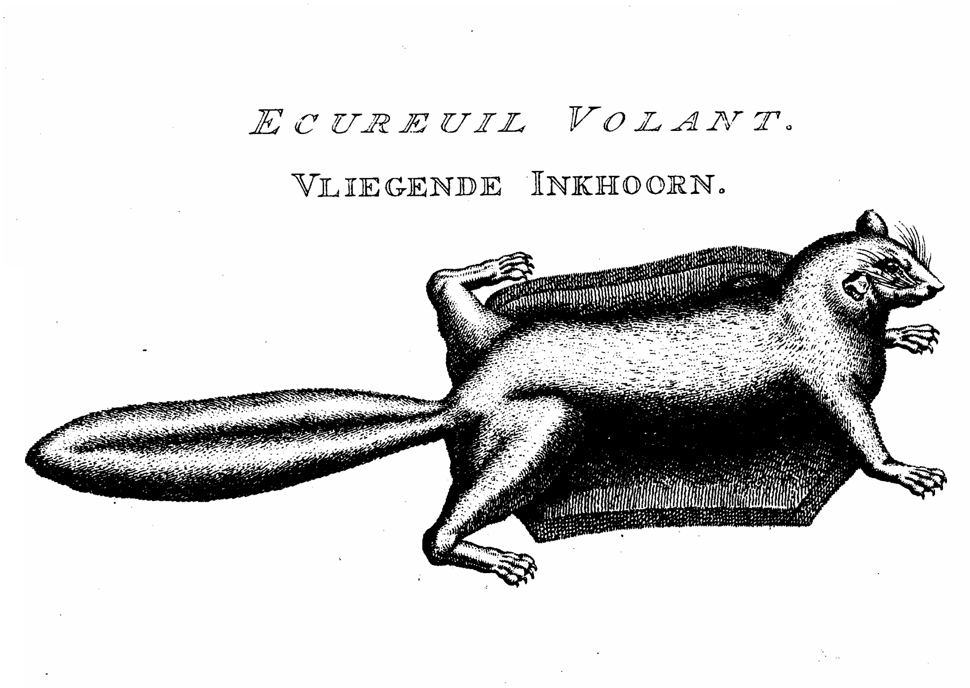
CHAPTER 4: FURTHER DATA MINING ON FAUNAL EVOLUTION IN THE INDO-MALAYAN REGION

> “The curling locks of her bright flowing hair are purest gold; her smooth forehead the Elysian Plain; her brows are two celestial bows; her eyes two glorious suns; her cheeks two beds of roses; her lips are coral; her teeth are pearl; her neck is alabaster; her breast marble; her hands ivory; and snow would lose its whiteness near her bosom. Then, for the parts that modesty has veiled, my imagination, not to wrong them, chooses to lose itself in silent admiration; for nature boasts nothing that may give an idea of their incomparable worth”
>
> Don Quixote on his Dulcinea of Toboso, Cervantes



Drawing of a flying squirrel from the Philippines [in Historische Beschrijving der Reizen of Nieuwe en Volkome Verzameling van de Allerwaardigste en Zeldzaamste Zee- en Land-Togten, Vol 18 (1759)]. This is presumably a *Hylopetes* or *Petinomys* species, which the authors described as the size of a hare and the colour of a fox, although confusingly the authors claim that this animal also occurs in Pulo Condor (=Con Son, offshore SE Vietnam), where at present no flying squirrels exist.

4.1 FOSSIL VERTEBRATES

In this section, I provide an overview of the fossil faunas of SE Asia, with an emphasis on Java, Borneo, Sumatra, and the Malay Peninsula. As much as possible I have attempted to accurately assess species occurrence in the fossil record, although I realize that the data are incomplete, especially for mainland Asia. Still, what matters is not that the fossil record is incomplete—and that my compilation is an incomplete representation of that fossil record—but whether data incorporated in the fossil record are adequate to test my hypotheses, i.e. I am interested in the occurrence of certain species and species groups, and how and when they were replaced by others. Thus, I use the fossil record in combination with my palaeoenvironmental and palaeogeographical reconstructions and with data on phylogenetics to generate and test hypotheses that spring from my new biogeographical model.

Fossil vertebrates of Java

Shutler and Braches (1985) summarised the major changes in Java's faunal composition since the likely arrival of the first mammals. They estimated this event at approximately 2.7 Mya, while van den Bergh et al. (1996) estimated it at 2.0 Mya. Recently, however, the first arrival of mammals on Java was tentitatively pushed back some 3 Myr by Kramer et al. (2001), who found fossilized bovid remains in West Java below a deposit that was aged at 5 Myr. If these dates are correct and the fossils are autochthonous, then mammals have occurred in Java since the Early Pliocene. Interestingly, von Koenigswald (no year mentioned, in van Bemmelen 1970, p. 650) described a fossil tooth of Pliocene age, of what could be a rhinoceros. However, the dating of this specimen is problematical and the specimen may in fact be a modern Javan Rhinoceros (*Rhinoceros sondaicus*) and unlikely to be of Pliocene age. The Cidulang vertebrate fauna, found in this area, also remains stratigraphically unresolved. It alternates with marine strata assigned to the Late Pliocene, which would fit the date of the first mammals on Java of 2.7 Mya (Shutler & Braches 1985), or 2.0 Mya by van den Bergh et al. (1996).

The Late Pliocene–Early Pleistocene mammals of Java included large species such as the elephant-like *Archidiskodon* (=Elephas planifrons Maglio 1973), a hippopotamus, a rhino, several pig species and several deer. These species showed a clear relationship with the Indian Siwaliks fauna, and the fauna was hence named Siva-Malayan fauna. Furthermore, carnivores like *Lutra robusta* and *Felis* sp. have been found and possibly a Bamboo Rat of the genus *Rhizomys* (Hooijer 1952; Medway 1971). All these species appear to be good swimmers and it is possible that, at that time, Java was reached by cross-sea dispersal. This picture remains through the Satir fauna (2–1.5 Myr) where all species (proboscideans, cervids and hippos) are good swimmers, and where the impoverished fauna indicates to van den Bergh et al. (1996) that Java was still an island reached by sweepstake dispersal. However, as Heaney (1985) pointed out, this may also be attributed to preservation or collection matters; archaeological research in Java rarely used finely meshed sieves and small mammal remains, if present, could have remained unnoticed. Indeed, recent exploration for micro fauna fossils have revealed species such as *Chiropodomys gliroides*, the Common Pencil-tailed Tree-mouse, and several species of *Mus* and *Rattus* in the Late Pliocene–Early Pleistocene Satir and Kali Glagah faunas (van der Meulen and Musser 1999).

The composition of the Middle Pleistocene Trinil fauna, which includes several forest species such as *Pongo pygmaeus* and *Symphalangus syndactylus*, suggests at least a partially forested Java. Note that van den Bergh et al. (1996) did not accept the presence of the two latter species, but Kaifu et al. (2001) presented convincing evidence of their occurrence. It also suggests that these poor dispersers and poor swimmers reached Java via a land connection. It is interesting that de Vos et al. (in Musser 1982b) suggested that, based on the relatively low species number of the Trinil fauna and the development of an endemic like *Duboisia*, Java must have been isolated from the Asian mainland in Middle Pleistocene (ca. 900–800 Kya, but note that dating by Larick et al. (2001) suggested a much older age for the Trinil fauna: 1.5–1.4 Mya). However, *Duboisia* has also been described from the Malay Peninsula (Hooijer 1963b), and was therefore not endemic to Java (unless Malayan fossils were misidentified). Heaney (1985) did not agree with de Vos et al.'s hypothesis, because of the presence on Java of a large number of ungulate and carnivore species at that time, which are typically quite rare on islands. Also, Heaney pointed out that the recovered fossils of the 'depauperate' Trinil fauna represent only a portion of the original fauna, and that the processes of preservation or collection systematically underrepresented the more abundant smaller species. A fauna such as that described from Trinil, consisting for a significant part of large ungulates, primates, and carnivores, would be unique among tropical island faunas. In fact, Heaney considered the Trinil fauna typical for a full continental fauna, suggesting that Java was then connected to the other islands of the Sunda Shelf area, and that much of the Trinil fauna occurred also on Borneo and Sumatra. Van der Meulen and Musser (1999) proved Heaney largely right when they discovered a Middle Pleistocene (Trinil, Grenzbank) rodent fauna on Java. Interestingly, because of the predominance of *Rattus* species, they considered the faunal composition to be more of an Indochinese than Sundaic character. The open woodland environment deduced from the larger mammal association was confirmed by the presence of the wide-toothed *Rattus* sp. A, which was presumably a grassland species.

A collection of fossil bird remains from Trinil provides some insight into the vegetation of the area at the time of deposition and possibly also into the climate in higher latitude areas. Finds of *Leptoptilos* cf. *dubius* (an Adjutant Stork) and *Ephippiorhynchus* cf. *asiaticus* (Black-necked Stork of India, SE Asia—but not Sundaland—and Australia) suggest the presence of grassy areas, mud banks, mangroves, swamps, or open and lightly wooded areas, which also seems to fit the picture for *Pavo muticus* (Green Peafowl) habitat (MacKinnon & Phillipps 1993; Simpson & Day 1996). The presence of *Branta* cf. *ruficollis* (a goose of western Siberia), a northern winter migrant whose southern limit of the wintering range is presently much further north, could indicate colder climate at higher altitudes. Similarly, the presence of *Tadorna tadornoides* (Australian Shelduck), a southern Australian endemic, suggests that colder conditions existed in Australia some 900–800 Kya, forcing birds to migrate north into island SE Asia (Weesie 1982). During deposition of the Watualang beds, the presence on Java of *Grus grus* (Common Crane), a temperate species, also indicates colder conditions in mainland Asia. Weesie (1982) suggested that the two colder periods of late Trinil and Watualang might have been separated by a warmer one, during which Java was an island.

The Trinil conditions changed during the deposition of the Kedung Brubus sediments when a wave of Asiatic mammals entered the region, probably during a glacial maximum (Musser 1982b). The Kedung Brubus fauna, which has been aged at 0.8–0.7 Myr or 1.3–0.8 Myr (see Larick et al. 2001), brought in several new medium to large-sized mammals (*Rhinoceros unicornis*, *Tapirus indicus*, *Manis palaeojavanica*, *Hyaena brevirostris*, *Lutrogale palaeoleptonix*) (Brandon-Jones 1998), and seems to be characterised by open woodland species (van den Bergh et al. 1996). A fauna similar to the Kedung Brubus fauna was found in Citarum, West Java (Aziz & de Vos 1999), which indicates that at that time there was probably a land connection between Central and West Java. Batchelor (1979) suggested that, following the Kedung Brubus fauna, during inter-glacials the major extinctions occurred of the savannah-adapted land mammals because of their geographical isolation and the unsuitability of increasingly homogenous, dense rainforest habitat. Other species that persisted into the Ngandong fauna but then perished included: *Panthera palaeojavanica*, *Stegodon trigonocephalus*, and *Hippopotamus sivalensis* (Medway 1971). The Ngandong fauna itself has been dated at between 46 and 27 Kyr by some and at 300 Kyr by others (see Westaway 2002, for an overview). *Homo sapiens* arrived ca. 110 Kya, or possibly later, while between 110 and 70 Kya *Pongo* and *Hylobates* probably arrived on Java through a continuous humid forest cover with Sumatra/Borneo (van den Bergh et al. 1996) (but note that the latter two genera might have been present on Java at an earlier stage as well). This so-called Punung fauna existed between 80–60 Kya (van den Bergh, 1999). Along with *Sus scrofa* and *Pongo pygmaeus*, it brought a number of species associated with tropical wet evergreen forest. Brandon-Jones (1998) suggested that *Pongo* disappeared from Java round 50 Kya, whereas Dobson (1953-54) found indications that the species may have persisted into the 17th century. Other species that occurred in the Punung fauna but have disappeared from Java since then include Siamang *Symphalangus syndactylus*, Golden Cat *Catopuma temmincki*, Asian Tapir *Tapirus indicus*, Serow *Naemorhedus sumatraensis*, Asian Elephant *Elephas maximus*, Moonrat *Echinosorex* sp., and *Sus barbatus*.

Finally; the early Holocene fauna of Java in Sampung, included the following species: *Nycticebus coucang*; *Presbytis cristata*; *Macaca fascicularis*; *Homo sapiens*; *Lepus nigricollis*; *Ratufa bicolor*; *Callosciurus notatus*; *Hystrix brachyurus*; *Cuon alpinus*;

Amblonyx cinerea; *Paradoxurus hermaphroditus*; *Panthera tigris*; *P. pardus*; *Neofelis nebulosa*; *Prionailurus bengalensis*; *F. rubiginosa* (doubtful record); *F.* cf. *chaus* (?); *Elephas* sp.; *Rhinoceros sondaicus*; *Sus scrofa*; *Tragulus javanicus*; *Muntiacus muntjak*; *Cervus unicolor*; *Bos* (*Bibos*) *javanicus*; and *Bubalus*? *palaeokerabau* (Medway 1971). Van den Brink (1982) also reported *Axis kuhli* from the Holocene deposits at Wajak, East Java. This species now only occurs on Bawean Island in the Java Sea. Table 4.1 provides an overview of the fossil mammals of Java.

	Tjidulang (3 - 2 Myr)	Kali Glagah (2 Myr)	Satir (2 - 1.5 Myr)	Bukuran	Ci Saat (?- 1.51 Myr)	Trinil (900 Kyr)	Kedung Brubus (700 Kyr)	Ngandong (195 Kyr and onwards)	Punung (80 - 60 Kyr)	Holocene Caves (10 Kyr)	Recent
Primates											
Homo erectus					?	■	■	■			
Homo sapiens									■	■	■
Pongo pygmaeus					?				■	?	?
Symphalangus syndactylus					?				■		
Hylobates moloch											■
Nycticebus coucang										■	■
Trachypithecus auratus						■	▤	▤	▤	■	■
Presbytis comata						?					■
Macaca fascicularis						■	▤	■	▤	■	■
M. nemestrina									■		
Pholidota											
Manis palaeojavanica							■				
Manis javanica										■	■
Rodentia											
Hystrix brachyurus						■	▤	▤	■	■	
Hystrix javanica										■	▤
Hystrix gigantea			lacking stratigraphical information								
Maxomys sp.						■					
Rattus trinilensis						■					
Rattus aff. *tiomanicus*						■					
Rattus sp. A						■					
Rattus sp. B.						■					
Rattus sp. C.						■					
Rattus sp. indet.						■					
Mus sp.		■									
Rattus sp.		■									
Chiropodomys gliroides					■						
Rattus sp.					■						
Carnivora											
Lutra robusta		■									
Lutra lutra											■

Lutra sumatrana											■
Amblonyx cinerea										▨	▨
Lutrogale palaeoleptonyx							■				
	Tjidulang (3 - 2 Myr)	Kali Glagah (2 Myr)	Satir (2 - 1.5 Myr)	Bukuran	Ci Saat (?- 1.51 Myr)	Trinil (900 Kyr)	Kedung Brubus (700 Kyr)	Ngandong (195 Kyr and onwards)	Punung (80 - 60 Kyr)	Holocene Caves (10 Kyr)	Recent
Lutrogale robusta			lacking stratigraphical information								
Melogale personata											■
Mydaus javanensis											■
Arctogalidia sp.										■	■
Arctictis binturong											■
Paradoxurus hermaphroditus										■	■
Prionodon linsang											■
Viverricula indica											■
Mustela lutreolina											■
Martes flavigula										■	■
Herpestes javanicus											■
Hyaena brevirostris							■				
Cuon javanicus										■	
Cuon javanicus (=*alpinus*)											■
Megacyon sp.			lacking stratigraphical information								
Megantereon sp.			lacking stratigraphical information								
Panthera sp.					?						
Panthera tigris						■	■	■	■	■	■
Panthera pardus					?	?					■
Prionailurus viverrinus											■
Prionailurus bengalensis						■	▨	▨	▨	■	■
Homotherium zwierzyckii						■					
Homotherium ultimum			lacking stratigraphical information								
Mececyon trinilensis						■					
Hemimachairodus zwierzyckii			lacking stratigraphical information								
Ursus malayanus									■	■	
Proboscidea											
Mastodon bumiajuensis		■									
Elephas planifrons	■	■									
Elephas hysudrindicus							■	■			
Elephas maximus									■	■	
Elephas indonesicus			lacking stratigraphical information								
Tetralophodon bumiajuensis		■	■								
Stegodon trigonocephalus		■	▨	▨	■	■	■	■			
Stegodon cf. *elephantoides*				■							
Stegodon ? *hypsilophus*							?				
Perissodactyla											
Tapirus indicus						■	■	■	■	■	
Rhinoceros sondaicus						■	■	▨	■	■	■
Rhinoceros unicornis kendengindicus							■				

Nestoritherium cf. *sivalense*			lacking stratigraphical information								
Artiodactyla											
Merycopotamus nanus	■										
	Tjidulang (3 - 2 Myr)	Kali Glagah (2 Myr)	Satir (2 - 1.5 Myr)	Bukuran	Ci Saat (?- 1.51 Myr)	Trinil (900 Kyr)	Kedung Brubus (700 Kyr)	Ngandong (195 Kyr and onwards)	Punung (80 - 60 Kyr)	Holocene Caves (10 Kyr)	Recent
Merycopotamus dissimilis			lacking stratigraphical information								
Hexaprotodon sivalensis	■	■	■	■	■	▤	■	■			
Sus stremmi		■									
Sus brachygnathus		■	▤	▤	▤	■	▤	?			
Sus macrognathus							■	■			
Sus sp.									■		
Sus scrofa vittatus									■	■	■
Sus verrucosus										■	■
Cervus (*Rusa*) *stehlini*		■									
Cervus problematicus		■				■					
Cervus hippelaphus (=timorensis)			■	▤	■	■				■	■
Cervus sp.							■	■			
Cervus palaeojavanicus					■	■					
Axis lydekkeri		■	■	▤	■	■	■				
Axis kuhli										■	
Antilope saatensis					■	■					
Duboisia santeng					■	■	■				
Muntiacus muntjak					■	■	■	▤	■	■	■
Bubalus palaeokerabau						■	■	■		■	
Bubalus arnee									■	■	
Leptobos? problematicus			lacking stratigraphical information								
Epileptobos groeneveldtii							■				
Bos palaesondaicus						■	■	■			
Bos sp.									■		
Bos javanicus										■	■
Capricornis sumatraensis									■		
Tragulus javanicus										■	■

Table 4.1. Faunal list of Java's fossil sites (Medway 1971; Hooijer 1975; Aimi & Aziz 1985; van den Bergh et al. 1996).

Fossil vertebrates of Sumatra, Borneo, Palawan, and the Malay Peninsula

Late Tertiary and Quaternary fossils are rare in Sumatra. Dubois investigated some caves in the Padang Highlands in 1890 and found some subfossils of 15 mammal species from several thousand years ago. The bulk of the material originates from three caves, i.e., the Lida Ajer Cave near Pajakombo, and the Sibrambang Cave and

Djamboa Caves near Tapisello (de Vos, 1983), and contained *Homo sapiens, Panthera tigris*, *Helarctos malayanus*, *Elephas maximus*, *Tapirus indicus*, *Dicerorhinus sumatrensis*, *Capricornis sumatraensis*, *Cervus* (*Rusa*) sp., *Sus barbatus*, *S. scrofa*, *Presbytis melalophos*, *Macaca nemestrina*, *M. fascicularis*, *Hylobates* sp., *Trachypithecus cristatus*, *Symphalangus syndactylus*, *Pongo pygmaeus* (named P. duboisi by Drawhorn 1994), *Hystrix brachyura*, and *Bos javanicus*. This fossil record gives a very incomplete picture of the faunas that have lived in the Sumatra region, as I expect these to be at least 10 Myr old [based on the estimated time of divergence of *Nesolagus netscheri*, a Sumatran endemic, from its nearest relative on the Asian mainland (see Chapter 4.2)].

Fossil finds from Borneo are also rare. Stromer (1931) described fossil finds of *Choeromorus* and *Anthracotherium* (Suidae) from the Melawi River area in West Kalimantan province, dated by him as Eocene. These fossils have not been studied since, and their present museum location is unknown. These very old finds may indicate that mammals occurred on Borneo at least by the Early Oligocene and possibly earlier. The next finds date back to Middle Pleistocene times (ca. 900 Kyr) and include *Elephas namadicus*, which was found near Samarinda in East Kalimantan. The same species and *Stegolophodon lydekkeri* were recovered from unstratified deposits in Brunei, dated at approximately 800 Kyr. Both these species were absent on Java, indicating that an ecological barrier existed and that the species reached Borneo by a north-western land-bridge (Medway 1971). Also in Brunei, but much later (ca. 80 Kyr), the Pleistocene elephant (*Elephas maximus*) occurred (Hooijer 1972). Recently, Cranbrook et al. (2000) described fossils of *Hippopotamus (=Hexaprotodon*), which they considered to be morphologically similar to *H. sivalensis*, and of *Stegodon*, which was most like *S. elephantoides*; these finds presumably originated from Late Pliocene to Middle Pleistocene deposits in Indonesian Borneo and were likely recovered by Indonesian gold miners near Sintang, West Kalimantan.

The more complete fossil records in Borneo are all of Late Pleistocene to Holocene age. They include the finds from the Niah and Bau Caves in Sarawak, the Madai Caves in Sabah, and recently discovered cave deposits in the Berau region of East Kalimantan. These are all modern faunas, albeit with a distribution range that was considerably different from that found in the present. For instance *Melogale*, the Ferret Badger, and *Hylomys suillus*, the Lesser Gymnure, can now only be found at high altitudes, whereas these species occurred at sea-level during the LGM (Medway 1964; Majid 1982). Also remains of *Manis palaeojavanica* (Medway 1971), *Panthera tigris*? (Hooijer 1963a; Harrison 1998), *Rhinoceros sondaicus*, *Cuon alpinus* (repudiated by Medway 1964), and *Tapirus indicus* (Hooijer 1963a) have been found in the Holocene deposits, while none of these species presently occurs on Borneo (for further discussion of tiger and tapir occurrence refer to Meijaard 1999a; Meijaard & van Strien in press).

