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DIVERSITY OF CENOZOIC MAMMALS IN THAILAND: PALEOENVIRONMENT AND AGE UPDATED

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ABSTRACT

Various mammalian fossils have been discovered from Paleogene, Neogene, and Quaternary sediments in the northern, central, northeastern, and southern regions of the country as a result of our intensive investigations in Thailand. These new discoveries play an important role in both taxonomy and evolution of mammals and also give indications about paleo- environments, climates, and biogeography. Furthermore, the discoveries provide new information about Thailand's ancient biological diversity and are important for dating the deposits in which they were found. Knowing the age of deposits improves the precision of stratigraphic correlations.
Key words: mammal, paleoenvironment, Thailand, Continental Tertiary

PALEOGENE AND NEOGENE MAMMALIAN FOSSILS IN THAILAND

Continental Tertiary basins in Thailand have provided numerous mammalian fossils. The oldest mammal locality in Thailand originates from Krabi basin, Krabi Province, Peninsular Thailand and is of late Eocene age. Late Oligocene mammals have been recorded from Nong Ya Plong Basin, Phetchaburi Province in Central Thailand. Several Middle Miocene mammals have been discovered in the northern intermontane basins; Mae Moh, Mae Teep, Li and Chiangmuan and late Miocene mammals from Khorat sand pits in northeastern Thailand. Numerous Quaternary mammals have been found mostly in caves and in some terrace deposits.

Krabi Basin

Krabi basin is located in Krabi Province, Peninsular Thailand and lies in a N-S direction following major geological trend of the area. The basin is bounded by Jurassic and Triassic rocks on the east and south, and by Carboniferous and Permian rocks on the west and north-west. Tertiary beds were generally identified by the presence of thin beds of lignite or lignitic clay (Markiat et al., 1984). The basin covers a surface of about 364 km^2. The sediments are composed of mudstones, shales, carbonaceous clays and lignite seams. There is only one main lignite seam in the basin which is 15-20 m thick.
The fossiliferous layers in Krabi coal mine are located in the carbonaceous clay and in the main lignite seam. The fauna from Krabi coal mine consists of crocodiles, colubrid snake (Rage et al., 1992), geoemydid turtles (Claude et al., 2007). Mammals from Krabi basin are represented by several new forms such as fruit bat (Ducrocq et al., 1993); dermoptera: *Dermotherium major* (Ducrocq et al., 1992); primates: *Siamopithecus eocaenus* (Chaimanee et al., 1997; Chaimanee et al., 2000), *Wailekia orientale* (Ducrocq et al., 1995), *Muangthanhinius siami* (Marivaux et al., 2006); Carnivores: *Miacis thailandicus* (Ducrocq et al., 1992) *Nimravus* cf. *intermedius* and *Hoplophoneus* sp. (Peigné et al., 2000); rodent: *Baluchimys krabiense* (Marivaux et al., 2000); suids: *Egatochoerus jaegeri* (Ducrocq, 1994), *Siamochoerus banmarkensis* (Ducrocq et al., 1998); anthracotheriid: *Siamotherium krabiense* (Suteethorn et al., 1988), *Anthracotherium chaimanei* (Ducrocq, 1999), *Anthacokeryx thailandicus* (Ducrocq, 1999) and *Bothriogenys orientalis* (Ducrocq, 1999); tragulid: *Archaeotragulus krabiensis* and *Krabimeryx primitivus* (Metais et al., 2001) and helohyid: *Progenitohyus thailandicus* (Ducrocq et al., 1997).
The age of Krabi basin given by mammalian assemblage and magnetostratigraphic dating corresponds to the C13R chron of the paleomagnetic time scale of Berggren et al. (1995), late Eocene of about 34 Ma (Benammi et al., 2001). The paleoenvironment of Krabi basin corresponds to a tropical swamp with low seasonality**.**

Nong Ya Plong Basin

Nong Ya Plong basin is located at Phetchaburi Province, Central Thailand. The basin is a small isolated basin 6 km wide and 15 km long. This locality yields many mammalian fossils such as rodents *Fallomus ladakhensis* (Marivaux et al., 2004), flying lemurs *Dermotherium chimaera* (Marivaux et al., 2006), fruit bat, rhinocerotids, anthracotheres, mustelid carnivores *Chaprongictis phetchaburiensis* (Peigné et al., 2006). This fauna indicates a late Oligocene age and a tropical forest environment nearby a swamp.

