Esposito *et al.*, 2002). For these reasons, the attribution of the fauna to the early Late Pleistocene by Van den Bergh (1999) is preferred here.

Sumatra The material collected by Dubois, as early as 1888, originates from three distinct caves: the Lida Ajer Cave near Pajakombo, the Sibrambang Cave, and the Djamboe (Jambu) Cave near Tapisello. The fauna was subsequently studied by Hooijer (1947), who assigned Holocene age to these faunas. However, Drawhorn (1994) used amino acid racemization to date the Lida Ajer Cave fauna from 80 to 60 kyr. The Lida Ajer Cave has yielded two teeth of *H. sapiens*, one upper central incisor and one upper left molar associated with 16 other mammalian taxa, including Asian elephant, orangutan, *Hylobates,* all taxa indicative of a rain forest environment. Almost all of these fossil mammal taxa are also present in Sibrambang Cave and have been described by Hooijer in several publications between 1947 and 1962. De Vos (1983) also mentioned additional taxa such as *Rusa* sp., *Muntiacus muntjak, S. vittatus*, and *S. barbatus*.

Borneo The Late Pleistocene of Borneo is famous for its historical discovery of the first Southeast Asian modern human skull and associated rich mammalian fauna at Niah Cave (*see* Interactions with Hominids). Several levels have been excavated in recent years and have yielded abundant mammal fossils, from large mammals to rodents (Medway, 1972), including *H. sapiens* (**Fig. 6**). The sequence possibly dated back to more than 40 kyr. One white marker bed, which may correspond to ash from the Toba eruption, has been dated to 32.6 kyr BP. From the fossiliferous level, 30 extant species of mammals, including six primates (*H. sapiens*, orangutan, *Hylobates, Macaca*, *Semmopithecus*, and *Nycticebus*) have been reported with more than eight rodents and insectivores and more than ten species of bats. Asian elephant is also present and, with orangutan, characterizes the Sundaic Late Pleistocene faunal assemblage. Only one extinct species, a pangolin, *Manis palaeojavanica*, occurs, and the overall assemblage is characteristic of rain forest. Therefore, it demonstrates that this part of Borneo was a rain forest refuge at that time and that *H. sapiens* were already adapted to rain forest environments.

Flores Island endemic vertebrates have been recorded for many years from Flores (Sondaar *et al*., 1994; Van den Bergh *et al*., 1996; Morwood *et al*., 1998) including dwarf *Stegodon*, giant rat, *Hooijeromys*, and Komodo dragon. However, the recent discovery, in the Liang Bua Cave of a dwarf human skeleton described under the name *H. floresiensis*, interpreted as an island dwarf endemic *H. erectus* and dated to 18 kyr, changes the understanding of the faunal evolution of that island. The dwarf *Homo* is associated with an endemic fauna, with a dwarf *Stegodon*, a Komodo dragon, and endemic rats. According to the different absolute dates provided by Morwood *et al*. (2004), this dwarf human and associated fauna occurs during a time interval spanning 74–37.7 kyr up to 18 kyr in the cave. This discovery testifies to the long isolation of Middle Pleistocene immigrants including *H. erectus*, and furthermore, stone tools as old as 800 kyr have been reported (Morwood *et al*, 1998). Therefore, the FAD of the mainland mammals recorded from Holocene sediments (Van den Bergh *et al*., 1996) should be younger, from shortly after the LGM, and modern *H. sapiens* may have immigrated simultaneously when the deep-water barrier isolating flores during most of the Middle Pleistocene became shallower.

Figure 6 Dry screen method was used to separate fossils from cave sediments.