In Palawan, an excavation of Late Pleistocene–Holocene deposits by Reis et al. (2001) revealed the following mammals: *Crocidura palawanensis*, *C.* sp., *Cynopterus brachyotis*, *Eonycteris spelaea*, Pteropididae sp., *Emballonura* cf. *alecto*, *Megaderma spasma*, *Hipposideros diadema*, *Rhinolophus* sp., Rhinolophidae sp., Vespertilionidae sp., Chiroptera sp., *Macaca fascicularis*, *Hylopetes nigripes*, *Sundasciurus* sp., Sciuridae sp., *Chiropodomys calamianensis*, *Maxomys panglima*, *Rattus* cf. *norvegicus*, *Rattus* sp., Muridae sp., *Hystrix pumila*, Rodentia sp., *Amblonyx cinereus*, and *Sus barbatus* [note that *S. barbatus ahoenobarbus*, the subspecies from Palawan, has recently been elevated to species level, *S. ahoenobarbus* (Groves 2001c) and appears to be only distantly related to *S. barbatus* (Lucchini et al. in prep.)].

Similar to Sumatra, Borneo, and Palawan, fossils other than plants are not common on the Malay Peninsula, and Middle Pleistocene fossils have been identified only for the following species: cf. *Cynogale*, *Elephas namadicus*, *Rhinoceros sondaicus*, *Sus* sp., *Hippopotamus* sp., *Cervus* (?*Rusa*) sp., *Duboisia santeng*, *Bibos* and/or *Bubalus* sp. (Hooijer 1963a). Apart from these, a collection of vertebrate bone fragments was found in a mine near Batu Gajah in the southern Kinta Valley. This yielded identifications of a rhinoceros, a suid, and a deer ("probably *Hydropotes* and possibly *Muntiacus*") (A.D. Hooijer, personal communication in Stauffer 1973). Further elephant teeth were found in north Kinta and near Raub, Pahang (Savage, 1937 and Richardson, 1939 both in Stauffer 1973), while recently, the fossilized remains of a large mammal were discovered at the roof of the Gua Naga Mas Cave at a height of about 37 m above the ground. H.D. Tjia apparently described this fossil in 2000 (In

Warisan Geologi Malaysia 3: 209-218), but this publication could not be obtained. Internet sources refer to a cat, possibly a leopard. The fossils are younger than 228 Kyr (Ros Fatihah Muhammad et al. 2000).

Fossil vertebrates of Thailand and Indochina

Below I provide an overview of the fossil record of Thailand and Indochina, although I know this to be far from complete, as I have not exhaustively searched the available literature on this subject. The main sources that I have used include Cuong (1985 in Olson & Ciochon 1990) who provided faunal lists of Late Pleistocene and Holocene sites in Vietnam (Table 4.2) and Chaimanee (1998), who compiled the Late Tertiary and Quaternary rodent faunas of Thailand (Table 4.3). Other sources include Ducrocq et al. (1994), who described the Miocene fauna of northern Thailand, and Tougard et al. (Tougard et al. 1998), who described the late Middle Pleistocene fauna of northern Thailand.

	Tham Khuyen 300,000 - 200,000	Thum Wiman Nakin 350,000 - 80,000	Tham Hai	Tham Om	Hang Hum I 140,000 - 80,000	Hang Hum II 140,000 - 80,000	Lang Trang	Keo Leng 30,000 - 20,000
Primates								
Gigantopithecus blacki	■		?					
Homo erectus	■		■					
Homo sapiens				■	■	■		■
Nomascus cf. *concolor*	■							
Macaca cf. *assamensis*	■							■
Macaca cf. *mulatta*								■
Macaca nemestrina		■						
Macaca sp.	■		■	■	■	■	■	■
Pongo pygmaeus "weidenreichi"			■					■
Pongo pygmaeus pygmaeus						■		
Pongo pygmaeus spp.	■	■					■	
Semnopithecus sp.	?		?		?			■
Trachypithecus/Presbytis sp.							■	
Insectivora								
Crocidura fuliginosa		■						
Hylomys suillus		■						
Rodentia								
Atherurus cf. *macrourus*								■
Atherurus sp.	■		▤	■	?			
Bandicota savilei		■						

Callosciurus finlaysoni		▓						
Cannomys badicus		▓						
	Tham Khuyen 300,000 - 200,000	Thum Wiman Nakin 350,000 - 80,000	Tham Hai	Tham Om	Hang Hum I 140,000 - 80,000	Hang Hum II 140,000 - 80,000	Lang Trang	Keo Leng 30,000 - 20,000
Chiromyscus chiropus		▓						
Chiropodomys gliroides		▓						
Hapalomys delacouri		▓						
Hylopetes spadiceus		▓						
Hystrix sp.	▓							
Hystrix subcristata	▓	▓	▓	▓	▓	▓		▓
Hystrix brachyura							▓	
Leopoldamys sabanus		▓						
Maxomys cf. *niviventer*		▓						
Maxomys surifer		▓						
Menetes berdmorei		▓						
Mus caroli		▓						
Mus pahari		▓						
Mus shortridgei		▓						
Niviventer bukit		▓						
Niviventer confuciacus		▓						
Petaurista petaurista		▓						
Rattus argentiventer		▓						
Rattus koratensis		▓						
Rattus rattus		▓						
Rhizomys sp.				▓				
Rhyzomys cf. *troglodytes*	▓				▓	▤		▓
Vandeleuria oleracea		▓						
Carnivora								
Nyctereutes sp.					▓			
Ailuropoda melanoleuca	▓	■	▤	▓				▓
Ursus malayanus	▓						▓	
Ursus thibetanus kokeni	▓	▓	▓	▓	▓	▓	▓	▓
Arctonyx collaris cf. *rostratus*	▓		▤	▓	▓	▓	▓	▓
Crocuta crocuta ultima		▓			▓			
Cuon javanicus antiquus					▓			
Cuon sp.	▓		▤	▓	▤	▓	▓	
Felis sp.				▓				
Neofelis nebulosa						▓		
Neofelis nebulosa cf. *primigenia*					▓			
Panthera pardus			▓	▤	▓	▓	▓	?
Panthera tigris		▓	▓	▓	▓		▓	?
Catopuma temmincki				▓			▓	
Lutra lutra		▓						
Lutragale perspicilata							▓	
Martes flavigula		▓						
Paguma larvata		▓		cf.	▓			

Paradoxurus sp.						▒		
Paradoxurus cf. *hermaphroditus*	▒	▒	▤	▤	▒	▤		▒
	Tham Khuyen 300,000 - 200,000	Thum Wiman Nakin 350,000 - 80,000	Tham Hai	Tham Om	Hang Hum I 140,000 - 80,000	Hang Hum II 140,000 - 80,000	Lang Trang	Keo Leng 30,000 - 20,000
Viverra cf. *zibetha*				▒				
Proboscidea								
Elephas cf. *namadicus*				▒		▒	▒	
Elephas namadicus	?					▒		
Stegodon orientalis	▒		▒	▒	▒	▤	▒	▒
Perissodactya								
Dicerhorinus sumatrensis							▒	
Rhinoceros sinensis	▒		▒	▒	▒	▒		▒
Rhinoceros sp.				▒				
Tapirus (Megatapirus) augustus	▒		▤	▒	▒	▤		▒
Tapirus indicus							▒	
Tapirus indicus cf. *intermedius*					▒			
Tapirus sp.	▒		▒	▒				
Artiodactyla								
Tragulus javanicus		▒						
Elaphodus sp.				▒				
Muntiacus muntjak cf. *margae*				▒				
Muntiacus muntjak	▒	▒					▒	▒
Muntiacus sp.				▒				▒
Axis porcinus		▒						
Bibos gaurus cf. *grangeri*					▒			
Cervus unicolor	▒	▒	▤	▒	▒	▒	▒	▒
Cervus cf. *unicolor*			▒					
Cervus eldi		▒						
Cervus sp.	▒		▤	▒	▒	▤		▒
Bibos gaurus spp.	▒			▒				?
Bos frontalis		▒						
Bos sauveli		▒						
Bubalus bubalis	▒	▒	▤	▒	▒	▤	▒	▒
Capricornis sumatraensis		■		▒			▒	▒
Caprinae gen. et sp. indet.						▒		
Naemorhedus goral		▒						
Sus scrofa	▒	▒	▒	▒	▒	▒	▒	▒
Sus sp.	▒			▒				▒
Sus cf. *lydekkeri*	▒				▒			▒
Sus cf. *officinalis*					▒			

Table 4.2. Fossil mammals of Indochina and Thailand after Olson and Ciochon (1990); Tougard and colleagues (1996; 1998), and Long et al. (1994).

Chaimanee et al. (1993) described mammal fossils from the Thai Peninsula and from southern mainland Thailand. The deposits were tentatively dated as late Early–early

Middle Pleistocene and contained many species that still occur in that area. In addition to these species, Chaimanee and her colleagues found remains of *Exilisciurus exilis*, a pygmy squirrel now restricted to Borneo, *Iomys horsfieldi*, a flying squirrel which lives presently only in Malaysia, Sumatra, Borneo, and Java. Also, *Hylopetes phayrei*, another flying squirrel presently only occurs further north on the Asian mainland (and was recently also described from Vietnam, see Dao & Cao 1990), while *Vandeleuria oleracea*, an arboreal mouse presently only occurs in the mainland part of Thailand and not on the peninsular (Chaimanee et al. 1993). It is unclear whether these species are the same as the present-day ones, or whether the fossils belong to closely related species that have become extinct. Both Bornean species of *Exilisciurus* (*E. exilis* and *E. whiteheadi*) occur in tall and logged Dipterocarp forest (but are separated by altitude), and *Iomys horsfieldi* occurs in lowland and hill forests, plantations, and gardens with tall trees (Payne et al. 1985). *Hylopetes phayrei* is found in partly cleared forest near cultivation at an elevation of 1,000 m, while *Vandeleuria oleracea* is a small mouse that lives in tall cane (Lekagul & McNeely 1977). These data provide a somewhat mixed palaeoenvironmental signal, with two species of forest or open forest extending their range from the south, one open forest species extending its range from the north, and one grassland species extending its range from the north. Including the fossil species that are still extant on the Thai peninsula, i.e. *Petaurista petaurista*, *Hylopetes spadiceus*, *Petinomys vordermanni*, *Hapalomys longicaudatus*, and *Chiropodomys gliroides*, leads to a clearer palaeoenvironmental interpretation. The former three occur in tall and logged forest, with especially *P. petaurista* being able to survive in rather open areas (Payne et al. 1985), while the latter two species are murids restricted to bamboo vegetation (Lekagul & McNeely 1977). It appears from this that, at the time of the fossil deposition, a rather open forest vegetation type existed on the Thai Peninsula with grasses and bamboo, possibly related to drier and/or cooler climatic conditions. When wetter and/or warmer conditions led to a denser forest type, the four locally extinct species were outcompeted by the ones that remained. This interpretation is, however, tentative, as the ecological characteristics of extinct populations are unknown.

Further Middle Pleistocene palaeoenvironmental information from Thailand is provided by fossil finds of *Hadromys humei* (see Chaimanee & Jaeger 2000c), a rat associated in India with tropical and subtropical monsoon habitats in oak parkland, where it lives on dry hillsides covered with tall grasses at between 1,150 and 1,320 m (Musser, 1987 in Chaimanee & Jaeger 2000c). Fossils of *H. humei* have been found in 10 sites in eastern, northern central/southern and peninsular Thailand, which is much further south than the species' present range in northeastern India and southern China. The layers in which the fossils were discovered are characterized by faunal remains of the Middle Pleistocene *Stegodon-Ailuropoda* zone, and an overlying deposit also suggested an age of >137 Kyr. A Late Pliocene–Early Pleistocene *Hadromys*-related fossil from Thailand suggests that this group of Murinae was formerly more diversified in Thailand and that Thailand may have been its area of origin and evolution (Chaimanee & Jaeger 2000c). Chaimanee and Jaeger (2000c) concluded that the fossil record indicate that *H. humei* was distributed throughout Thailand in the Middle Pleistocene, with a southern limit extending to the Songkla Province near the Thai-Malay border. This and data by Chaimanee (1998) suggest a predominance of evergreen forests with patches of grasslands for the Middle Pleistocene of Thailand, but with significantly lower temperatures and humidity than today. Table 4.3 provides an overview of the Late Pliocene–Holocene microfauna of Thailand.

	Late Pliocene	Early Pleistocene	Middle Pleistocene	Late Pleistocene	Holocene
Muridae					
Ratchaburimys ruchae	■	■			
Prohadromys varavudhi n. g. n. sp.	■	■			
Saidomys siamensis n. sp.	■	■			
Hadromys humei		■	■		
Hapalomys delacouri			■		
H. longicaudatus			■	■	■
H. khaorupchangi n. sp.		■	■		
Hapalomys sp. indet.	■	■			
Chiropodomys gliroides	■	■	■	■	■
C. maximus n. sp.			■		
Pichecheir parvus		■	■		
P. peninularis n. sp.		■	■		
Vandeleuria oleracea	■	■	■	■	■
Maxomys surifer	■	■	■	■	■
Bandicota savilei			■	■	■
B. indica			■	■	■

Berylmys berdmorei			■	■	■
	Late Pliocene	Early Pleistocene	Middle Pleistocene	Late Pleistocene	Holocene
Leopoldamys sabanus			■	■	■
L. minutus n. sp.	■	■			
Niviventer fulvescens			■	■	■
N. gracilis n. sp.			■		
Rattus sikkimensis			■	■	■
R. rattus			■	■	■
R. jaegeri n. sp.	■	■			
Rattus sp. Indet.			■		
Mus shortridgei	■	■	■	■	■
M. pahari			■	■	■
M. cookii	■	■	■	■	■
M. cervicolor			■	■	■
M caroli	■	■	■	■	■
Sciuridae					
Belomys pearsonii			■	■	■
B. thamkaewi n. sp.			■	■	
Iomys horsfieldi			■		
Petaurista petaurista	■	■	■	■	■
Hylopetes phayrei	■	■	■	■	■
H. spadiceus	■	■	■	■	■
Petinomys setosus			■	■	■
Nannosciurus melanotis			■		
Rhinosciurus laticaudatus	■	■	■	■	■
Tamiops macclellandi			■	■	■
Callosciurus finlaysonii			■	■	■
Menetes berdmorei	■	■	■	■	■

Table 4.3. Fossil murids and sciurids from Thailand (after Chaimanee 1998)**.**

4.2 BACKGROUND INFORMATION ON PHYLOGENY, EVOLUTION AND BIOGEOGRAPHY OF SELECTED SE ASIAN MAMMALS

In this chapter I have compiled all available information on the phylogeny of groups of mammal species and as much as possible the estimated divergence times between taxa in these groups. The main aim is to link the phylogenetic data to the palaeoenvironmental reconstructions to see whether changes in land connections or environmental conditions can be correlated to the timing of divergence between taxa.

Insectivora

Erinaceidae

Ruedi and Fumagalli (1996) analysed the sequence variation of the cytochrome *b* gene from several taxa of gymnure (genus *Hylomys*) that were sampled throughout SE Asia and the Sunda islands (Fig. 4.1). The phylogenetic reconstructions indicated that *H. suillus* is paraphyletic and demonstrated the existence of a Sundaic clade composed of all island taxa, as opposed to those from the continent.

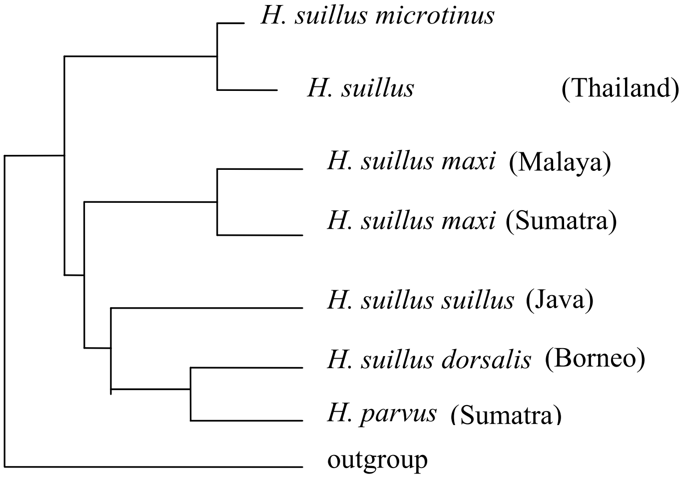


Figure 4.1. Phylogeny of the *Hylomys* group (after Ruedi and Fumagalli, 1996).

The data indicate that rapid radiation occurred, suggesting that the separation of the islands may have been perceived as a simultaneous event rather than as a succession of vicariant events. The estimated divergence times suggested that this radiation predated the climatic fluctuations of the Pleistocene, unless a much faster rate of cytochrome-*b* evolution was assumed. Based on a *cyt-b* sequence divergence rate at third position transversions of 1.8%/Myr, the divergence between *H. suillus* and *H. parvus*, for instance, could date back to between 1.5 and 4.7 Myr (mean 4.0), and that among all *Hylomys* populations to between 1.5 and 6.6 Myr (mean 5.0) (Ruedi & Fumagalli 1996). If the latter is considered to represent the split between an Indochinese and Sundaic faunal group this may have occurred between the MIO 4 and PLIO 3 stages (see Chapter 3.5).

Soricidae

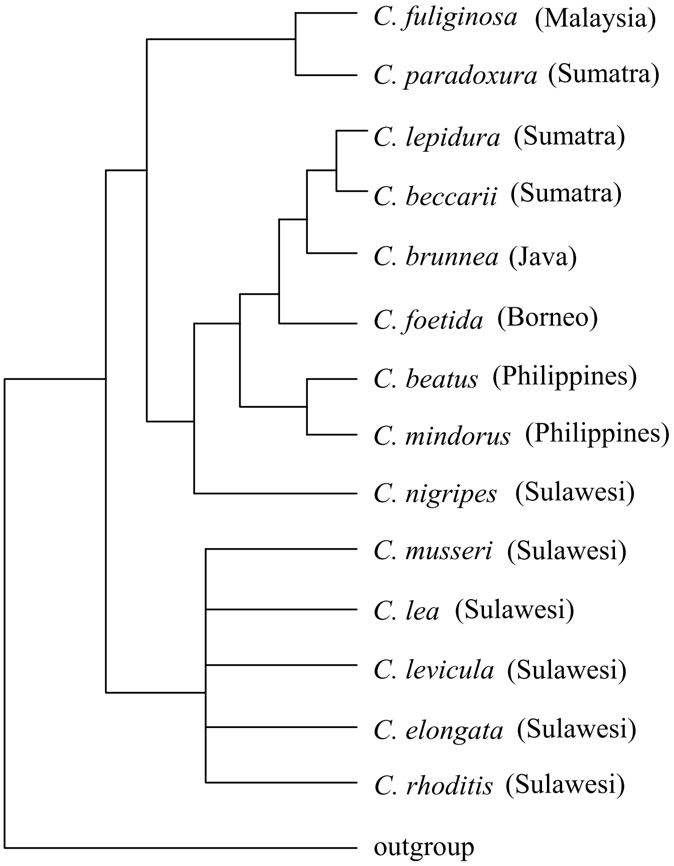


Figure 4.2. Phylogenetic relationships (consensus tree) for a selected number of *Crocidura* species (after Ruedi 1996; Ruedi et al. 1998)**.**

SE Asian shrews of the genus *Crocidura* consist of 20 species in Sundaland and Sulawesi. A phylogenetic analysis of this genus offers an insight in processes that have led to the rapid radiation within this group (Ruedi 1995, 1996) (Fig. 4.2), including two dispersal waves from Borneo to Sulawesi, as suggested by Ruedi et al. (1998). No divergence times were provided and it is not yet possible to link these events to the palaeogeographical model. Considering the many species that have evolved, however, it is likely that the divergence events occurred during the Pliocene, or even Miocene, and no later than the Early Pleistocene.

Kitchener et al. (1994a) described the genetic variation for *Crocidura maxi* based on electrophoretically detected loci. A dendrogram of the genetic distances between specimens from different islands revealed three primary clusters, separating the western Nusa Tenggara (Bali and Sumbawa) from the eastern Nusa Tenggara populations (Komodo, Flores and Alor) and the south-eastern Maluku population (Aru island). Genetic distances varied between 0.022 and 0.254 (Nei index), which would translate in separation times of between 1.3 Myr and 110 Kya (assuming a conversion factor of $5 * 10^6$D), which I tentatively link with a Middle–Late Pleistocene lowstand (possibly PLEI 4).

Scandentia

Tupaiidae

This family is endemic to the Indomalayan Region (Corbet & Hill 1992), and biogeographic patterns indicate an origin of the genus in the Borneo area (Yasuma 1996). Allocation of early Tertiary fossils to Tupaiidae is uncertain, but more definite evidence of former occurrence beyond the present range was provided by finds in the Siwaliks (Miocene-Pliocene) (Jacobs 1980) and in Yunnan, China (Late Miocene) (Qiu 1986). Interestingly, Emmons (2000) stated that all species of *Tupaia* retain morphological adaptation for arboreality, although most of them are now terrestrial. She suggested that all species derive from an arboreal ancestor that evolved into terrestrial species, which then specialized according to dietary niches.

