A review of the Cainozoic small mammal fauna of Thailand with new records (Chiroptera; Scandentia; Eulipotyphla) from the late Pleistocene

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In October 2010, a team comprising scientists from The Prince of Songkla University in southern Thailand and the Harrison Institute in the United Kingdom collected samples of a fossiliferous deposit in Khao Kao Cave, which is situated in an Ordovician limestone hill range in Thailand's Songkhla Province.

Analysis of the numerous teeth, jaws, and other bones present in the samples has resulted in the identification of fifteen species of small mammal representing the orders Chiroptera, Scandentia and Eulipotyphla, all but one known from the living fauna. Eleven of the species are recorded for the first time from the Pleistocene of Thailand including an extinct bat species new to science, which is described. Optically Stimulated Luminescence (OSL) dating of the deposit indicates a late Pleistocene age of 16.35 ± 2.67 Ka, although a small number of rogue grains among the mineral population suggests the presence of material older than 200 Ka. The history of fossil small mammal research in Thailand is summarised.

KEY WORDS: Chiroptera, Scandentia, Eulipotyphla, Thailand, Pleistocene, Eptesicus sp. nov., new records, OSL dating

Introduction

The following sections outline the history of palaeontological small mammal research in Thailand. The six epochs (Eocene, Oligocene, Miocene, Ploicene, Pleistocene and Holocene) to which fossilised small mammal remains can be dated, are treated in chronological order. The introduction concludes with details of the present study, which comprises an analysis of a late Pleistocene deposit from southern Thailand.

Eocene (56.0-33.9 Ma) (Tables 1a-c)

Evidence of the earliest mammal fossil-bearing locality in Thailand was uncovered in 1987 during palaeontological excavations in the Krabi Basin in south-eastern peninsular Thailand (Fig. 1). The excavations yielded a second lower molar of a large adapid primate and cranial, mandibular, and dental remains of a new genus of anthracothere (*Siamotherium*) (Suteethorn *et al.*, 1988). The basin is the only known Eocene fossil locality in Thailand and comprises three open cast pits: Wai Lek, from which the most complete Eocene mammalian fauna in SE Asia is known (Marivaux et al., 2000); Ban Pu Dam, and Bang Mark. The pits share a coal seam, from which most of the fossil mammals have been recovered. The coal seam is located between overlying lacustrine and underlying fluviatile sediments with a thickness of 175 m (Marivaux et al., 2006; Ducrocq et al., 1993). Based on faunal and magnetostratigraphic analysis, the sedimentary deposits of the three pits are considered to fall within an age range of 34.5 to 33.5 Ma (late Eocene to early Oligocene) (Marivaux et al., 2000) while faunal and palaeomagnetic data suggest that the main lignite seam occupies an age range of 34.8 to 33.7 Ma (latest Eocene to earliest Oligocene) (Marivaux et al., 2006).

Fossil remains representing more than 30 species of mammal have been recovered from Krabi Basin (Marivaux *et al.*, 2000). Although the majority of material may be attributed to medium to large herbivores, two orders (Insectivora and Rodentia), two families (Chiroptera: Pteropodidae and Rodentia: Ctenodactylidae), and two species (*Baluchimys krabiense* and *Dermotherium major*) of small mammal are present (Table 1).

Based on mammalian fossil material recovered from lignite seams in the basin's open cast pits by scientists from La Mission Paléontologique Française en Thaïlande, Ducrocq *et al.* (1992a) report the presence of a new genus of Galeopithecidae (Dermoptera) based on the morphology of two lower molars (m2-m3) situated in a lower jaw fragment. The material is discussed in more detail in Ducrocq *et al.* (1992b), where it is assigned to *Dermotherium major* Ducrocq *et al.*, 1992. The latter authors state that the material represents the first fossil record of the order Dermoptera. In addition to the dermopteran material, Ducrocq *et al.* (1992a) assign a single third upper molar to an indeterminate form of rodent of the family Ctenodactylidae, although the material is listed as representing the less distinct group 'Ctenodactyloidea' by Ducrocq *et al.*, 1995.



Figure 1. Map of Thailand showing Tertiary fossil collection sites. Sedimentary basins are represented by darker coloured areas.

Following further analysis of material from Wai Lek pit, Ducrocq *et al.* (1993) assigned an isolated, lower right molar (p3 or p4) to an indeterminate genus and species of the megachiropteran family Pteropodidae (Old World fruit bats). This is the earliest megachiropteran tooth known, predating *Archaeopteropus transiens* Meschinelli, 1903 from the early Oligocene of Venice.

In an update of the fossil taxa reported from the Krabi Basin (see Ducrocq *et al.*, 1992a), Ducrocq *et al.*, 1995 added to the list an indeterminate family of the Order Insectivora and two different but indeterminate families of rodent.

Marivaux *et al.*, 2000 described a new species of baluchimyine rodent, *Baluchimys krabiense*, based on a left maxilla with a P4 and M1-M3 recovered from the main coal seam in Bang Mark pit. The authors refer several isolated molars recovered from a lens of microconglomerates within a lacustrine deposit about 25 m above the principal coal seam to the same species.

Oligocene (33.9–23.03 Ma) (Tables 1a-c)

In August 2001, a joint Thai-French team from the Department of Mineral Resources, Bangkok (Thailand) and l'Institut des Sciences de l'Évolution, Montpellier (France), surveyed coal mines in the Nong Ya Plong Basin (Fig. 1) in Phetchaburi Province. From one of these, the coal seam of the Cha Prong pit, the team made preliminary identifications of rodents, dermopterans, chiropterans, carnivores, artiodactyls, and perissodactyls, the same mentioned without detail by Marivaux et al. (2004). In further analysis of material recovered from Cha Prong pit, Marivaux et al. (2004) referred two mandibles and isolated teeth (lower molars and premolars) to the extinct diatomyid rodent, Fallomus ladakhensis Nanda & Sahni, 1998. It is suggested that the Nong Ya Plong locality is of Oligocene age, based on the co-occurrence at the collection site of material representing a 'typically late Oligocene rhinocerotid' and on the basis that F. ladakhensis was described originally from the Oligo-Miocene Kargil Formation in Ladakh, India (Marivaux et al., 2004).

The Nong Ya Plong Basin remains the only Oligocene site known in Thailand. The sedimentary deposits of the basin's coal mines are characterised by mudstones and sandstones interspersed with lignite seams (Marivaux *et al.*, 2004).

Miocene (23.0-5.33 Ma) (Tables 1a-c)

The known Miocene small mammalian fauna of Thailand is restricted to six sedimentary basins in the north-west of the country: Chiang Muan, Lampang, Li, Mae Moh, Phitsanulok and Pong. A seventh basin, Mae Teep, has produced mastodon tusks and molars but no small mammal material. Chiang Muan Basin is located in the district of the same name in Phayao Province in north-western Thailand. The basin is composed of 'Tertiary sandstone, claystone, carbonaceous claystone, and coal' (Thasod *et al.*, 2007).

Taxon	late Eocene 37.8-33.9 Ma	late Oligocene 28.1-23.0 Ma			mid	dle Miocene 15.97-11	.63 Ma		
	KRABI BASIN	NONG YA PLONG BASIN	CHIANG MUAN BASIN	LAMPANG BASIN	LI BASIN	MAE MOH BASIN	PHITSANULOK BASIN	PONG B	ASIN
		Cha Prong pit		Had Pu Dai	Mae Long		Nong Hen I (A) well	Huai Siew quarry	Ban San Klang
CHIROPTERA			1	Indet. 24					
Pteropodidae	Gen. et sp. indet. 25, 27			11001.24					
Microchiroptera sp. indet.	Cont of op. mode. 20, 21								
"Rhinolophoidea"					indet. 50				
Rhinolophidae					indet. 50				
ttminolophus yongyuthi					50				
Hipposideridae					Indet. 24				
ttpposideros felix					50				
††Hipposideros khengkao					50				
Megadermatidae									
Megaderma sp.					50				
Emballonuridae			<u> </u>				Indet. 24. 43		
?Taphozous sp.					50				
Molossidae					Indet, 24				
††Mormopterus nonghenensis							24, 43		
††Rhizomops (Tadarida) mengraii					50				
"Vespertilionidea"					indet. 50		Indet. 43		
Vespertilionidae					Indet. 24		Indet. 24, 43		
†la lanna					50				
SCANDENTIA									
Tupaiidae					Indet. 24				
††Tupaia miocenica					50				
DERMOPTERA									
Cynocephalidae (Galeopithecidae)									
†Dermotherium major	22,23,25								

Table 1a. Fossil Chiroptera, Scandentia and Dermoptera from late Eocene to middle Miocene sites in Thailand. $\dagger =$ genus (and species) extinct, $\dagger \dagger =$ species extinct.

Taxon	late Eocene 37.8-33.9 Ma	late Oligocene 28.1-23.0 Ma			middle	Miocene 15.97-11.63	Ма		
	KRABI BASIN	NONG YA PLONG BASIN	CHIANG MUAN BASIN	LAMPANG BASIN	LI BASIN	MAE MOH BASIN	PHITSANULOK BASIN	PONG BA	
		Cha Prong pit		Had Pu Dai	Mae Long		Nong Hen I (A) well	Huai Siew quarry	Ban San Klang
EULIPOTYPHLA	Family indet. 25								
Erinaceidae				Indet. 24	Indet. 24				Indet. 24
tcf. Galerix					24				
††Hylomys engesseri					50				
cf. Hylomys					24				
tcf. Mioechinus					50				
++Neotetracus butleri					50				
†Thaiagymnura equilateralis					50				
Talpidae									
ttScapanulus lampounensis					50				
†XX cf. Desmanuella "minuscule"					24				
"Talpini"					24				
RODENTIA	Family x 2 indet. 25						Indet. 24, 43	Indet, 24	
Baluchimyidae									
†Baluchimys krabiense	44								
Scuiridae				Indet. 24					Indet. 24
?Atlantoxerus sp.					24,31,49,50				
Ratufa maelongensis					24, 50, 51				
Gliridae				Indet. 24					
Platacanthomyidae									
†Neocometes orientalis					24, 50, 51				
+Neocometes cf. orientalis						14			
Castoridae									
+Steneofiber siamensis .			65			65			
Rhizomyidae									
†Prokanisamys benjavuni					24,31, 49, 50	14			
Cricetidae									
†Democricetodon kaonou					50				
†Democricetodon sp.					24, 51				
†Potwarmus thailandicus					24, 31,40,49, 50				
†Potwarmus sp.				24					
†Spanocricetodon janvieri					50				
†Spanocricetodon khani					24,31,49				
†Spanocricetodon sp.					24,31,49				

Table 1b. Fossil Eulipotyphla and Rodentia (Baluchimyidae, Sciuridae, Gliridae, Platacanthomyidae, Castroidae, Rhizomyoidae and Cricetidae) from late Eocene to middle Miocene sites in Thailand.

 \dagger = genus (and species) extinct, \dagger = soecies extincs, XX = invalid species.

Taxon	late Eocene late Oligocene 37.8-33.9 Ma 28.1-23.0 Ma								
	KRABI BASIN	NONG YA PLONG BASIN	PLONG BASIN CHUANG MUAN BASIN LAMPA		LI BASIN	MAE MOH BASIN	PHITSANULOK BASIN	PONG BASIN	
		Cha Prong pit		Had Pu Dai	Mae Long		Nong Hen I (A) well	Huai Siew quarry	Ban San Klang
		1	1						1
RODENTIA	Family x 2 indet. 25						Indet. 24, 43	Indet. 24	
Ctenodactylidae	Indet. 22								
"Ctenodactyloidea"	Indet. 25								
†(F)Diatomyidae									
†Diatomys liensis					24,31,49,50				
†Diatomys sp.				24	40				24, 59
†Fallomus ladakhensis		46							

Table 1c. Fossil Rodentia (Ctenodactylidae and Diatomyidae) from late Eocene to middle Miocene sites in Thailand. $\dagger(F) = family extinct, \dagger = genus (and species)extinct, \dagger \dagger = species extinct.$

Taxon	late Pliocene to early Pleistocene 3.6-0.78 Ma		early Pleistocene		early to late middle Pleistocene		early mid	early to die Pleistocene 75-500 Ka	middle Pleistocene	middle to early late Pleistocene	
	KHAO ANGHIN	KHAO SAMNGAM	KHAO KHLONGWAN	SARABURI	KHAO PANAM	KHAO RUPCHANG 1	BAN NASAN	KANCHANABURI 2	CAVE of the MONK	KHAO CHONGKRACHOK	KHAO SINGTO
CHIROPTERA			1	1							
Pteropodidae											
Cynopterus sp.				11			11	11		11	
Rhinolophidae											
Rhinolophus sp.										11	
Hipposideridae											
Hipposideros sp.				11							
Molossidae				indet. 11							

Table 1d. Fossil Chiroptera from late Pliocene to middle /early late Pleistocene sites in Thailand.

Taxon	early F	late Pliocene to early Pleistocene 3.6-0.78 Ma		early Pleistocene		early to late middle Pleistocene		late early to early middle Pleistocene c. 875-500 Ka		middle to early latePleistocene	
	KHAO ANGHIN	KHAO SAMNGAM	KHAO KHLONGWAN	SARABURI	KHAO PANAM	KHAO RUPCHANG 1	BAN NASAN	KANCHANABURI 2	CAVE of the MONK	KHAO CHONGKRACHOK	KHAO SINGTO
EULIPOTYPHLA						I				1	
Soricidae											
Crocidura sp. 1							11				
RODENTIA											
Scuiridae									indet. 62		
Belomys pearsonii					6,10			6,10, 11			
Callosciurus cf. finlaysoni	6							6		6	
Callosciurus sp.								11			
Hylopetes phayrei		6			6		6	6,11			
Hylopetes spadiceus		6			6	6	6	6,11			
Menetes berdmorei		6						6			
Menetes sp.								11			
Petaurista petaurista		6									
Rhinosciurus laticaudatus		6									

Table 1e. Fossil Eulipotyphla and Rodentia (Sciuridae) from late Pliocene to middle/early late Pleistocene sites in Thailand.

Taxon	late Pliocene to early Pleistocene 3.6-0.78 Ma		early Pleistocene			y to late Pleistocene	early mide	early to die Pleistocene 75-500 Ka	middle Pleistocene	middle to early late Pleistocene	
	KHAO ANGHIN	KHAO SAMNGAM	KHAO KHLONGWAN	SARABURI	KHAO PANAM	KHAO RUPCHANG 1	BAN NASAN	KANCHANABURI 2	CAVE of the MONK	KHAO CHONGKRACHOK	KHAO SINGTO
RODENTIA											
Muridae									indet. 62		
Bandicota savilei								6			
Bandicota sp.								11			
Chiropodomys gliroides		6			6	6	6,11			6	6,11
Hadromys humei					6,9	6,8,9	6,9	6,9			
††Hapalomys khaorupchangi						6					
Hapalomys sp.		6									
††Leopoldamys minutus	6	6									
Leopoldamys sabanus					6			6			
Leopoldamys (sp.)		8						11			
Maxomys surifer		6,8	6			6,8	6				
Mus caroli		6									
Mus cervicolor					6			6			6
Mus cookii		6			6	6	6			6	
Mus shortridgei		6	6		6	6	6	6			
Mus sp.			11				11	11		11	11
Niviventer fulvescens						6,8	6	6			6
Niviventer (sp.)		8	11	11		8	11	11			
Pithecheir parvus							6				
††Pithecheir peninsularis						6					
†Prohadromys varavudhi		6									
†Rachaburimys ruchae	6	6,13	6,13	13							
††Rattus jaegeri	6	6									
Rattus rattus						6,8					
Rattus sikkimensis (= andamanensis)					6	6,8	6	6			
Rattus sp.								6			
Rattus sp. 1								11		11	
Rattus sp. 2			11	11			11	11			
†Saidomys siamensis		6	6								
Vandeleuria oleracea		6			6	6	6,11	11			
Hystricidae						l Č					
Atherurus cf. macrourus									62		
Hystrix cf. brachyura									62		
Hystrix sp.					6.65						

Table 1f. Fossil Rodentia (Muridae and Hystricidae) from late Pliocene to middle / early late Pleistocene sites in Thailand. $\dagger =$ genus (and species) extinct, $\dagger \dagger =$ species extinct.

Taxon		late middle Pleistocene c. 500-130 Ka									late Pleistocene	Holocene 11.7-0 Ka
	KHAO NAPHUNG	KHAO NOH	KHAO RUPCHANG 2	KHAO TAKLA	KHAO TINPET	KHAO TOI 1	KHAO TOI 2	PHA BONG CAVE	SNAKE CAVE	CRYSTAL CAVE	KHAO KAO CAVE	KANCHANABURI 1
CHIROPTERA												
Pteropodidae												
Cynopterus sp.		11				11						
Eonycteris spelaea											•	
Pteropus sp.									7,60			
Rousettus amplexicaudatus											•	
Microchiroptera sp. indet.									60			
"Rhinolophoidea"											•	
Rhinolophidae												
Rhinolophus sp.		11					11					
Hipposideridae												
Hipposideros diadema												
Hipposideros larvatus											•	
Hipposideros pomona												
Hipposideros sp.					11							
Emballonuridae												
Taphozous sp.											•	
?Taphozous sp.											•	
Vespertilionidae												
††Eptesicus chutamasae n. sp.											•	
SCANDENTIA												
Tupaiidae												
Tupaia sp.											•	

Table 1g. Fossil Chiroptera and Scandentia from late middle Pleistocene to Holocene sites in Thailand. $\dagger \dagger =$ species extinct, $\bullet =$ this paper.