Indochinese Province

The Indochinese Province fauna of the middle and Late Pleistocene is characterized by a peculiar mammalian assemblage comprising of *Stegodon orientalis, Ailuropoda melanoleuca baconi* (giant panda), and orangutan. The fossil record of these species dates from the early Middle Pleistocene, and they survived until the Late Pleistocene or even close to the present day. Some even migrated southward to reach the Sundaic Province at an early time and, in the case of *Stegodon*, this probably occurred in several waves. Orangutan and modern human, in contrast, reached Sundaland only during the end of the last interglacial or the beginning of the last glacial, and giant panda never immigrated there. Biochronologically, the Pleistocene period is subdivided by the FAD and LAD of different species. The Early Pleistocene is characterized by a primitive species of panda, *Ailuropoda minuta, Gigantopithecus*, and several other species which also survived in the earliest Middle Pleistocene. This later period (*see* Mid-Pleistocene of Southern Asia) is characterized by a short-faced hyena (*Hyaena brevirostris sinensis*) which is replaced after migration or extinction by the spotted hyena (*Crocuta crocuta ultima*) whose origin and FAD is problematic. For Kurten (1956), the spotted hyena had reached Southeast Asia between 480 and 450 kyr. It also immigrated to Northern China, where it was found in the upper layer of the Choukoutien *H. erectus* locality. Another biochronological marker is *H. sapiens* whose appearance seems to correspond to the end of the Middle Pleistocene. The Late Pleistocene fauna of that province can be therefore characterized by the local or total extinction of some mammal species. Giant panda survived in Southern China whereas orangutans survived in Borneo and Sumatra. A similar history has been elaborated for rodents by Chaimanee (1998). Early Pleistocene and early Middle Pleistocene rodent faunas contain several extinct genera, which became extinct before the late Middle Pleistocene, a period that is characterized by the presence of extant species no longer native to Thailand, such as *Hadromys humei, Hapalomys delacouri, Pithecheir parvus, Nannosciurus melanotis*, and *Iomys horsfieldi*. Finally, the Late Pleistocene rodent assemblage is characterized by the progressive local extinction of these 'exotic' rodents and by the immigration of some large-sized flying squirrels originating from South China.

Vietnam Several early to Middle Pleistocene mammal faunas are known, but so far only one rich Late Pleistocene locality has been reported, the Lang Trang Cave from North Vietnam with 23 species of large- and medium-sized mammals (Vu *et al*., 1996; Long, 1996). Its age has been estimated between 80 and 60 kyr. Primates are represented by *Macaca, Semmopithecus*, and orangutan. *S. orientalis* and *Elephas namadicus* are associated with giant panda and tapir, indicating a forest environment of early Late Pleistocene age. No human remains have been collected so far from the cave which represents the LAD for *E. namadicus*. The Ma U'Oi Cave in Northern Vietnam (Bacon *et al*., 2004) has yielded a small fauna with six species of large mammals including *Elephas* and *Homo* sp. and four species of rodents.The age is uncertain since the fauna has a modern composition with no extinct species. The Keo Leng fauna from Northern Vietnam has an 'estimated' age of 30–20 kyr (Kha, 1976; Olsen and Ciochon, 1990). It has yielded a rich mammalian fauna of 27 species including *H. sapiens*. Orangutan, giant panda, *Megatapirus augustus*, and *S. orientalis* are indicative of a late Middle Pleistocene assemblage, thereby casting doubts on its estimated age. If confirmed, it would indicate that the previously mentioned taxa, with the exception of modern human, survived until the LGM or even later in the Indochinese Province.

Thailand No precisely dated Late Pleistocene mammal fauna has been reported from Thailand, since most Thai caves and fissure fillings have been dated to the late Middle Pleistocene (Chaimanee, 1998). Among them, the fossiliferous layer of Tham Wiman Nakin Cave in Northeastern Thailand (*see* Mid-Pleistocene of Southern Asia) has been dated as older than 169 kyr, using speleothems covering the main fossiliferous layer (Esposito *et al*., 2002). However, uranium–thorium ages obtained from mammalian teeth gave confusing results due to leaching and diagenesis. *Homo*, orangutan, giant panda, and modern Asian elephant therefore existed in Thailand before the last interglacial. Only one fissure-filling locality, the Crystal Cave near Kanchanaburi in Central West Thailand, has yielded a rodent fauna that may be of Late Pleistocene age. It consists of only extant species associated with an unusual large species of flying squirrel, which has been interpreted as a large-sized species, that shifted its range southward during a cold period, as predicted by Bergmann's rule (Chaimanee and Jaeger, 2000a). Many Pleistocene prehistoric excavations, such as Lang Rongrien rockshelter and Moh Kiew Cave in Peninsular Thailand near Krabi, and Spirit Cave and Tham Lod rock shelter near Mae Hong Son in North Thailand, have yielded mammalian remains which have not been published so far. They consist of only modern species. In addition, recent palynological data obtained from three localities in Thailand confirm the hypothesis of a drier and cooler climate during the LGM (White *et al*., 2004), with a fagaceous–coniferous forest in northeast Thailand (Penny, 2001).

Cambodia Only one cave fauna in Cambodia, Phnom Loang (Beden *et al*., 1972) from Kampot Province shows a composition which could correspond with either a Late Pleistocene or a late Middle Pleistocene age, no absolute dating being presently available. Here, Javan rhinoceros (*Rhinoceros sondaicus*) is associated with spotted hyena. Nearby caves have shown the presence of orangutan, Asian elephant, and tapir. The presence of a spotted hyena supports a late Middle Pleistocene age rather than a Late Pleistocene one. In that last case, the *C. crocuta ultima* LAD would be latest Middle Pleistocene.