A genetic and morphological analysis of Bornean Tupaiidae by Han et al. (2000) suggests that the relationships between the species may be related to the older tectonic history of the island, rather than the glacially induced Late Pleistocene sea-level and vegetation changes. Their phylogenetic tree based on DNA hybridization (Fig. 4.3) is similar to the one provided by Dene et al. (1978, in Han et al. 2000). Han and colleagues hypothesized an Oligocene origin of the Tupaiidae in the Bornean area, originally leading to the progenitors of *Tupaia montana* and *T. javanica*. After this the

Tupaiidae may have experienced a relatively recent adaptive radiation in Borneo leading to newer species.

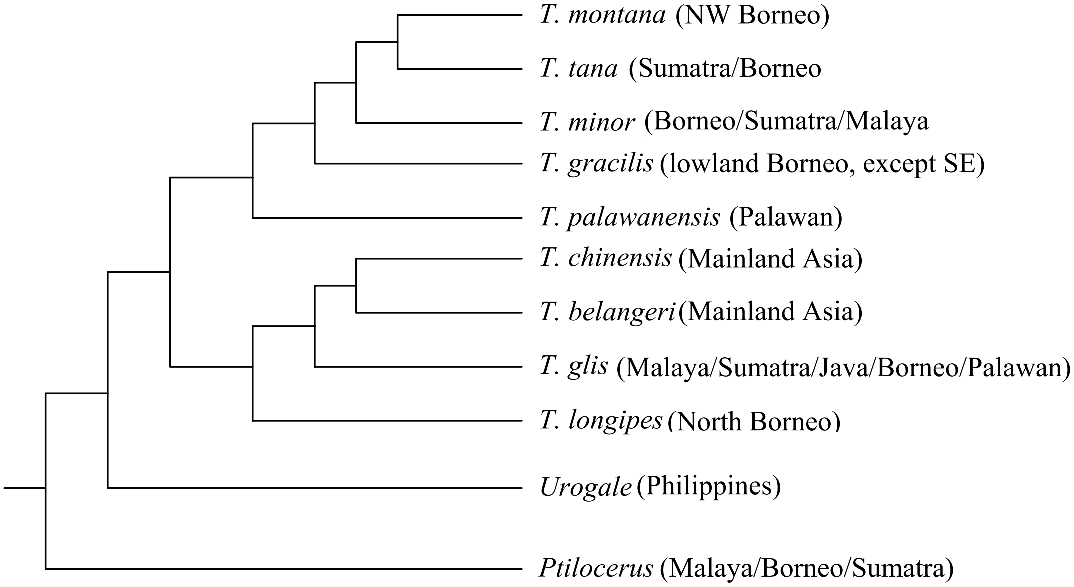


Figure 4.3. Immunological divergence tree of the Tupaiidae (after Han et al. 2000)

The sequence of species divergence in Fig. 4.3. matches the findings by Staffors and Thorington (1998) who studies carpal morphology of Tupaiidae. They found that *Ptilocercus* showed a highly derived carpal morphology that may be related to its relatively greater arboreality. *Dendrogale* exhibited what is most likely the ancestral tupaiid carpal morphology, with the derived carpal morphologies of *Tupaia*, *Urogale*, and *Anathana* (the Madras Tree shews) being identical to each other. This suggests that the latter three genera diverged after the split between *Ptilocercus* and *Dendrogale*, with one lineage ending up in the Philippines (*Urogale*), one in India (*Anathana*) and one in Sundaland and Indochina (*Tupaia*). The phylogenetic data are insufficient to link them to the palaeoenvironmental model.

Finally, Hirai et al. (2002) provided evidence for the distinctness of *T. glis* and *T. belangeri*, two species that have often been considered as subspecies of *T. glis* that were more-or-less separated at the Isthmus of Kra (see Corbet & Hill 1992). According to observations by Hirai and his colleagues, the two species exist sympatrically and they are probably reproductively isolated. The difference between these species is also expressed in differences in mtDNA, although those data remain unpublished (H. Hirai, *in litt.* 9 May 2003).

Chiroptera

Pteropodidae

Genetic distances between various fruit bat species of the genus *Cynopterus* indicate that the genus underwent rapid speciation in the Indonesian archipelago, some 1 Mya. This led to a lineage containing species of Java and the lesser Sundas and one with species from Sulawesi, Sumatra and the Mentawai Islands, and Borneo, Java, and Bali. Further inter-specific divergence occurred in the Late Pleistocene (Schmitt et al. 1995). The Sulawesi species seems to have diverged from the others in its clade during the Early Pleistocene (PLEI 1), whereas the two lineages of Sumatra/Mentawai and Borneo/Java/ Bali diverged in the late Middle Pleistocene (PLEI 4–5) (assuming a Nei's estimate of codon substitution of 10^{-7}). Figure 4.4. shows the phylogenetic relationships among several *Cynopterus* species from the Indonesian archipelago.

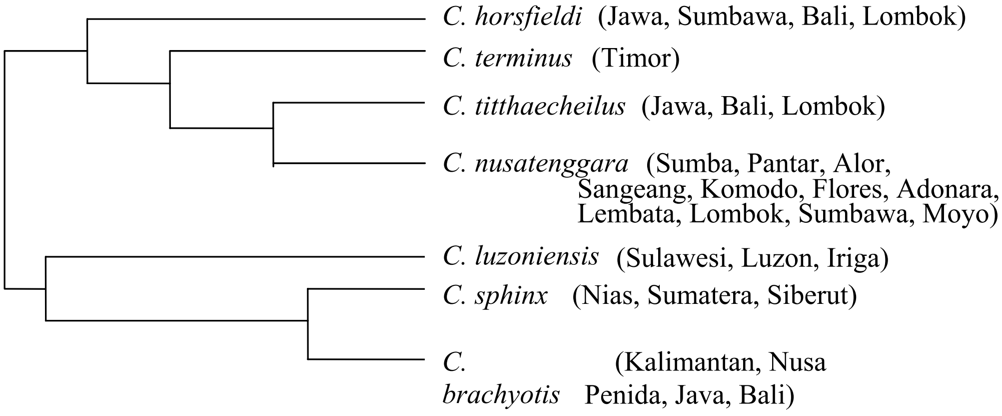


Figure 4.4. Phylogenetic relationships among Cynopterus fruitbats in the Indonesian archipelago (after Schmitt et al. 1995)**.**

Vespertilionidae

The genus *Myotis* had a burst of diversification during the Late Miocene–Early Pliocene (Ruedi & Mayer 2001) in a yet unknown part of Asia. In their molecular research, Ruedi and Mayer included several *Myotis* species that now occur in the Sundaic Region, including *M. horsfieldii* (Borneo, Java, Malaya, and Asian mainland, including India), *M. hasseltii* (Borneo, Java, Malaya, and Asian mainland)*, M.*

macrotarsus (Borneo and Philippines), and *M. montivagus* (N. Burma, S. India, S. China, NE Thailand, Malaya, and Borneo). The former three had a common ancestor some 6 Mya, while *M. montivagus* seemed to have diverged from the Asian mainland species *M. mystacinus* some 7–8 Mya. Many species in this genus are associated with forest areas and open waters, and although little is known about the ecology of the earliest *Myotis* species, it is possible that their rapid evolution during stages MIO 4 – PLIO 2 is related to the considerable drying that was taking place on the Asian mainland. Fragmentation of once contiguous forest areas may have resulted in vicariant speciation with *Myotis*.

Pholidota

Manidae

The pangolins (Manidae) are a family of the Afrotropical and Indomalayan Regions, with three representatives in the latter: *Manis pentadactyla* (Asian mainland), *M. crassicaudata* (Indian peninsula), and *M. javanica* (Sundaic subregion). Little is known about the phylogenetic relationships among the Asian species, although recent morphometric research by Gaudin and Wible (1999) strongly suggested that the Asian species are a monophyletic group. Zhang and Shi (1991) described two colour morphs of *M. pentadactyla*, which can be consistently separated based on their mtDNA (which suggests that they may be distinct taxa); their divergence time was estimated at 0.6 Mya. If this estimate is correct, then the divergence within Asian species of *Manis* would have occurred before that time, i.e. pre-Middle Pleistocene. The divergence data are as yet insufficient to link them to any of the palaeogeographical stages. Finally, the giant pangolin *Manis palaeojavanica* occurred in northern Borneo around 40 Kyr, after which it became extinct. Remains of this anteater have been found only in much older deposits of Middle Pleistocene age in Java (Hooijer 1960). We do not know the phylogenetic affinity of this species to the extant ones, but Hooijer (1960) thought it to be a large, closely related version of *M. javanica*.

Primates

All Asian primates except the lorises (Family Lorisidae) belong to the suborder Haplorrhini. Based on DNA analysis and fossil evidence Goodman et al. (1998)

recently described the branching sequence among the main primate groups within this suborder. The following approximate ages were found for a number of primate taxa that presently still occur in SE Asia: Suborder Tarsiiformes, between 45 and 40 Mya; Family Lorisidae, 23 Mya; Superfamily Cercopithecoidae, 25 Mya; Tribe Cercopithecinae, 14 Mya; Subtribe Papionina (to which the macaques belong), 7 Mya; Subfamily Homininae, 18 Mya; Subtribe Hylobatina, 8 Mya; and Tribe Hominini (to which both *Pongo* and *Homo* belong), 7 Mya. Jablonski (1993) suggested that episodic immigrations played a major role in shaping the primate faunas of the Asian Neogene. Before the Miocene, undoubted catarrhines (i.e. old world monkeys, apes and humans) were absent from Asia, and the primate fauna comprised lorisiformes, a tarsier and a number of adapids (an extinct lemur-like group). Catarrhines appear to have arrived from Africa during two sea-level lowstands in the Miocene. A first wave coincided with the opening of a corridor between Afro-Arabia and Eurasia at 16.5 Mya, while a second wave that include the thick-enameled hominoids like *Sivapithecus* and *Dryopithecus* occurred at 12 Mya (Bernor et al., in Jablonski 1993).

Lorisidae

The lorises of the genus *Nycticebus* occur from Bangladesh and Assam to Vietnam, the Malay Peninsula and on Sumatra, Java, Borneo, Bangka, Tioman, the Natuna Islands, and the Sulu Archipelago. Presently, 3 species are recognized, *Nycticebus coucang* of the Malay Archipelago, *N. bengalensis* of NE India, Bangladesh and China west of Yunnan, and *N. pygmaeus* east of the Mekong River, while the existence of a possible fourth species in North Vietnam, *N. intermedius*, was rejected by Groves (1971). Groves (1998) recently indicated, however, that the genus might be of much greater complexity than previously assumed. Within *N. coucang* three subspecies are presently recognized, with the very closely related *N. bengalensis* a further member of this group. *N. bengalensis* (N. of Kra) represents the most northerly and largest form, *N. c. javanicus* (Java) is slightly smaller, while *N. c. coucang* (Malaya, Sumatra) and *N. c. menagensis* (Borneo, Mindanao), the two equatorial subspecies, are smallest (Ravosa 1998).

In research on the phylogenetics of the genus, Zhang et al. (1993a) found that *N. coucang* and *N. pygmaeus* diverged from each other ca. 2.7 Mya, which in line with results from DNA research by Lu et al. (2001), who estimated that *N. coucang* and *N.*

pygmaeus separated 3 Mya. This split can thus be related to the PLIO 4 stage and may have been the result of the contraction of wet evergreen forests to some refuges at the time of the severe Late Pliocene glacial. Furthermore, Zhang and his colleagues found that divergence among the *N. coucang* subspecies might have begun 0.3 Mya, although it must be noted that all their specimens originated from China and Indochina, and divergence between the other subspecies of *N. coucang* may have occurred earlier. The mechanism behind the divergence of *N. coucang* subspecies is unclear, but could be related to the effects of the break-up of Sundaland after the PLEI 4 lowstand.

Tarsiidae

Tarsiers form an ancient radiation, in mammalian terms, and they could have diverged from the other primates as early as 45–40 Mya (Goodman et al. 1998). In addition, the morphological variation found between the *Tarsius* species suggests separation which is more in line with what one would expect when comparing genera rather than species. They are extinct on mainland Asia, but tarsier fossils of Miocene age have been found there.

It is unclear how the species of tarsier came to have their current distribution and evolutionary patterns. Groves (1998), who interpreted the findings of Musser and Dagosto (1987, in Groves 1998), suggested that the genus can be divided into two informal groups: (1) *Tarsius syrichta* (southern Philippines) and *T. bancanus* (Sumatra, Borneo and intervening islands); and (2) *T. spectrum* (Sulawesi and neighbouring islands) and *T. pumilus* (Sulawesi highlands). Groves (1998) mentioned that a fifth species (*T. sangirensis*) can be found on the Sangihe Islands, north of Sulawesi, and recent investigations have revealed that there are probably several more distinct species on Sulawesi and some of its smaller islands (Sangihe, Selayar). Differences between the species of Sundaland, Sulawesi, and the Philippines are such that generic differentiation among them is warranted (C. Groves, pers. comm., 29 May 2003). Groves (pers. comm.) thinks that tarsiers initially dispersed from Borneo to Sulawesi, then the Bornean form evolved into a Philippine-like tarsier that dispersed to the Philippines. This could have happened some 8–7 Mya (Groves, pers. comm.), i.e. during stages MIO 3 – MIO 4.

Cercopithecidae

The family of Cercopithecidae consists of two extant subfamilies, The Colobinae (the leaf-eating monkeys) and the Cercopithecinae (the cheek-pouch monkeys) (Groves 1993). The Asian genera of the former family are *Nasalis* (the Proboscis Monkey), *Simias* (the Pig-tailed Langur), *Presbytis* (leaf monkeys), *Pygathrix* (Doucs), *Rhinopithecus* (Snub-nosed Monkeys), *Semnopithecus* (langur), and *Trachypithecus* (langur). The Cercopithecinae consist of only one Asian genus, *Macaca*, while 10 other genera occur in Africa (Page et al. 1999b). Table 4.4 shows some of the branching times within the Asian members of the Cercopithecidae using a local molecular clock, DNA-DNA hybridization clock and fossil-based estimates [adapted from Page et al. (1999b)].

Branch point	Local (Mya)	DNA-DNA hybridization clock (Mya)	Fossil-based estimates (Mya)	Corresponding biogeographical stage
Colobinae vs. Cercopithecinae	15–14	14	ca 14–12	MIO 2
Asian colobines vs. African Colobines	10–9	10	ca. 13–12	MIO 2 – MIO 3
Nasalis vs. *Trachypithecus*	6–5	n/a	ca. 4–3	MIO 4
Macaca vs. rest of Papionini	8	7	ca. 8–7	MIO 3 – MIO 4
Macaca mulatta vs. other macaques	4	n/a	n/a	PLIO 1 – PLIO 2
M. nigra vs. *M. nemestrina*	4	n/a	n/a	PLIO 1 – PLIO 2

Table 4.4. Estimates of branching times within the family Cercopithecidae (Page et al. 1999b)**, and corresponding biogeographical stages as discussed in Chapter 3.**

Judging from the number of sites at which they are represented macaques were by far the most successful of the cercopithecids, with distributions in the Middle Pleistocene extending from Manchuria to Sundaland and Sulawesi (Jablonski 1993). Genetic analysis of macaques indicates that macaques originated in Africa, and probably entered Eurasia via north-east Africa at 6–5.5 Mya (Tosi et al. 2000). Then, as early as

4.5 Myr (Morales & Melnick 1998) or 4.0 Mya (Page et al. 1999b), the ancestral species of the Sulawesi macaques crossed over from Sundaland to Sulawesi, probably leaving behind the ancestor of the Pig-tailed Macaque (*Macaca nemestrina*). These estimates appear to be in conflict with fossil finds that indicate that the genus *Macaca* did not appear in Asia until the latest Pliocene or Pleistocene (Jablonski 1993), therefore either the cross-over to Sulawesi occurred more recently (more like 3–2 Mya) or the fossil record is incomplete. Data from Evans et al. (1999), and also from Froehlich et al. (1996) are more in line with a Late Pliocene or Pleistocene macaque dispersal to Sulawesi, as they suggest one or possibly two macaque invasions from the Borneo/Java area to Sulawesi at that time.

In a recent paper, Abegg and Thierry (2002) proposed a new model for macaque evolution based on a reinvestigation of phylogenetic and palaeoenvironmental literature. They suggested that an ancestral *Macaca silenus*-like stock colonized mainland and insular SE Asia by land during warmer phases of the Late Pliocene (probably coinciding with PLIO 3). First, it became isolated in several refuges during an early and intense glacial episode of the Pleistocene (possibly at PLIO 4 or PLEI 1). Macaque populations survived in South India (as a proto *silenus*-stock), in the Indochinese peninsula or in the Sunda Shelf area (as a proto-*nemestrina*), in Sulawesi where it dispersed by sea rafting (as a *maurus*-like or *tonkeana*-like ancestor of the several Sulawesi species), and in the Mentawai Islands area, which it reached by land. Secondly, during ongoing climatic cycles, the ancestral pre-glacial stock diversified in various glacial refuges but only the proto-*nemestrina* was able to successfully recolonize the Sunda Shelf and Indochinese peninsula. When the colonization of the Mentawai Islands and Sulawesi took place, the Pig-tailed Macaque (*nemestrina*) did not exist as such but only as a form then closely related to the progenitors of Lion-tailed Macaque (*silenus*), Sulawesi, and Mentawai macaques. Consequently, the Pig-tailed Macaque should not be considered as the progenitor of Mentawai and Sulawesi macaques. Abegg and Thierry suggested that the proto-*silenus* group dispersed into Sumatra during the Pliocene, before spreading to the Mentawai Island area during the Late Pliocene–Early Pleistocene glacial. This glaciation might have brought down sea-level to about 200 m BPL, thus permitting a terrestrial entry to the Mentawai Islands. This long isolation time for the Mentawai macaques, allowed for considerable differentiation from its *silenus*-like ancestor, and recent morphological (Kitchener & Groves 2002) and behavioural (Abegg & Thierry 2002) data suggest that the Mentawai macaques should be considered distinct species (*M. pagensis* and *M. siberu*), rather than subspecies of *M. nemestrina*. The palaeoenvironmental reconstructions by Abegg and Thierry also suggested that, when macaques dispersed to Sumatra, all of Sumatra was connected to Sundaland, but it may be more likely that macaques dispersed along the Asahan Arch, as also suggested for the early *Presbytis* dispersal into Sumatra (see Appendix 3). If this is correct, the dispersal of macaques into Sumatra may have occurred earlier (MIO 4 to PLIO 1) when the Asahan Arch still existed (unless this arch remained emerged for longer).

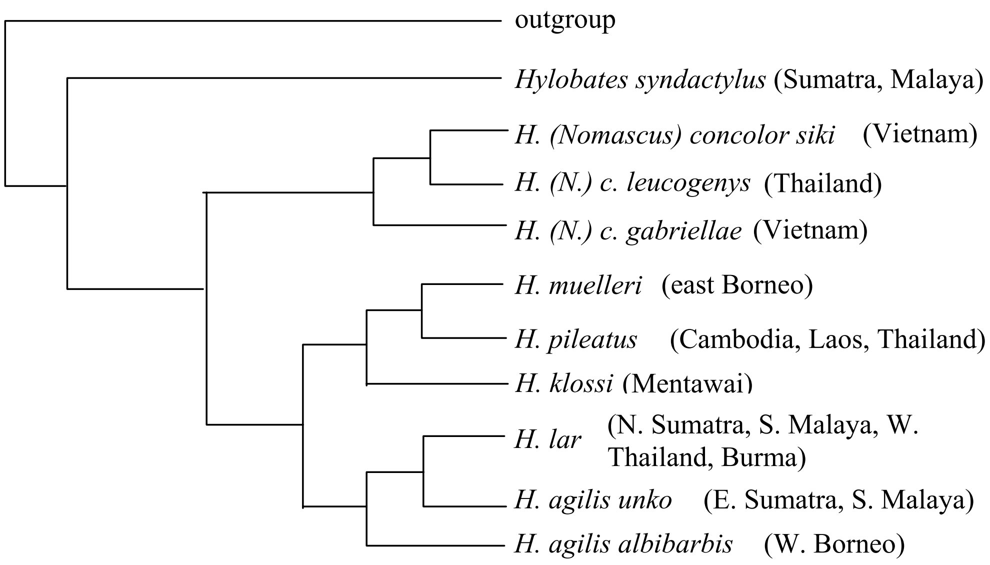
The migration route and timing of divergence of the ancestral Asian colobines into SE Asia may be similar to that of macaques, although Zhang et al. (1993b) suggested that this happened much later during the Late Pliocene or Early Pleistocene. Colobines migrated from Africa to India and dispersed into south India, Burma, Malaya and Sundaland. The evolution of *Presbytis* was discussed in detail by Meijaard and Groves (in press-a) (see Appendix 3).

Sarich (1970 in Zhang et al. 1993b) estimated that the split between *Nasalis* (Proboscis Monkey) and *Presbytis* occurred approximately 5 Mya, after which *Simias* and *Nasalis* split. Interestingly, a Siwalik fossil exists named cf. *Presbytis sivalensis*, which has been aged at 7.2 Mya, and if this is indeed a *Presbytis*, the split between *Nasalis* and *Presbytis* is likely to be an older one. *Nasalis larvatus* is a Bornean endemic of coastal and riverine forest, with its closest relative (*Simias concolor*) on the Mentawai islands west of Sumatra; no relatives of these species occur on Sumatra. Such a distribution pattern can only be explained if an ancestral species went extinct on Sumatra, while surviving on the Mentawai islands and in Borneo.