Taxon		_	late middle to late Pleistocene	late Pleistocene	Holocene 11.7-0 Ka							
	KHAO NAPHUNG	KHAO NOH	KHAO RUPCHANG 2	KHAO TAKLA	KHAO TINPET	KHAO TOI 1	KHAO TOI 2	PHA BONG CAVE	SNAKE CAVE	CRYSTAL CAVE	KHAO KAO CAVE	KANCHANABURI 1
EULIPOTYPHLA		1				1	<u>г г</u>					1
Erinaceidae												
Hylomys suillus						-			7.60		•	
Soricidae									7,00		•	
Crocidura attenuata		-				-					•	
Crocidura allenuala Crocidura fuliginosa							<u> </u>		7.60			
Crocidura hilliana									7,60			
Crocidura indichinensis							I				<u>.</u>	-
Crocidura indocrimensis Crocidura vorax											•	
							-				•	
Crocidura sp.						11					•	
Crocidura sp. 1							8.2					
Crocidura sp. 2						11	11					
Suncus etruscus												
RODENTIA												-
Scuiridae												
Belomys pearsonii				6,10			6,10		6,10			
††Belomys thamkaewi										10		
Callosciurus finlaysoni									7,60	10		
Callosciurus cf. finlaysoni									6			
Exilisciurus exilis						11						
Hylopetes phayrei				6		6,11			6	10		6,11
Hylopetes spadiceus	6			6		6,11			6,7,60	10		6,11
lomys horsfieldii						6,11	6,11					
Menetes berdmorei				6		6			6,7,60	10		
Nannosciurus melanotis						6						
Petaurista petaurista						11			6,7,60	10		
Petinomys setosus		6				6						
Petinomys vordermanni						11						
Tamiops cf. macciellandi						6						
Tamiops sp.						11						
Spalacidae												
Cannomys badius									7.60			

Table 1h. Fossil Eulipotyphla and Rodentia (Sciuridae and Spalacidae) from late middle Pleistocene to Holocene sites in Thailand. \dagger ⁺ = species extinct, • = this paper.

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Taxon					ddle Pleistocen 500-130 Ka	e				late middle to late Pleistocene	late Pleistocene	Holocene 11.7-0 Ka
	KHAO NAPHUNG	KHAO NOH	KHAO RUPCHANG	KHAO TAKLA	KHAO TINPET	KHAO TOI 1	KHAO TOI 2	PHA BONG CAVE	SNAKE CAVE	CRYSTAL CAVE	KHAO KAO CAVE	KANCHANABURI 1
	101110110						1	0/102			0/112	
RODENTIA												
Muridae												
Bandicota indica									6.8			
Bandicota savilei	6								7.60			
Berylmys berdmorei									6			
Chiromyscus chiropus									7,60			
Chiropodomys gliroides		6		6	91	6,11	6,11		6,7,60			6.11
tt Chiropodomys maximus					6							
Hadromys humei	6,9	6,9	9						6.8.9	9		
Hapalomys delacouri									6,7,30, 60			
Hapalomys longicaudatus				6	6.11	6.11			7.30			
Leopoldamys sabanus					6	6			6,7,8,60	10		6
Leopoldamys (sp.)					11	11			10.101.00			- 11
Maxomys (= Niviventer) cf. niviventer									7,30,60			
Maxomys surifer	6					6			6,7,8,60			
Mus caroli									7.60			
Mus cervicolar	6	6							6,7,60			6
Mus cookii	6								6,7,60			6
Mus pahari						6			6,7,60			
Mus pahari gairdneri						1			8			
Mus shortridgei	6	6		6					6,7,60	10		
Mus sp.		11		-	-11	-11				1.4		- 11
Mus sp. 1 & II									7,30, 60			
Niviventer bukit (= fulvescens)									7,60			
Niviventer confucianus									7,60			
Niviventer fulvescens						6			6,8			
Niviventer gracilis									6			
Niviventer (sp.)						11						
Pithecheir parvus						6						
Rattus argentiventer									7,60			
Rattus koratensis (= andamanensis)									7.60			
Rattus rattus				6		6			6,7,8,60			
Rattus sikkimensis (= andamanensis)		6		6		6			6.8	10		
Rattus sp.				-		-			7,30,60			
Rattus sp. 1						-11	11					
Rattus sp. 2		11			- 11	11			1			-18
Vandeleuria oleracea	6					1			6,7,60			
Hystricidae	ľ								.0,1,00			
Atherurus cf. macrourus												
Hystrix hodgsoni subcristatus (= brachyura)									7,30,60			
Hystrix cf. brachyura						1			1,00,00			1
Hystrix sp.						1		66	66			1

Table 1i. Fossil Rodentia (Muridae and Hystricidae) from late middle Pleistocene to Holocene sites in Thailand.†† = species extinct.

Fossil material has been recovered within the basin from the upper seam in Chiang Muan open-pit coal mine, the latter being 300 m in width and in excess of 1 km in length (Thasod *et al.*, 2007). The age of the coal seam was considered to be 13.5-10 Ma based on palaeomagnetic analysis and the examination of mammalian remains (Thasod *et al.*, 2007) whilst later magnetostratigraphic analysis indicated an age of 12.4-12.2 Ma for the upper seam (Suraprasit *et al.*, 2011).

Lampang Basin is one of the largest Tertiary basins in northern Thailand (Ducrocq *et al.*, 1995). The age of the basin's fossil mammal-bearing sites near the village of Had Pu Dai (known also as Nah Nai Yod) is regarded as being approximately 16-14 Ma (middle Miocene) (Ducrocq *et al.*, 1995).

Li Basin has been regarded as late Eocene based on fossil plant remains (Endo, 1963), Oligocene based on palynological evidence (Ratanasthien, 1984) and subsequently as late early Miocene (19-18 Ma) (Mein & Ginsburg, 1985) and middle Miocene (16-11 Ma) (Jacobs *et al.*, 1989). Ducrocq *et al.* (1995) considered that the mammalian fauna of Li Basin is 'younger than 17 Ma and therefore ... middle Miocene'. Mein & Ginsburg (1997) suggested that the age of Mae Long, the sole locality within Li Basin from which small mammals fossils have been recovered, is 18.5-17.8 Ma, which would place the locality in the late early Miocene. Based on a comparison of the fossil small mammal fauna recovered from Mae Moh Basin and that of Li, however, Chaimanee *et al.* (2007) considered the age of Li Basin to be the same as the two main fossil-bearing lignite

seams in the Mae Moh Basin, namely 13.3-13.12 Ma (late middle Miocene). Fossil remains of large mammals (one suid, an indeterminate form of anthracothere, one rhinocerotid and one stegodontid) have been found in a lignite seam at Ban Na Sai in Li Basin but no fossil small mammal fauna is known from the locality (Ducrocq *et al.*, 1994).

Mae Moh Basin contains the largest coal mine in Thailand with fossil mammals and other vertebrate and invertebrate taxa having been recovered from several lignite seams in the mine. The basin is 16 km long and 6.5 km wide and is bounded by Triassic marine deposits (Ducrocq *et al.*, 1995). The age of Mae Moh's principal lignite seams, as mentioned above, is 13.3-13.12 Ma (Chaimanee *et al.*, 2007).

Phitsanulok Basin is a deep and expansive syncline containing alluvial and lacustrine sediments. Fossil mammal remains have been found in light grey, sideritic clay between 887 and 894 m below ground level in a well-core drilled by the Thai Shell Exploration and Production Company Ltd through the crest of a ridge separating the main part of the basin from the Phrom Phiram sub-basin. The clay matrix was considered part of a rare (late early to middle) Miocene karstfill in fractured Permian limestone (Legendre *et al.*, 1988).

Pong Basin contains two fossil-bearing localities, Huai Siew quarry and Ban San Klang, that have yielded small mammal remains. The sedimentary deposits at Huai Siew comprise a red, sandy marl interspersed with consolidated sands (Ginsburg, 1989) but the locality has produced little

in the way of small mammal fossil material. Ducrocq *et al.* (1995) considered Huai Siew to be early middle Miocene Min age. The Ban Sang Klang locality occurs in 'an outcrop of beige silts and clays of fluvial origin' (Ducrocq *et al.*, the 1994) and is seemingly younger than Huai Siew, the fossiliferous deposits of which are probably overlain directly by those of the Ban Sang Klang Formation (Ducrocq *et al.*, provide the Ban Sang Klang Formation (Ducrocq *et al.*, provid

1995). All mammalian fossil material has been recovered from an outcrop of pedogenetic clays containing numerous crab remains (Ducrocq *et al.*, 1995). The basins, which were created by the movement of the

Red River fault and the Wang Chao fault during the collision of the Indian and Asian tectonic plates (Nagaoka & Suganuma, 2002), occur in the northernmost section of the Indo-Malay arc, which describes a course from Chiang Mai in north-western Thailand through Peninsular Malaysia to the Indonesian Archipelago (Ginsburg *et al.*, 1988). The basins of northern Thailand overlie pre-Cretaceous areas and are continental whereas the basins found in peninsular Thailand are marine, lacustrine, or fluvial in origin.

In 1980, a Franco-Thai palaeontological expedition, directed by Rucha Ingavat of the Department of Mineral Resources in Bangkok, undertook research on vertebrate fossils spanning the periods from the Carboniferous to the Quaternary in the basins of Mae Moh, Li and Pong in northern Thailand. In the course of this expedition, the first Miocene small mammalian fossils from Thailand were collected by Jean-Michel Mazin of Le Centre National de la Recherche Scientifique in Paris and Benjavun Ratanasthien from Chiang Mai University. The material, which was intermixed with organic matter and the remains of 'freshwater molluscs ... fish vertebrae and teeth, turtle plates, snake vertebrae' and avian bones (Jaeger et al. ,1985), was gathered from clay deposits at Mae Long, one of four sub-basins of the Li Basin and the main basin's only vertebrate-bearing locality. Part of the fossil material was described by Jaeger et al. (1985), who assigned a single molar (a right M3) to the extinct rodent genus, Diatomys, and a left m1, a left M1, a right M2, a left m3 and a left M3 to a new extinct species of primitive murine, Antemus thailandicus Jaeger, Tong, Buffetaut, & Ingavat, 1985, the species being moved subsequently to the extinct cricetid rodent genus, Potwarmus Lindsey, 1988 (see Musser & Carleton, 2005: 1251).

During the course of October, 1983, in excess of 100 mammalian jaws and teeth representing early to middle Miocene terrestrial mammals were extracted from the Nong Hen I(A) well-core drilled by the Thai Shell Exploration and Production Company Ltd in Phitsanulok Basin in northern Thailand. The fossil material was termed the 'Nong Hen Local Fauna'. Much of the recovered remains was considered to represent a new, extinct species of molossid bat, *Mormopterus nonghenensis* Legendre, Rich, S., Rich, T., Knox, Punyaprasiddhi, Trumpy, Wahlert, & Napawongse Newman, 1988, a genus first known from the Oligocene of Brazil. Material representing the taxon included maxillary fragments, an upper incisor, upper and lower canines, lower second premolars, upper and lower

fourth premolars, and upper and lower molars (M1, M2, M3, m1-2, and m3) (Legendre *et al.*, 1988). The material recovered from the well-core is considered to differ from the European Miocene forms of the genus *Mormopterus* on the basis of a more reduced hypocone on the first and second molars (M1 and M2), myotodont lower molars, the presence of a linguodistal groove on the upper incisor, and a rudimentary metaconid on the fourth premolar (p4).

Having examined other fossil specimens from the wellcore, Legendre *et al.* (1988) adjudged a single molar (m1 or m2) to represent an indeterminate form of the bat superfamily 'Vespertilionoidea' (corrected to 'Vespertilionidae indet.' in a list of taxa from the Miocene basins of northern Thailand produced by Ducrocq *et al.* (1994), a single incomplete molar (M1 or M2) to belong to an indeterminate species and genus of the family Emballonuridae (Sheathtailed bats), a sole gliriform incisor to represent an indeterminate form of rodent, and two enamel fragments from a bunodont molar to belong to an unidentified, larger mammal.

In 1984, Pierre Mein of the Université de Lyon and Léonard Ginsburg of the Muséum National d'Histoire Naturelle in Paris undertook fieldwork also at Mae Long in the Li Basin, during which they washed and sieved almost two tons of sediment. In addition to confirming the presence of Antemus thailandicus based on the recovery of some 300 teeth, Mein & Ginsburg (1985) referred a single damaged right premolar tentatively to the extant sciurid rodent genus Atlantoxerus (?Atlantoxerus sp.) and recorded the extinct cricetid rodent, Spanocricetodon khani de Bruijn, Hussain, & Leinders, 1981, based on two upper molars, and possibly a smaller cricetid (?Spanocricetodon sp.) based on a fragment of a molar (M1-2). The authors name a new extinct rhizomyid rodent, Kanisamys benjavuni. Mein & Ginsburg stress the affinities to Prokanisamys, into which genus subsequent authorities, such as Ducrocq et al. (1994), consider the species to fall) based on 23 teeth, and a new extinct pedetid rodent, Diatomys liensis, based on eight teeth (Mein & Ginsburg, 1997 removed Diatomys from the family Ctenodactyloidea on the basis that the genus shows no saltatorial adaptation and placed it in a new family, the Diatomyidae). Material representing Potwarmus thailandicus (Jaeger, Tong, Buffetaut, & Ingavat, 1985), Spanocricetodon khani de Bruijn, Hussain & Leinders, 1981, Prokanisamys benjavuni (Mein & Ginsburg, 1985), ?Atlantoxerus sp., Forsyth Major, 1893 and Diatomys liensis Mein & Ginsburg, 1985 had been gathered previously from Li Basin by the 1980 Thai/French study mentioned above but details of the collection, which was examined by L. Ginsburg, were not published until 1988 (Ginsburg et al., 1988).

In 1989, a right m1, a left m2, a right M1, and a left M2 recovered from the clays of Mae Long Reservoir in the Li Basin gave rise to the description of a new species of an extinct platacanthomyid rodent, *Neocometes orientalis* Mein *et al.*, 1990. A single left M1-2 extracted also from the Reservoir enabled the same authors to describe *Ratufa maelongensis* as a new extinct species of an extant genus

of sciurid rodent. Mein *et al.* (1990) state that this is the first record of a fossil *Ratufa*. An m1 and M2 recovered from the same site are referred by Mein *et al.* (1990) to the extinct cricetid rodent genus, *Democricetodon*.

Suteethorn *et al.* (1990) offered the first description of the middle Miocene locality of Ban San Klang in the Pong Basin, in which hominoid primate remains were discovered by the first author. Rodent teeth (molars and premolars [Ducrocq *et al.*, 1994]) were also recovered and these were assigned to the extinct rodent genus *Diatomys*.

A list of taxa recorded from the Miocene basins of northern Thailand is presented in Ducrocq et al. (1994) and this, excepting the taxa hereinbeforementioned, includes an indeterminate form of Tree shrew (Tupaiidae) from Mae Long; indeterminate forms of erinaceid mammal (Erinaceidae) from Mae Long, Ban San Klang and Had Pu Dai in the Lampang Basin with further material possibly representing the extinct erinaceid genus Galerix and the extant genus Hylomys from Mae Long; material that compares favourably with a talpid soricomorph, Desmanella 'minuscule' (see Note below) from Mae Long, and an unidentified mole of the tribe Talpini also from Mae Long. Bats (Chiroptera) are represented by material from the extant families Hipposideridae (Leaf-nosed bats) from Mae Long (Hipposideridae indet.), Vespertilionidae (Evening bats) from Mae Long (Vespertilionidae indet.) and Molossidae (Free-tailed bats) from Mae Long (Molossidae indet.). Material representing an indeterminate family of Chiroptera was found at Had Pu Dai. The presence of indeterminate forms of rodent has been determined from teeth marks found on a bone at Huai Siew quarry in the Pong Basin. Indeterminate scuirid rodent material has been identified at Ban San Klang and Had Pu Dai while fossil dormouse material of the family Gliridae has been recorded at Had Pu Dai. The family Cricetidae is represented at Had Pu Dai by unspecified material from the extinct genus Potwarmus (as Potwarmus sp.), while material representing the extinct genus of hystricomorphous sciurognathous rodent Diatomys has been identified at Had Pu Dai (as Diatomys sp.).

Note – The author of the specific form '*minuscule*' cannot be determined, which would indicate that it is an invalid taxon. It would seem that this French adjective is being used simply to mean a 'very small' *Desmanella*'. B. Engesser, pers. comm.).