Mae Moh Basin

The Mae Moh coal mine is part of the Miocene intermontane Mae Moh basin in northern Thailand. It represents the largest open coal mine of Thailand. Its stratigraphy has been divided established by Corsiri and Crouch (1985) which subdivided it into three formations. The lowest unit is part of Huai King Formation and consists of sandstones, claystones and conglomerates (15 to 320 meters thick). The overlying Na Khaem Formation, which is 300 to 420 meters thick, contains the main coal-bearing units, interbedded with claystones, mudstones and sandstones. Five coal zones (identified as S, R, Q, K and J coals from bottom to top of the Na Khaem Formation) are present. These coal seams, Q and K which have been and are still intensively excavated for mining, are rich in vertebrate fossils including mammals, turtles, fishes and crocodiles; they also yield invertebrate fossils such as gastropods (Songtham et al., 2005), bivalves and plant remains such as wood, leaves and charophytic algae (Soulié-Märsche et al., 1997). The uppermost units are part of Huai Luang Formation, comprising a sequence of red-brown and grey sandstones, mudstones and siltstones with occasional sandstones and conglomerates. It contains also the uppermost coal seam (I coal seam).

The mammalian fossils have been predominantly collected from the coal beds. But due to the intense mining activity and the concentration of that mining activity in the center of the basin, where coal layers were thickest, very few mammalian remains have been recovered during the last twenty years. The fossil remains mostly consisted of isolated fragments of large mammals; mainly proboscideans and rhinos**.** The thickest coal layers becoming exhausted, mining work moved towards the paleo-shores of the lacustrine basin where coal layers become thinner, but with an increasing abundance amount of fossil mammal remains, sometimes less fragmentary, especially in the Q and K coals beds. However, large mammals discovered in Mae Moh are still scarce. Proboscideans are represented by two forms, *Stegolophodon* cf. *latidens* Tassy et al. 1992 and an indetermined Gomphothere. Rhinos are represented by cf. *Gaindatherium* sp., pigs by *Conohyus thailandicus*, deers by *Stephanocemas* cf. *rucha* Ginsburg and Ukkakimapan, 1983, Amphicyonid carnivores by *Maemohcyon potisati* Peigné et al., 2006 and otters by *Siamogale thailandica* Ginsburg et al. 1983. Small mammals from this coal mine are rodents and insectivores (Chaimanee et al., in press).

This sequence made by the three formations characterizes the Mae Moh Group which rests unconformably on marine Triassic limestones. The magnetostratigraphy of the Na Khaem Formation which includes the mammalian fossil layers has been investigated and resulted in a very precise calibration. According to Benammi et al. (2002), the mammalian bearing coal beds of Na Khaem Formation have been deposited between 13.5 and 12.1 Ma. The fossiliferous Q and K coal beds are precisely dated beween 13.3 and 13.1 Ma, corresponding to the C5AAR chron of the paleomagnetic time scale of Berggren et al. (1995). The paleoenvironment of MaeMoh basin corresponds to a tropical forest with a significative amount of temperate floral elements.

ChiangMuan basin

Chiang Muan Basin is a small Tertiary basin located in Chiang Muan District of Payao Province. It is about 8 km wide and 25 km long. According to Strogen (1994), Chiang Muan sedimentary sequence can be subdivided into three formations, Chiang Muan Sandstone Formation, Ban Sa Mudstone Formation, and Pha Lad Formation. The Chiang Muan Sandstone Formation is composed of fluviatile conglomerates, sandstones, siltstones and mudstones. Deposition occurred in a subsiding faulted half-graben on a surface of eroded basement strata. The Ban Sa Mudstone Formation is composed of fluvio-lacustrine, palustrine and swamp mudstone, siltstone, limited sandstones and coals, deposited under a regime of increased subsidence and sedimentation rates. The lower coal seam, which represents the main coal seam, is about 10-20 m thick and the upper coal seams consists of 3-4 thin coal beds. The Pha Lad Formation marks a basin wide transgression of sheet flood, debris-flow and floodplain conglomerate, sandstone, siltstone and limited mudstone. This formation was deposited above a major unconformity under a regime of decreased subsidence rate.

Mammalian fauna found from the lower and the upper coal seams consists of hominoid primate, *Khoratpithecus chiangmuanensis* Chaimanee et al., 2003, large mammal fossils such as mastodons (*Tetralophodon*), pigs (*Propotamochoerus* and *Conohyus*), and ruminants (*Eotragus*, *Protragocerus*, and *Siamotragulus*). On the basis of the fossil mammal assemblages found in the neighboring basins of northern Thailand, Ducrocq et al. (1994) argued for late Early to Middle Miocene age for the Thai intermountain basins. Geological investigations suggest that these deposits are of Middle Miocene age and obviously older than 10.6 Ma, in as much as the major discontinuity that has affected the area is usually dated about 11 Ma (Remus et al., 1993; Strogen, 1994).