Discussion

Several conclusions can be reached from this review. The most important is the lack of absolute dating and the huge imprecision concerning the age of most of these mammalian faunas. The second is that the complex geographic history of Southeast Asia makes it nearly impossible to construct a global biochronological timescale. Local faunal evolution is strongly related to the main geographical changes induced by sea-level changes and by neotectonic uplift or subsidence. Only in the more stable Indochinese Province, a reliable biochronological scale potentially could be established, but more accurate dating would be necessary.

Late Pleistocene Local and Global Extinctions

Giant panda is today confined to a small range in Southern China at high altitude, with a temperate climate, where it feeds mostly on temperate bamboos. Tougard *et al.* (1996) have suggested that climatic cooling and an associated altitudinal drop of vegetation zones caused the extension of the temperate bamboo range on which the giant pandas fed. This would explain their wide Pleistocene expansion. Simultaneously, the same cause could explain the spread of the spotted hyena, which is clearly an open woodlands and grassland species, and its replacement of the short-faced hyena. Both giant panda and spotted hyena never reached the Sundaic Province, probably because of rain forest barriers. Orangutan was also widespread in the Indochinese Province during the Middle Pleistocene and migrated later on to the Sundaic Province, where it still survives until today. No data are available concerning the extinction of orangutan in the Indochinese Province, but Bacon *et al.* (2001) described an orangutan skeleton from Hao Bin Province (northernVietnam) that seems to be of very recent age, suggesting a long survival of that species and supporting an anthropic cause for its extinction. Other species have become extinct in both provinces, such as *Megatapirus* in the Indochinese Province and *Duboisia santeng* in the Sundaic Province, before the Late Pleistocene. But again, these events are not yet accurately dated and their causes are unknown. A similar situation occurs for the rodents, with the grassland species *Hadromys humei* becoming extinct before the Late Pleistocene (Chaimanee and Jaeger, 2000b).

Changing Biogeography and the Fluctuating Boundary between the Indochinese and Sundaic Faunal Provinces

Both of these provinces are characterized by a small number of taxa during most of the late middle and Late Pleistocene. Not only extant forms such as *Macaca assamensis, Ursus thibetanus*, giant panda, but also extinct ones such as *Crocuta, S. orientalis, E. namadicus*, and *Megatapirus* can be considered as typical markers of the Indochinese Province. The extant gibbon (*Hylobates syndactylus*) and the pig (*S. barbatus*) for the living species, and *Stegodon trigonocephalus* and *Duboisia santeng* for the extinct taxa, are also characteristic of the Sundaic Province. But many other species were common to both provinces such as *H. sapiens*, tiger, Malayan bear, wild dog (*Cuon alpinus*), tapir, rhinocerotids (*R. sondaicus* and *Dicerorhinus sumatraensis*), wild pig, buffalo, muntjac, Sumatran goat, and several rats, and squirrels. Progress in taxonomic work may increase this list, especially when more small mammals are taken in account. Their association clearly defines a Southeast Asian mammalian assemblage. But the real question concerns the past location of the 'paleo-Kra Isthmus' and its fluctuations. The fossil record yields little information with the exception of a perceptible southward extension of this boundary during glacial periods. The fauna from Tambun locality next to Kuala Lumpur in Malaysia, the age of which is not well established (Hooijer, 1962), contains *E. namadicus*, indicating a southward expanded Indochinese Province fauna. Some extant grassland rodent species, such as *Hadromys humei*, presently restricted to Northeast India and South China, have been found in a late Middle Pleistocene locality close to the Thai–Malay border (Chaimanee and Jaeger, 2000b). On the other hand, some Sundaic rats, presently not living in Thailand, such as *Pithecheir parvus*, extended their range northward. Similar examples occurred among squirrels. However, as very few rodents have been described from the Pleistocene localities of Sundaland, it is difficult to follow the complicated history of the fluctuating boundary between these provinces. Nevertheless, many species of rodents showed a larger latitudinal range than today and many ranges did overlap in a much broader ecotone with high small-mammal biodiversity.