In the years following the fieldwork undertaken in the Li Basin in 1984 by Pierre Mein and Léonard Ginsburg, Ginsburg returned to Li's Mae Long locality alone and, during the course of five expeditions, sampled some sixteen tons of clay from the site. The findings were the subject of a number of papers: Mein & Ginsburg (1985) (Rodentia); Ginsburg & Mein (1987) (Tarsiidae); Ginsburg (1988) (primates); Mein *et al.* (1990) (Rodentia); Ginsburg *et al.* (1991) (Mammalia). The combined results of the authors' excavations at Mae Long are set out in Mein & Ginsburg (1997), in which the authors enumerate 23 small mammal taxa including five new species of bat, one new species of tree shrew, four new species and one new genus of insectivore, and two new rodent species. Mein & Ginsburg (1997) detailed nine bat taxa present at Mae Long. The authors referred to eleven teeth comprising three canines, four premolars, and four molars to a new, extinct species of Rhinolophus (Rhinolophus yongyuthi), an m1 and m2, with dental morphology similar to the extinct genus Brachipposideros Sigé, 1968, to the superfamily Rhinolophoidea (Rhinolophoidea indet.), a right M3 and a left m1 to a new, extinct species of Hipposideros (Hipposideros felix), 26 teeth comprising six canines, four premolars, and 16 molars to a further new, extinct species of Hipposideros (Hipposideros [Brachipposideros] khengkao), a well-preserved p2 to the genus Megaderma Geoffroy, 1810b (as Megaderma sp.), a fragment of an m2 to the genus Taphozous Geoffroy, 1818 (as ?Taphozous sp.), a canine, an upper and lower fourth premolar, an upper and lower first molar, two upper second molars, an upper third molar, and an incomplete lower molar to a new, extinct species of Rhizomops (Rhizomops mengraii), which is treated as a synonym of *Tadarida* Rafinesque, 1814 by Simmons (2005), a P4, a left and a right M2 and a M3 to a new, extinct species of Ia (Ia lanna) and one complete and one incomplete lower molar to the superfamily Vespertilionoidea (Vespertilionoidea indet.).

A single left M2 gave rise to a new, extinct species of Tree shrew (Tupaia miocenica), which remains the only Miocene representative of the genus (Mein & Ginsburg, 1997). Five insectivore taxa from Mae Long are discussed by Mein & Ginsburg (1997), who attribute 44 complete and partial teeth to a new, extinct species of Hylomys (Hylomys engesseri), a P3, a lower canine, and a lower first molar to an indeterminate genus of Erinaceidae that may, on the basis of a similarity in the dental morphology of the P3, represent the extinct genus Mioechinus Butler, 1948, an M1, two M2's, and an m3 to a new, extinct species of the extant genus Neotetracus (Neotetracus butleri), two M1's, an M2 and an M3, and an m2 to a new, extinct, erinaceid genus (Thaiagymnura), the type species of which they name as T. equilateralis, and a P4, an M2, an m1 and an m2 to a new, extinct species of the extant talpid insectivore genus, Scapanulus (Scapanulus lampounensis).

Mein & Ginsburg (1997) identified material representing eight rodent taxa from Mae Long, six of which had been described previously from the locality (?*Atlantoxerus* sp. Forsyth Major, 1893, see Mein *et al.*, 1990, *Ratufa maelongensis* Mein, Ginsburg, & Ratanasthien, 1990, *Diatomys liensis* Mein & Ginsburg, 1985, *Prokanisamys benjavuni* Mein & Ginsburg, 1985, *Potwarmus thailandicus* (Jaeger, Tong, Buffetaut, & Ingavat, 1985) and *Neocometes orientalis* Mein, Ginsburg, & Ratanasthien, 1990), but two of which the authors describe for the first time. A single m1 gave rise to a new species of the extinct genus *Democricetodon* (*Democricetodon kaonou*) while four upper second molars and fragments of an M3, an m1-2 and an m3 are placed in a new species of the extinct genus, *Spanocricetodon* (*Spanocricetodon janvieri*).

As a result of fieldwork undertaken at the Mae Moh coal

mine by Yaowalak Chaimanee and colleagues from the Bureau of Geological Survey, Bangkok, l'Université Montpellier II, and l'Université de Poitiers, Chaimanee et al. (2007) recorded the presence in two of the mine's lignite seams of the first small mammal remains from the Mae Moh Basin. The authors attribute two lower first molars, a single upper first molar, two lower second molars, an upper second molar, an upper third molar and a lower jaw fragment supporting the posterior section of the first molar and a complete second molar to the extinct glirid rodent genus, Neocometes and tentatively to the specific form N. orientalis Mein, Ginsburg, & Ratanasthien, 1990. A single molar (M1) was referred to the extinct rhizomyid rodent Prokanisamys benjavuni (Mein & Ginsburg, 1985). Both Neocometes cf. orientalis and Prokanisamys benjavuni had been reported previously from Mae Long in the Li Basin (Mein et al., 1990; Mein & Ginsburg, 1997).

After fieldwork conducted at Mae Moh Basin and Chiang Muan coal mine, Suraprasit *et al.* (2011) name a new extinct species of beaver *Steneofiber siamensis*, based on a left maxilla with P4 and M1, a right mandible with p4-m2 and a few incisor fragments from Mae Moh and '15 isolated cheekteeth' (including P4, M1, M2, M3, P4, p4, m1, m2, and m3) from Chiang Muan. The records are the first for the family Castoridae from South-East Asia and represent the southernmost known limit of castorid rodents (Suraprasit *et al.*, 2011).

Late Pliocene to early Pleistocene (3.6–0.78 Ma) (Tables 1d-f)

Fossil rodent remains have been recovered from Khao Anghin and Khao Samngam, two Permian limestone hills lying in eastern Ratchaburi Province, some 30 km inland from the north-western corner of the Bight of Bangkok. Fossils were collected in fissure fillings from sediments of red calcareous clay by Yaowalak Chaimanee and colleagues from the Thai-French Vertebrate Paleontology Project.

The geological age of Khao Samngam is estimated, on the age of its fauna, to be 3.5-2.5 Ma (late Pliocene to very early Pleistocene) (Chaimanee & Jaeger, 2000a). As it is considered that Khao Anghin may be of a similar age to Khao Samngam (Chaimanee, 1998: 35), Khao Anghin is treated here also as a late Pliocene to early Pleistocene site. Two further fissure fillings, Khao Khlongwan in Prachaup Khiri Khan Province and Saraburi in the province of the same name, may be late Pliocene or early Pleistocene in age (Chaimanee, 1998). As the numerical age of the boundary between the Pliocene and the Pleistocene epochs has been changed from 1.8 Ma to 2.59 Ma (Gradstein & Ogg, 1996; Gradstein et al., 2012) - it was 1.8 Ma at the date of Chaimanee's 1998 paper - and because it appears that no exact dating of the deposits has been carried out, Khao Khlongwan and Saraburi are discussed under the following section headed 'Pleistocene' together with other fissure fillings of that epoch.

There are no apparent fossil small mammal records from

the early or middle Pliocene of Thailand.

Chaimanee *et al.* (1996) described a new genus and species of extinct stephanodont murid rodent from Khao Samngam, which they name *Rachaburimys ruchae*. The diagnosis was based on 14 first molars (M1), 11 second molars (M2), 17 third molars (M3), 17 first lower molars, 29 lower second molars, and a single lower third molar. Further molars of the species recovered from both Khao Samngam and Khao Anghin are discussed by Chaimanee (1998).

Chaimanee (1998) described three new extinct species and one new extinct genus and extinct type species of murid rodent based on material gathered at Khao Samngam and Khao Anghin. The presence at both localities of the extinct species Leopoldamys minutus is affirmed from 316 upper and lower molars recovered from Khao Samngam and seven upper and lower molars from Khao Anghin. The extinct genus and species Prohadromys varavudhi was named from a fragment of a right upper maxilla containing an M1 together with two lower first molars and an isolated upper first molar from Khao Samngam. The extinct genus and species Saidomys siamensis is named from an upper first molar, two upper second molars, two upper third molars, three lower first molars and two lower second molars recovered also from Khao Samngam while 211 upper and lower molars from Khao Samngam and one upper first molar from Khao Anghin gave rise to a new extinct species, Rattus jaegeri.

Further material analysed from Khao Samngam enabled Chaimanee (1998) to report from that locality the following extant taxa: the sciurid rodents Hylopetes phayrei (Blyth, 1859) (based on one m1 and one m2), Hylopetes spadiceus (Blyth, 1847) (two first upper molars and single examples of M2, M3, m1, and m2), Menetes berdmorei (Blyth, 1849) (five fourth upper molars, 11 first upper molars, nine second upper molars, four third upper molars, 15 first lower molars, a single second lower molar and four third lower molars), Petaurista petaurista (Pallas, 1766) (one M2 and one m1), Rhinosciurus laticaudatus (Müller, 1840) (a single p4); and the murid rodents, Chiropodomys gliroides (Blyth, 1856b) (17 first upper molars, ten second upper molars, ten lower first molars, seven lower second molars, and one lower third molar), Hapalomys sp. (one M3 and one m3), Maxomys surifer (Miller, 1900) (two first upper molars), Mus caroli Bonhote, 1902 (67 first upper molars, 20 second upper molars, three third upper molars, 63 lower first molars, and 36 lower second molars), Mus cookii Ryley, 1914 (three first lower molars and one second lower molar), Mus shortridgei (Thomas, 1914) (one M1, one M2, and one m2) and Vandeleuria oleracea (Bennett, 1832) (four first upper molars, two second upper molars, and nine first lower molars). From Khao Anghin, Chaimanee (1998) recorded the sciurid rodent Callosciurus cf. finlaysonii (Horsfield, 1823) based on two fourth upper premolars, four first upper molars, one deciduous premolar, a single fourth lower premolar, four first lower molars, three second lower molars and four third lower molars.

Chaimanee & Jaeger (2000a) referred to 'the presence of ... *Niviventer* ... at Khao Samngam ...', but added at a later point in the same publication that '*Niviventer* makes it[s] first appearance in the Thai fossil record [at Khao Rupchang]', the latter an early middle Pleistocene site.

Pleistocene (2.59-0.0117 Ma) (Tables 1d-i)

Including Khao Kao Cave, there are twenty Pleistocene sites in Thailand from which fossil small mammal remains have been recovered. They are mainly fissure fillings in Permian limestone but material has been collected additionally from cave sites, quarries, and mines. Details of the sites, which appear in alphabetical order below andin geochronological order in Tables 1a-i, are as follows.

Ban Nasan – This is a narrow fissure filling in a large cave located within a Permian limestone hill. Fossil material was recovered from red calcareous sediments. The locality lies just south of Ban Nasan District in Surat Thani Province, central peninsular Thailand. The age of the deposit is considered to be late early to early middle Pleistocene, approximately 0.5–0.875 Ma. (Chaimanee, 1998: 235).

Cave of the Monk – The cave is located within a Permian limestone karst formation near the village of Ban Fa Suai in Chiang Dao Wildlife Sanctuary, northern Thailand. Fossil rodent material was recovered in clay deposits within two pits dug approximately 100 m from the entrance. The cave, which has an elevation of 900 m, is characterised by a network of chambers, galleries, and corridors extending over 1 km.Examination of faunal remains would suggest that the deposit is of middle Pleistocene age (Zeitoun *et al.*, 2005: 257).

Crystal Cave – Fossilised remains of small mammals have been collected from a fissure filling in Permian limestone within the cave, which is located in Kanchanaburi Province in western Thailand. The locality has an estimated age of late middle to late Pleistocene based on faunal comparisons with other fossil localities in Thailand (Chaimanee & Jaeger, 2000c).

Kanchanaburi 2 – This is a fissure filling located in a Permian limestone hill in the vicinity of the village of Tung Nagarat in Kanchanaburi District, western Thailand. The sedimentary deposits from which small mammal remains have been recovered are composed of calcareous silts with iron concretions (Chaimanee, 1998). Amphibian and reptile remains are also present. The site is older than Kanchanaburi I (see the section entitled 'Holocene', below), with the deposits having an indicative age of approximately 875,000 to 500,000 years (late early to early middle Pleistocene) (Chaimanee, 1998).

Khao Chongkrachok – Small mammal remains were found in a fissure filling located in a Permian limestone hill in the coastal area of Prachaup Khiri Khan Province in peninsular Thailand. The sedimentary deposits comprise 'red calcareaous silty sands' (Chaimanee, 1998). No direct dating of the fossiliferous deposits appears to have been undertaken but recovered material contains only extant forms. All rodent taxa collected at the locality are known also from Snake Cave (see below), to which Khao Chongkrachok is likened in terms of its geochronological age (Chaimanee *et al.*, 1993).

Khao Khlongwan – A former limestone quarry occupying a coastal site in Prachaup Khiri Khan Province some 10 km south of Khao Chongkrachok. Fossilised rodent remains were recovered from red, sandy, calcareous sediments indicative of a fissure filling in a hill of Permian limestone (Chaimanee, 1998). The locality is regarded as late Pliocene to early Pleistocene with a maximum age of approximately 3 Ma and a minimum age older than 1 Ma (Chaimanee, 1998). The locality is treated here as a Pleistocene site for the reasons given in the section 'Late Pliocene to early Pleistocene', above.

Khao Naphung – A further fissure filling of red, sandy, calcareous sediments in a Permian limestone outcrop. The site is located in Krabi Province in southern peninsular Thailand and is considered to fall within an age range of approximately 500-130 Ka in the late middle Pleistocene (Chaimanee, 1998).

Khao Noh – A former limestone quarry situated about 35 km NW of the confluence of the Nam Mae Ping and the Mae Nam Nan rivers in Nakhon Sawan Province, central Thailand. Fossil-bearing sediments are consistent with a fissure filling containing fragmented limestone. Chaimanee (1998) indicates an age range of the deposit of approximately 500-130 Ka (late middle Pleistocene).

Khao Panam (= 'Forest Thorn Hill') – This is a Permian limestone outcrop (Pope *et al.*, 1978) and an old phosphate mine (Chaimanee, 1998), in which numerous small mammal remains have been recovered from calcareous, sedimentary deposits and soil pockets. Large mammals including *Hippopotamus* and *Hyaena* are known from the locality as well, but the remains of these are not found with those of the microvertebrates. The locality lies in Lampang Province in northern Thailand and is considered to be younger than 780,000 years based on palaeomagnetic analysis (Chaimanee, 1998).

Khao Rupchang 1 – Fossil small mammals were collected from calcareous clay deposits in a fissure filling near a cave entrance in Khao Rupchang, a sizeable outcrop of Ordovician limestone on the Thai-Malaysian border. Karst scenery dominates the area, which is characterised by numerous caves. The cave from which the deposits were recovered is frequented by tourist groups that enter the area principally to visit a notable Chinese temple nearby. The deposit is considered to be early middle Pleistocene by Chaimanee (1998: 42), but the wider range of early to late middle Pleistocene is inferred by Chaimanee & Jaeger (2000a: 187).

Khao Rupchang 2 – A single fossil rodent species, *Hadromys humei* (Thomas, 1886), is known from Khao Rupchang 2. The locality is a fissure filling dated as 'middle Pleistocene' based on the occurrence of *H. humei* at Snake Cave (see below), the deposits of the latter locality having been dated with accuracy (Chaimanee & Jaeger, 2000b). Khao Rupchang 2 is treated herein as late middle Pleistocene, however, as Snake Cave may be regarded as falling more precisely into that subdivision of the stage (Esposito *et al.*, 1998). It is probable that the fissure filling occurs in the same Ordovician limestone range as Khao Rupchang I but information on the locality is scant, the site being mentioned only, it would appear, by Chaimanee & Jaeger (2000b), who did not supply substantive details.

Khao Singto – Fossil rodent remains were retrieved from calcareous sandstone sediments in a fissure filling at Khao Singto, a limestone quarry located in Prachinburi Province in south-eastern Thailand, about 40 km from the Cambodian border. It seems that the locality has not been dated in any detail but analysis of its fossil fauna would indicate a probable age range of middle to early late Pleistocene (Chaimanee *et al.*, 1993).

Khao Takla – Lying half a kilometre or so from Khao Panam, Khao Takla in Lampang Province is a disused limestone quarry in which small mammal remains and a few large mammal teeth have been found in fissure filling deposits characterised by reddish limestone rocks. The age range of the locality is adjudged to be roughly 500-130 Ka (late middle Pleistocene) (Chaimanee, 1998).

Khao Tinpet – At Khao Tinpet, a former limestone quarry in Chumporn Province in central peninsular Thailand, fossilised small mammal remains were recovered from sediment collected from a fissure filling in an isolated outcrop of Permian limestone.

The deposit is considered to fall into an age range of approximately 500-130 Ka (late middle Pleistocene) (Chaimanee, 1998).

Khao Toi 1 – Several vertebrate taxa were identified from calcareous deposits taken from a fissure filling at Khao Toi, which is a former limestone quarry in Phang Nga Province in south-western peninsular Thailand. The age range of the deposits, which contained also amphibians and reptiles, is estimated to be 500-130 Ka (late middle Pleistocene) (Chaimanee, 1998).

Khao Toi 2 – A second fissure filling located within Khao Toi quarry in Phang Nga Province. The faunal composition of the filling resembles that of Khao Toi 1 although fewer taxa have been recorded as less fossiliferous matrix has been analysed. The date of the sedimentary deposits is considered to be the same as Khao Toi 1 (late middle Pleistocene) (Chaimanee, 1988).

Pha Bong Cave – The only apparent mention of this cave is in van Weers (2005), who refers to the occurrence of *Hystrix* during the Pleistocene. No information is given on the age of the Pha Bong deposit although the specimens recovered from Pha Bong 'do not differ significantly' from those found in Snake Cave (van Weers , 2005). The location of the cave, itself, is not identified but it would seem reasonable to assume that the cave is situated in the vicinity of the village of Pha Bong in Mae Hong Son Province, northwestern Thailand.

Saraburi – Fossil-bearing calcareous silts were collected from a limestone quarry in Saraburi Province in south central Thailand. The quarry is situated in an outcrop of Permian limestone with the fossiliferous deposits judged to be late Pliocene to early Pleistocene in age with an earliest date of approximately 3 Ma and a latest date of more than 1 Ma (Chaimanee, 1998). The locality is treated here as a Pleistocene site for the reasons given in the section 'Late Pliocene to early Pleistocene', above.