Concerning the Tertiary fossils, a major result concerns the discovery and description of *Khoratpithecus chiangmuanensis* This is the first time that an undisputed ancestor of extant large-body ape has been discovered. It delivers therefore many informations concerning the reconstruction of the common ancestor to all extant apes, Asian and African, and about our own ancestors. The absence of any corresponding fossil in Africa suggests that they may have evolved elsewhere and perhaps in Southeast Asia, before migrating to Africa at about 11-8 Ma.

The paleoenvironment of Chiang Muan basin as indicated by plant pollens corresponds to a tropical swamp forest in which one species of swamp tree, *Syzygium* widely dominated the swamp forest. We also argumented that a tropical vegetation corridor may have existed between

tropical Africa and Asia ~12 Ma ago. This corridor was probably used as a dispersal way between Africa and Southeast Asia and explains also the resemblance between some extant plant taxa of African and Southeast Asian rain forests.
Benammi et al. (2004), proposed a magnetostratigraphic correlation of Ban Sa Formation with chron C5ABn–C5n.2n, and an age of the fossil assemblage which is Middle Miocene between 13.5 and 10 Ma.

Khorat basin

Khorat sandpits are located along Mun River in Nakorn Ratchasima Province. Stratigraphic sections were studied from two open sand pits in the area (Somsak sand pit, and the Siam sand pit). Both pits were excavated to a level extending about 20-30 m below the natural surface. We also investigated the sediments from a bore hole made by the Department of Mineral Resources next to Siam sand pit, about 500 m northeast of Somsak sand pit. The bore hole reached 114 m and ended in an evaporitic layer. Below the top soil, the section displays two sand units, an upper unit of yellowish sands (7.6 m thick) and the lower unit of organic matter rich sands and gravels (51 m thick). These sandy units overlie a 50 m thick unit of red and grey clays, of late Mesozoic or early Cenozoic age, attributed to the Phu Thok Formation. The evaporitic layer at the bottom of the bore hole pertain to the Maha Sarakham Formation.
The lower, organic-rich sand unit yields most of the vertebrate fossils. These sands correspond to fluviatile channel deposits with intense cross-bedding and contain fish, turtle and crocodile fossils. Organic-rich clay lenses, between 5 to 30 cm thick and rich in pollen, are interbedded within these sands. Fossil tree trunks and wood fragments occur at multiple levels in that unit. The mammalian fossils collected from this sand unit indicate a late Miocene age for this level of the Somsak sand pit. They consist of hominoid primates, *Khoratpithecus piriyai* Chaimanee et al., 2004; *Hipparion*, remains of which are scanty and consist of a large and a small form; the proboscideans *Prodeinotherium* and *Deinotherium* cf. *indicum, Gomphotherium* sp., *Stegolophodon* sp., and a primitive *Stegodon*; the rhinocerotids *Chilotherium palaeosinense*, *Brachypotherium perimense* and *Alicornops complanatum*; the pigs *Hippopotamodon* cf. *sivalense* and *Propotamochoerus* cf. *hysudricus*; and the anthracotheres *Merycopotamus medioximus* and *Microbunodon milaensis*. Bovid and giraffid remains are also abundant. Two complete carapaces of the giant land turtle cf. *Colossochelys atlas* were also collected. Bunopas et al. (1999) and Haines et al. (2004) have interpreted these deposits as being Quaternary in age, but the abundant mammalian fauna displays no trace of reworking and clearly characterizes a late Miocene faunal assemblage.
The upper sand unit, which shows an average thickness of 6-7 m, differs in color from the underlying sand unit and rests unconformable on top of it. Sediments from the upper sand unit consist mostly of yellowish sands and gravels, with some clay lenses that are rich in organic matter, leaves and seeds. The lowermost part of that unit consists of gravel and reworked tektites that we collected in-situ with abundant tree trunks. These tektites are related to the widespread tektites debris field that resulted from an impact event dated at 0.8 Ma in northeastern Thailand (Howard et al., 2003). In places, patches of top-soils can be observed above the upper sand unit, yielding pottery fragments, modern human skeletal remains and Holocene mammals.
Biostratigraphic data derived from the mammalian fauna of the lower sand layer from Somsak sand pit suggest a broad correlation with the upper Nagri to the lower Dhok Pathan Formations of the Siwaliks. This would indicate an age interval between 10 to 6 Ma. The Siwalik fossil record has been precisely dated by paleomagnetic studies (Barry et al., 2002), so that the stratigraphic ranges of Siwalik fossil species, based on first and last occurrences, are precisely calibrated. Late Miocene localities in China lack marine intercalations and volcanoclastic sediments, and are therefore dated solely on the basis of local mammal biostratigraphy. Compared to biostratigraphic data from the Siwaliks (Barry et al., 2002), we can propose a more precise time interval for the lower Somsak sand unit. The first occurrence of *Hipparion* in the Siwaliks is now estimated at 10.7 Ma. The range of *Deinotherium* spp. in South Asia is dated between 12.9 Ma for their first occurrence and 8 Ma for their last occurrence. The pig *Hippopotamodon sivalense* is bracketed between 10.2 and 7.2 Ma. Anthracotheriids are represented in the Somsak sand pit by two taxa, *Merycopotamus medioximus* Lihoreau et al., 2004 and *Microbunodon milaensis* Lihoreau et al., 2004. The three rhinocerotids are known from Dhok Pathan Formation in the Siwaliks and the Shanxi red clays in China, indicating an age bracketed between 9 and 7 Ma (P.O. Antoine, pers. com.). The giant land turtle cf. *Colossochelys atlas*, which is present in the Siwaliks since Chinji levels, disappears from Siwalik section at about 8 Ma (J. Head, pers. com.). Using the concurrent ranges of Siwalik large mammals, we can estimate the age of the fossiliferous level in the Somsak sand pit as occurring between the first occurrence of *Hippopotamodon sivalense* at 10.2 Ma and the last occurrence of *Deinotherium spp.* at 8 Ma. This interval is similar to that indicated by the range of *Merycopotamus medioximus* (between 10.6 and 8.1 Ma) and *M. milaensis* (between 10.3 and 9.2 Ma) in the Siwaliks. However, the Siwaliks strata were deposited at more northern latitude than Khorat and did not belong to the same climatic and vegetational province as Thailand. There is strong and convincing evidence of increasing seasonality occurring during late Miocene in the Siwaliks with a progressive increase in the abundance of C4 plants, starting at about 10 Ma (Morgan et al., 1994; Nelson, 2003).
Fossil wood (C. Vozenin-Serra, pers. com.) and pollen (Sépulchre, 2003) from the Somsak lower sand unit show that an evergreen tropical gallery-forest occurred in the immediate vicinity, indicating a less seasonal climate than in the Siwaliks. Instead, the associated palynoflora suggests a wetter and more tropical environment during