Hylobatidae

The Hylobatidae appear to be the only family of primates that emerged in Asia during the Late Tertiary (Jablonski 1993). Wu and Pan (1984) described what they thought to be a Late Miocene gibbon with affinities to *Nomascus concolor*, but Groves (pers. comm.) consideres this to be dubious. Hall et al. (1998) confirmed that the extant gibbons are a monophyletic group, but their data could not resolve the evolutionary relationships between the gibbon subgenera. The four gibbon genera *Nomascus* (east Asia), *Symphalangus* (Sumatra and Malaya), *Hylobates* (SE Asia) and '*Bunopithecus*' (Assam, north Burma, and Bangladesh) are thought to have diverged from each other 6 Mya, while the species within *Hylobates* are estimated to have radiated 3.5 Mya (Hayashi et al. 1995). Recent phylogenetic research by Chatterjee (2002) indicated that the gibbon radiation may have begun much earlier than suggested above, i.e. around 10.5 Mya, and probably in Indochina. Between 10.5 and 8.6 Mya (MIO 3) gibbons radiated southwards to Sumatra. Subsequently, they differentiated into two types of gibbon on Sumatra, representing the genera *Symphalangus* and *Hylobates*. A third radiation, approximately 8–7 Mya, saw the dispersal of *Bunopithecus* into Burma, Assam, and Bangladesh. At around 5–3 Mya (PLIO 1 – PLIO 3) there was a second radiation of genus *Hylobates*, involving dispersal onto the islands of Borneo, Mentawai and Java (Chatterjee 2002). Note that Groves' (2001b) examination of *Bunopithecus* led him to doubt whether it belonged to *Hylobates*, and also, the name *Bunopithecus* should probably be restricted to a fossil species, and a new name is needed for this genus. Phylogenetic investigations by Roos and Geissmann (2001) suggested a closer relationship of *Bunopithecus* to *Symphalangus*, albeit with weak bootstrap support. .

Figure 4.5. Phylogenetic relationships among gibbons (after Garza & Woodruff 1992)



Garza and Woodruff (1992) provided a phylogenetic tree for gibbon species (Fig. 4.5). Their data suggest that *H. agilis* is closely related to *H. lar*, whereas the Bornean *H. muelleri* is more closely related to *H. pileatus* from Cambodia, Laos and east Thailand and to *H. klossi* from Java. If we apply Hayashi et al.'s (1995) divergence estimate to this tree, then it appears that a split between the Indochinese *Nomascus* and Sundaic *Hylobates* clade occurred sometime during the Early Pliocene, and may be related to the PLIO 2 highstand.

Hominidae

The apparent dependence of non-human apes on tropical and subtropical forest environments in Asia was crucial to their fate during the latest Tertiary and Quaternary. *Sivapithecus* disappeared from the fossil record of the Pakistani Siwaliks around 7.4 Mya at about the time when forests were displaced by grasslands, and it is possible that some of the larger-bodied apes from drier regions of southern China became extinct for a similar reason (Jablonski 1993). The only surviving hominids with Asian origins are the Orang-utans (*Pongo pygmaeus*). Orang-utans occurred throughout SE Asia in the Middle to Late Pleistocene, including the southern Chinese provinces, Vietnam, Laos, Thailand, and Burma (Nisbett & Ciochon 1993). At 23 Kyr, the species still existed in Vietnam, but, after 18 Kyr, the species became extinct in that region (Ciochon et al., 1990 in Nisbett & Ciochon 1993), probably because of the combined effects of over-hunting and climate change.

The two sub-species of the orang-utan (*P. pygmaeus pygmaeus* and *P. pygmaeus abelii*; now elevated to species level) that occur on Borneo and Sumatra respectively are now thought to be separated 1.1. Myr (Warren et al. 2001), between 1.5 and 1.7 Mya (Zhi et al. 1996), 2.3 ± 0.5 Mya (Zhang et al. 2001), or around 2.5 Mya (Uchida 1996). These estimates contradict statements by several authors (e.g. Kahlke 1972; von Koenigswald 1981) that dispersal, and the likely associated mixing of gene pools, between Borneo and Sumatra continued until the Late Quaternary. Warren et al. (2001) also found that, approximately 860 Kya, the Bornean orang-utans diverged into four or possibly more sub-populations, i.e. Sabah, East Kalimantan, Southwest and Central Kalimantan, and Northwest Kalimantan and Sarawak. This seems to agree with findings by Xu and Arnason (1996), Arnason et al. (1996) and Muir et al. (2000) who reported considerable inter-island divergence in Borneo, suggesting that the

Bornean subspecies diverged into different populations 1–0.5 Mya. It is also noteworthy that the morphological variation within orang-utans in Borneo is significant (Groves et al. 1992), suggesting that populations in East Borneo have had a different history compared to those in the southwest. Interestingly, within the Sumatran orang-utans the maximum divergence appears to be much greater than within the Bornean orang-utan, 9% as opposed to 0.4% (Muir et al. 2000), although Zhang et al. (2001) found the opposite for a different part of the genome. Muir et al. (2000) found three very different Sumatran haplotypes, which they consider the result of an extended period of isolation of at least three groups that joined together in the present Sumatran population relatively recently. They suggest that most of the Sumatran orang-utans were extirpated as a result of the Toba explosion (see Chapter 3.4), and that the present population of northern Sumatra is the result of recolonizations from three or four sources: Borneo, mainland Asia, southern Sumatra, and Java. Muir et al. provided a detailed palaeoenvironmental scenario dating back to 300 Kya for the genetic divergence that they found in orang-utans. It is unclear how this scenario can be reconciled with the much older divergence time estimates by for instance Warren et al. (2001) and Zhang et al. (2001). Zhang et al. (2001) opposed the idea that Bornean orang-utans contributed to the modern Sumatran orang-utan gene pool, as their data did not support this. Zhang et al. also detected a population expansion of the Sumatran orang-utan (rather than a bottleneck), which they dated at approximately 82 Kya (note that this is in the vicinity of the Toba eruption that occurred 70–74 Kya, see Chapter 3.4). It remains unclear how all of this fits Drawhorn's (1994) finding that an Orang-utan population existed in the Padang Highlands during the Middle Pleistocene–Holocene, which was dentally distinct from both *P. pygmaeus* and *P. abelii* (and also from the extinct Asian mainland form, which he called *P. p. weidenreichi*); in fact, Drawhorn thought this population so distinct that he assigned full species status, i.e. *P. duboisi*, with two chronological subspecies: the younger *djamboensis* and older *lidaajerensis* (note that these names are invalid as the nomeno-typical subspecies *P. d. duboisi* has not been described). Interestingly, Drawhorn suggested that instead of chronological subspecies, the Jambu sample might be a temporally mixed composite of *P. duboisi* and *P. a. palaeosumatrensis*. Under this hypothesis, the disappearance of *P. duboisi*, and the emergence of *P. abelii*, would coincide with the onset of the terminal Pleistocene glaciation (PLEI 5), which could then mean that the present-day Sumatran Orang-utan is of recent mainland Asian origin (only arriving on Sumatra during the Late Pleistocene). This is supported by the close dental similarity between a Vietnamese fossil Orang-utan and *P. p. palaeosumatrensis* (Bacon & Long 2001).

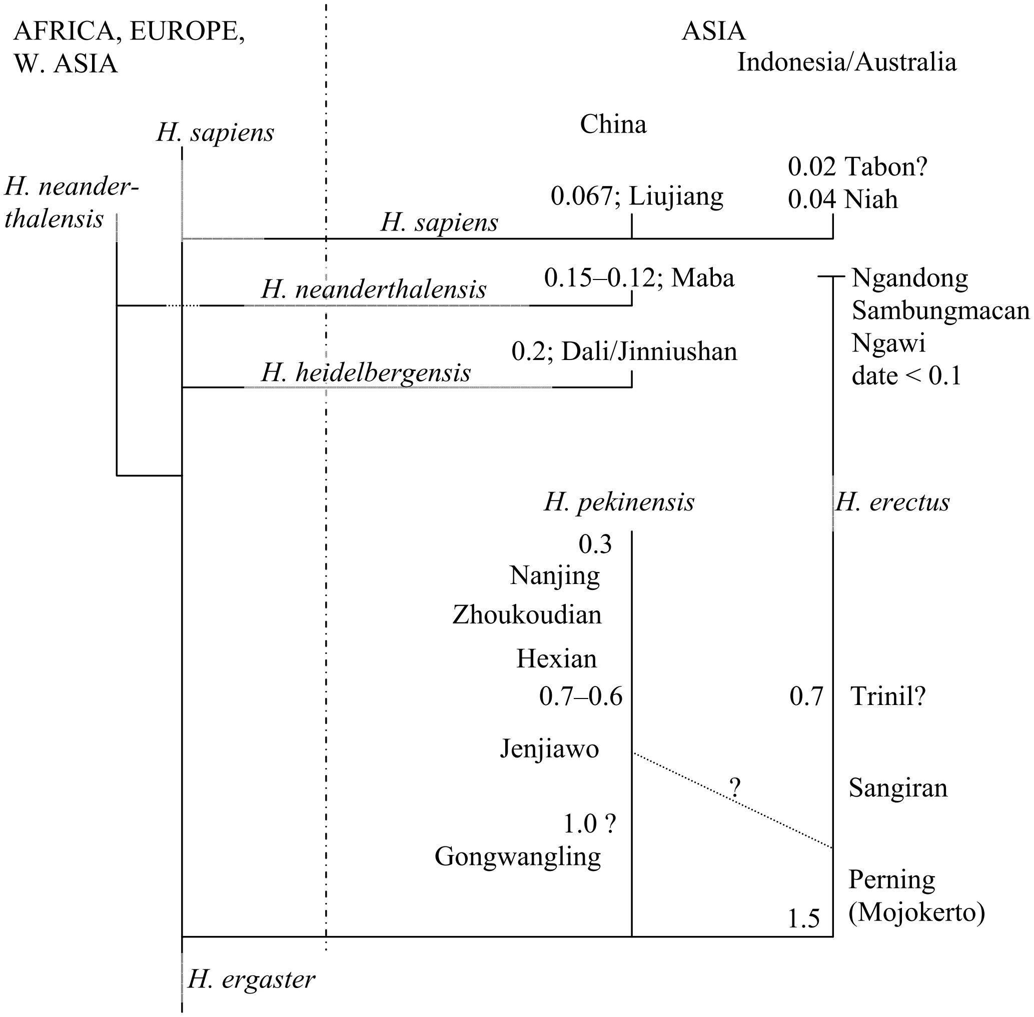


Figure 4.6. Phylogenetic relationships among Asian hominids (Groves, pers. comm.). Also shown are the main fossil localities, and their estimated ages.

The Javan Middle–Late Pleistocene Orang-utan of the Punung Fauna appears to be more closely related to *P. pygmaeus/abelii* than to *P. duboisi*, and Drawhorn assigned it to *P. p. javensis*. If we assume that *P. duboisi* was the only Orang-utan on Sumatra before the Late Pleistocene, then the Javan Orang-utan probably arrived from Borneo or directly from the Asian mainland. Kaifu et al. (2001) recently claimed to have found evidence that *Pongo* was present on Java in Late Early–Middle Pleistocene, at which time a land bridge probably existed between Java and the Malay Peninsula.

Recent finds of an advanced *Homo sapiens* skull in Ethiopia (White et al. 2003) appears to lend strong support to the 'Out of Africa' theory, which claims that *H. sapiens* evolved in Africa, spread through the rest of the world, and replaced other hominids. Swisher et al. (1994) suggested that the earliest specimens of *Homo* from Java date back to 1.8 Myr, but this has been contested by de Vos and Sondaar (1994). Recent dating suggests that *H. erectus* had arrived in Central Java before 1.51±0.08 Myr (the Bapang/Sangiran Formation contact), although *H. erectus* fossils in the Bapang Formation are much more common than in the upper units of the Sangiran Formation (Larick et al. 2001). Statistical comparison between *H. erectus* fossils from Java and from China suggest that the two population are morphologically distinct, while there is a small possibility of the existence of two distinct anatomical morphs within the Indonesian *H. erectus* (Antón et al. 2002). Fig. 4.6 shows the phylogenetic relationships between Asian hominids.

Rodentia

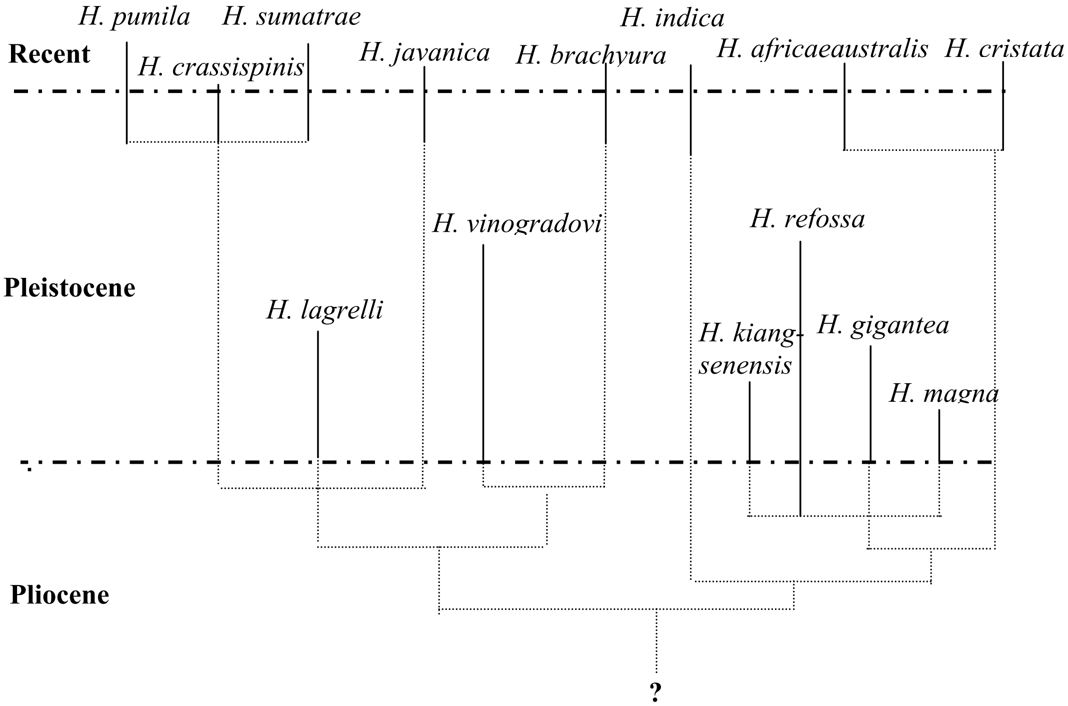
Hystricidae

The porcupines (Hystricidae) are a family of Africa, the S. Palaearctic, and the Indomalayan Region; there are 3 genera of which one, *Atherurus*, is often separated in its own subfamily, the Atherurinae. Of the other two genera, *Hystrix* is widespread, whereas *Trichys* is restricted to the Sundaic Subregion (Corbet & Hill 1992). Based on skull measurements, van Weers (1976) recognized only one species in the genus *Trichys*, without subspecific division. The species, *Trichys fasciculata*, occurs on Sumatra, Borneo and Peninsular Malaysia, but not on Java. The lack of subspecific subdivision may suggest relatively recent separation between the populations.

The group of short-tailed porcupines in Sundaland of the genus *Hystrix* is divided into two subgenera, i.e. *Acanthion* and *Thecurus.* Within *Thecurus*, van Weers (1978) recognized three species, *H. crassispinis* from Borneo, *H. sumatrae* from Sumatra, and *H. pumila* from the Philippine islands of Balabac, Palawan and Busuanga. Within the subgenus *Acanthion*, van Weers (1979) recognised two species, *H. brachyura*, which occurs throughout SE Asia and on Sumatra and Borneo, and *H. javanica*, which is found on Java and on many of the lesser Sunda islands.

Three fossil porcupine species have been found in Java (see section on Fossil Vertebrates of SE Asia), *H.* (=*Acanthion*) *brachyurus*, *H. javanica*, and *H. gigantea*, while van Weers and Zheng (1998) also mentioned a fourth fossil species from Java, *H. lagrelli*, which was also found in China. The first appeared in the fossil record in the Middle Pleistocene and disappeared after the LGM, while *H. javanica* was first found in the Holocene. Van Weers and Zheng (1998) proposed the phylogenetic relationships among living and fossil species of *Hystrix* as shown in Fig. 4.7. Van Weers and Zheng's phylogeny suggests that in the Late Pliocene a split occurred between species that ended up on Java (*javanica*, *lagrelli*), Borneo [*crassispinis*, and closely related *pumila* (Palawan) and *sumatrae* (Sumatra)], and China (*lagrelli*). This could have happened when existing land bridges between Java and Borneo, and between Borneo and the Asian mainland became disconnected during PLEI 1.

Figure 4.7. A hypothetical phylogeny of the genus Hystrix (after van Weers and Zheng



1998). Solid lines are certain, whereas the dotted lines are hypothetical.

Finally, because the Sundaic genus *Trichys* must have separated from *Hystrix* before the species within the latter genus started to diverge (assuming monophyly in *Hystrix*), a Pliocene (before Late Pliocene) divergence of *Trychis* from *Hystrix* is likely, and may be related to the Early–Middle Pliocene separation between the Sundaic and Indo-Chinese faunas that possibly occurred during PLIO 2.

Muridae

Watts and Baverstock (1995) suggested that the first murines arose in southern Asia about 20 Mya from an unknown ancestor. At 15 Myr, one lineage reached northern Pakistan and, by about 12–10 Myr, had given rise to the ancestors of, among others, *Mus* and possibly the ancestor of the clades now found in the Southeast Asian/Australasian region. Between 10 and 8 Mya, ancestral species had reached New Guinea and began to speciate relatively rapidly (Watts & Baverstock 1996). After splitting off from the lineage leading to *Mus*, murine speciation led to three distinct clades, a SE Asian clade, a New Guinea clade and an Australian clade. Within the Southeast Asian clade three main groupings arose: (1) *Maxomys*; (2) *Leopoldamys*, *Niviventer* and *Tokudaia*; and (3) a large group containing, among others, *Rattus*, *Sundamys*, *Bandicota*, and *Berylmys* (Watts & Baverstock 1994, 1996).

Chaimanee (1998) suggested a slightly different scenario, with an estimated origin of the Murinae in southern Asia between 12.5 and 11.8 Mya. The earliest murine species belong to the genus *Progonomys*, which spread subsequently to all other Old World continents about 11.8 Mya. Chaimanee suggested that the most likely evolutionary scenario in Asia was as follows: the speciation of *Progonomys* in Asia led rapidly to the differentiation of *Karnimata* (a large murine of the *Arvicanthis* group); between 11.8 and 8 Mya, the radiation of murines in SE Asia was very rapid, and presumably continued between 9 and 6 Mya, although for the latter period there is no documentation. Figure 4.8 shows a strict consensus tree of relationships among Asian murines based on dental morphology (after Chaimanee 1998).

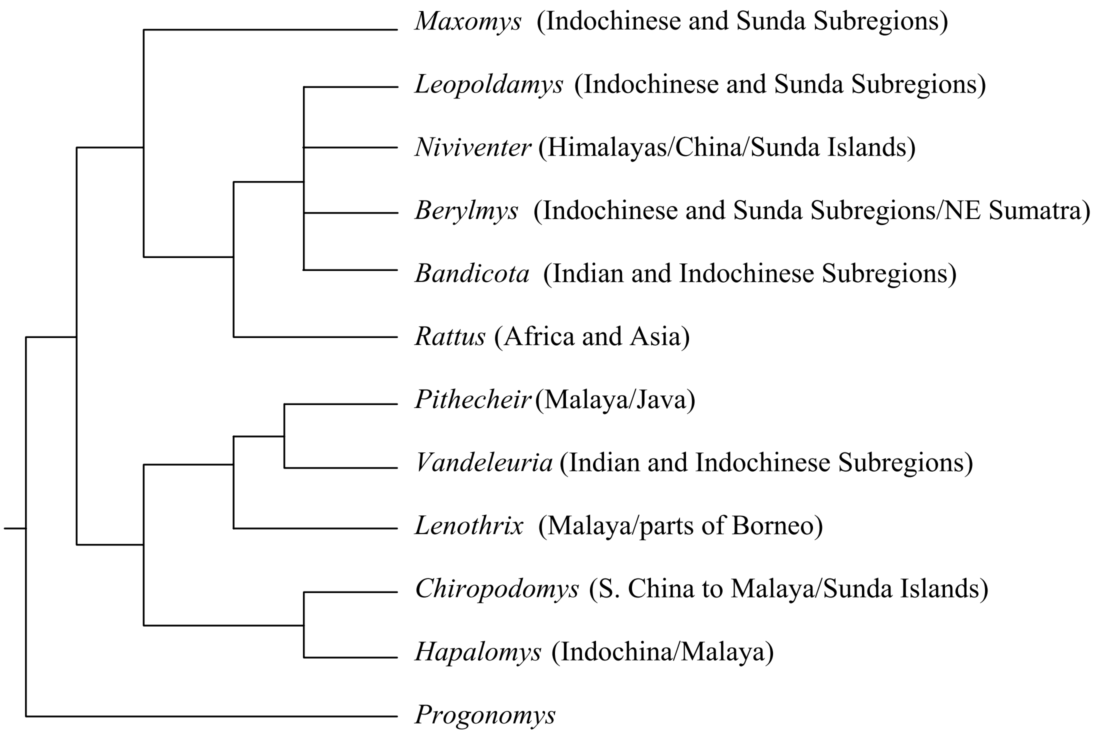


Figure 4.8. Strict consensus tree of Asian murine genera (after Chaimanee 1998)

	Ruedas and Kirsch (1997)		Chevret (in Ruedas and Kirsch)	
Rattus vs. *Mus* (calibration date)	10	12.2	10	12.2
Rates (%/Myr)	2.6	2.1	1.8	1.4
Rattus vs. *Sundamys*	2.1	2.5		
Rattus/*Berylmys* vs. *Leopoldamys*/*Niviventer*	4.4	5.4	5.4	6.6
Rattus vs. *Bandicota*	2.1	2.5	2.5	3.0
Rattus vs. *Berylmys*	2.6	3.3	3.7	4.5
Leopoldamys vs. *Niviventer*	2.7	3.3	3.4	4.1
Rattus vs. *Maxomys*	6.1	7.6	6.7	8.2
Maxomys rajah vs. *M. whiteheadi*	3.4	4.3	4.2	5.1
Diversification of *Maxomys*	3.9	4.8		

Table 4.5. Comparison of some divergence dates (in Mya) within the Muridae, calibrated against two proposed times for the separation of the Mus and Rattus lineages (10.0 and 12.2 Mya). Table adapted from Ruedas and Kirsch (1997).