Snake Cave - This locality, known equally as Thum Wiman Nakin, is located within Permian marine limestone some 6 km (Chaimanee, 1998 states 'about 17 km') from Chulaphorn Dam in Khon San District, Chaiyaphum Province, north-east central Thailand (Ginsburg et al., 1982; Esposito et al., 1998). Numerous vertebrate taxa have been recovered from the cave, the fossiliferous deposits of which are rich in both large and small mammal remains. Chaimanee (1998) recorded the collection of material from three sites within the cave, which she terms the 'main layer', 'upper layer', and 'roof'. In the main layer, fossil rodent, bat, insectivore, amphibian, and reptile remains were recovered from 15 m³ of sedimentary deposit, which was excavated from a depression near the cave entrance. The upper layer comprises a seemingly unrelated sedimentary deposit occurring about 15 m from the cave entrance and at a more elevated point than the main layer. From the upper layer, the same author collected several rodent species from an unconsolidated sandy, clay matrix on top of a thick layer of calcite. The roof relates to the ceiling of a single cavity lying approximately 2 m below the upper layer. Murine rodent remains were recovered from calcareous sediments, from which the ceiling was formed.

Snake Cave's deposits were regarded initially as late middle Pleistocene (Ginsburg *et al.* 1982). Subsequently, Tougard *et al.* (1996) suggested an age range between 350,000 and 80,000 years based on Uranium/Thorium (U/Th) datings of dentine and enamel of mammalian teeth (Bovidae, Suidae and Rhinocerotidae) together with 'calcite from stalagmitic floors' (Tougard *et al.* 1996). U/Th dating of fragments of enamel from large mammals and calcite in the main layer of Snake Cave led Chaimanee (1998) to propose a youngest age for the deposit of 169,000 \pm 15,000 years (late middle Pleistocene). In order to determine specifically the age of the locality, Esposito *et al.* (1998) dated two sites within Snake Cave using the ²³⁰Th/²³⁴U-method. The first site (96EP) is close to the cave-mouth, the second site (96GS) is at the bottom of the cave. The isochron ages of 96EP and 96GS are 96 ± 4 Ka and $137^{+7}/_{-6}$ Ka, respectively. The Th/U age of 96 GS is $132^{+11}/_{-10}$ Ka. Fossil teeth are found in 96GS and are 'presumably older' than the Th/U and isochron dates given as they are 'embased in the bottom surface of this calcitic level' (Esposito *et al.*, 1998). A 'lower age limit of 130 Ky [Ka]' was attributed to the 'fossiliferous level' (Esposito *et al.*, 1998).

Between January and April 1978, a team of scientists from the University of California's Department of Anthropology and Chiang Mai University's departments of Anthropological survey of over 40 caves and fissures in the vicinity of Chiang Mai in north-western Thailand. Tentative identification of fossils recovered from brecchia blocks in one of the caves (18°47'N, 99°14'E) indicated the presence of small mammal material representing the sub-order Megachiroptera and the family Muridae. Owing to the cautious identification of the material, these records are not included in Tables 1d, f, g, i). Fragmentary fossilised material of larger mammals (Artiodactyla) was collected from all three caves.

Pope *et al.*, (1978) considered the caves to fall within a tentative age range of early to late Pleistocene based principally on analysis of the elevation and geomorphology of the sites.

During fieldwork carried out in the course of 1979 and 1980, the same team, with the inclusion of two further scientists from the University of California and the University of Kansas, recovered reptile, chelonian, and mammal remains, including molars and incisors of *Hystrix* sp. from a soil pocket within brecchia at Khao Panam in Lampang Province . The presence of fossils at Khao Panam had been identified first by Achan Sujit of Chiang Mai University's Department of Geological Sciences (Pope *et al.*, 1978).

In 1980 scientists from France (E. Buffetaut, L. Ginsburg, P. Janvier and M. Martin) and Thailand (R. Ingavat, N. Satayarak and V. Sutteetorn) undertook an examination of fossil sites in the north of Thailand, during the course of which they made a collection of Pleistocene fossils at Snake Cave. Fossil material from the locality had been discovered initially by a security guard from Chulaphorn Dam, the same lying at the head of the Chulaphorn Reservoir, some 6 km from the cave. The Thai-French team unearthed mainly isolated teeth and some complete and incomplete bones of primates, rodents, carnivores, perissodactyls and artiodactyls (Ginsburg et al., 1982). The rodent material represented two species of Marmoset rat (Hapalomys delacouri Thomas, 1927 and Hapalomys longicaudatus Blyth, 1859), a species of Maxomys (= Niviventer) that compared favourably with Niviventer niviventer (Hodgson, 1836), the Malayan porcupine (Hystrix hodgsoni subcristatus (= subcristata Swinhoe, 1870) = H. brachyura Linnaeus, 1758), two indeterminate species of murid rodent and one indeterminate species of the genus

Rattus.

Wet-screening of material from Snake Cave undertaken during the course of 1991 and 1992 enabled Chaimanee & Jaeger (1993) to add without detail to the initial list from the locality prepared by Ginsburg et al. (1982) an unidentified species of Fruit bat (Pteropus sp.), the gymnure, Hylomys suillus Müller, 1840, the shrew, Crocidura fuliginosa (Blyth, 1856a), the squirrels, Callosciurus finlaysoni (Horsfield, 1823), Hylopetes spadiceus (Blyth, 1847), Menetes berdmorei (Blyth, 1849) and Petaurista petaurista (Pallas, 1766), the Lesser Bamboo rat, Cannomys badius (Hodgson, 1841) and the murid rodents, Bandicota savilei Thomas, 1916b, Chiromyscus chiropus Thomas, 1891, Chiropodomys gliroides (Blyth, 1856b), Leopoldamys sabanus (Thomas, 1887), Maxomys surifer (Miller, 1900), Mus caroli Bonhote, 1902, M. cervicolor Hodgson, 1845, M. cookii Ryley, 1914, M. pahari Thomas, 1916a, M. shortridgei (Thomas, 1914), Niviventer bukit (= fulvescens (Gray, 1847)), N. confucianus (Milne-Edwards, 1872), Rattus argentiventer (Robinson & Kloss, 1916), R. koratensis [= andamanensis (Blyth, 1860)], R. rattus (Linnaeus, 1758) and Vandeleuria oleracea (Bennett, 1832).

In the years prior to 1993 the Thai-French 'Mission Paléontologique', which included scientists from the Department of Mineral Resources in Bangkok and the Palaeontology Department of l'Université Montpellier II in France, recovered fossilised small mammal remains including isolated teeth, incomplete jaws with intact teeth and bone fragments from 11 fissure-fillings in Pleistocene localities in central, western and peninsular Thailand (Ban Nasan, Kanchanaburi 1 & 2, Khao Chongkrachok, Khao Khlongwan, Khao Noh, Khao Singto, Khao Tinpet, Khao Toi 1 & 2 and Saraburi). The collection, which represented exclusively extant taxa, comprised two shrew species of the genus Crocidura. one species each of the bat genera, Cynopterus, Hipposideros and Rhinolophus and the squirrel genera, Callosciurus, Menetes and Tamiops, the squirrel, Exilisciurus exilis (Müller, 1838) (which is now restricted to Borneo), the flying-squirrels, *Iomys horsfieldi* (Waterhouse, 1838) (restricted currently to Malaysia, Sumatra, Java, and Borneo), Hylopetes phayrei (Blyth, 1859), Hylopetes spadiceus (Blyth, 1847), Petinomys vordermannii (Jentink, 1890) and Belomys pearsonii (Gray, 1842), the Marmoset rat, Hapalomys longicaudatus Blyth, 1859, the Tree mice, Chiropodomys gliroides (Blyth, 1856b) and Vandeleuria oleracea (Bennett, 1832, a single species each of the murid rodent genera Bandicota, Mus, Niviventer and Leopoldamys and two species of Rattus.

Following the further study by scientists from the Thai-French Mission Paléontologique of deposits from Snake Cave, Tougard *et al.* (1996) produced a revised list of the mammal taxa from that locality, which added to the indices of Ginsburg *et al.* (1982) and Chaimanee & Jaeger (1993) an indeterminate species of Microchiroptera and removed therefrom the Greater Marmoset rat, *Hapalomys longicaudatus* Blyth, 1859. No detail attends the addition and removal mentioned.

Chaimanee et al. (1996) described the extinct murid rodent

Ratchaburimys ruchae from the Pleistocene sites of Khao Khlongwan and Saraburi based on a first upper molar and a first lower molar, respectively. The taxon is recorded by the same authors from the Pliocene locality of Khao Samngam.

Based principally on the examination of isolated teeth recovered from all of the sites detailed at the start of this section other than the Cave of the Monk, Crystal Cave, and Khao Rupchang 2, Chaimanee (1998) presented a detailed analysis of Pleistocene material representing the families Sciuridae and Muridae. The author identified 36 species from the 16 localities comprising ten sciurid rodents and 26 murid rodents. She named the following four new species of extinct murid rodent: Pithecheir peninsularis (based on an upper first molar, two lower first molars, and two lower third molars from Khao Rupchang 1), Chiropodomys maximus (three first upper molars, five second upper molars, two second lower molars, and one third lower molar from Khao Tinpet), Hapalomys khaorupchangi (two upper first molars, two upper second molars, a single upper third molar, one lower first molar, and a single lower third molar from Khao Rupchang [1]) and Niviventer gracilis (23 upper and lower molars from the main layer of Snake Cave).

Ratchaburimys ruchae and *Saidomys siamensis*, which Chaimanee (1998) named as new taxa from the Pliocene site of Khao Samngam, are recorded by the same author also from Khao Khlongwan (both species) and Saraburi (*R. ruchae*).

The ten sciurid rodent and the remaining 20 murid rodent species represent nine genera and 13 genera respectively and are listed, together with the sites from which evidence of their presence has been recovered, in Tables 1e, f, h, i, wherein they are identified by the number '6'.

Chaimanee & Jaeger (2000b) recorded the murine rodent *Hadromys humei* (Thomas, 1886), based on isolated molars gathered from eight middle (to early late) Pleistocene karstic fissure fillings in peninsular Thailand (Ban Nasan, Khao Naphung, Khao Rupchang 1, and Khao Rupchang 2), central Thailand (Khao Noh, Kanchanaburi 2, and Crystal Cave) and northern Thailand (Khao Panam) and two deposits at Snake Cave (main and upper layers). *H. humei* is classified currently as endangered and is restricted to north-eastern India (Molur & Nameer, 2008).

In a continuation of their work on Thailand's Pleistocene small mammal fauna, the same two authors described a new, extinct species of flying squirrel, *Belomys thamkaewi* from Crystal Cave in central Thailand based on 157 molars and premolars recovered from a fissure filling in Permian limestone (Chaimanee & Jaeger, 2000c). They referred to the presence of fossil material of the extant species *Belomys pearsonii* (Gray, 1842) from fissure fillings at Kanchanaburi 2 in western Thailand, Khao Panam and Khao Takla in northern Thailand, Khao Toi 2 in peninsular Thailand, and Snake Cave in north-eastern Thailand. The authors indicate that the following extant taxa have been recovered from the deposit at Crystal Cave: the squirrels *Callosciurus* cf. *finlaysoni* (Horsfield, 1823), *Menetes*

berdmorei (Blyth, 1849), Petaurista petaurista (Pallas, 1766), Hylopetes phayrei (Blyth, 1859) and Hylopetes spadiceus (Blyth, 1847) and the murid rodents, Leopoldamys sabanus (Thomas, 1887), Rattus sikkimensis (= andamanensis (Blyth, 1860)) and Mus shortridgei (Thomas, 1914).

During the course of their discussion of the evolutionary diversification and radiations of *Rattus* during the Plio-Pleistocene in Thailand, Chaimanee & Jaeger (2000a) referred to the presence of the subspecies *Mus pahari gairdneri* (Kloss, 1920) at Snake Cave. The comment is made, however, without detail.

Zeitoun et al. (2005) presented preliminary data on dental and osseous fossil material recovered from clay deposits within the Cave of the Monk at Ban Fa Suai in northern Thailand, a site that was discovered originally by a team from the Thai/French palaeontological survey mentioned above that was looking primarily at human migration patterns in the region. Thirteen families, 21 genera and 34 species of large mammal were identified in the material collected. Small mammal fossils recovered are considered by the authors to represent indeterminate forms of the families Sciuridae and Muridae and two porcupine taxa, Atherurus cf. macrourus (Linnaeus, 1758) and Hystrix cf. brachyura (Linnaeus, 1758). Much of the material from the site exhibited signs of gnawing by porcupines. The total osseous and dental remains recovered amounted to 3,930 items, approximately 690 of which were complete teeth. Pursuant to an examination of upper and lower porcupine molars (M1/2, n=11; m1/2, n=15) contained in the collections of the Geological Survey Division, Bangkok, van Weers (2005) reported the possible presence of either Hystrix indica Kerr, 1792 or the extinct species H. kiangsenensis Wang, 1931 in Snake Cave and Pha Bong Cave. The author states that firm identifications are not possible in the absence of skull material.

Holocene (0.0117–0 Ma) (Tables 1h, i)

The only small mammal fossils recovered in Thailand from a Holocene site were collected by scientists from the Department of Mineral Resources in Bangkok and the Palaeontology Department of l'Université Montpellier II, France, during the course of the Thai-French 'Mission Paléontologique', which investigated 11 fossil-bearing localities prior to 1993 in central, western, and peninsular Thailand. All of the sites were considered at the time to be of Pleistocene age (Chaimanee *et al.*, 1993) but a single site, Kanchanaburi 1, was placed subsequently in the Holocene (Chaimanee, 1998).

Fossil material was recovered at the Kanchanaburi 1 locality from three sites situated within Lang Kamnan Cave, which lies in the same Permian limestone hill as Kanchanaburi 2 (see the section entitled 'Pleistocene', above), from which it is about 1 km distant. The sites were originally the subject of excavations by members of the Department of Archaeology at Bangkok's Silpakorn University. The fossiliferous sediments comprise 'clayey silts with some calcareous concretions, iron concretions, shell fragments, plant disturbations and vertebrates' (Chaimanee, 1998). The age of the sediments was considered initially to be similar to the late middle Pleistocene deposits of Snake Cave in Chaiyaphum Province (Chaimanee *et al.*, 1993: 46) but Chaimanee (1998, p. 230) attributed an age of 8,000 to 4,000 years to the material from Kanchanaburi 1 based on dating carried out on archaeological remains from the area.

The material recovered from Kanchanaburi 1 by the 'Mission Paléontologique', which comprised mainly dental and osseous items, all representing extant taxa, was recorded initially by Chaimanee *et al.* (1993) and more precisely thereafter by Chaimanee (1998), who reported the presence of the sciurid rodents *Hylopetes phayrei* (Blyth, 1859) (based on an M2, an M3, and an m3) and *H. spadiceus* (Blyth, 1847) (one M2) and the murid rodents, *Chiropodomys gliroides* (Blyth, 1856b) (one M1, an M3, and an m1), *Leopoldamys sabanus* (Thomas, 1887) (one m2), *Mus cookii* Ryley, 1914 (an M1and a m1) and *M. cervicolor* Hodgson, 1845 (an M1 and an m1).

Present study

In October 2010 a team comprising scientists from the Prince of Songkla University, Hat Yai, Thailand, and the Harrison Institute, Sevenoaks, UK, undertook fieldwork at Khao Kao Cave in Songkhla Province, southern Thailand, from where the team recovered approximately 60 kg of fossiliferous material from three separate, but adjacent, locations. The deposits (9.85 kg of which have been analysed to date) have yielded mainly isolated teeth and broken limb bones but jaws, either edentulous or with some intact dentition, were also present. So far, 15 species representing eight genera, seven families, one superfamily and three orders of small mammal have been distinguished and specimens of these are described below. Eleven of the species, one of which is new to science, are recorded for the first time from the late Pleistocene of Thailand.

Locality data

Khao Kao Cave ($6^{\circ}42'27''$ N, $100^{\circ}16'38''$ E) = 'White Hill' Cave – This cave is situated in Songkhla Province in the same Ordovician limestone range on the Thai-Malaysian border as the Khao Rupchang localities mentioned above, from which it is roughly 1 km distant. The area is about 100 m above sea level with the cave entrance lying approximately 25 m above ground level. A high chamber dominates the interior of the cave, the floor of which is strewn with large limestone boulders. Fossiliferous sedimentary deposits consistent with a fissure filling were collected from three adjacent locations next to a narrow ledge about three metres above the surrounding floor level and some seven metres above the cave's threshold. Hardened deposits containing the jaws, bones, and teeth of small mammals (Fig. 2) were removed from the ceiling areas of two small recesses (locations 1 & 3) while similar fossil material was extracted from location 2, the same comprising a number of horizontal furrows in the limestone, in which a fine, powdery deposit had accumulated. The furrows were approximately 30 cm above the ledge. Luminescence dating of the fossiliferous deposit indicates that the matrix was formed in its current position c.16,000years ago but contains material derived from a substantially older context dating back to more than 200,000 years.

Materials and methods

Calcareous fossil-bearing matrix (see Fig. 2) was removed manually from the ceiling areas of locations 1 and 3 using a hammer and chisel. A 1³/₄ inch paint-brush was used to sweep the fine fossiliferous deposits from location 2 into a garden trowel held horizontally in the grooves of the rock surface. All collected material was sealed in plastic containers before being removed for laboratory analysis.