the late Miocene at Somsak, similar to that of the late middle Miocene Chiang Muan locality (Chaimanee et al., 2003). Pollen of tropical trees including *Alchornea*, *Bauhinia*, *Nauclea* and *Phyllantus* have been recorded, although hydromorphic plants such as Cyperaceae and ferns dominate the pollen spectra, suggesting that large areas of the floodplain were covered by grassland. Some fossils mammals, including the hominoid, pigs and *Deinotherium*, also attest to the presence of a tropical gallery-forest. Therefore, several mammal species that disappear from the Siwaliks sequence because of local climatic changes may have survived longer in a more southerly refuge. Thus, their last occurrence in Thailand may have been more recent than the Siwalik record would suggest. For these reasons, one should be extremely careful concerning the biostratigraphic value of the last occurrence ages of Siwalik mammal species for calibration of the Thai biochronologic time-scale. Instead, data that are less dependent upon climatic changes should be used, such as the first occurrences of other mammalian taxa. According to Barry et al. (2002), the earliest hippopotamid fossils to be recorded in Asia occur in the Siwaliks at 5.9 Ma or possibly in an older layer dated at 7.4 Ma. Hippopotamid remains have been recovered in the lower sand unit at Somsak, but they are rare despite the fact that the habitat was very suitable for them. In addition, the exact stratigraphic provenance of these hippos is unknown. If they come from the same level as the hominoid, the hippos would indicate an age younger than 7.4 Ma. We interpret these data to suggest that these Khorat hominoid deposits are older than 5.9 Ma, the age of the first occurrence of *Merycopotamus dissimilis* in the Siwaliks, which is considered as the descendant of *M. medioximus* (Lihoreau, 2004), the only *Merycopotamus* species recorded from Somsak pit. This would limit the possible age range of this fossiliferous lower Khorat sand unit to a probable age range of 7.4 to 5.9 Ma.