Bergmann's Rule and Size Changes

One common feature of Pleistocene fossil mammal communities concerns their composition and the large size of their constituent species. As in other parts of the world at the same time, large herbivores were more numerous than they are at present. Despite the lack of updated taxonomic studies, six or more large herbivores, two proboscideans and four bovids, have coexisted in these Southeast Asian faunas. Pleistocene herbivores are usually larger than their living representatives. Many factors are involved in controlling adult size of mammals. The most common is Bergmann's rule, which stipulats that warm-blooded animal size increases according to a decreasing mean temperature gradient. This has been demonstrated for the extant *Macaca fascicularis* by Fooden and Albrecht (1993). Hooijer (1949) uses this principle to explain the progressive size decrease of Sundaland mammals, such as orangutans, Javan rhinoceros, tapirs, tigers, and even rodents (Medway, 1972). However, many other factors could have played an important or additional role including interspecific competition and island isolation.

Conclusions

The Late Pleistocene mammalian faunas of Southeast Asia are very incompletely known. Many localities have not yet been dated with modern methods and their inferred ages sometimes correspond only to rough estimations. However, some general conclusions can be drawn from the available data. First, the beginning of this period corresponds to the immigration of modern humans in the area. Some scanty human remains attest to the occurrence of *Homo* before 169 kyr in Thailand and in several other places in the Indochinese Province, but the fossils are not sufficiently complete to identify these remains to species level. The faunas were distributed into two distinct provinces but their boundary, located today in the Thai Peninsula at the Kra Isthmus, was situated further south during most of the Late Pleistocene. Rodent faunas suggest that the transition area, which is sharp today, was much more latitudinally extended. During these periods, savanna was widely expanded and many species were occupying that niche. Probably, many extant forest herbivores were also living in the savanna during the Late Pleistocene as indicated by recent unpublished isotopic studies. Sea-level and climatic changes permitted some exchanges between the two provinces, allowing *H. sapiens*, orangutan, and some other species to reach the biotas of the Sundaic Province. Orangutan's present distribution range in Sumatra and Borneo appears also to be a refuge area and not as a center of origin. In the Sundaic Province, many endemic species, including *H. floresiensis*, differentiated through island evolution as a consequence of isolation. It is expected that in future more evidence of island evolution will be discovered. The history of the Late Pleistocene fauna consists of the progressive range reduction and the local to total extinction of several species. Two main periods of climatic changes may be responsible for these events. First, the Late Glacial Maximum, some 20 ka, corresponded to an important cooling and extension of savanna. It was followed, about 10 ka, by the Holocene warming which was associated with a dramatic expansion of the rain forest that led to the present biogeographic situation. The causes of the local extinctions, as those of the spotted hyena, *Stegodon*, giant panda, and orangutan in the Indochinese Province, are not well understood, since the importance of the human factor cannot yet be evaluated (*see* Late Pleistocene Megafaunal Extinctions). Finally, the modern distribution of mammals has developed only very recently, after a long period of relative stability during the middle and Late Pleistocene.

See also: **Vertebrate Records**: Late Pleistocene Megafaunal Extinctions; Mid-Pleistocene of Southern Asia. **Vertebrate Studies**: Interactions with Hominids.

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Late Pleistocene Mummified Mammals

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Introduction

These well-preserved ice age (Pleistocene about 2 Myr to 10 ka) mammal specimens are the 'crown jewels' of their kind. Along with a few closely observed, beautifully executed depictions of Paleolithic cave art, they give us the best idea of the appearance of the now-extinct mammals.

The mummies have also yielded important information on: (1) taxonomic relations and dispersal history through the study of ancient DNA; (2) soft tissue structure; (3) paleodiet based on gut contents and associated feces; (4) paleopathology; (5) parasites; (6) predators and scavengers through the study of tooth-puncture marks in the skin and gnaw marks on the bone; and (7) paleoclimatic evidence inferred from plant remains in gut contents, ground squirrel nesting grasses, fecal pellets, and seed caches, as well as from the nature of enclosing sediments.

At least 16 species of ice age mammals have been mummified: woolly mammoth, Shasta ground sloth, Jefferson's ground sloth, Patagonian ground sloth, woolly rhinoceros, Yukon horse, steppe bison, helmeted muskox, Harrington's mountain goat, caribou, giant moose, black-footed ferret, collared pika, snowshoe hare, arctic ground squirrel, and vole. Among the best of these specimens are: (1) 'Dima,' a 40-kyr-old baby woolly mammoth from Siberia; (2) a 10-kyr-old Shasta ground sloth from New Mexico; (3) 'Blue Babe' a 36-kyr-old steppe bison from Alaska; (4) an 18-kyr-old subadult helmeted muskox also from Alaska; (5) a woolly rhinoceros from Ukraine; and (6) a 40-kyr-old black-footed ferret from Yukon.

Most are preserved by a type of freeze-drying in frozen ground (permafrost) of Siberia, Alaska, and Yukon, and date from 50–25 and 15–10 ka.