In the laboratory, material from locations 1 and 3 was transferred to plastic bowls and covered with a fresh solution of 10% acetic acid (CH₃CO₂H) every 24 hours. During each change of acid, any separated teeth, jaws, and bones were recovered by rinsing the dissolved matrix by hand through a plastic sieve with a 0.8 mm mesh using a rosehead watering gun attached to a domestic hose. The calcareous matrix dissolved at a rate of 13.62 grammes per hour. Material from location 2 was covered in 10% acetic acid for a single 24 hour period before being rinsed with cold water in an electric sieving machine for a further six hours. Separated fossilised material was recovered by rinsing the matrix by hand as described above. The material from the three locations was dried before being sorted using a Leica MZ8 stereomicroscope. Drawings of specimens were made using the said Leica microscope with a drawing arm attachment fitted.

Abbreviations used in the text and in Tables 2 to 19 are as follows:

al	first lower antemolar
A1	first upper antemolar
a2	second lower antemolar
A2	second upper antemolar
a3	third lower antemolar
A3	third upper antemolar
a4	forth lower antemolar
с	lower canine
С	upper canine
C(alv.)	alveolus of the upper canine
C(alv.)-M.	3 distance from the most anterior part of the
	alveolus of the upper canine to the most pos-
	terior part of the third upper molar
c(alv.)-m3	(alv.) distance from the most anterior part of
	the alveolus of the lower canine to the most

the alveolus of the lower canine to the most posterior part of the alveolus of the third lower molar



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Figure 2. Fossiliferous matrix adhered to the ceiling area of a small recess inside Khao Kao Cave.

C-M3	distance from the most anterior part of the upper canine to the most posterior part of					
	the third upper molar					
c-p2	distance from the most anterior part of the					
	lower canine to the most posterior part of					
	the second lower premolar					
c-p3(alv.)	distance from the most anterior part of the					
	lower canine to the most posterior part of					
	the alveolus of the third lower premolar					
Gy	"Gray" (unit of absorbed radiation meas-					
	urement)					
HZM	Harrison Zoological Museum (now the					
	Harrison Institute)					
i1	first lower (mandibular) incisor					
I1	first upper (maxillary) incisor					
I2	second upper incisor					
I3	third upper incisor					
IC	interorbital constriction (shortest distance					
	across the interorbital region)					
Ka	thousand years ago					
М	mandible length from the most posterior part					
	of the condyle to the most anterior part of					
	the mandible including the lower incisors					
	(where present)					

Ma	million years ago
m1	first lower molar
M1	first upper molar
M1(alv.)-M3	B distance from the most anterior part of the
	alveolus of the first upper molar to the most
	posterior part of the third upper molar
m1(alv.)-m3	
	of the alveolus of the first lower molar to the
	most posterior part of the alveolus of the
	third lower molar
m1-m3	distance from the most anterior part of the
	first lower molar to the most posterior part
	of the third lower molar
M1-M3	distance from the most anterior part of the
	first upper molar to the most posterior part
	of the third upper molar
m2	second lower molar
M2	second upper molar
M2-M3	distance from the most anterior part of the
	second upper molar to the most posterior
	part of the third upper molar
m3	third lower molar.
M3	third upper molar
MPL	median palatal length (distance from most

	anterior part of the centre line of the palate to the most anterior part of the centre line of
	the mesopterygoid space)
MSL	median skull length (distance from the most
	anterior part of the nasal bulb to the lambda)
p1	first lower premolar
p1-m3	distance from the most anterior part of the
-	first lower premolar to the most posterior
	part of the third lower molar
p2	second lower premolar
p3	third lower premolar
p4	fourth lower premolar
P4	fourth upper premolar
P4-M3	distance from the most anterior part of the
	fourth upper premolar to the most posterior
	part of the third upper molar
RW	rostral width (distance across the front of the
	orbits at their most anterior point).

For dating by optically stimulated luminescence (Aitken, 1998), the exposed outer parts of a small block of the cemented matrix (KKC03 sample A: laboratory code X5142) were removed under low intensity laboratory safe-lighting from purpose-built yellow LED's emitting at ~594nm. The preparation procedures were designed to yield pure quartz from the natural sediment sample. Sand-sized quartz grains were extracted following standard preparation procedures involving wet sieving (180-250 μ m) and successive treatments with hydrochloric acid (HCl) to remove carbonate and then concentrated hydrofluoric acid (HF) (48%) for 100 minutes to dissolve feldspar grains and to remove (etch) the outer surface of quartz grains (the only part exposed during burial to natural alpha radiation). Any heavy minerals present were subsequently removed by gravity separation using a sodium polytungstate solution at 2.68 g/cm⁻³. Finally, the sample was re-sieved to remove heavily etched grains. The prepared sand-sized quartz grains were mounted on 1 cm diameter aluminium discs as small aliquots of 3-4 mm diameter using viscous silicone oil

Optically stimulated luminescence (OSL) measurements were made in an automated Risø luminescence reader (Bøtter-Jensen, 1997; 2000) using a single aliquot regenerative-dose (SAR) post-infrared (IR) blue OSL measurement protocol (Murray & Wintle, 2000; Banerjee et al., 2001; Wintle & Murray, 2006). Dose rate calculations are based on the concentration of radioactive elements (potassium, thorium and uranium) within the sample. The beta dose rate was derived from elemental analysis by inductively coupled mass spectrometry (ICP-MS) and inductively coupled atomic emission spectroscopy (ICP-AES) using a fusion sample preparation technique. In the absence of in situ radioactivity measurements and because of the proximity of the sample to the cave wall (15-20 cm), the gamma dose rate was estimated to originate 50% from the limestone bedrock. The OSL age estimate includes an additional 3% systematic error to account for uncertainties in source calibration. Dose rate calculations are based on Aitken (1985). These incorporated beta attenuation factors (Mejdahl, 1979), dose rate conversion factors (Adamiec & Aitken, 1998) and an absorption coefficient for the water content (Zimmerman, 1971). The contribution of cosmic radiation to the total dose rate was calculated as a function of latitude, altitude, burial depth and average over-burden density based on data by Prescott & Hutton (1994). Due to the extensive thickness of the cave roof (>50 m) the contribution of the cosmic dose rate to the total dose received by the quartz mineral grains may be considered to be negligible. Likewise, the contribution of the bedrock to the external gamma dose received by the quartz grains within the sedimentary matrix can be considered to be small (0.17Gy/Ka) due to the low concentration of radioisotopes within limestone. The dose rate is dominated by the beta dose rate originating from the sediment itself but which was also found to be very low (2.5% potassium, 0.6 ppm thorium and 2.3 ppm uranium). The calculated age estimate was obtained from dividing the palaeodose by the estimated total dose rate. The geologic timescale used throughout this paper follows Gradstein et al. (2012).

Material with the specimen prefix 'KK' is housed either at the Prince of Songkla University, Hat Yai, Thailand or at the Harrison Institute, Sevenoaks, UK. The single specimen with the prefix 'HZM' is retained in the collections of the Harrison Institute.

Systematic palaeontology

In this section, the sequence of orders, families, genera, and species follows Wilson and Reeder (2005). Subfamilies have been omitted.

Order Chiroptera Blumenbach, 1779 Family Pteropodidae Gray, 1821. Genus *Eonycteris* Dobson, 1873. *Type species – Macroglossus spelaeus* Dobson, 1871a.

Eonycteris spelaea (Dobson, 1871) - (Lesser) Dawn bat, Cave Fruit bat, Dobson's Long-tongued Fruit bat Plate A, Table 2

1871a Macroglossus spelaeus Dobson, p. 105, 106 [Farm Caves, Moulmein, Tenasserim, Burma (Myamnar)].

Material examined – Right mesial ramal fragment with c, p1, p2 and alveolus of p3 (KK1).

Discussion – The material compares with a Recent specimen from Perak, Malaysia (HZM 1.73960), differing only in its more robust canine, which is, however, morphologically similar with a concave distal surface. It may be noted that lower canine size and the length of the diastema between p1 and p2 are both variable in this species with the canines of adult males usually larger. This fragment was derived probably from a male. Recent records have been summarised by Bumrungsri et al. (2006).

This is the first fossil record of the genus *Eonycteris* from Thailand. *Eonycteris spelaea* is a current, widespread species in SE Asia, where it has been recorded from Nepal, south-western and north-eastern India, the Andaman Islands, Myanmar, southern China, Thailand, Indochina, Malaysia, Indonesia, and the Philippines (Simmons, 2005). In 2003, it was known to be present in Khao Kao Cave in large numbers (S. Bumrungsri, pers. comm.).

Tooth		n Crown length		Crown w	width
10001	n	range	mean	range	mean
с	1	1.66-1.66	1.66	1.41-1.41	1.41
p1	1	1.22-1.22	1.22	0.83-0.83	0.83
p2	1	1.63-1.63	1.63	0.93-0.93	0.93
Toothrow		Length			
c-p2	1		5	.25	
c-p2 c-p3 (alv.)	1		7	.60	

Table 2. Measurements (in mm) of the crown length and crown width of teeth of *Eonycteris spelaea* (Dobson, 1871) recovered from Khao Kao Cave, Thailand.

n = number of teeth.

Genus Rousettus Gray, 1821

Type species – Pteropus egyptiacus E. Geoffroy, 1810a.

Rousettus amplexicaudatus (E. Geoffroy, 1810) - Geoffroy's rousette Plate B, Table 3

1810 *Pteropus amplexicaudatus* Geoffroy, p. 96, pl. 4 (Timor I).

Material examined – Incomplete mandible with p1, p2, p3, m1, m2, m3 sin., p2, p3 dex. (KK2); distal right ramus with m1, m2, m3, coronoid and condyle intact (KK3).

Discussion – These two fragmentary jaws are identified by their size, the presence of six post-canine cheekteeth in KK2, and a subcircular third lower molar in both specimens (see Andersen, 1912: 42).

These specimens represent the first fossil record of the genus *Rousettus* from Thailand. *Rousettus amplexicaudatus* is an extant taxon and is distributed widely across the region, where it is known from Myanmar, Thailand, Cambodia, Malaysia, Indonesia, the Philippines and north-western Oceania.

Superfamily Rhinolophoidea Gray, 1825

Rhinolophoidea indet.

Plate C, Table 4

Tooth		Crown length		Crown w	vidth
Tooth	n	range	mean	range	mean
p1	1	1.08-1.08	1.08	1.00-1.00	1.00
p3	1	2.03-2.03	2.03	1.26-1.26	1.26
p4	1	2.30-2.30	2.30	1.58-1.58	1.58
m1	2	2.45-2.45	2.45	1.58-1.62	1.60
m2	2	2.07-2.08	2.08	1.56-1.58	1.57
m3	2	1.27-1.30	1.29	0.91-0.92	0.92
Toothrow			Len	ıgth	
TOULITOW		rang	e	mear	<u>n</u>
p1-m3	1	12.36-12	12.36-12.36		5
m1-m3	2	6 22-6	25	6.24	Ú

Table 3. Measurements (in mm) of the crown length and crown width of teeth of *Rousettus amplexicaudatus* (E. Geoffroy, 1810) recovered from Khao Kao Cave, Thailand. n = number of teeth.

Discussion – The morphology of this isolated left upper first molar would indicate that it is representative of a small rhinolophoid bat, the specific identity of which it is not possible to determine in the absence of more complete material.

Tooth	n	Crown length	Crown width
M1	1	1,57	1,89

Table 4. Dental measurements (in mm) of Rhinolophoidea indet.from Khao Kao Cave, Thailand.n = number of teeth.

Family Hipposideridae Lydekker, 1891 Genus *Hipposideros* Gray, 1831

Type species – Vespertilio speoris Schneider, 1800.

Hipposideros diadema (E. Geoffroy, 1813) - Diadem Leafnosed bat

Plates B, D; Table 5

1813 *Rhinolophus diadema* Geoffroy, p. 263, pls 5, 6 (Timor I)

Material examined – Cranium with P4 dex., M1 sin. et dex., M2 sin. et dex., M3 sin. et dex.; left zygoma broken (KK5).

Discussion – This specimen compares well with Recent examples of the species although the cheekteeth P4-M3 are distinctly heavier, suggesting a Pleistocene form.

This is the first fossil record of *Hipposideros diadema* from Thailand. The genus has been recorded from the Pleistocene sites of Khao Tinpet and Saraburi ([11], Chaimanee *et al.*, 1993) while two earlier extinct forms of Leaf-

nosed bat, *H. felix* and *H. khengkao*, are known from the middle Miocene locality of Mae Long in the Li Basin (Mein & Ginsburg, 1997).

Hipposideros diadema is an extant species with a broad distribution from mainland SE Asia through Indonesia and the Philippines to the islands of north-western Oceania (Simmons, 2005).

Cranium	n		
MSL	1	26.00	
RW	1	9.72	
IC	1	3.72	
MPL	1	4.44	

Teeth		Crown length	Crown width
P4	1	2.30	2.55
M1	1	3.00	3.00
M2	1	2.88	3.12
M3	1	1.44	2.40
Toothrow		Len	gth
P4-M3	1	9.1	12
M1-M3	1	7.2	

Table 5. Cranial and dental measurements (in mm) of *Hipposideros diadema* (E. Geoffroy, 1813) from Khao Kao Cave, Thailand.

n = number of specimens.

Hipposideros larvatus (Horsfield, 1823) - Intermediate Leaf-nosed bat Plates C, D; Table 6

1823 Rhinolophus larvatus Horsfield, part 6, pl. (Java).

Material examined – Right maxilla with alveoli of C, P3; P4, M1, M2, M3 *in situ* (KK6); P4 sin. (KK7).

Discussion – The maxilla (KK6) is derived from a medium-sized *Hipposideros*. The alveoli of the small premolar (P3) and the canine (C) indicate that the former tooth was extruded from the toothrow and that the latter tooth and the P4 were in close proximity. M3 is slightly reduced with two commissures, the second about three-quarters as long as the first. The specimen agrees in all essentials with *H. larvatus* and falls into the size range of that species. The isolated P4 (KK7) may belong to the same taxon but is slightly larger.

This material represents the first fossil record of *Hipposideros larvatus* from Thailand. For other records of the genus from fossil sites in Thailand, see '*Discussion*' within the *Hipposideros diadema* entry above. *Hipposideros larvatus* is an extant, widespread species in SE Asia, ranging from Bangladesh and north-eastern India through southern China, Myanmar, Thailand, Indochina, Malaysia, and Indonesia.

Tooth	n	n Crown length		Crown w	vidth	
10011	ш	range	mean	range	mean	
P4	2	1.79-2.18	1.99	1.79-2.11	1.95	
M1	1	2.37-2.37	2.37	2.24-2.24	2.24	
M2	1	2.37-2.37	2.37	2.43-2.43	2.43	
M3	1	1.25-1.25	1.25	2.02-2.02	.02 2.02	
Toothrow			Length			
Toothrow		rang	range		n	
P4-M3	1	6.98-6	.98	6.98	3	
M1-M3	1	5.44-5	.44	5.44	4	

Table 6. Dental measurements (in mm) of *Hipposideros larvatus* (Horsfield, 1823) from Khao Kao Cave, Thailand. n = number of teeth/toothrow measurements taken.

Hipposideros pomona Andersen, 1918 - Andersen's Leafnosed bat; Pomona Leaf-nosed bat Plate C; Table 7

1918 *Hipposideros pomona* Andersen, pp. 380, 381 (Haleri, North Coorg, southern India).

Material examined – Left maxilla with alveolus of M1 and M2, M3 *in situ* (KK8).

Discussion – Specimen KK8 is a left maxillary fragment with the alveolus of the first upper molar and the second and third upper molars in place. These elements match perfectly the same elements in HZM 1.30502, which is a female *H. pomona* collected in Cuc-Phuong National Park in Vietnam.

This is the first fossil record of *Hipposideros pomona* from Thailand. For other records of the genus from fossil sites in Thailand, see '*Discussion*' under *Hipposideros diadema* above. *Hipposideros pomona* is an extant species with a broad range in SE Asia, where it is known from southwestern and north-eastern India, Bangladesh, Myanmar, south-eastern China, Indochina, Thailand, and Peninsular Malaysia (Simmons, 2005; Corbet & Hill, 1992).

Tooth	n	Crown length	Crown width
M2	1	1,57	1,06
M3	1	0,93	1,47
Toothrow		Len	gth
M1(alv.)-M3	1	3,0	65
M2-M3	1	3, 2,	37

 Table 7. Dental measurements (in mm) of *Hipposideros po-mona* Andersen, 1918 from Khao Kao Cave, Thailand.

 n = number of teeth/toothrow measurements taken.

None of the hipposiderid species mentioned above was recorded from Khao Kao Cave during a survey in 2003 although a few *Hipposideros cineraceus* and *H. lylei* were observed (S. Bumrungsri, pers. comm.).

Family Emballonuridae Dobson, 1875 Genus *Taphozous* E. Geoffroy, 1818 *Type species – Taphozous perforatus* E. Geoffroy, 1818.

Taphozous sp.

Plate A; Table 8

Material examined – Edentulous right ramus (KK10).

Discussion – This edentulous jaw is smaller than *Taphozous longimanus*, *T. melanopogon*, and *T. theobaldi* but it could derive from *T. perforatus*. Precise identification is not possible in the absence of dentition.

Taphozous is an extant and common genus throughout the Old World tropics and subtropics, ranging from Mauritania in western Africa to Queensland in north-eastern Australia. *Taphozous longimanus, T. melanopogon* and *T. theobaldi* are known to occur in Thailand (Bumrungsri *et al.*, 2006). The nearest locality to Khao Kao Cave from which extant forms of *T. perforatus* have been recorded is Jabalpur in the central Indian state of Madhya Pradesh (Khajuria, 1965).