In addition, preliminary results of paleomagnetic data indicate normal polarity for the upper part of the lower sand unit (M. Benammi, pers. com.). According to its normal polarity, the lower sand unit could correspond to at least 6 different normal periods, including C4 5n.2n (10.9-9.9 Ma), 4An (9.05-8.7 Ma), 4n.2n (8.05-7.6 Ma), 4n.1n (7.5 Ma), 3Bn (7 Ma) and C3 An.1-2n (6.5-5.9 Ma). Sedimentary and/or paleomagnetic data do not allow us to favor one interval rather than another. But if we exclude the earliest interval on the basis of biochronologic arguments already discussed previously, only 5 possible normal intervals remain, between 9.05 and 6 Ma, suggesting a median value of 7.5 Ma. Available biochronologic data are unfortunately not constrained enough to exclude some of the possible correlations between 9 and 6 Ma, if no hippos in that layer, or between 7.4 and 5.9 Ma if hippos are present. Ongoing taxonomic work on additional fossil mammal taxa, combined, with additional magnetostratigraphic analyses, may help to constrain more precisely the age of the hominoid-bearing stratum at Somsak sand pit.

A nearly complete lower jaw of a more derived ape, *Khoratpithecus piriyai* has been discovered in a sandpit of Late Miocene age (about 9-7 Ma), Chalermprakiet District, Nakhon Ratchasima Province (Chaimanee et al., 2004). It is clearly a relative of the Chiang Muan ape and is also a close relative of the extant orangutan, indicating that Thailand was a center of evolution for orangutan and perhaps all other modern apes. The jaw has been found in river channels deposits, associated to crocodile, fish and fresh water turtles. Surprisingly, remains of a terrestrial giant turtle also known from India, *Colossochelys*, have been also fossilized, probably washed out from the river strands during floods. Many bone and teeth fragments of land mammals are associated and document a typical Late Miocene South Asian fauna, with short necked *Sivatherium*-like extinct giraffes, rhinos, *Dinotherium*, pigs, anthracotheres and antilopes. To interpret all these new data, it was also necessary to improve the dating of all these Tertiary basins. In the absence of marine deposits and of volcanic rocks, we focused on the magnetostratigraphy of these deposits.

Khok Sung Sand pit

Khok Sung sand pit is situated in Nakorn Ratchasima Province, Northeastern Thailand. Concerning the Pleistocene, a rich and diversified Middle Pleistocene mammalian fauna has been excavated from ancient river deposits at Khoksung sandpit in Nakon Ratchasima Province which has delivered outstanding fossils like a complete skull of a spotted hyaena which is presently extinct in Asia (Chaimanee, 2006), several complete skulls of a long snouted gavial, a fish eating crocodile, also extinct in Thailand. Associated to an extinct elephant, *Stegodon* and deers, buffalos, gaur and banteng remains, it represents the best preserved Middle Pleistocene fossil assemblage from Thailand. Usually these animal remains are only documented from caves where their remains have been fragmented by predators and by porcupines. Therefore mostly isolated teeth are left in cave sediments. From such caves we have also discovered spotted hyaena in the Peninsula Thailand near Nakhon Si Thammarat Province and in several other places in Northern Thailand, where they are associated with remains of giant panda, orangutans and many micromammals (Chaimanee, 1998). These fossils indicate that the climate and vegetation was rather different from today, with heavier rain fall and more extended grassland areas at some periods. This interpretation has been recently confirmed by the carbon stables isotopes extracted from the teeth of these fossil animals. Further work is going on actively to reconstruct the communities and the paleoenvironments of the Pleistocene mammal communities in Thailand.

CONCLUSIONS

Fossil mammals are well represented for their biochronological and paleoenvironmental contributions. Several Tertiary basins in Thailand have beeen precisely dated by combining biochronological data and magnetostratigraphical studies. There are two Paleogene basins rich in mammalian fauna have been discovered,

Krabi basin of late Eocene age located in the Peninsular Thailand and Nong Ya Plong basin of late Oligocene age in Central Thailand. There are several Neogene basins in Northern Thailand that have yielded rich mammalian fauna, most of them being of middle Miocene age. Concerning the paleoenvironments, Thailand has always remained in the tropical domain during the Tertiary. But the tropical environments have considerably varied through time from rain forests to dry open grassland. Swamp and lake deposits are over represented due to the numerous Tertiary basins. But at some periods, temperate floras appear to have been represented by a significant percentage of taxa, as in the Mae Moh basin around 13.1-13.2 Ma. Not only older localities as Krabi, but also younger localities as Chiang Muan, display a high tropical component. Climate dramatically changed during the ice ages in Pleistocene, where important latitudinal shifts occurred, some taxa of northern areas such as giant panda and *Hadromys humei* (an Assam rat) moved southwards until Thai-Malay border (Chaimanee & Jaeger, 2000). Additional discoveries will allow tofill the gaps and bring more detailed understanding of the diversity and history of Thai fossil mammals. From our data, Thailand appears clearly as a “paleo hot spot” of mammalian diversity.

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