Maxomys, Niviventer, Leopoldamys, Rattus, Sundamys, Bandicota, Berylmys clade

Ruedas and Kirsch (1997) pointed out a likely important role of the collision of the Philippine Arc with the Eurasian continental margin (Hall 1996, 1998) in the evolution of SE Asian murids. For instance, their data for the initial diversification of the genus *Maxomys* suggest cladogenesis at ca. 4.8 Mya (see below), as is the cladogenesis of the *Niviventer-Leopoldamys* clade from the *Rattus-Sundamys-Bandicota-Berylmys* clade at ca. 5.4 Mya (note that this divergence sequence does not fully agree with Chaimanee's phenetic relationships in Fig. 4.8). Chaimanee (1998) suggested that *Maxomys* originated as a Sundaic group, as there are no fossils of this genus anywhere in S. China, while *Rattus* similarly appears to be of Sundaic origin. This could suggest that the Sundaic *Maxomys* split from its Indochinese sister groups during the PLIO 2 highstand.

Based on DNA hybridization data, Ruedas and Kirsch (1997) suggested an arrangement of two species groups within the *Maxomys* genus: one consisting of an unresolved trichotomy among *M. ochraceiventer* (N. Borneo), *M. rajah* (Malaya/Sumatra/Borneo) and *M. whiteheadi* (Peninsular Thailand and Malaya/Sumatra/Borneo) (albeit suggestive of a closer relationship between *M. rajah* and *M. whiteheadi*), and another pairing of *M. bartelsi* (W. and C. Java) and *M. surifer* (Sundaic and Indochinese Subregions) as the sister group to the other three species. They estimated the divergence date of *M. bartelsi* and *M. surifer* to be about 4 Myr (see Table 4.5), and the split could be related to the separation of West Java from Sundaland between PLIO 1 and PLIO 2.

It appears that the *Rattus* group evolved in central Indonesia, and that only relatively recently it spread to the Asian mainland (Watts & Baverstock 1994). Further biogeographic information was derived from the evolution of the *Niviventer*/*Leopoldamys* group that appears to be centred on mainland Asia. Further work on the Asian Muridae largely confirms the above phylogeny (Usdin et al. 1995; Verneau et al. 1997, 1998). *Rattus* sensu stricto, *Sundamys*, *Berylmys*, and *Bandicoota* are on a separate branch of the phylogenetic tree than *Maxomys*, *Niviventer*, and *Leopoldamys*, with the latter two grouping on a separate branch. Verneau et al. (1998) provided the divergence timing of some of the subfamilies within this phylogenetic tree, based on a base substition rate of 1.1%/Myr. Five divergence events were clustered between 5.5 and 7 Mya and could be related to the climatic cooling and drying during MIO 4; five events were clustered tightly around 2.7 Mya, and appear to be related to the severe PLIO 4 glacial. This latter period of evolution defines an intense speciation event that gave rise to five lineages: *Berylmys bowersi*, *Sundamys muelleri*, *Rattus fusciceps*, *Bandicoota bengalensis*, and the lineage that gave rise to several other *Rattus* species (see Fig. 4.9). *Maxomys* was the first group to split off from *Rattus sensu lato* between 7.3 and 5.7 Mya. After this, a 3 Myr period of apparent stasis occurred, followed by an episode of intense speciation in the Late Pliocene–Early Pleistocene (PLIO 4) (Verneau et al. 1998).

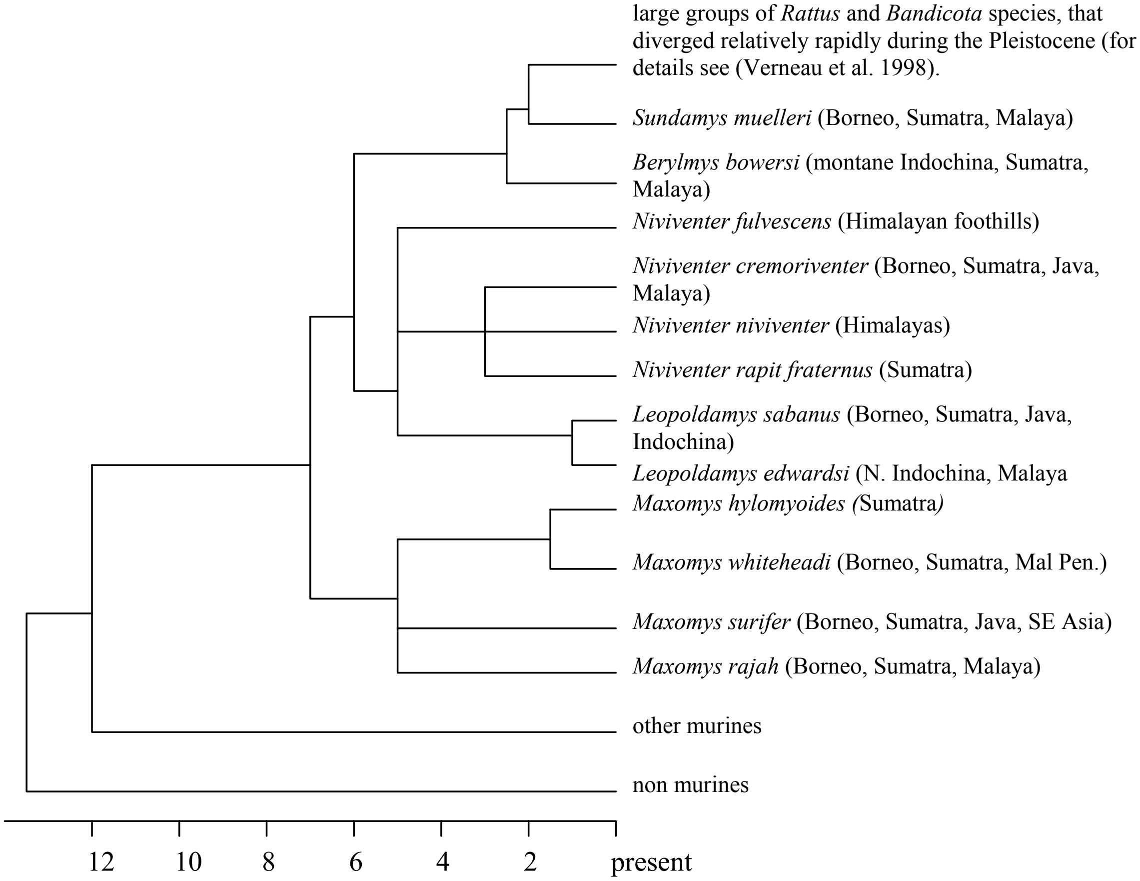


Figure 4.9. Phylogenetic relationships and divergence time estimates for SE Asian Muridae (after Verneau et al. 1998).

Chaimanee (1997 in Chaimanee & Jaeger 2000a) claimed that during the Late Pliocene/Early Pleistocene, *Rattus sensu lato* was represented by a single species in Thailand, although the possibility of older material cannot be excluded. Further species included the extant *Maxomys surifer*, *Ratchburimys ruchae*, and an extinct species of *Leopoldamys*. Also, several species of *Saidomys* and cf. *Hadromys* were present, which exhibit adaptations for grazing and that have extant relatives living in grasslands or open woodlands. Early Pleistocene rodent faunas of Thailand record the appearance of modern species of the *Rattus* group. However, the occurrence of grassland species such as *Hadromys humei* and high altitude species such as *Mus* (*Coelomys*) *pahari gairdneri* suggests that drier and cooler conditions than today prevailed. The distribution and ecology of these species indicates that until the late Middle Pleistocene a dry evergreen forest vegetation persisted in Thailand. In both Thailand and South China, the number of *Rattus* species increased through the Pleistocene from one or two species in the Late Pliocene to 5–10 extant species, while during this interval the number of other members of the Murinae, apart from *Rattus sensu lato* gradually decreased (Chaimanee & Jaeger 2000a). Chaimanee and Jaeger (2000a) related the rapid Pleistocene radiation of *Rattus*, which seems to have spread northwards from a southern refugium, to the development of evergreen forests after the relatively drier and more seasonal vegetation types of the Pliocene.

Musser (1973) investigated the two closely related species *Niviventer cremoriventer* and *N. langbianis*, which are separated by the Isthmus of Kra. Several authors have included *langbianis* as a subspecies of *cremoriventer* (see Corbet & Hill 1992), but they appear to be morphologically distinct. Likhnova et al. (2000) further found that *langbianis* was the most phylogenetically distinct of three *Niviventer* species (including *fulvescens* and *tenaster*), but their research did not include *cremoriventer*. Musser (1973) found that there appear to be two subspecies of *N. cremoriventer* on Sumatra, one in the north that is very similar to *N. c. cremoriventer* from the Malay/Thai Peninsula, and one in the south, *N. c. mengurus*, that is similar to those from Bangka and Belitung, and to a lesser extent to those from Borneo (*R. c. kina*). The Nias subspecies, *N. c. barussanus*, is most like *N. c. cremoriventer*, but decidedly larger, while the Javan subspecies (*N. c. cretaceiventer*) is morphologically similar to *N. c. cremoriventer* from the Malay/Thai Peninsula. Based on this there appear to be two or three general groups in *R. cremoriventer*: (1) the form on the Malay/Thai Peninsula, in north Sumatra, on Nias, and on Java; (2) the form in south Sumatra, on Bangka and Belitung; and (3) the Bornean form. The genus *Niviventer* probably evolved in the Late Pliocene of China because that is where the earliest fossils (*N. preconfuscianus*) were found (Zheng, 1993 in Chaimanee 1998). The divergence between the 3 subspecies groups described by Musser therefore took place during the Pleistocene, although the mechanism behind the divergence remains unclear.

Mus

Sourrouille et al. (1995) investigated the phylogenetic relationships of the Sumatran endemic mouse *Mus crociduroides*. Marshall (1977) and Musser and Newcomb (1983) considered this species to belong to the subgenus *Coelomys*, supposedly together with the Javan mountain endemic *M. vulcani*, *M. pahari* from Darjeeling, Sikkim, Burma, Yunnan, S. Sichuan, Thailand, Laos, and Vietnam, *M. mayori* from Sri Lanka, and *M. famulus* from the Nilgiri Hills in S. India (Corbet & Hill 1992). Sourrouille et al. (1995), using complete sequences of mitochondrial 12S rDNA, could neither confirm nor reject the monophyly of this subgenus as not all *Coelomys* species were included in their research. They did, however, find strong support for a close relationship between *M. crociduroides* and *M. pahari*. Sourrouille et al. (1995) did not provide a divergence time estimate for these two species, but the branch lengths in their Figure 2, combined with an average mtDNA evolution rate in *Mus*, estimated at 7.1 ± 2.3 % per Myr (after She et al, 1990 in Catzeflis et al. 1992) would suggest separation in the late Middle Pleistocene. The genus *Mus* was already established on Java in the Early–Middle Pleistocene (van der Meulen and Musser 1999), and the late Middle Pleistocene connection between Java and Sumatra may have been the same one that was used by species of the Punung Fauna.

Vandeleuria, Chiropodomys, Hapalomys, Pithecheir, Kadarsonomys clade

Musser and Newcomb (1983) suggested that *Lenothrix* and *Pithecheir* have the aspects of old endemics of Sundaland, relicts left over from an earlier time in the history of the Sunda region and the early evolution of rats there. The Grey Tree Rat *Lenothrix canus*, the only species in its genus, is restricted to northern Borneo and the Sumatran island of Tuangku (Corbet & Hill 1992), although S.E. Page et al. (1999a) also described the species from south Central Kalimantan. The two *Pithecheir* species are restricted to Java and Peninsular Malaysia (Corbet & Hill 1992), and based on the absence of fossils on the Asian mainland, Chaimanee (1998) suggested that this group remained isolated in the Sundaic Subregion for millions of years. Emmons (1993) described a new genus and species of rat from Sabah, *Pithecheirops otion*, which she considered closely related to the other two old endemic genera *Pithecheir* and *Lenothrix*. The data are insufficient to link the group's evolution to palaeogeographies.

The occurrence of two or three species of *Hapalomys* in the Late Pliocene deposits of S. China (between 2 and 1.8 Mya) demonstrates that this genus developed its modern characters in Asia (Chaimanee 1998). Musser and Newcomb (1983) proposed an Indochinese origin of the extant species of this genus, which was confirmed by fossil finds (Chaimanee 1998). The related group *Chiropodomys* probably also evolved on the Asian mainland, judging from the primative characters of a 2 Myr old fossil from China (*C. primitivus*), although the majority of the present-day species are of Sundaic affinity. Most likely, in the Pliocene or Pleistocene, *Chiropodomys* entered Sundaland, where it diverged. Musser (1979) separated the 5 species (but see below) of *Chiropodomys* into 2 groups, the first consisting of 3 species (*C. karlkoopmani*-Mentawai and Pagai Islands; *C. calamianensis*-Busuanga and Calamian Islands; and *C. major*-N. Borneo), and the second containing 2 species (*C. gliroides*-mainland Asia and Sunda Islands; *C. muroides*-N. and C. Borneo). Musser and Carleton (1993) reassigned the Bornean subspecies of *C. gliroides* to species level (*C. pusillus*), and Chaimanee (1998) named a new fossil species from the Isthmus of Kra, *C. maximus*. The latter species is much larger than other members of the genus, and it appears that its type locality (Khao Tinpet, N 10º 54', E. 99º 15') was once isolated from the rest of the group's range, possibly as an island. The geographic ranges of Musser's two groups suggest that the first three species first evolved in Sundaland, and were then pushed to the periphery by the arrival of the second group of species with a more central distribution; it is unclear when and how these events took place.

Sciuridae

The squirrel family, Sciuridae, is an ancient group of mammals, with the earliest fossil squirrel, *Douglassciurus jeffersoni*, known from the Late Eocene, ca. 36 Mya, in western North America. In a recent paper, Mercer and Roth (2003) provided a complete phylogeny of the family based on nuclear and mitochondrial DNA sequence analyses (Fig. 4.10). Their results argue against the long-standing practice of separating all tree and ground squirrels into a group distinct from flying squirrels. Instead they found that the flying squirrels formed a monophyletic clade with the New World tree squirrels. A second major lineage embraces the Indo-Malayan tree squirrels together with two African genera. Furthermore, their analysis suggested that a single lineage of squirrels crossed Wallace's Line to give rise to the genera of Sulawesi (*Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*) between 11.4 and 10.5 Mya.

One of the most unexpected results of Mercer and Roth's work was that the Bornean endemic Tufted Ground Squirrel (*Rheithrosciurus macrotis*) is nested within a clade comprising most of the tree squirrels of the New World. This can only be explained by either the complete extinction of all relatives distributed across Asia or long distance dispersal. Also remarkable was that *Ratufa*, the Giant Squirrels, constituted a monotypic lineage that split off from the other squirrels at a very early stage. Fossils of *Ratufa* have been found in northern Pakistan and were dated at ca. 8.8 Myr (Barry et al. 2002), which shows the considerable age of this genus.

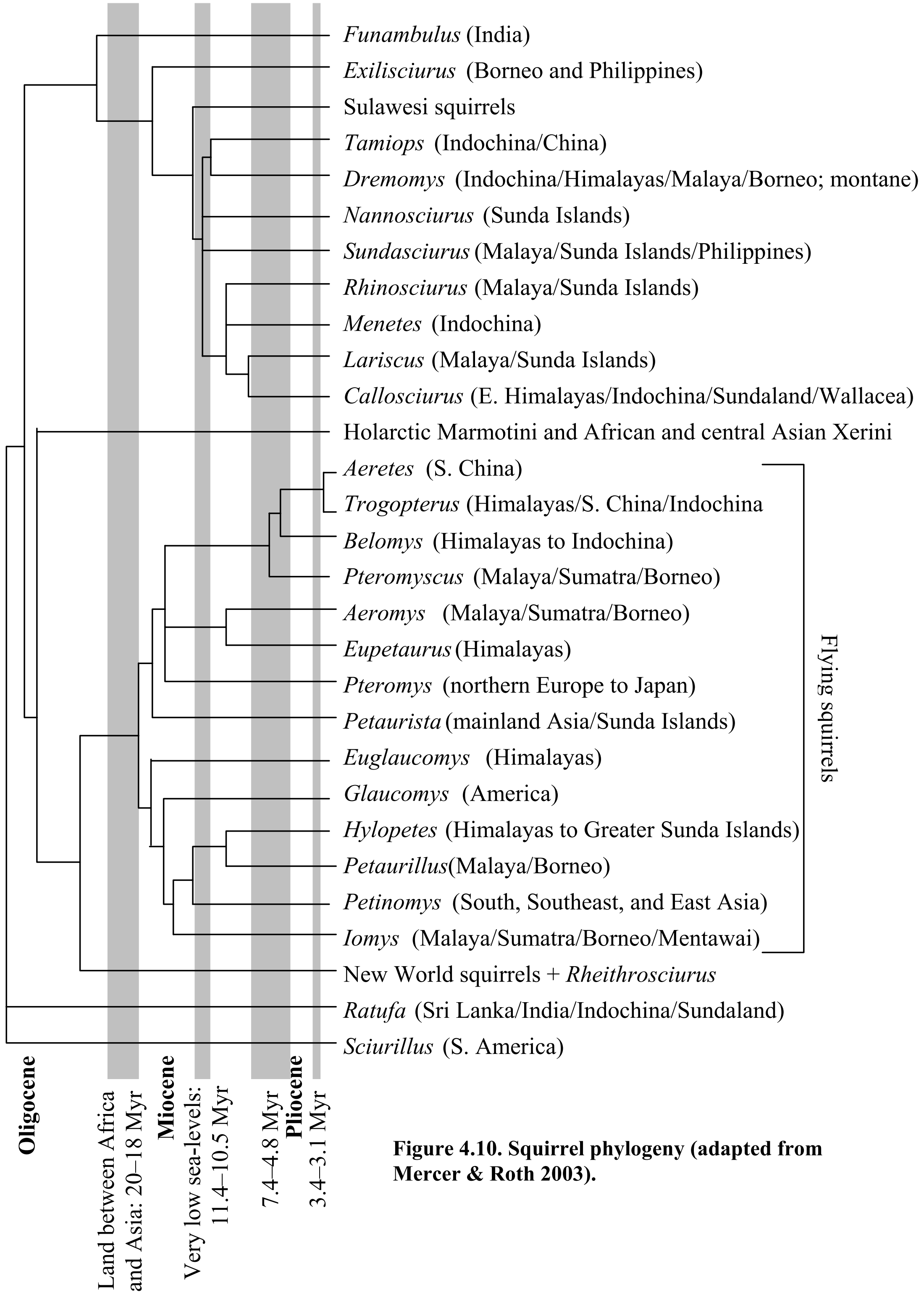


Figure 4.10. Squirrel phylogeny (adapted from Mercer & Roth 2003).

Flying squirrels

The phylogeny of Asian flying squirrels is still very much unresolved, and even the monophyly of the group has not yet been established (Oshida et al. 1996). Hight et al. (1974), while recognizing a close relationship between *Petaurista* and *Pteromys*, suggested that flying squirrels evolved from more than one stock because of the apparent large evolutionary distances between the genus *Iomys* from Southeast Asia and other flying squirrels. The flying squirrels minus *Iomys* appear to be monophyletic. The first genus to split off from this group was *Belomys* (*Trogopterus*), a flying squirrel of dense forest of China and high altitude areas of Indochina and India (Oshida et al. 2000b); no divergence time for this taxon has been estimated. The next group to split off, probably during the Oligocene, contained the *Hylopetes* and *Petinomys* genera, from which, at about 29 Mya, the New World genus *Glaucomys* diverged.

Clearly Oshida et al.'s phylogeny differs considerably from the one presented in Fig. 4.10. Oshida et al. (2000b) hypothesized that after the Oligocene-Miocene radiation of flying squirrels in Europe, the ancestral stock of *Glaucomys* may have migrated to North America, while at the same time the ancestor of *Hylopetes* and *Petinomys* migrated to South and SE Asia. *Hylopetes* and *Petinomys* diverged from each other approximately 2.2 Mya (Oshida et al. 2000b) (but see the very different estimate in Fig. 4.10). The group containing the widespread *Petaurista* genus and the north and east Asian *Pteromys* diverged, with a split between the two genera occurring between 28 and 38 Mya (Oshida et al. 2000b), but note that Mercer and Roth's data suggest a more recent evolution within the flying squirrels (compare Figs. 4.10 and 4.11).

The phylogeny of Oshida and colleagues coincides well with the morphometrics-based phylogeny of Thorington et al. (2002) (Fig. 4.11). Thorington and colleagues also concluded that the monophyly of the *Hylopetes* and *Petinomys* clade is strongly supported, and it would be interesting to know how long ago the primarily Sundaic *Petinomys* (which has one species in Sri Lanka) diverged from *Hylopetes* that has most species on the Asian mainland. They also found strong support for the monophyly of a clade consisting of *Petaurista* and the Chinese endemic *Aeretes melanopterus* (Thorington et al. 2002). Most divergence times among the existing

Petaurista species were estimated at Late Miocene to Pliocene (see Table 4.6) (Oshida et al. 1996; 2000a). It would be interesting to know whether the divergence of these arboreal species coincided with the fragmentation of once contiguous forest areas.