Toothrow	n	Length	
c(alv.)-m3(alv.)	1	9.00	
m1(alv.)-m3(alv.)	1	5.4	
М	1	15.13	

Table 8. Dental measurements (in mm.) of *Taphozous* sp. fromKhao Kao Cave, Thailand.

n = number of toothrow measurements taken.

?Taphozous sp.

Plate C; Table 9

Material examined - M3 sin. (KK11).

Discussion – This isolated M3 is larger than the same element of *Taphozous longimanus*, *T. melanopogon* and *T. perforatus*, but is too small to be derived from *T. theobaldi*. Even its generic identity must remain uncertain at present; the second commissure is longer than usual in *Taphozous*, giving the tooth a more triangular outline. Further intact material of this genus is needed to make a more precise identification.

Teeth	n	Crown length	Crown width
P4	1	2.30	2.55
M3	1	1.15	2.18

Table 9. Dental measurements (in mm) of ?*Taphozous* sp. fromKhao Kao Cave, Thailand.

n = number of toothrow measurements taken.

Family Vespertilionidae Gray, 1821 Genus *Eptesicus* Rafinesque, 1820

Type species – Eptesicus melanops Rafinesque, 1820 (= *Vespertilio fuscus* Beauvois, 1796).

Eptesicus chutamasae Harrison & Pearch, sp. nov. - Chutamas's serotine. Figure 3a, b; Plate E, Table 10

Type material – **Holotype**: right maxilla with alveoli of I1, I2, C and P4-M3 *in situ* (HZM 1.39818). The holotype is the only known specimen.

Type locality – Khao Kao Cave, Songkhla Province, Thailand.

Stratum typicum – Calcified cave deposit (late Pleistocene).

Etymology – We name this taxon in honour of Prof. Chutamas Satasook, Dean of the Faculty of Science at the Prince of Songkla University, Hat Yai, Thailand.

Diagnosis – Cheekteeth robust (P4-M3: 6.78 mm.), distinctly larger than *Eptesicus serotinus* (Schreber, 1774). Styles of M1 to M3 much more prominent, especially the parastyle of M3, which projects beyond the metastyle of M2, tending to curve round it buccally.

Description – Small upper premolar absent. M1 and M2 are robust and dilambdodont, their parastyles extruding buccally beyond the metastyles of the preceding teeth. M3 is transversely elongate, robust, and narrow from its anterior to its posterior point, its parastyle extruding similarly and tending to curl round the metastyle of M2. It possesses two commissures with a vestige of a third (Fig. 3a), the second one short and only one third as long as the first. Measurements of a series of Recent *Eptesicus serotinus* in the collections of the Harrison Institute are given in Table 11.

Alveoli originally present for two upper incisors, the second smaller and situated slightly distally (Fig. 3a). The alveolus of the canine is robust. No alveolus exists for a small upper premolar between the canine and P4, where the palatal bone is complete.

The rounded infraorbital foramen is situated above P4 and just below the upper border of the anterior root of the zygomatic arch and above and mesial to the anterior root of M1, which is exposed in the specimen (Fig. 3b). The palatal emargination is present and quite small, its distal border attaining the mesial third of the alveolus of the canine. The maxillary dental formula is: I2 C1 P1 M3: 7.

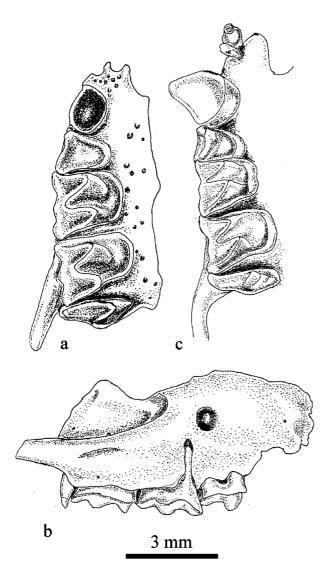


Figure 3. a, c. *Eptesicus chutamasae* sp. nov. Right maxilla with alveoli of 11, 12, C; P4-M3 *in situ* (holotype) (HZM 1.39818): a. occlusal view; c. buccal view. 3b. *Eptesicus sero-tinus* (HZM 41.8487 – nr Hollingbourne, Kent, U.K.): right toothrow, occlusal view.

Teeth	n	Crown length	Crown width
C(alv.)	1	1.70	1.30
P4	1	1,60	1.86
M1	1	2.30	2.43
M2	1	2.30	2.75
M3	1	1.09	2.50
Toothrow		Lei	ngth
C(alv.)-M3	1	7.	92
P4-M3	1	6.	78
M1-M3	1	5.	44

Table 10. Dental measurements (in mm) of *Eptesicus chuta-masi*sp. nov. from Khao Kao Cave, Thailand.

n = number of teeth/toothrow measurements taken.

Tooth	n	Crown	length	Crown	width	
1 00011		range	mean	range	mean	
С	14	1.50-1.90	1.74	1.40-1.75	1.62	
P4	14	1.15-1.45	1.28	1.40-1.85	1.62	
M1	14	1.90-2.10	2.01	1.70-2.25	1.99	
M2	14	1.90-2.10	1.98	1.90-2.40	2.18	
M3	14	0.90-1.20	1.00	1.70-2.10	1.97	
т 4			Len	ıgth		
Toothrow	n	rang	e	mean	mean	
C-M3	14	6.8-8.10		7.60		
P4-M3	14	5.30-6.35		5,97	7	
M1-M3	14	4.30-5	.20	4.82		

Table 11. Dental measurements (in mm.) of *Eptesicus serotinus*(Schreber, 1774) from Algeria, Germany, Hun-gary, Israel, Italy,Spain, and the United Kingdom.

n = number of teeth/toothrow measurements taken.

Discussion – This maxilla is readily distinguishable from Recent *Eptesicus serotinus* because of its very robust dentition: the P4-M3 are all very significantly larger to such a degree that it has to be regarded as a distinct, probably ancestral species.

The teeth reveal some distinctive morphological features. The protocone lobe of P4 is more elongated and narrower than in the Recent species. Furthermore, the styles of M1-M3 are much more prominent, especially the parastyle of M3, which projects well beyond the metastyle of M2, tending to curl round it buccally, making this element much longer than the M3 of *E. serotinus* (see Fig. 3a, c).

Eptesicus serotinus is an extant species and is known in Thailand today from Thung Yai Naresuan and Huai Kha Khaeng wildlife sanctuaries in western Thailand (Robinson *et al.*, 1995) and from Chiang Mai (Lekagul & McNeely, 1977), in which latter location it is represented by the subspecies, *Eptesicus serotinus andersoni* Dobson, 1871b, a taxon that has smaller and narrower ears than the typical form. *Eptesicus serotinus* is the only genus and species that compares favourably with HZM 1.39818.

This unique specimen appears distinct from any other Thai microbat examined and is worthy of taxonomic distinction as a new fossil taxon, with closest affinity to *Eptesicus*.

Comparative notes on other extant vespertilionid bats of a similar size – Eptesicus dimissus Thomas, 1916c – Thomas (1916c) states only, in respect of the dentition, that C-M3 is 6.2 mm. *E. chutamasae* C(alv.) - M3 is 7.92 mm.

Eptesicus pachyotis (Dobson, 1871) – In his original description of *E. pachyotis*, Dobson (1871b) gives little information other than external measurements. Lekagul & McNeely (1977, p. 222) state (of *E. pachyotis*): 'The teeth are very small, with the outer upper incisor $\frac{1}{2}$ or less the height of the inner incisor. The minute upper premolar is lacking'.

Eptesicus serotinus (Schreber, 1774) (HZM 41.8487) – From near Hollingbourne, Kent, England (Fig. 3b). A

small upper premolar is absent. The dentition is essentially similar but considerably smaller. M3 is less elongate and does not curl round the metastyle of M2 but terminates just internally to it or level with it.

Ia io Thomas, 1902 (HZM 2.30522) – From Cuc Phuong National Park, Vietnam. This large vespertilionid possesses a small upper premolar in the inner angle between C and P4. Its M3 is less elongate with the parastyle not curling round the metastyle of M2. Its teeth are clearly more robust.

Nyctalus noctula (Schreber, 1774) (HZM 41.16246) – From St. Xavier's School, Godavari, Nepal. This species possesses a small upper premolar, which is squeezed internally between C and P4. The teeth are smaller: M3 is less elongate with the crown length about half the crown width. *Otonycteris hemprichii* Peters, 1859 (HZM 13.11878) – From Qarat Kabrit, Oman. This taxon is distinguishable by the presence of only one upper incisor. M1 has a dominant, projecting metastyle. M3 is much less elongate and its parastyle does not curl round the metastyle of M2. The dentition is distinctly smaller in size. No small premolar is present.

Scotophilus heathii Horsfield, 1831 (HZM 8.7299) – From Mirzapur, India. The dentition of this species is the closest morphological match but only one upper incisor is present. M1 and M2 lack mesostyles and their buccal borders are strongly retracted. M3 is elongated and narrow but the parastyle does not curve round the metastyle of M2.

Order Scandentia Wagner, 1855 Family Tupaiidae Gray, 1825 Genus *Tupaia* Raffles, 1821

Type species – Tupaia ferruginea Raffles, 1821 (= *Sorex glis* Diard, 1820)

Tupaia sp.

Plate F; Table 12

Material examined – m2 dex. (KK12).

Discussion – This single tooth is distinguishable as a *Tupaia* because of the small cingular projection mesially, just buccal to the paracone. The tooth is distinctly smaller than *Tupaia belangeri* (HZM 1.32313) from Kyaikto, Myanmar and could belong to *Tupaia minor*.

Mein & Ginsburg (1997) described a large fossil *Tupaia* (*T. miocenica*) from the middle Miocene of Mae Long in the Li Basin based on an upper M2 measuring 3.57×4.79 mm (Mein & Ginsburg, 1997: 804). It is clearly larger than this late Pleistocene form, which is rather small.

Tooth	n	Crown length	Crown width	Tri W	Tal W
m2	1	3.26	1.90	2.50	2.24

Table 12. Dental measurements (in mm.) of *Tupaia* sp. from Khao Kao Cave, Thailand. n = number of teeth.

Order Eulipotyphla Waddell, Okada, & Hasegawa, 1999 Family Erinaceidae Fischer, 1814 Genus *Hylomys* Müller, 1840

Type species – Hylomys suillus Müller, 1840.

Hylomys suillus Müller, 1840 - Short-tailed gymnure Plates F, G; Table 13

1840 Hylomys suillus Müller in Temminck, p. 50. Mt. Gede, western Java.)].

Material examined – Right mandibular ramus with p4 (KK2); left edentulous mandibular ramus (KK35); I3 (KK30); P4 (KK23-KK29, KK54, KK55, KK64); M1 (KK13-KK15, KK17, KK63, KK82, KK92); M2 (KK19-KK20, KK20a-KK22, KK65, KK66, KK84, KK93); M3 (KK67, KK91); i2 (KK223); p4 (KK2, KK31, KK32, KK53, KK77, KK79); m1 (KK37, KK37a-KK41, KK56, KK71, KK74, KK76, KK80, KK83); m2 (KK42-KK51, KK57, KK72, KK78, KK86-KK88); m3 (KK52, KK68-KK70, KK73, KK75, KK89).

Discussion – Teeth of this species are plentiful in this deposit and are readily recognisable by comparison with Recent specimens, from which they do not differ significantly. Apparently the most common eulipotyphlan insectivore in Thailand (Lekagul & McNeely, 1977), *Hylomys suillus*, seems to have been equally abundant during the Pleistocene.

Tougard *et al.* (1996) referred to the presence of the taxon in late middle Pleistocene deposits at Snake Cave in Chaiyaphum Province while the extinct species, *Hylomys engesseri* Mein & Ginsburg, 1997 is documented from the middle Miocene of Mae Long in the Li Basin.

Tooth	n	Crown le	ength	Crown width	
10001	n	range	mean	range	mean
13	1	0.77-0.77	0,77	0.51-0.51	0,51
P4	10	1.98-2.56	2,28	1.86-2.94	2,43
M1	7	2.10-2.62	2,43	2.50-2.94	2,77
M2	9	2.00-3.12	2,28	2.30-2.75	2,55
M3	2	1.54-2.30	1,92	1.50-1.92	1,71
i2	1	0.68-0.68	0,68	1.35-1.35	1,35
p4	6	1.70-2.40	1,97	1.09-1.31	1,20
ml	12	2.88-3.25	3,01	1.65-2.10	1,83
m2	16	2.30-2.70	2,47	1.47-1.92	1,66
m3	7	1.85-2.15	1,93	1.20-1.45	1,30

Table 13. Measurements (in mm.) of the crown length and crown width of teeth of *Hylomys suillus* Müller, 1840 recovered from Khao Kao Cave, Thailand. n = number of teeth.

- 80 -

Family Soricidae Fischer, 1814 Genus *Crocidura* Wagler, 1832

Type species - Sorex leucodon Hermann, 1780

Crocidura attenuata Milne-Edwards, 1872 - Asian Grey shrew.

Figure 4d; Plates H, I; Table 14

Material examined – Cranial fragment with I1 (KK169); right maxillary fragment with A1, A2, A3, P4 (KK165); right maxillary fragment with P4, M1, M2 (KK141); left maxillary fragment with P4, M1, M2 (KK150); right maxillary fragment with M1 (KK131); left maxillary fragment with P4, M1 (KK166); I1 (KK170); M2 (KK155); M3 (KK157); right ramus with a3, m1, m2, m3 (KK95); right ramus with a3, m1, m2, m3 (KK96a); right ramus with m1, m2 (KK98); right proximal ramus with a2, m1, m2, m3 (KK160); right distal ramus with i1, m1, m2, m3 (KK102); right distal ramus with m1, m2, m3 (KK163); right distal ramus with m1, m2 (KK99); right distal ramus with m2, m3 (KK153); right distal ramus with m2 (KK101); right ramal fragment with m1, m2 (KK97); right ramal fragment with m1 (KK156); right ramal fragment with m2 (KK164); left ramus with part i1; a1, a2, m1, m2 (KK151); left ramus with i1, m1 (KK100); left ramus with a2, m1, m2 (KK109); left ramus with a2, m1, m2, m3 (KK167); left ramus with m1, m2, m3 (KK96b); left ramus with m1, m2, m3 (KK161); left ramus with m1, m2 (KK152); left distal ramus with m1, m2, m3 (KK154); left distal ramus with m1 (KK159); left proximal ramus with a2, m1, m2, m3 (KK168); left ramal fragment with p4 (KK162).

Tooth	n	Crown l	ength	Crown width	
1 0011	11	range	mean	range	mean
I1	2	1.15-1.47	1,31	0.42-0.64	0,53
A1	1	1.08-1.08	1,08	0.90-0.90	0,90
A2	1	0.64-0.64	0,64	0.64-0.64	0,64
A3	1	0.80-0.80	0,80	0.64-0.64	0,64
M1	4	1.47-1.70	1,58	1.79-2.10	1,97
M2	3	1.31-1.50	1,42	1.55-2.08	1,85
M3	1	0.61-0.61	0,61	1.28-1.28	1,28
P4	3	1.50-1.61	1,55	1.09-1.55	1,39
i1	2	2.00-3.03	2,52	0.50-0.56	0,53
a2	3	1.02-1.09	1,07	0.72-1.06	0,92
a3	3	0.56-1.06	0,84	0.56-0.78	0,69
p4	1	1.54-1.54	1,54	1.41-1.41	1,41
m1	18	1.21-1.62	1,49	1.02-1.30	1,09
m2	18	1.38-1.56	1,47	0.80-1.25	1,01
m3	11	1.02-1.19	1,11	0.65-0.90	0,76

Table 14. Measurements (in mm.) of the crown length andcrown width of teeth of *Crocidura attenuata* Milne-Edwards,1872 recovered from Khao Kao Cave, Thailand.n = number of teeth.

Discussion – This is the first fossil record from Thailand of this widespread Asian shrew, which ranges from southern China south through the Indian subcontinent and Indochina to southern Peninsular Malaysia and probably Sumatra (Corbet & Hill, 1992).

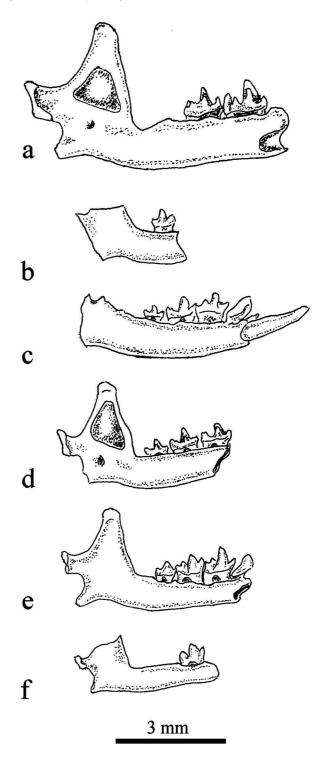


Figure 4. Relative sizes of soricid mandibular fragments from Khao Kao Cave, Thailand.

a. Crocidura fuliginosa (KK57); b. C. hilliana (KK186); c. C. vorax (KK108); d. C. attenuata (KK96b): e. C. indochinensis (KK207); f. Suncus etruscus (KK53).

¹⁸⁷² Crocidura attenuata Milne-Edwards, p. 231, pls38B, 39A (Moupin, Sichuan, China).

Crocidura fuliginosa (Blyth, 1856a) - South-East Asian shrew.

Figure 4a; Plates H, J; Table 15

1856	Sorex fuliginosa Blyth, p. 362 (Schwegyin, near
	Pegu, Burma).
1012	Crocidura dracula Thomas n 686 (2near Mong-

1912 *Crocidura dracula* Thomas, p. 686 (?near Mong tze [Mengtsz], S. Yunnan, China).

Material examined – Intact skull with complete dentition (KK55); left maxillary fragment with M1 (KK59); M2 (KK61); left distal ramus with a2, m1, m2, m3 (KK56); left distal ramus with m1, m2 (KK57).

Discussion – This is the largest shrew found in the fauna, contrasting strongly with the tiny *Suncus etruscus* (Savi, 1822) (see below). Hutterer (2005) considered *Crocidura dracula* Thomas, 1912 to be a synonym of *C. fuliginosa* (Blyth, 1856a).

Crocidura fuliginosa is recorded without detail from late middle Pleistocene deposits at Snake Cave in Chaiyaphum Province (Chaimanee & Jaeger, 1993). Today, the species occupies an extensive range from north-eastern India through Myanmar, southern China, Indochina, Thailand, Malaysia, and western Indonesia (Hutterer, 2005; Corbet & Hill, 1992).

Tooth		Crown length		Crown width	
10011	n	range	mean	range	mean
P4	1	2.10-2.10	2,10	2.40-2.40	2,40
M1	2	2.00-2.30	2,15	2.35-2.43	2,39
M2	2	1.60-1.70	1,65	2.30-2.43	2,37
M3	1	0.90-0.90	0,90	1.70-1.70	1,70
m1	2	1.92-1.98	1,95	1.31-1.31	1,31
m2	2	1.72-1.79	1,76	1.22-1.28	1,25
m3	1	1.28-1.28	1,28	1.02-1.02	1,02

Table 15. Measurements (in mm.) of the crown length andcrown width of teeth of *Crocidura fuliginosa dracula* Thomas,1912 recovered from Khao Kao Cave, Thailand.n = number of teeth.

Crocidura hilliana Jenkins & Smith, 1995 - Hill's shrew Figure 4b; Plates H, I; Table16

1995 Crocidura hilliana Jenkins & Smith, p. 103 (Wat Tham Maho Lan, Ban Nong Hin, 48 km south of Loei, Loei Province, north-eastern Thailand, 17°06'N., 101°53'E., altitude 575 m).

Material examined – Right ramus with i, m1, m2 (KK184); right maxilla with M1, M2 (KK183); right maxilla with part P4, M1, alveolus of M2 (KK182); distal right ramus with m3 (KK181, KK186); m3 sin. (KK185).

Discussion – This is the first fossil record of *Crocidura hilliana* from Thailand. Recent specimens of this species are known only from central and north-eastern Thailand

and from Lao PDR. The taxon is slightly smaller than *C*. *fuliginosa* (see Hutterer, 2005).

Tooth	n	Crown length		Crown width	
	n	range	mean	range	mean
M1	2	1.54-1.79	1,67	2.05-2.11	2,08
M2	1	1.34-1.34	1,34	1.98-1.98	1,98
m1	1	1.66-1.66	1,66	1.09-1.09	1,09
m2	1	1.60-1.60	1,60	0.96-0.96	0,96
m3	4	1.09-1.18	1,14	0.64-0.77	0,72

Table 16. Measurements (in mm.) of the crown length and crown width of teeth of *Crocidura hilliana* Jenkins & Smith, 1995 recovered from Khao Kao Cave, Thailand. n = number of teeth.

Crocidura indochinensis Robinson & Kloss, 1922 - Indochinese shrew

Figure 4e; Plates I, K; Table 17

1922 Crocidura indochinensis Robinson & Kloss, 1922: 88. Dalat, Langbian Plateau, Annam, Vietnam, 5,000 ft.

Material examined – Left maxillary fragment with I1 (KK204); right maxillary fragment with A3, P4 (KK206); right maxillary fragment with P4 (KK212); right ramus with a3, m1, m2, m3 (KK207); right ramus with a3, m1, m2 (KK215); right ramus with m1, m2, m3 (KK208, KK210); left ramus with m1, part m2, m3 (KK202); right ramus with m1, m2 (KK145, KK205); A1 dex. (KK200); P4 dex. (KK209); P4 sin. (KK213); M1 sin. (KK211); M2 dex. (KK134, KK201, KK203); M2 sin. (KK135, KK214).

Discussion – This is the first fossil record of *Crocidura indochinensis* from Thailand. The current range of the species extends from northern Myanmar through the northern areas of Thailand, Lao PDR, and Vietnam to south-eastern China (Hutterer, 2005). *C. indochinensis* is not known to occur in southern Thailand other than in the fossil form discussed here.

Tooth		Crown	length	Crown width	
10011	n	range	mean	range	mean
I1	1	1.34-1.34	1,34	0.64-0.64	0,64
A1	1	1.09-1.09	1,09	0.70-0.70	0,70
A3	1	0.83-0.83	0,83	0.64-0.64	0,64
P4	4	1.54-1.79	1,63	1.22-1.54	1,40
M1	1	1.34-1.34	1,34	2.11-2.11	2,11
M2	5	1.25-2.10	1,45	1.30-1.89	1,73
a3	2	0.96-1.05	1,01	0.74-0.96	0,75
m1	7	1.40-1.55	1,47	0.95-1.25	1,06
m2	6	1.30-1.45	1,4	0.90-1.10	1,00
m3	3	1.10-1.12	1,11	0.75-0.80	0,78

Table 17. Measurements (in mm.) of the crown length andcrown width of teeth of *Crocidura indochinensis* Robinson &Kloss, 1922 recovered from Khao Kao Cave, Thailand.

n = number of teeth.

Crocidura vorax Allen, 1923 - Voracious shrew Figure 4c; Plate L;Table 18

1923 Crocidura vorax Allen, p. 8 (Ssu Shan, Likiang [Lijiang] Range, Yunnan, China, 12,000 ft).

Material examined – Cranial fragment with I1 sin, A3 dex, P4 dex., M1 dex. (KK218); right maxillary fragment with M1, M2, M3 (KK220); right maxillary fragment with M1, M2 (KK127); right maxillary fragment with P4, M1 (KK143); left maxillary fragment with I1, A1, A2, A3, P4, M1, M2 (KK142); left maxillary fragment with P4, M1, M2 (KK128, KK129); left maxillary fragment with P4, M1 (KK124); right ramus with i1, m1, m2, m3 (KK108); right ramal fragment with i1, a1, a2, m1, m2 (KK219); right ramal fragment with m1, m2, m3 (KK104); left ramal fragment with part i1, part a4, m1 (KK106); I1 sin. (KK216); m3 sin. (KK217).

Discussion – This is the first fossil record of *Crocidura vorax* from Thailand. The species is known currently from India, Thailand, Lao PDR and from Vietnam to southern and central China (Hutterer, 2005).

	n	Crown	length	Crown	width
Tooth	n	range	mean	range	mean
I1	3	1.45-1.73	1,59	0.54-1.15	0,84
A1	1	1.35-1.35	1,35	0.85-0.85	0,85
A2	1	0.72-0.72	0,72	0.70-0.70	0,70
A3	2	0.80-0.90	0,85	0.58-0.70	0,64
M1	8	1.38-1.85	1,67	1.65-1.95	1,87
M2	5	1.28-1.63	1,47	1.70-1.91	1,84
M3	1	0.64-0.64	0,64	1.28-1.28	1,28
P4	7	1.34-1.55	1,45	1.60-1.90	1,72
i1	2	2.25-2.70	2,48	0.50-0.75	0,63
a1	1	0.97-0.97	0,97	0.64-0.64	0,64
a2	1	1.02-1.02	1,02	0.74-0.74	0,74
m1	4	1.41-1.65	1,52	0.96-1.05	1,00
m2	3	1.41-1.45	1,42	0.90-0.97	0,93
m3	3	1.09-1.15	1,11	0.70-0.80	0,73

Table 18. Measurements (in mm) of the crown length and crownwidth of teeth of *Crocidura vorax* Allen, 1923 recovered fromKhao Kao Cave, Thailand.n = number of teeth.

Tooth	n	Crown length		Crown width	
		range	mean	range	mean
i1	1	1.86-1.86	1,86	0.38-0.38	0,38
m1	2	1.06-1.20	1,13	0.77-0.80	0,79
m2	2	1.02-1.20	1,11	0.70-0.80	0,75

Table 19. Measurements (in mm) of the crown length and crownwidth of teeth of *Suncus etruscus* (Savi, 1822) recovered fromKhao Kao.

n = number of teeth.

Crocidura sp.

Material examined – Fragmentary jaws, either edentulous or with partial dentition (KK122); humerus (KK221, KK222).

Discussion – The genus *Crocidura* is widespread throughout SE Asia (Hutterer, 2005; Corbet & Hill, 1992) with five species recorded herein from Khao Kao Cave. The genus is known additionally from the Pleistocene sites of Ban Nasan, Khao Toi 1, and Khao Toi 2, (Chaimanee *et al.*, 1993) and also from Snake Cave (Tougard *et al.*, 1996; Chaimanee & Jaeger, 1993). The very partial nature of the dentition present in the new material referred to here prohibits accurate identification of the specimens.

Genus Suncus Ehrenberg, 1833

Type species – Suncus sacer Ehrenberg, 1833 (= *Sorex murinus* Linné, 1766)

Suncus etruscus (Savi, 1822) - Savi's Pygmy shrew; Etruscan shrew

Figure 4f; Plates I, K; Table 19

1822 Sorex etruscus Savi, p. 60 (Pisa, Italy).

Material examined – Right ramus with m1, m2, and alveolus of m3 (KK53); left ramus with m1 (KK95); i1 (KK54).

Discussion – These specimens resemble closely in their morphology and minute size a specimen from Rapallo, Italy (HZM 1.1010).

This is the first fossil record of *S. etruscus* from Thailand. The current geographical distribution of the species is broad with the taxon occurring from southern Europe and northern Africa to southern China (Hutterer, 2005).

The diversity of soricids found in Khao Kao Cave is remarkable, with at least six species present. They are mainly distinguishable by their relative sizes (see Fig. 4; Pls H,J,K,L; Tabs 14-19).

OSL dating

OSL measurements obtained from multiple (n=24) aliquots of quartz mineral grains extracted from the fossiliferous Khao Kao Cave deposit provided a mean weighted palaeodose of 10.3 ± 1.5 Gy. The dose rate was determined to be around 0.63+/-0.05Gy/Ka and the age calculation resulted in an OSL estimate of 16.35 ± 2.67 Ka.

Although the OSL age estimate of 16.35 ± 2.67 Ka. for the fossiliferous Khao Kao Cave deposit represents the last exposure of the majority of grains to daylight, the luminescence measurements also revealed the presence of high outliers (n=3) most likely to be caused by a small number of rogue grains among the mineral population that may not

have been fully reset at the time of deposition. Instead, they are likely to have retained a residual signal from a previous event and this observation suggests that the sediment may be derived, at least in part, from elsewhere in the cave system and that the sampled faunal assemblage may not necessarily be in a primary context. In future, more advanced single grain dating on grains extracted from a larger sample of the fossiliferous matrix using a focused green laser beam may allow a better understanding of the equivalent dose distribution within the mineral grain population. By basing the age calculation on the maximum palaeodose determination of 166.80±8.1Gy, an age in excess of 200 Ka may be postulated.

Discussion

OSL dating of the deposit

The data available to us at present are insufficient to explain the geological history of Khao Kao Cave, particularly the presence in the fossiliferous matrix of grains that may indicate a date older than 200 Ka. It might be the case that parts of the original sedimentary deposit were washed out by water inundation from above and replaced over time with a new layer of fossiliferous breccia, which, itself, was eroded partially by a subsequent water cycle, exposing the surface of the fossiliferous deposit seen today. A theory of this nature was propounded by Bacon et al. (2006) in relation to fissure fillings in Triassic limestone at Tan Vinh quarry in northern Vietnam. The older and younger deposits at Tan Vinh, however, were identifiable by the difference in the density and coloration of each. In the case of Khao Kao Cave, the fossil matrix appears uniform in coloration and fossiliferous content although that part of the deposit nearest the wall of the cave seems somewhat more consolidated than the outer part.

A marine inundation of Khao Kao Cave (even a significant event such as a tsunami) in the late middle Pleistocene is improbable as sea levels did not reach more than roughly 25 m above the present sea level during this time (Woodruff & Turner, 2009). Khao Kao Cave lies some 27 km from the sea at a current elevation above sea level of approximately 125 m. It is quite possible, however, that the cave was subjected to marine inundations in the Miocene, Oligocene, and Eocene as global sea levels reached heights in excess of 125 m above current levels during those epochs (Woodruff, 2003).

A number of crab claws have been recovered in the fossiliferous matrix from Khao Kao Cave. These have not been identified but it is probable that they represent terrestrial rather than marine species owing to the presence of land crabs in southern Thailand (P. Soisook, pers. comm).

This is the first time a late Pleistocene fauna has been described from Thailand and this serves to fill, to some extent at least, the hiatus in palaeontological knowledge of this part of the epoch to which Chaimanee & Jaeger (2000: 187) draw attention.

Fauna

Other than *Eptesicus chutamasae* sp. nov. all taxa listed in this paper from Khao Kao Cave are extant and known currently from Thailand. The bat species *Eonycteris spelaea*, *Rousettus amplexicaudatus*, *Hipposideros diadema*, *H. larvatus* and *H. pomona*, and the eulipotyphlan species *Hylomys suillus*, *Crocidura attenuata*, *C. fuliginosa* and *Suncus etruscus* are known additionally from the region in which the cave is situated (Corbet & Hill, 1992; Hutterer, 2005; Bumringsri et al., 2006).

Chiroptera – Eighteen rhinolophid bat species have been recorded from Thailand (Bumrungsri *et al.*, 2006) but a lack of identifiable material means that it cannot be determined if any of these is represented by the left first upper rhinolophoid molar recovered (KK9).

The emballonurid bat species of the subfamily Taphozoinae that are known from southern Thailand are *Saccolaimus saccolaimus*, *Taphozous longimanus* and *T. melanopogon*. A further species of *Taphozous*, *T. theobaldi*, occurs in Thailand and this is known at present only from central areas of the country. Further material is necessary to show whether any of these species is represented by the edentulous right ramus (KK10) or the left M3 (KK11).

Scandentia – Two species of Tree shrew (*Tupaia belangeri* and *T. glis*) occur in Thailand. *Tupaia belangeri* is found north of the Isthmus of Kra (Han *et al.*, 2008) while the range of *T. glis* extends south of the Isthmus through Malaysia and into Indonesia (Han, 2008). Based on recent specimens, it would seem reasonable to surmise that the second right lower molar (KK12) is more likely to represent *T. glis* than *T. belangeri*. To confirm this identification, however, further material is required.

Eulipotyphla – The genus *Crocidura* is well represented both in the samples taken from Khao Kao Cave and throughout Thailand and SE Asia (Corbet & Hill, 1992; Hutterer, 2005). The fragmentary jaws (KK122) and two humeri (KK221, KK222) may be attributed to one or more of these species.

The shrews, *Crocidura hilliana*, *C. indochinensis* and *C. vorax* occur in central and northern parts of Thailand but these species are not known currently from the southern part of the country (Chiozza, 2008a,b; Lunde, 2008). Shrews' high metabolic rate makes them especially dependent on food availability and the absence of a particular food source caused by temperature increases since the end of the Pleistocene and during the Holocene may account for the current retracement of these three taxa northwards.

The species' diversity in the 9.85 kg of fossiliferous matrix processed so far from Khao Kao Cave is high. Analysis of the material has enabled 11 taxa new to Thailand's fossil record to be identified with the numbers of known bat and eulipotyphlan species each being doubled by the addition of material identified herein. As well as the bat, tree shrew and eulipotyphlan taxa mentioned above, jaws, teeth, and bones of rodents were recovered from the fossiliferous matrix within Khao Kao Cave. This material is undergoing analysis currently and it is hoped that the results will be made available in a subsequent publication.

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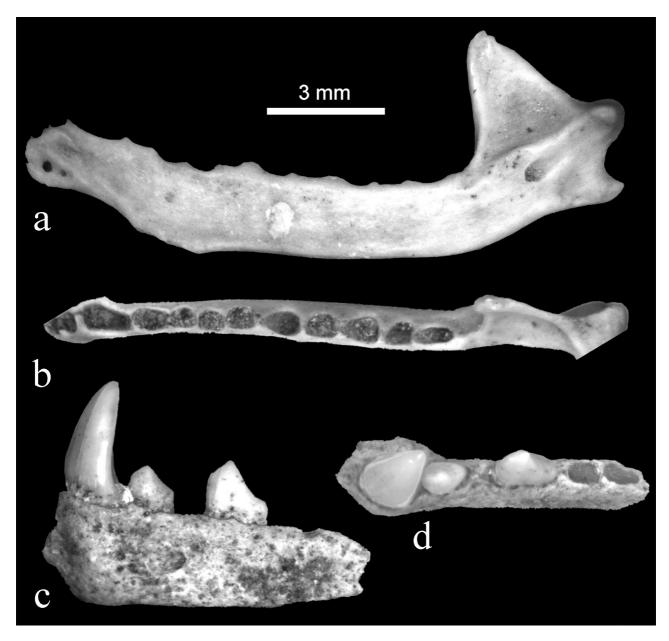


Plate A. a, b. *Taphozous* sp., edentulous right ramus (KK10): a. lingual view; b. occlusal view; c, d. *Eonycteris spelaea* (Dobson, 1871), right mesial ramal fragment with c, p1, p2, and alveolus of p3 (KK1); c. buccal view; d. occlusal view.