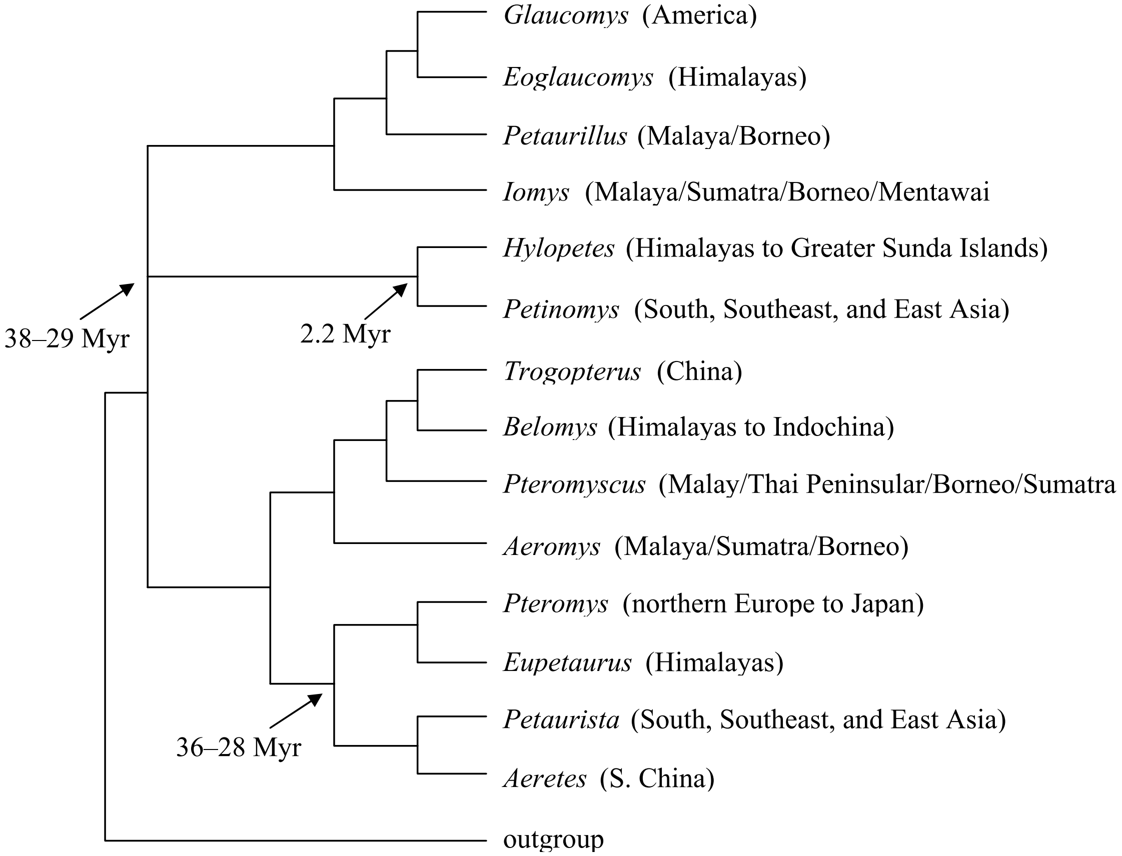


Figure 4.11. Strict concensus tree of flying squirrel phylogeny (after Thorington et al. 2002), with some of the divergence time estimates of Oshida et al. (2000b).

Oshida et al. (2001a) also analysed the phylogenetic relationships within the genus *Petaurista*, on the basis of sequence comparison of a part of the mitochondrial cytomchrome *b* gene, but because there are such large discrepancies between the divergence estimates of Oshida and colleagues and Mercer and Roth that I have left the detailed study of *Petaurista* out of this thesis. It should be noted, however, that the centre of species diversity of *Petaurista* appears to lie on the Asian mainland, with only 2 out of 9 (or 10) species reaching the Sundaic Subregion. These two, *P. petaurista* and *P. elegans* seem to have their centre of distributional gravity in Sundaland, although both also have populations on the Asian mainland (as far as

Pakistan for *P. petaurista*). Oshida et al. (2000a) did not provide estimates for the divergence between these two species and their nearest relative, but from other divergence times estimates I deduce that both species evolved in the Late Miocene–Pliocene. Abundant fossils of *P. petaurista* indicated that this species became widespread in Thailand after the Pliocene (Chaimanee 1998), which, assuming that the species originated in the Sundaic Subregion, would suggest that the species dispersed into the Asian mainland at that time.

Chaimanee and Jaeger (2000b) described the new species *Belomys thamkaewi* from late Middle to Late Pleistocene deposits in western Thailand. This species has not been found in the same location as the more widespread *B. pearsonii*. The occurrence of fossil *B. pearsonii* all over Thailand during the Pleistocene and of *B. thamkaewi* in lowlands of west Thailand during the Late Pleistocene is rather surprising as this genus is supposed to live in rather temperate forest, high latitude and an elevation of about 1,500–2,400 m a.s.l. (Mitchell, 1979 in Chaimanee & Jaeger 2000b). Middle and Late Pleistocene climatic fluctuations are probable causes for these range shifts.

Callosciurus

Oshida et al. (2001b) investigated the phylogenetic relationships between 5 of the 15 species of *Callosciurus*, i.e. *C. caniceps* (Thailand and Malay peninsula), *C. erythraeus* (mainland SE Asia, but absent from central Thailand), *C. finlaysonii* (Indochina and Thailand), *C. nigrovittatus* (Malay peninsula, Sumatra, and Java), and *C. prevostii* (Borneo, Sumatra, and Malay peninsula). Because of the small number of species used in the research the study could not completely explain phylogenetic relationships in the genus. *C. nigrovittatus* was closely related to *C. prevostii* with 100% bootstrap values in MP and NJ trees and with 100% support in an ML tree. The divergence time between them was estimated at 4.4–5.0 Myr (PLIO 1 – PLIO 2). The two species occur sympatrically in Sumatra and the southern Malay peninsula, but *C. nigrovittatus* does not occur on Borneo, and *C. prevostii* is absent from Java. The divergence between the two species might therefore have happened when two land areas became disconnected, one of which was connected to Java, and the other to Borneo.

Carnivora

Bininda-Emonds et al. (1999) established the phylogeny of all carnivores using a combination of published fossil and molecular studies, which they analysed using a supertree construction (Fig. 4.12).

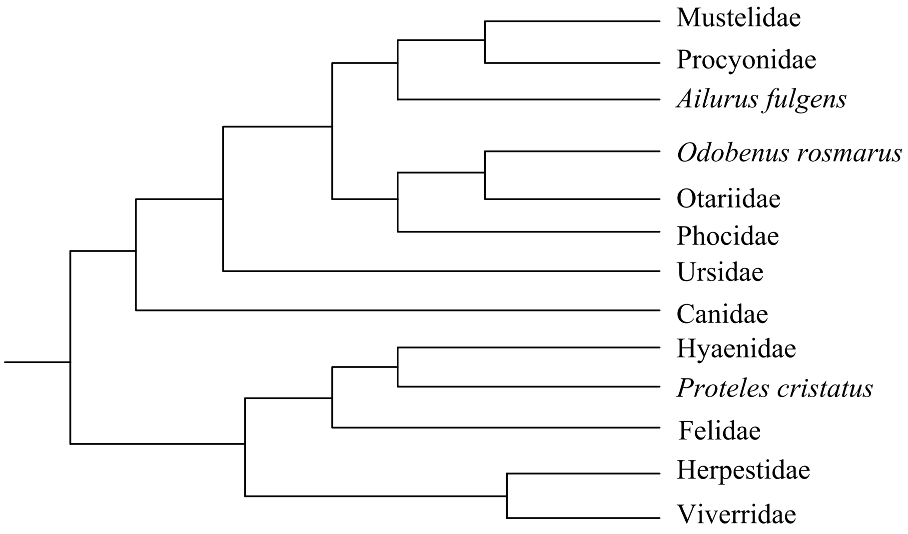


Figure 4.12. The composite tree for the higher groups of carnivores (after Bininda-Emonds et al. 1999).

Canidae

The Canidae diverged from other carnivores some 50–40 Mya, during the Eocene. However, the extant canids have radiated from a common ancestor more recently, about 10 Mya (Vilà et al. 1999). The extant Canidae form a diverse group of wolf-, jackal-, and fox-like carnivores that includes about 36 species. Twenty-three of these were included in a molecular study by Wayne et al. (1997), who used cytochrome *b* sequences to assess phylogenetic relationships among these species. Their different phylogenetic approaches used produced similar topologies with the following generalized sequence divergence. The most basal species are the Raccoon Dog (*Nyctereutes procyonoides*) of Japan and China, Grey Fox (*Urocyon cinereoargenteus*) of North America, and the Bat-eared Fox (*Otocyon megalotis*) of sub-Saharan Africa. Following these early divergences, two monophyletic groups split off: the Red Fox-like canids, and the Wolf-like (genera *Canis* and *Cuon*) and South American canids. The genus *Canis* does not appear to be monophyletic, because the

Side-striped Jackal *Canis adustus*, forms a sister group to the other *Canis* species and *Cuon* (the Dhole); in some scenarios the latter group also contains *Chrysocyon brachyurus* (Maned Wolf) and *Speothos venaticus* (Bush Dog). Here, I am primarily interested in the Asian members of the Wolf-like canids group for which the phylogeny is reproduced in Fig. 4.13.

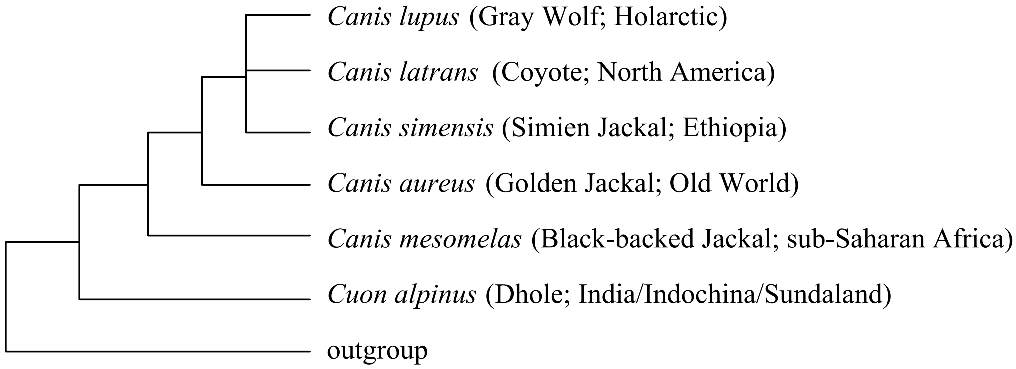


Figure 4.13. Phylogenetic relationships among Asian canids (after Wayne et al. 1997).

Wayne et al. (1997) did not provide an estimated time of divergence of the *Cuon* lineage from the other canids, but their sequence divergence data and their fossil-based rate of mtDNA divergence suggests that this happened between 6.3 and 5.1 Mya, i.e. during MIO 4. The evolution of these communal species that hunt in packs may be related to the increasing availability of open areas towards the end of the Miocene.

Fossil specimens of *Cuon* have been found as far as Europe where, in the Late Pliocene–Late Pleistocene, *C. priscus*, *C. alpinus fossilis*, and *C. a. europaeus* occurred (Schütt 1973; Baryshnikov 1996). The species or its ancestors also occurred in China and on Java. According to Schütt (1973), the radiation of the genus *Cuon* did not start until the Early Pleistocene, as no earlier fossils have been found. She suggested that this radiation started at a time when older, related species, such as *Mececyon* sp., *Megacyon* sp. and *Xenocyon* sp. started to decline, and it is possible that either *Megacyon* or *Xenocyon* where ancestral to *Cuon* (Schütt 1973). It is yet unclear how the palaeogeographical model can be related to the evolution of *Cuon*.

Ursidae

The classification of bears seems excessively split for such a small and recently evolved family. Taxonomists have placed each species of bear in its own genus at one time or another, and other genera, declared on the basis of one or a few specimens, have been shown to be no more than subspecies, local populations, or colour phases (Lekagul & McNeely 1977).

In a study of molecular genetic-distance estimates among the Ursidae, Goldman et al. (1989) estimated that between 22.4 and 32.3 Mya, the ancestors of the procyonids (racoons) and the ursids split into two lineages. Ten Myr after that event, the Red Panda (*Ailurus fulgens*) split from the line that led to the racoon. An ancestor of the Giant Panda (*Ailuropoda melanoleuca*) split from the ursid line 22–18 Mya, and the South-American Spectacled Bear (*Tremarctos*) split from the line leading to the ursine bears 15–10.5 Mya. Based on this, the Spectacled Bear has been considered a very primitive bear and has been alternatively placed in its own monotypic genus (*Tremarctos*) or subfamily (Zhang & Ryder 1993).

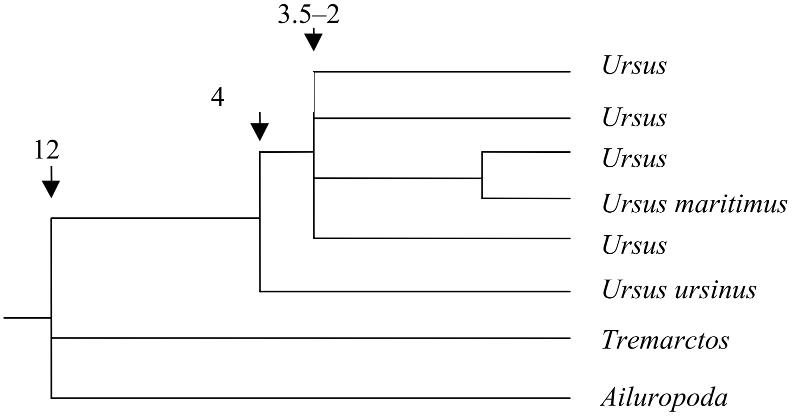


Figure 4.14. The phylogenetic relationships between bears species (after Waits et al. 1999). Numbers refer to the estimated divergence times at each node.

The origin of the Ursinae (true bears) is placed in the Late Miocene, approximately 7 Mya by Talbot and Shields (Talbot & Shields 1996). However, Waits et al. (1999), based on more extensive data, placed the divergence of the Ursinae at about 4 Myr. This seems to fit data from the fossil record, because at about 4 Mya the genus *Ursus* first appeared in northern China's fossil deposits (Kurten, 1968 in Flynn et al. 1991).

Several genetic studies have failed to resolve the phylogenetic resolution of the species within the Ursinae, which suggest that rapid radiation occurred leading to four ancestral bear lineages. This included the lineage leading to Asiatic Black Bear (*U. thibetanus*) and to American Black Bear (*Ursus americanu*s), the lineage of the Malayan Sun Bear (*U. malayanus*), and the lineage leading to the Brown Bear (*U. arctos*) and Polar Bear (*U. maritimus*) (Waits et al. 1999, also Waits, 1996). The initial rapid radiation occurred some time between 3.5 and 2 Mya (PLEI 3 – PLEI 4), while the emergence of Polar Bears from within the Brown Bears occurred in the last 1 Myr (Waits et al. 1999), or very recently (Late Pleistocene) according to Mazza and Rustioni (1994).

Figure 4.14 coincides reasonably well with Mazza and Rustioni's (1994) phylogeny, which was based on bear fossils and their morphology. They suggested that the *U. malayanus* lineage split from a group of primitive *U. minimus*-*U. thibetanus* bears in Asia in the Late Pliocene. These bears (*U. minimus*-*U. thibetanus*) were widespread during the Pliocene, from Europe, including Britain to East Asia. They disappeared from Europe in the Late Pliocene, probably because of worsening climatic conditions, but they survived in Asia. In the Late Pliocene, this led to an Asian lineage of *U. minimus*-*U. thibetanus* which eventually gave rise to the modern Asiatic black bear. *U. namadicus*, the Indian equivalent of the European *U. minimus*, may have been the direct ancestor of *U. thibetanus*. During the Middle–Late Pleistocene, *U. minimus*-*U. thibetanus* remigrated to Europe, presumably during interglacials, but they disappeared from Europe during the early Late Pleistocene (Mazza & Rustioni 1994). If indeed, *U. thibetanus* orinated approximately at the same time as *U. malayanus*, and the ancestor of the former can be traced back to India, it is possible that *U. malayanus* evolved in another tropical or subtropical parts of Asia, i.e. Sundaland or mainland SE Asia. *U. malayanus* only appeared on Java during the Late Pleistocene with the tropical Punung fauna, and the limited morphological and genetic differentiation of *U. malayanus* from Borneo, Sumatra, Malaya, and the Asian mainland suggests that the species dispersed into Sundaland relatively recently (see Chapter 6.1).

Felidae

In spite of the intensity and scope of cat research, there remains considerable uncertainty regarding the evolutionary relationship among the 37 living cat species. A major reason for this uncertainty is the rather recent radiation producing all extant species within the last 10 Myr (Janczewski et al. 1995). O'Brien (1996) and Johnson and O'Brien (1997) provided overviews of the phylogenetic relationships among the Felidae (Fig. 4.15).

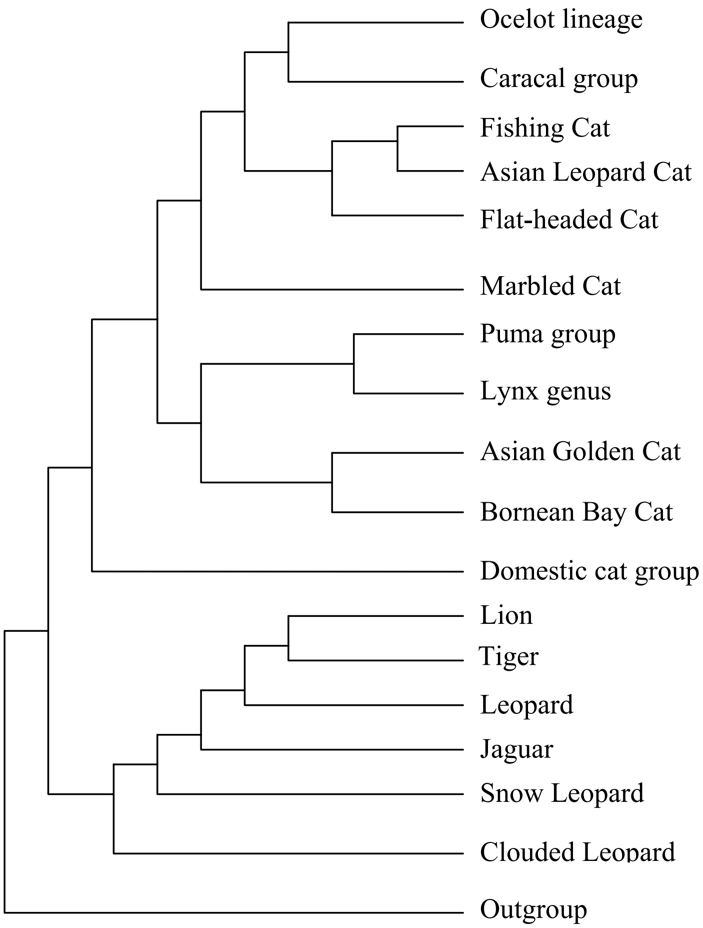


Figure 4.15. Phylogenetic relationships among selected living cat species (after Johnson & O'Brien 1997).

Figure 4.15 coincides well with the more recent phylogenetic data by Mattern and McLennan (2000), although in the latter phylogeny the Marbled Cat is more closely linked with the *Catopuma* group (Bay and Golden Cat).

Of the species that presently occur in Southeast Asia, Johnson and O'Brien (1997) made the following consensus estimates of the lineages' divergence times. The Bornean Bay Cat (*Catopuma badia*) and Asian Golden Cat (*Catopuma temmincki*) are distantly related, but form a well-supported monophyletic clade. The two species of *Catopuma* diverged ca. 5.4 Mya (7 Myr in O'Brien, 1996) from the lineages leading to the *Panthera* group (which includes, among others, the tigers and leopards). With the Bay Cat being restricted to Borneo, this may suggest that isolation of the island occurred before the start of the Pliocene (in fact, this was estimated at 3.2 Ma by Bininda-Emonds et al. 1999, although they consider this estimate to be very tentative). It could be that the two species diverged when Borneo first became an island during PLIO 3, or if *temmincki* is considered to be of Indochinese affinity and *badia* of Sundaic affinity, then it is possible that the two lineages separated during PLIO 2 when the Sundaic and Indochinese subregions may have become separated. It should be noted, however, that Mattern and McLennan (2000) suggested a process of sympatric speciation associated with an increase in body size in *C. temmincki*. More generally, these latter authors suggested that vicariant speciation appears to have played a limited role in the Felidae.

Asian Leopard Cat (*Prionailurus bengalensis*), Fishing Cat (*P. planiceps*) and Flat-headed Cat (*P. viverrinus*) are closely related and form a strongly supported clade in a DNA-based phylogeny. These three species probably diverged from a common ancestor some 3.95 Mya (Johnson & O'Brien 1997). According to Mattern and McLennan (2000) these species evolved sympatrically associated with movement into thicker forest, coupled with the origin of climbing ability in *bengalensis*. It could also be that these species evolved as the result of allopatric speciation, when high sea levels during PLIO 2, may have split Sumatra from the rest of Sundaland and Sundaland from the Asian mainland; ecological specialization of the 3 species would then have occurred after their initial divergence and was not the direct cause of it.