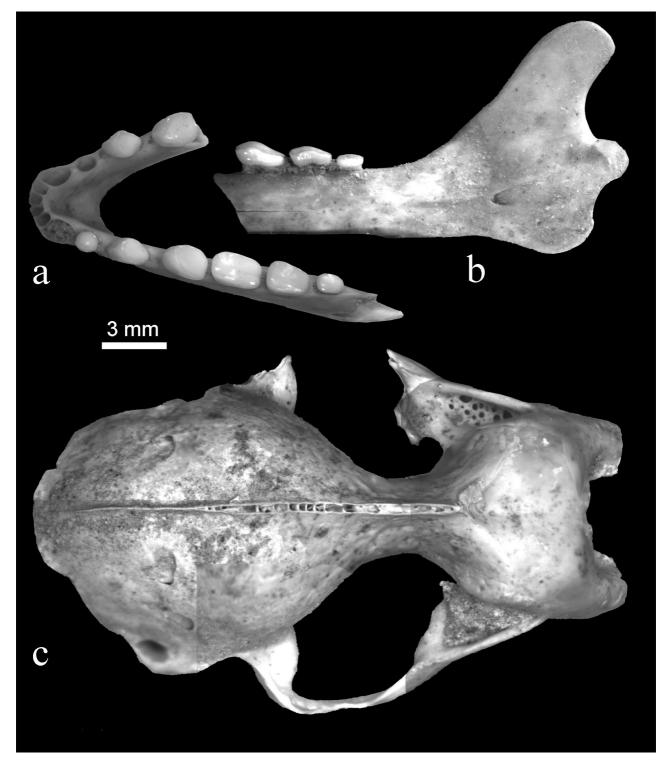


Plate B. a, b: *Rousettus amplexicaudatus* (E. Geoffroy, 1810), a. incomplete mandible with p1, p2, p3, m1, m2, m3 sin., p2, p3 dex. (KK2), occlusal view; b. distal right ramus with m1, m2, m3 (KK3), lingual view; c: *Hipposideros diadema* (E. Geoffroy, 1813, intact cranium (KK5), dorsal view.

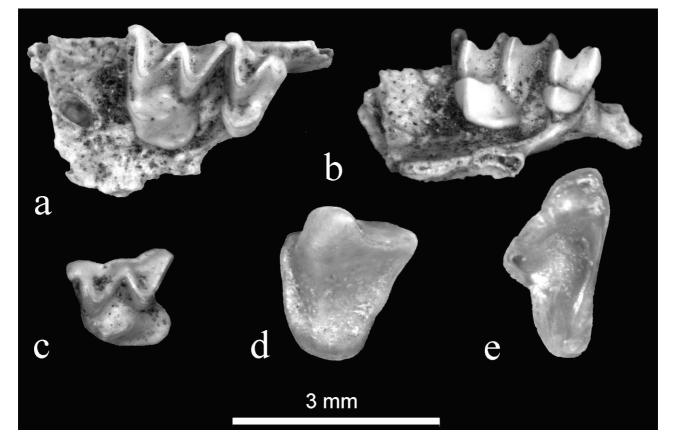


Plate C. a, b. *Hipposideros pomona* Andersen, 1918, left maxilla with alveolus of M1; M2, M3 *in situ* (KK8); a. occlusal view; b. oblique distal view; **c.** Rhinolophoidea indet., M1 sin. (KK9), occlusal view; **d**. *Hipposideros larvatus* (Horsfield, 1823), P4 sin. (KK7), occlusal view; **e**. *?Taphozous* sp., M3 sin. (KK11), occlusal view.

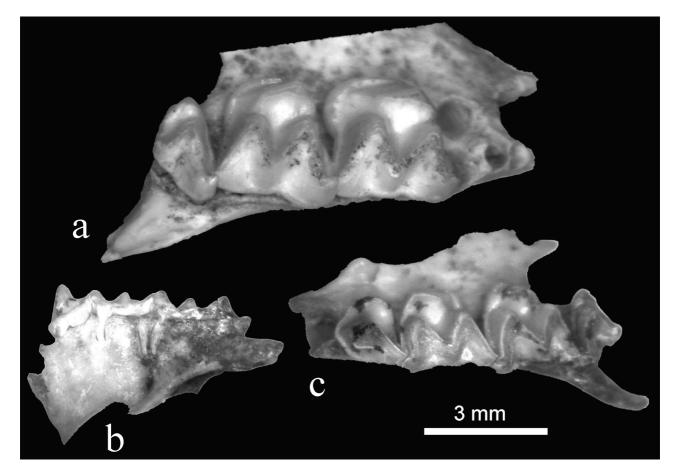


Plate D. a. *Hipposideros diadema* (E. Geoffroy, 1813), left maxillary toothrow with alveolus of P4; M1, M2, M3 in situ (KK5), occlusal view; **b, c.** *Hipposideros larvatus* (Horsfield, 1823), right maxilla with alveoli of C, P3; P4, M1, M2, M3 in situ (KK6); b. buccal view; c. occlusal view.

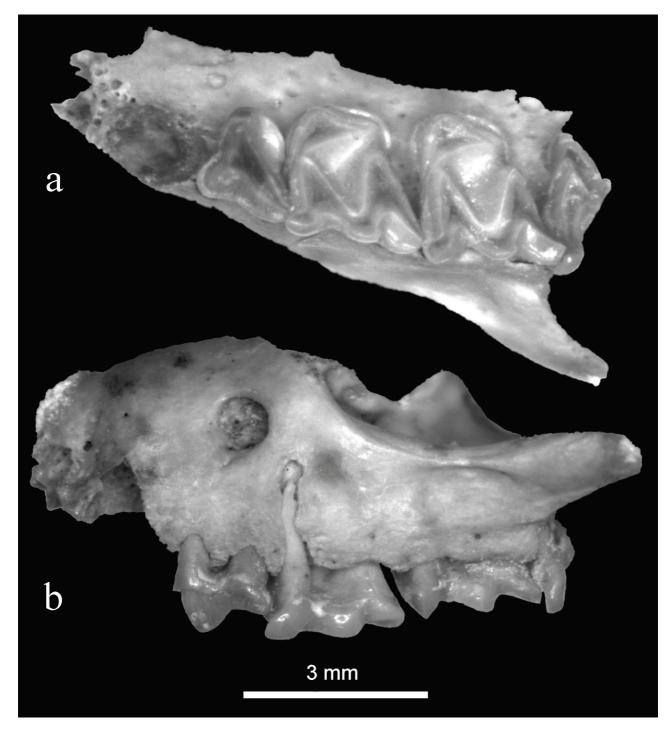


Plate E. *Eptesicus chutamasae* sp. nov., holotype (HZM 1.39818); right maxilla with alveoli of I1, I2, C; P4-M3 *in situ;* a. occlusal view; b. buccal view (image reversed).



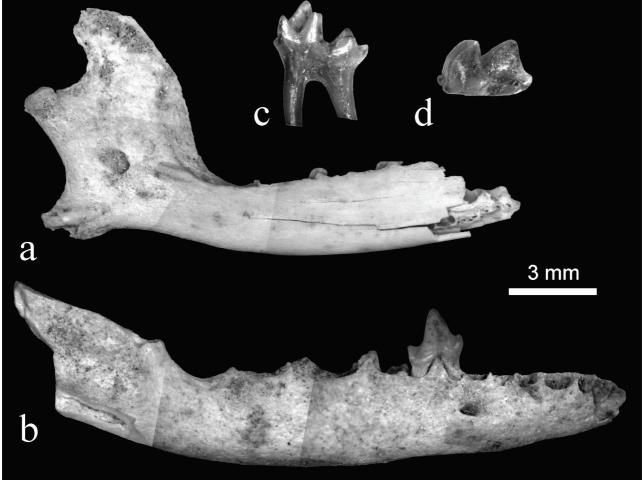


Plate F. a, b. *Hylomys suillus* Müller, 1840: a. left edentulous mandibular ramus (KK35); b. right mandibular ramus with p4 (KK2); **c, d.** *Tupaia* sp., m2 dex. (KK12); c. buccal view; d. occlusal view.

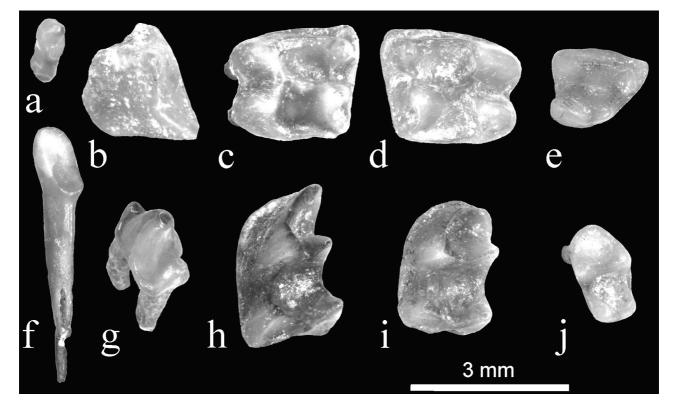


Plate G. a-j. *Hylomys suillus* Müller, 1840; a. I3 (KK30); b. P4 sin. (KK29); c. M1 sin. (KK92); d. M2 dex. (KK93); e. M3 sin. (KK91); f. i2 dex. (KK223); g. p4 sin. (KK53); h. m1 sin. (KK39); i. m2 sin. (KK46); j. m3 dex. (KK89) - occlusal views.

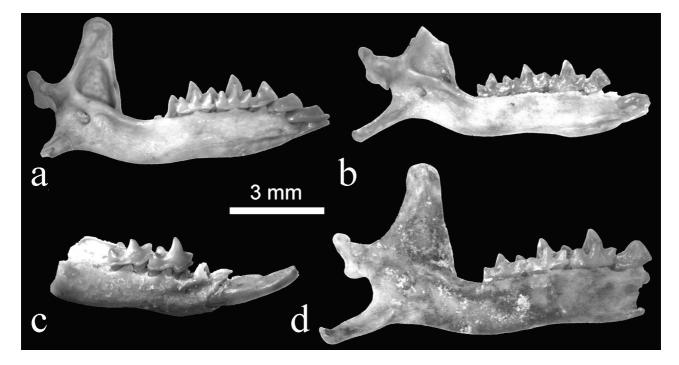


Plate H. a,b. *Crocidura attenuata* Milne-Edwards, 1872: a. left ramus with part i1, a1, a2, m1, m2 (KK151), lingual view; b. left ramus with a2, m1, m2, m3 (KK167), lingual view; c. *Crocidura hilliana* Jenkins & Smith, 1995, right ramus with i, m1, m2 (KK184), lingual view (image reversed); d. *Crocidura fuliginosa* (Blyth, 1856), left distal ramus with a2, m1, m2, m3 (KK56), lingual view.

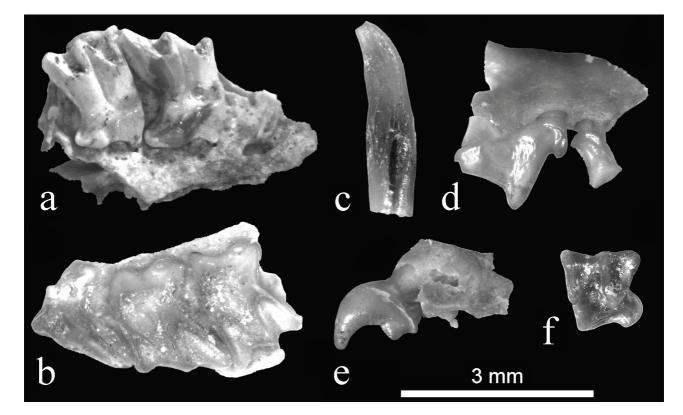


Plate I. a. *Crocidura hilliana* Jenkins & Smith, 1995, right maxilla with M1, M2 (KK183), occlusal view; b. *Crocidura attenuata* Milne-Edwards, 1872: left maxillary fragment with P4, M1, M2 (KK150), occlusal view; c. *Suncus etruscus* (Savi, 1822): i1 (KK54), lateral view; d-f. *Crocidura indochinensis* Robinson & Kloss, 1922; d. right maxillary fragment with A3, P4 (KK206), buccal view; e. left maxillary fragment with I1 (KK204), buccal view; f. M2 sin. (KK214), occlusal view.



Plate J. Crocidura fuliginosa (Blyth, 1856), intact skull with complete dentition (KK55); a. occlusal view; b. right lateral view.

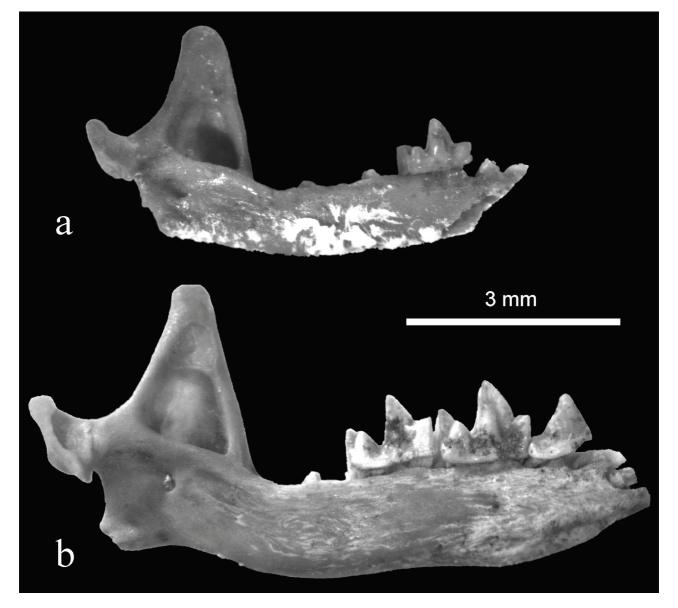


Plate K. a. *Suncus etruscus* (Savi, 1822): left ramus with m1 (KK95), lingual view; **b.** *Crocidura indochinensis* Robinson & Kloss, 1922, right ramus with a3, m1, m2 (KK215), lingual view (image reversed).

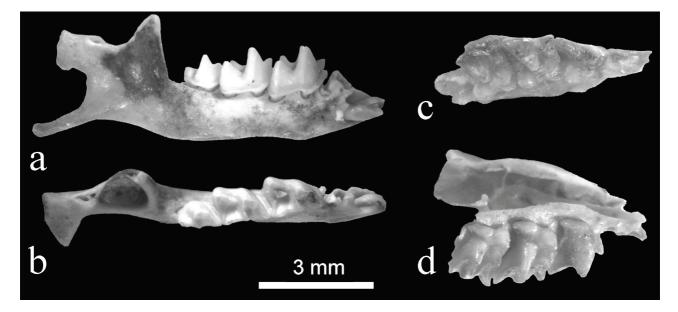


Plate L. *Crocidura vorax* Allen, 1923. **a**, **b**. right ramal fragment with m1, m2, m3 (KK104); a. buccal view, b. occlusal view (image reversed); **c**, **d**. right maxillary fragment with P4, M1, M2 (KK220): c. occlusal view; d. lingual view.

One of the papers in the present issue was erroneously sent for printing without proof reading, which necessitates the following

ERRATA

for the paper: A review of the Cainozoic small mammal fauna of Thailand with new records (*Chiroptera; Scandentia; Eulipotyphla*) from the late Pleistocene, by M.J. Pearch, S. Bumrungsri, J.-L. Schwenninger, D.J. Ward & D.L. Harrison, printed on pages 59-99 (not 98 as stated on the title page).

- p. 61. Table 1b. Caption should read: "Table 1b. Fossil Eulipotyphla and Rodentia (Baluchimyidae, Sciuridae, Gliridae, Platacanthomyidae, Castoridae, Rhizomyidae, and Cricetidae) from late Eocene to middle Miocene sites in Thailand.
 † = genus (and species) extinct, †† = species extinct, XX = invalid species.
- p. 74. Column 2. Line 40 should read: "(Myanmar)]."
- p. 78. Figure 3. Caption should read: "Figure 3. a, b. *Eptesicus chutamasae* sp. nov. Right maxilla with alveoli of I1, I2, C; P4-M3 *in situ* (holotype) (HZM 1.39818): a. occlusal view; b. buccal view. 3c. *Eptesicus serotinus* (HZM 41.8487 nr. Hollingbourne, Kent, U.K.): right toothrow, occlusal view.
- p. 78. Table 10. Caption should read: "Table 10. Dental measurements (in mm.) of *Eptesicus chutamasae* sp. nov. from Khao Kao Cave, Thailand. n = number of teeth/toothrow measurements taken.
- p. 78. Table 11. Caption should read: "Table 11. Dental measurements (in mm.) of *Eptesicus serotinus* (Schreber, 1774) from Algeria, Germany, Hungary, Israel, Italy, Spain, and the United Kingdom.
 n = number of teeth/toothrow measurements taken.
- p. 83. Column 2. Line 10 should read: "2005; Bumrungsri et al., 2006)."
- p. 84. Bibliography. The references "Dobson, G.E. 1871a ..." [column 1] to "(25) Ducrocq, S., Chaimanee, Y., Suteethorn, V. & Jaeger, J.-J. 1995 ..." (up to and including the words "*Journal of*") [column 2] should be deleted from their current position and inserted after the following reference: "Diard, P.M. 1820. Report of a meeting of the Asiatic Society of Bengal for March 10th., 1820. Asiatic Journal and Monthly Register for British India and its Dependencies 10: 477-478." [p. 85, column 2, lines 1-5 (part)].

The managing editor apologises for this inconvenience.

(AWJ)