Pardofelis marmorata, the Marbled Cat of the Himalayas, Indochina, and Sundaland, formed part of the radiation in a group including the genus *Lynx* (O'Brien 1996), although in the study by Johnson and O'Brien (1997), this species did not consistently associate with any other felid; a relationship with the Puma group was in that study more likely. Mattern and McLennan (2000) found a more likely close relationshio between *Catopuma* and *Pardofelis marmorata*. Finally, the radiation of the group containing *Panthera* and *Neofelis* (the Clouded Leopard) occurred some 6–5.5 Mya, according to O'Brien et al. (1987) and Johnson and O'Brien (1997), although in another paper O' Brien (1996) estimated that this radiation occurred in the Pleistocene. The origin of *Panthera* probably dates back to 3–2 Mya (Turner, 1987 in Johnson & O'Brien 1997). Meijaard (in press) discussed in detail the evolutionary history of Javan leopards (also see Appendix 4).

Tigers (*Panthera tigris*) probably originated in East Asia ca. 2 Mya from where one dispersal route led into the Indonesian islands (Hemmer, 1987, in Nowell & Jackson 1996). Fossil finds of tigers on Java date back to 900 Kya, or possibly to 1.2–1.0 Mya (van den Bergh et al. 1996). As Groves (1992) pointed out, the distributional history of the tiger is complicated possibly involving several migration waves and sub-species replacements (see Fig. 4.16). The primitive tiger stock spread from north-eastern Asia down into Java ca. 1 Mya, where it underwent change, and ca. 500 Kya it spread back north into China where it replaced the archaic form. The new northern tiger underwent further evolution, and ca. 100 Kya dispersed south, replacing the old Javanese type and evolving into the modern (recently extinct) Javan tiger (Groves 1992). The Sumatran tiger (*Panthera tigris sumatrae*) is the plesiomorphic sister taxon of the Javan tiger, which it resembles in stripe patterns while lacking the derived occiput shape (Groves 1992).

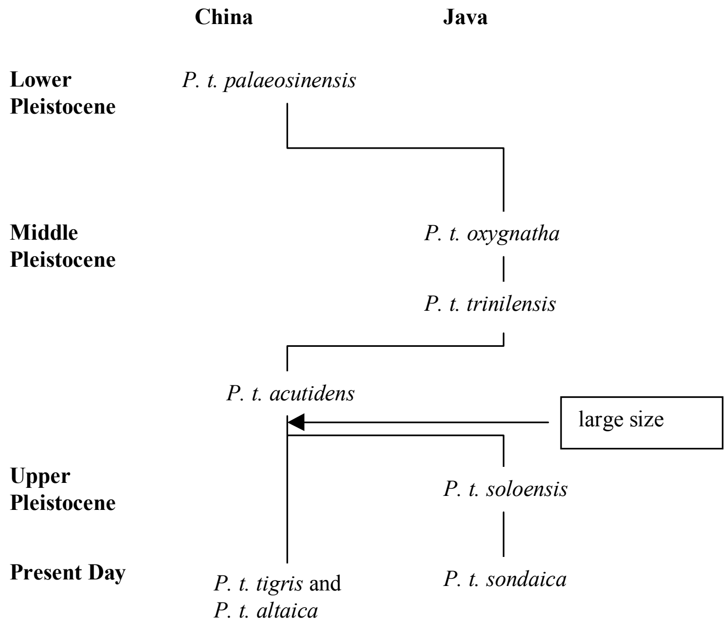


Figure 4.16. Tiger evolution in SE Asia (after Groves 1992)**.**

According to Cracraft et al. (1998), the Sumatran tiger was only recently separated from the populations in Peninsular Malaysia with slight genetic differences indicating isolation since the last glacial, while genetic research by Hendrickson et al. (2000) suggested that the Sumatran tiger is basal to the clade containing Bengal and Siberian tigers. This indicates that all mainland Asian tigers went extinct before or during the LGM (PLEI 5) (assuming that the time estimate by Cracraft et al. is correct), and that they reinvaded mainland Asia from Sumatra (and Java), during or just after the LGM. Tigers occurred on Java and Bali, but have never been found on Borneo (but see Meijaard 1999a), indicating that Borneo was physically or ecologically separated from the other islands before the arrival of the tiger.

Mustelidae

Schmidt-Kittler (1984) stated that the musteloid carnivores developed in two radiations. The earlier one originated in the Oligocene of Asia and gave rise to a great number of now extinct lineages, with maximum diversity in the Miocene. Towards the end of the Miocene, nearly the whole radiation went extinct, except for some New World lineages (Procyonidae) and the Red Panda *Ailurus fulgens*. As an offshoot of the earlier radiation, a second radiation arose and developed in the Early Miocene (for an alternative evolutionary scenario see Figure 4.12 at the start of the Carnivore section). This unit consisting of the Mustelidae led to the recent martens, weasels, badgers and otters. Divergence within the Eurasian Mustelidae primarily happened during the Early Pliocene, between ca. 5.8 and 3.7 Mya, with further speciation during the Early–Middle and Middle Pleistocene (Kurose et al. 2000), although Hosoda et al. (2000) suggested that this may have happened earlier, between 8 and 5 Mya. Kurose and colleagues did not include any of the SE Asian species in their research, but according to Schmidt-Kittler (1984) the Mustelidae were pushed south into Sundaland during the cooler periods of the Pliocene and Pleistocene leading to the presence of *Martes* and *Mustela*. Presumably this resulted in the divergence of Sundaic species like *Mustela nudipes* and *M. lutreolina*. Bininda-Emonds et al. (1999) estimated that the divergence between the SE Asian *Mustela* species (*M. lutreolina*-Java and S. Sumatra, above 1,000 m a.s.l.; *M. nudipes*-Sumatra and Borneo; *M. sibirica*-east

Himalayas, above 2,400 m. a.s.l.; and *M. strigidorsa*-northern Indochina to Himalayas, mainly hills) happened approximately 200 Kya.

Van Bree and Boeadi (1978) considered *M. lutreolina* to be externally similar to *M. lutreola*, the European Mink, but craniomorphologically it is much more like *M. sibirica*, the Siberian Weasel. Based on this, and the absence of *M. lutreolina* from the Malay Peninsula—the southern limit of *M. sibirica* is in Central Thailand, whereas *M. lutreolina* is restricted to the high mountains of Java and south Sumatra—van Bree and Boeadi (1978) suggested that *M. lutreolina* reached Java (and Sumatra) during much colder times. The biogeographic scenario may thus have been as follows. An ancestral species moved into Sundaland during a Pliocene or Pleistocene glacial period, after which the interglacial climatic conditions that followed isolated populations in cool climate habitats like the Javan, Sumatran, and mainland Asian mountains. The presence of *M. nudipes* throughout the lowlands of Thailand, Malaya, Sumatra, and Borneo would in this tentative scenario be a secondary adaptation to tropical conditions.

According to Hosoda et al. (2000), divergence within the genus *Martes* commenced during the Middle Miocene (14–10 Myr), when a group containing the ancestor of *M. flavigula*, the Yellow-throated Marten, diverged from another group which, among others, contained *M. foina*, the Stone Marten (but see above for a claim of much later divergence of this group). The data by Hosoda et al. are insufficient to speculate on the underlying causes of the speciation within *Martes*. The subgenus *Charronia* to which *M. flavigula* (SE Asia) and *M. gwatkinsii* (S. India) belong probably arose before the Pliocene (Stone & Cook 2002). A tentative estimate for the divergence time between these two species was provided by Bininda-Emonds et al. (1999). According to them, *M. flavigula* separated from *M. gwatkinsii* some 900 Kya (based on one estimate from the literature in Bininda-Emonds et al. 1999). These forest species (see, for instance, Lekagul & McNeely 1977; Payne et al. 1985) may have been separated as a result of the cooler and/or drier conditions in a Pleistocene glacial that could have led to the disappearance of suitable habitat in mainland Asia, although the species could also have diverged as a result of sympatric speciation.

According to Schmidt-Kittler (1984), the genera *Mydaus* and *Helictis* (=*Melogale*) were already established in Southeast Asia during the Miocene, although the earliest fossil finds attributed to *Mydaus* from Java only date back to the Holocene (see Section 4.1.). Bininda-Emonds et al. (1999) estimated the divergence time of the clade leading to *Mydaus*, and also *Meles* and *Arctonyx*, at 13.7 Myr, but this was done on a questionable assumption of a relationship between a clade's age and the logarithm of the number of species it contains, which would be strongly affected by (unnoticed) extinctions. Similarly, *Arctonyx* was estimated to having diverged from *Meles*—the Eurasian Badger—some 10.2 Mya. Bininda-Emonds et al. (1999) also provided an estimated divergence time for the two species of Ferret Badger in SE Asia, *M. javanensis* from Sumatra, Borneo, and Java, and *M. marchei* from Palawan. However, their estimate of 3.5 Mya is again based on an interpolation using a model under which a clade's age is proportional to the logarithm of the number of species it contains (after Purvis, 1995a in Bininda-Emonds et al. 1999). The distribution of *Melogale*, with one species in S. China, Indochina, Hainan and Taiwan, another species on Mt. Kinabalu, northern Borneo, and a third species on the mountains of Java, suggests a relict distribution of the two Sundaic species. Possibly these species entered Sundaland during colder times (Pliocene or Pleistocene) and where later restricted to mountainous habitats.

Koepfli and Wayne (1998) investigated the phylogenetic relationships among otters. Their analysis, which unfortunately excluded most of the SE Asian species, revealed that the otters are divided into three clades, one containing the North American River, Neotropical and Marine Otters (strong bootstrap support); another containing the Sea, Eurasian, Spotted-necked, Cape Clawless and Small-clawed Otter (moderate bootstrap support); and one containing the Giant Otter. The following evolutionary model was provided for Asia. The earliest lutrine genus, *Mionictis*, is found in Early Miocene deposits of both Europe and North America, with several species in each region. Most likely, rapid diversification then occurred during the Miocene. The Asian Small-clawed Otter (*Amblonyx cinereus*) split from its sister species the African Clawless Otter (*Aonyx capensis*) about 5 Mya (4.2 Mya in Bininda-Emonds et al. 1999). In the Late Miocene of China, the fossil species *Aonyx aonychoides* was found confirming that this lineage had diverged at that time. No records of *Amblonyx cinereus* fossils were found in the literature, apart from its Holocene appearance on Java (see Section 4.1), and the species may be a recent arrival in Sundaland. The common ancestry of the *Aonyx*-*Amblonyx* group with the Eurasian Otter (*Lutra lutra*) can be traced back to between 8 and 6.3 Mya. It is yet unclear how the other Asian otter species (*Lutra sumatrana* and *Lutrogale perspicillata*) fit in, but Koepfli and Wayne's results indicate that the genus *Lutra* is paraphyletic. This was also found by Bininda-Emonds et al. (1999) who suggested that *Lutrogale perspicillata*—the Smooth-coated Otter from mainland Asia and Sundaland was a sister species of *Lutra maculicollis* from Africa and *Pteronura brasilliensis* of South America and that these species separated some 300 Kya. *Lutrogale perspicillata* occurs throughout Asia, south of the Himalayas, including Indochina, the Malay Peninsula, Sumatra, Borneo, and Java (Corbet & Hill 1992). On Java, the species seems to be restricted to the western half of the island (van Bree 1969). Willemsen (1986) described otter fossils from the Kali Glagah and Kedung Brubus faunas on Java (respectively ca. 2 Mya and 700 Kya, although the former might lack stratigraphical information, see van den Bergh 1999), which he identified as *Lutrogale*. Von Koenigswald (1940 in Willemsen 1986) suggested morphological differences between the Kali Glagah and Kedung Brubus fossils, and named the species *Lutra palaeoleptonyx* and *Lutra robusta*, but according to Willemsem both these species belong to *Lutrogale*. This suggests that the genus *Lutrogale* is at least of late Early Pleistocene age, and has been present on Java since that time. The genus only appears in the fossil record of Thailand in the late Middle or Late Pleistocene, and it may therefore have been isolated on Java or in southern Sundaland for most of the Pleistocene. If this genus is indeed closely related to an African and South American species, and these taxa diverged sometime in the late Middle Pleistocene (Bininda-Emonds et al. 1999, also see above) it could have spread from southern Sundaland into the Americas and Africa. Such a rapid dispersal over very long distances followed by extinction in intermediate areas (N. America and west Asia) may, however, not be a very likely scenario.

Lutra lutra (the Eurasian Otter that occurs throughout mainland Asia and Europe, in Thailand, Sumatra, and Java, and possibly on Borneo) and *L. sumatrana* (the Hairy-nosed Otter from southern Indochina, southern Thailand, Sumatra, Java, and Borneo) separated approximately 200 Kya (Bininda-Emonds et al. 1999) (but the discussion above suggests that the estimates by Bininda-Emonds et al. may be rather inaccurate). Sivasothi (1999) suggested that the Indo-Malayan form of *L. lutra* might be a distinct species, while he further speculated that, although *L. lutra* has allegedly been reported from the Malay Peninsula, it may be absent there, so that the Sumatran and Javan subspecies (*L. l. barang*) form populations isolated from the mainland forms. In Sumatra, *L. lutra* appears to occur primarily in mountainous areas, based on records by Hoogerwerf (1937 in van Strien 2001) and Jacobson (1920 in van Strien 2001), while in Thailand their habitat is typically mountain streams and lakes (Lekagul & McNeely 1977). *L. sumatrana* is a species of coastal areas and larger inland river systems in Borneo (Payne et al. 1985) and Thailand (Lekagul & McNeely 1977). It could be that *L. lutra* descended into Sundaland during a presumably Late Pleistocene glacial period, after which it was pushed into mountainous areas when climatic conditions became warmer. Considering that its sister species *L. sumatrana* is restricted to Sundaland's lowlands and coasts, it is possible that ecological separation of the two species occurred in Sundaland, during an interglacial, after which the ancestral populations of *L. sumatrana* adapted to coastal conditions.

Viverridae

Veron and Heard (2000) investigated phylogenetic relationships within the Viverridae (Fig. 4.17). Relationships were generally poorly resolved, but indicated that the Viverridae is not a monophyletic family, and the Viverrinae (*Prionodon*, *Genetta*, *Civettictis*, *Viverricula*, and *Viverra*) not a monophyletic subfamily.

For the Asian members of this family Veron and Heard (2000) found that the Hemigalinae, which are endemic to Asia, and the Paradoxurinae probably originated in the Middle Miocene. Morphological studies, molecular results, and the fossil record shows that *Prionodon* constitutes a very different Asiatic lineage, distantly related to the palm civet and civet groups (e.g. Hunt 2001), which demonstrates that the presence of Viverridae in Asia resulted from different events (Veron & Heard 2000). Civet-like forms (*Viverra* or *Civettictis*-like) appear in the Middle Miocene of Europe, and then they can be found in the Plio-Pleistocene of Europe, Asia, and Africa, which reveals that the civets were more widely distributed in the past.

Hunt (2001) compared the skulls of the Asian Linsang *Prionodon pardicolor* with the living African Linsang *Poiana richardsoni*, and the extinct Oligocene aeluroid *Palaeoprionodon lamandani* from France. He found that the basicranium of *Prionodon* provided the link between *Palaeoprionodon* and *Poiana*. Hunt's data suggest that the subfamily Viverinnae is closely related to the Prionodontinae, because of their marked similarity in dental and basiocranial anatomy. But the other viverrid subfamilies (Paradoxurinae and Hemigalinae) probably stem from other early aeluroids of Eocene or Oligocene age. Based on the geographic restriction of the latter two subfamilies, Hunt (2001) suggested that the groups originated in the forested environments of Oligocene Indonesia.

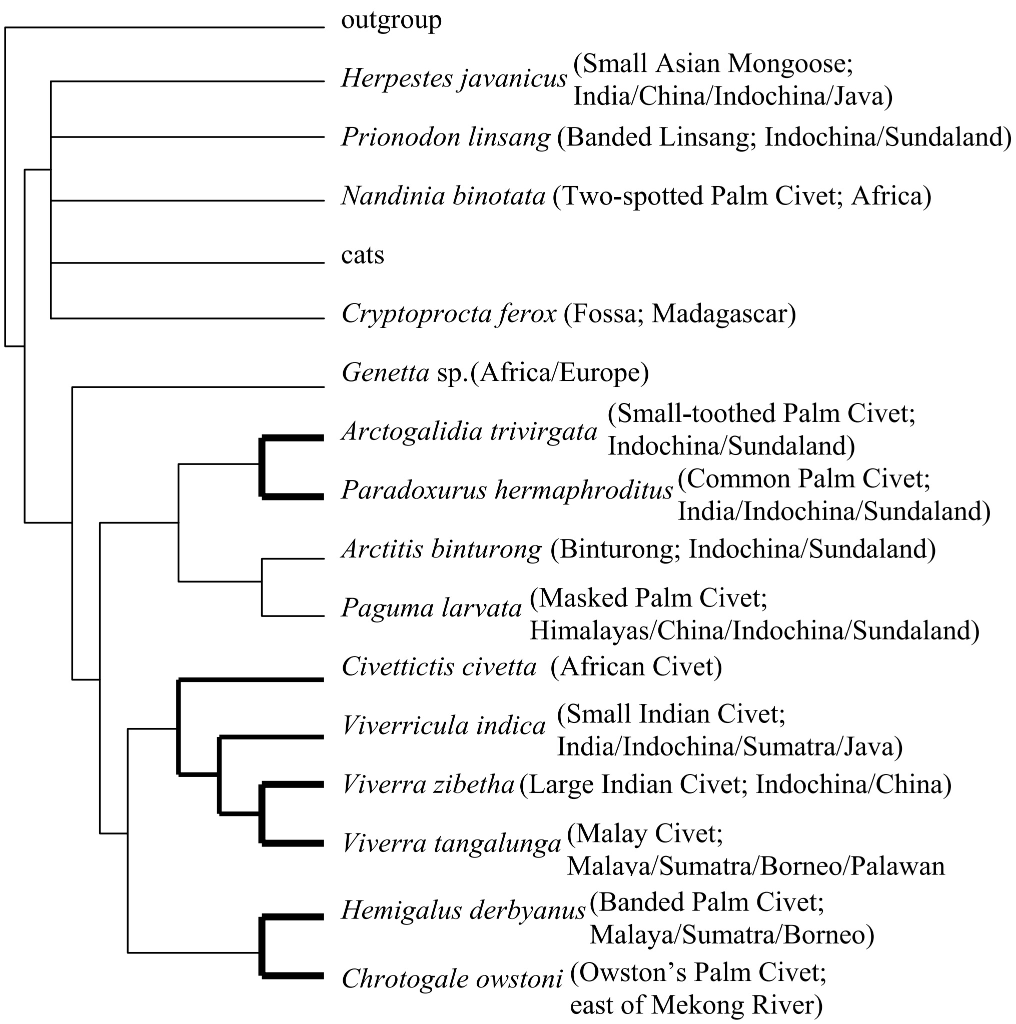


Figure 4.17. Phylogenetic relationships among viverrids (after Veron & Heard 2000). Double-bold lines had bootstrap support > 90%; single-bold between 55 and 90%; and normal lines had low bootstrap support.

Herpestidae

Asian fossils of *Herpestes* date back to the Miocene (Barry 1983), and at least 16 fossil species have been described (e.g. http://www.angellis.net/Web/PDfiles/carnivs.pdf). The first fossils of *Herpestes* on Java are only of Holocene age, and *Herpestes* could have arrived on Java during a Late Pleistocene glacial when Java was connected to Malaya by land, which was possibly covered by more open vegetation types. Both the craniometric analysis by Taylor and Matheson (1999) and the phylogenetic analysis by Bininda-Emonds (1999) suggest a sister-species relationship between *H. javanicus* (see Table 4.6) and *H. edwardsii* (Indian Grey

Mongoose), although it is unclear how the latter study came to that conclusion; it reported that there was no published information on the phylogeny of these species. Both species favour drier, more open habitats, as opposed to the mongooses of Borneo and Sumatra, *H. brachyurus* and *H. semitorquatus* that are more often found in closed forest habitats (see Payne et al. 1985). Not enough is known on the phylogeny of this group to develop a scenario for their present biogeography.

Species	**Range**
H. javanicus	S. China, Malaysia, Java
H. auropunctatus	Asian mainland [1]
H. brachyurus	Malaya, Sumatra, Borneo, Palawan
H. semitorquatus	locally in Sumatra and Borneo

Table 4.6. SE Asian mongoose species (after Taylor & Matheson 1999).

[1] Wells (1989 in Taylor & Matheson 1999) considered the supposed occurrence of *H. auropunctatus* in Malaya to be due to a previous misidentification, though the error continues to be perpetuated in the literature.

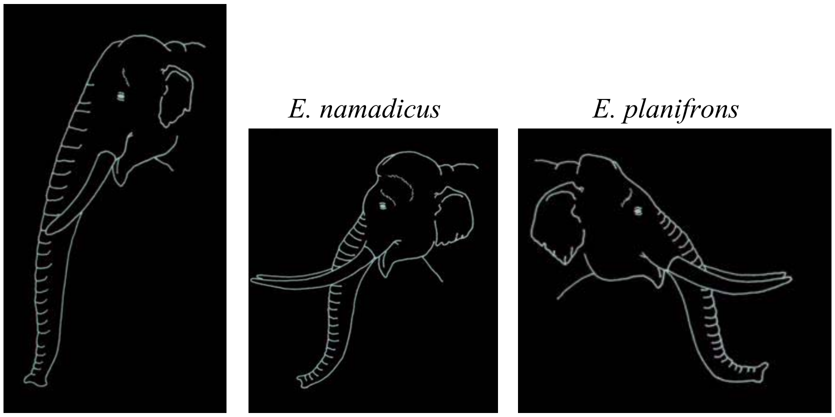
Taylor and Matheson (1999) investigated morphological similarities within the genus *Herpestes* using craniometric information (for SE Asian species see Table 4.7). Although these authors make no cladistic assumptions about primitive or derived states of characters, they think that their analysis provides some assessment of evolutionary relationships between species. One of their results strongly suggests that *H. javanicus* and *H. auropunctatus* are distinct, allopatric species. *H. javanicus* would then have a disjunct distribution with populations in Malaya and Java, but not in Sumatra and Borneo. The fact that *H. javanicus* is absent from Borneo and Sumatra may be due to its preference for grasslands and secondary growth (Lekagul & McNeely 1977), vegetation types that may not have naturally occurred in Borneo and Sumatra in recent times.

Proboscidea

Elephantidae

Fernando et al. (2000) dated the divergence between the African (*Loxodonta*) and Asian (*Elephas*) Elephants at 7–5 Mya, which seems to be supported by other data (see Fleischer et al. 2001). Molecular data by Thomas et al. (2000), however, suggested that *Elephas* initially split from the line leading to the *Loxodonta-Mammuthus* clade about 14.8 Mya, which is considerably older than the time suggested by Fernando et al. The *Elephas* lineage probably originated in Africa and diverged into a species complex with an Asiatic and African-European branch. Progenitors of the Asian branch invaded Asia in the Late Pliocene (ca. 3 Mya) leading to species such as *E. planifrons*, *E. hysudricus*, and derivatives. *E. maximus* likely evolved directly from *E. hysudricus*, perhaps during the last 200 Kyr (Maglio 1973). A Javan form, *E. hysudrindicus*, probably split off from the *E. hysudricus* lineage 1–0.8 Mya (Fleischer et al. 2001). In the Early Pleistocene, a second emigration out of Africa of the *Elephas* lineage occurred through *E. namadicus*. This species rapidly expanded in range and became dominant, occurring as the only elephant in parts of Asia, but went extinct in the Late Pleistocene (Maglio 1973).

Interestingly, genetic analysis revealed a phylogenetic discontinuity of two assemblages of haplotypes within mainland Asian elephants (*E. maximus*) with a sequence divergence corresponding to a divergence time of 3.5–2.5 Mya, according to Fernando et al. (2000), and 1.2 Mya according to Fleischer et al. (2001). As the latter authors conducted an independent test of their divergence estimate, it seems likely that the Asian clades diverged in Early–Middle Pleistocene. These two clades occur sympatrically, although Indonesian and Malaysian elephants appear to be restricted to one clade only. This could suggest that a Sundaic lineage was separated from the mainland Asian lineage during PLEI 2. Indian, Nepali, Burmese, and Thai elephants occur in both clades, and interestingly, Sri Lankan elephants were mostly found to belong to the clade of the Indonesian/Malaysian elephants, but high trade levels from and to Sri Lanka could explain this unusually high ratio of the Indonesian/Malaysian clade in Sri Lankan elephant populations (Fleischer et al. 2001). The split within this clade between the Indonesian (Sumatran) and Thai, Sri Lankan, and Indian elephants was roughly estimated to have occurred 0.57–0.12 Mya (Fleischer et al. 2001). An explanation for the split of Asian elephants into two clades is still needed. It is possible that an earlier population was split in two and these lineages were retained. But it can also not be ruled out that the two clades have been maintained in a single large population purely by stochastic lineage retention. Fleischer et al. appear to favour the former hypothesis. They speculate that the Indonesian/Malaysian clade could be descendants from haplotypes of *E. hysudrindicus*, whereas the other clade descended from those of the northern *E. maximus* (formerly *E. hysudricus*). These two forms later hybridised in the Late Pleistocene.


S. trigonocephalus

E. namadicus

E. planifrons

Figure 4.18. Recontructed heads of some of the elaphantids mentioned in the text (drawings from http://www.angellis.net/Web/muglist.htm)

The Javan dwarf elephant *"E." indonesicus*, presumably of Late Pliocene or Early Pleistocene age, appears to be closely related to the Sulawesi Pygmy Elephant (*Elephas celebensis*) (van den Bergh 1999). The latter descended from the prehistoric African elephant (*E. ekorensis*) and probably left the lineage of the modern Asian Elephant *E. maximus* about 3 Mya (Whitten et al. 1987b). More modern *Elephas* species, like *E. hysudrindicus* and possibly another species, occurred in Java in the Kedung Brubus fauna (0.8–0.7 Mya), while also *E. namadicus* (see Fig. 4.18 for some of these species) may have occurred simultaneously (van den Bergh 1999). Subfossil remains of *E. maximus* have been found on Java (80–60 Kya), on Borneo, and on Bangka (van den Bergh 1999), but never together with *E. hysudrindicus* (Fleischer et al. 2001). The mechanism behind the evolution of this group remains poorly understood, although one thing is clear; elephants swim very well and easily cross distances at sea of over 45 km. The wide distribution of fossil Elephantidae in Wallacea is probably the results of the group's considerable swimming powers (see Johnson 1980).

Perissodactyla

Rhinocerotidae

The living rhinoceroses are the descendants of a once much larger group of Tertiary rhinos. Within this group, most authors agree that the living forms should all be included in either a single subfamily (Groves 1983), or a single tribe (Prothero et al., 1986 in Morales & Melnick 1994). Four genera of rhino now remain, of which two occur in Africa, and two in Asia. The latter two are *Rhinoceros* (Indian and Javan Rhino, or the one-horned rhinos) and *Dicerorhinus* (Sumatran Rhino, or the two-horned rhino). Phylogenetic data suggest a split between the two-horned and one-horned rhinos at about 21.7 Mya (Morales & Melnick 1994), or 25.9 ± 1.9 (Tougard et al. 2001), which is consistent with the first appearance of *Dicerorhinus* types in the European fossil record (Heissig, 1989 in Morales & Melnick 1994). Xu and Anderson (1997), however, estimated this basal evolutionary divergence among extant rhinoceroses, i.e. one-horned vs. two-horned, at 27 Mya, although this grouping may be incorrect. Interestingly, Morales and Melnick (1994) found that within the Sumatran Rhinoceros two haplotypes existed that had diverged approximately 1 Mya (although they admitted that there could be considerable error in this estimate). One haplotype was found in Sumatra only, while the other occurred both in NE Borneo and Sumatra. The total sample size of 4 animals is too small to allow for accurate inferences about intraspecific variation (Morales & Melnick 1994). The Sumatran Rhinoceros (*Dicerorhinus sumatrensis*) on Sumatra was only recently separated from the Asian mainland with slight genetic differences indicating isolation since the last glacial (Amato et al. 1995). However, it was also found that separation times between the Sumatran Rhinoceros of Borneo and Sumatra had been much longer (Amato et al. 1995; Morales et al. 1997).

Morphological features of the Javan Rhinoceros (*Rhinoceros sondaicus*), as investigated by Groves and Guérin (1980), seem to indicate regional continuity in evolutionary development of the living Vietnam form and the subspecies from Java, Sumatra, the Malay Peninsula and Bengal. Tentatively it could be concluded from the data that the species has separately evolved in Cambodia and Vietnam, and in Java, Sumatra, the Malay Peninsula and Bengal, since the Middle Pleistocene. It should be noted, however, that the case for such regional continuity is weak.

Tapiridae

We know that in past geological epochs members of the tapir family were abundant over a large portion of the Earth's surface. Their fossil remains have even been dug-up in many European countries, and it is assumed that a predecessor of the modern tapirs migrated from Siberia across the Bering Strait and gave rise to the American tapirs. Tapiroids were most common during the Eocene, at which time they underwent prolific radiation. They consist of 6 to 8 distinct families, although the taxon is blatantly paraphyletic and in need of taxonomic revision (Schoch 1989). Presently, only the true tapirs (genus *Tapirus*) survive. The deteriorating climatological conditions at the end of the Tertiary probably restricted all species, among which the tapir (*Tapirus*), that had been widespread in the northern hemisphere during most of the Tertiary to parts of southern China and SE Asia (Jablonski 1993). The separation of the Asian Tapir from its present-day American relatives is now estimated to have occurred approximately 25–21 Mya (Ashley et al. 1996). Schoch (1989) hypothesized on the phylogenetic relationships among tapiroids, primarily based on dental character states; the relevant genera are shown in Fig. 4.19. If these relationships are correct, it is likely that *Tapirus* originated in N. America, from where it migrated to Europe and Asia, because the ancestral groups appear to be largely restricted to the New World.

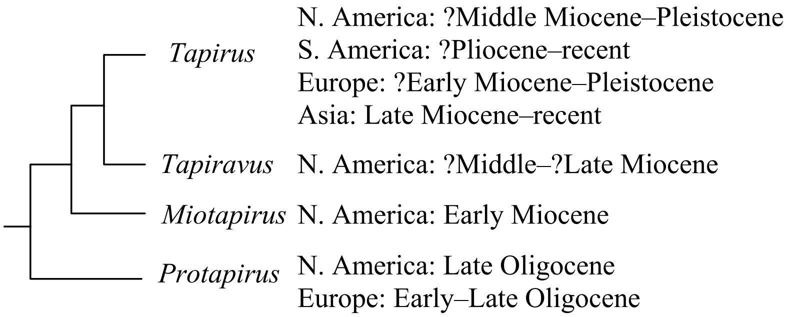


Figure 4.19. Hypothetical relationships among some of the living and fossil Tapiroidea (after Schoch 1989)**.**

Like many other SE Asian mammals, such as the Orang-utan or the Sumatran Rhinoceros, the Asian Tapir also used to be much more widely distributed than it is today. Pre-historic remains of the species were found in areas as far apart as southern Vietnam, south China, north-central India, north-west Borneo, central Java, and west Sumatra. The species seem to first appear in the fossil record of Java, Indo-China and the southern Chinese provinces of Szechwan and Yunnan in the Middle Pleistocene, some 170 Kya (Meijaard & van Strien in press). Up until the latest Pleistocene to Holocene, the tapir still existed on Java (van den Brink 1982). In Borneo fossil finds date back to between 19 and 8 Kya.

Artiodactyla

Suidae

Based on mtDNA sequences, Randi et al. (1996) estimated a time of origin of the Sulawesi babirusa (*Babyrousa babyrussa*) of 19–10 Mya. Considering that the land connection between southern Sulawesi and Borneo was severed some 50 Mya (Moss & Wilson 1998), this his suggested to some that a later land connection existed between Sundaland and Sulawesi (Weber 1902; Groves 1976), unless Babirusas dispersed through rafting or swimming (Musser 1987). The presence of two more genera of suids in Sulawesi (*Celebochoerus* and *Sus*), which must have split off from the main stock of Suidae at different times (Hooijer 1975), is indicative of several invasions of ancestral suid types to Sulawesi over a great length of time. It could be that at times of lower sea-levels pigs dispersed between Sulawesi and Borneo across shallow carbonate reefs (R. Hall, pers. comm., 1999), although also routes via the Philippines or the lesser Sunda islands have been suggested (Hooijer 1975).

In Malaysia, Borneo, Sumatra, and Java an ancestral species gave rise to the bearded pig (*Sus barbatus*) and to the Javan warty pig (*S. verrucosus*) some 5–2 Mya (Randi et al. 1996). Genetic analysis further indicated that the Indochinese warty pig (*S. bucculentus*) was genetically distinct from *S. scrofa*, while morphometric analysis placed the former species close to *S. verrucosus*, although only with weak statistical support. Stronger support was found for a clade including *S. scrofa*, *S. celebensis*, and *S. philippensis* (Groves & Schaller 2000). The Eurasian wild boar (*S. scrofa*) of Sumatra and Java probably entered the region during the late Middle Pleistocene, with the first fossil records of the species on Java occurring in the Punung Fauna (ca. 70 Kya). However, according to Medway (1971), the pig remains found in a Holocene (2.9 Kya) Malayan site (in western Pahang) were attributable exclusively to *S. barbatus*, and the absence of *S. scrofa* remains at such a late date is surprising. In Eurasia, the European and Asian *S. scrofa* populations diverged sometime in the

Middle Pleistocene (ca. 500 Kya) (Giuffra et al. 1999). Finally, recent archaeological finds by Morwood et al. (in press) indicate that during the Pleistocene an endemic pig, possibly related to *S. celebensis* and distinct from *S. scrofa*, occurred in Flores.

Based on dental morphology of pig fossils from Java, Badoux (1959) concluded that there is a striking resemblance between *Sus brachygnathus* Dubois and *S. barbatus*, and also between *Sus macrognathus* and *S. verrucosus*. Furthermore, he suggested that at least two pig species, i.e. *S. scrofa* and *S. barbatus* occurred in the Punung fissures of Java, while the presence of *S. verrucosus* is possible. Hardjasasmita (1987) largely agreed with this and added that *S. macrognathus* (and the subspecies *S. m. terhaari*) might be ancestors to *S. verrucosus*, but he did not consider *S. brachygnathus* to be closely related to *S. barbatus*. For suid evolution on Java, Hardjasasmita considered two possibilities: (1) *S. brachygnathus* is ancestral to *S. macrognathus*; (2) *S. macrognathus* evolved somewhere outside Java and immigrated together with several new faunal elements. Hardjasasmita favoured the former possibility, and he hypothesized that *S. brachygnathus* became extinct after the arrival of *S. scrofa*. Aimi (1989) considered *S. terhaari* a distinct taxon, with the most divergent characteristics in M_3 compared to *S. brachygnathus*, *S. macrognathus* and *S. stremmi*; based on the shape of the mandible Aimi suggested that *S. barbatus* is clearly different from all other taxa (*verrucosus*, *celebensis* (the extant species from Sulawesi), *brachygnathus*, *macrognathus*, *terhaari* and *stremmi*). If this is correct, then all Javan species may be chronospecies starting with *S. stremmi* in the Late Pliocene–Early Pleistocene, followed by *brachygnathus*, *macrognathus*, and *terhaari*. At the same time, *S. barbatus* would have evolved in the dipterocarp forests of Borneo and possibly Malaya and Sumatra. Lucchini et al. (in prep.) further discuss the evolution of SE Asian pig species (see Appendix 8). Overall it appears that allopatric speciation has played a major role in the evolution of SE Asian suids, with many species being restricted to certain islands.

Hippopotamidae

Holocene and recent hippos can be traced back to two genera, *Hexaprotodon* and *Hippopotamus*, each with one surviving and two recently extinct species. The two genera can be traced back to the Late Miocene as separate entities, while the family itself separated from its ancestors about 11 Mya (Groves & Grubb 1993). The first occurrence of *Hexaprotodon sivalensis* in Pakistan might be as old as 6.1 Mya or even 7.2 Mya, and can probably be related to the increased development of grasslands in this part of Asia (Barry et al. 2002). Pleistocene fossils of these species have been found on Java and Borneo (for the latter see Cranbrook et al. 2000), which indicates that very likely an open, swampy environment existed on these islands, with enough grasslands to feed these generally gregarious species (although we can clearly not know this for sure for the fossil species). On Java, hippos became extinct in the late Middle Pleistocene (they were last found in the Ngandong Fauna), and possibly, the increasingly dense forest vegegation, associated with the arrival of the Punung Fauna, eliminated suitable habitat.

Tragulidae

The chevrotains or mouse-deer (Tragulidae) are an ancient group of ungulates, with a shared history dating back to the Miocene. They are considered to be the sister-group of the remaining living Ruminantia (Groves & Grubb 1987). In southern Asia, they are found in fossil assemblages dated at ca. 18 Myr, although they reached their highest diversity with 5 named and 52 unnamed species at around 11.5 Mya (Barry et al. 1991) (MIO 3). Between 16 and 14 Mya, they were also common in the area which is now northern Thailand, although species diversity may have been low (Ducrocq et al. 1994). Tragulid fossils have been recovered from Miocene deposits in Thailand (Suteethorn et al. 1990 in Covert et al. 2001), and from Late Miocene deposits in Vietnam (Covert et al. 2001), but after 9 Mya, the tragulid family declined significantly in diversity in southern Asia (Barry et al. 1991), which may have been caused by the evolution of more open vegetation types. Presently there are three genera left, of which two, *Moschiola* and *Tragulus*, occur in the South and SE Asian region. Meijaard and Groves (in press-c) reviewed the taxonomy of *Tragulus* (see Appendix 5). No molecular phylogenetic data are as yet available for this group and it is not possible to link the evolution of tragulids to the palaeogeographical model.

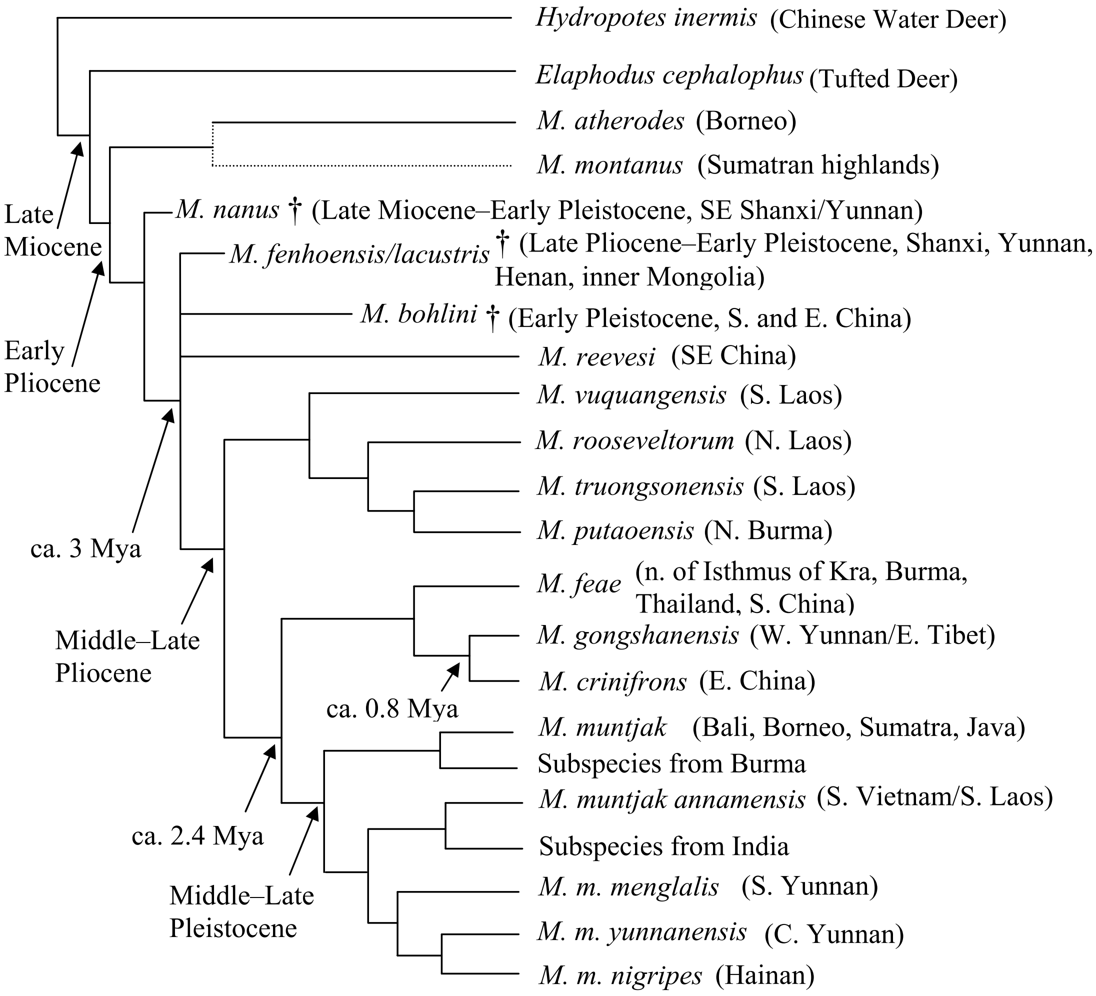
Cervidae

The Cervidae are a monophyletic family consisting of three principal clades. The one of interest to this study consists of the Cervini and the genus *Muntiacus*, and was found to be moderately-to-strongly supported in a phylogenetic analysis based on mitochondrial cytochrome *b* comparisons (Randi et al. 1998). Much research has been conducted on the phylogenetic relationships within the Cervini (for an overview see Meijaard & Groves in prep., and Appendix 7), but so far there has been little concordance between genealogies based on different nuclear and mitochrondrial loci and on morphological data. One of the reasons for this is that, because of the relatively recent evolution within this group, DNA research may pick up incompletely sorted lineages of ancestral polymorphisms, thereby giving a confused picture of inter-specific relationships. Also, Meijaard and Groves (in prep.) suggested that hybridisation may have occurred within this group and has led to the formation of new species.

The other SE Asian deer, the muntjacs are a fascinating group to study. Not only do they show some unusual karyotypic characteristics, with *Muntiacus muntjak* possessing the lowest diploid chromosome number in mammals, but also there have recently been several discoveries of new species of muntjac (Wang & Lan 2000). Muntjac-like deer (*Cervocerus*) first appear in the Late Miocene Hipparion fauna of China (Geist 1998). In a phylogenetic study of four species of mainland Asian muntjak it was found that *M. muntjak* (the most widely spread species; from India to Borneo) was sister-species to the three others, *M. gongshanensis* (Yunnan), *M. crinifrons* (SE China), and *M. reevesi* (S. China and Taiwan) (Lan et al. 1995). This contrasted with previous studies that had placed *M. crinifrons* at the base of the phylogenetic tree. The divergence between *M. muntjak* and the other muntjacs may have occurred at approximately 2.7 Mya (PLIO 4), although other estimates put this data later.

In Fig. 4.20, I have combined the results of several phylogenetic studies of this group (Wang & Xu 1986; Groves & Grubb 1990; Lan et al. 1995; Amato et al. 1999; Amato et al. 2000b; Wang & Lan 2000) in a phylogenetic tree which is most parsimonious with these data. The divergence timing within this group was inferred as follows. Wang and Lan (2000) estimated that *Elaphodus* and *Muntiacus* diverged about 3.7–1.9 Mya; *vuquangensis* separated from *reevesi* about 1.8–0.9 Mya; *feae* and *muntjak* shared a common ancestor 1.5–0.8 Mya; and the divergence between *crinifrons* and *gongshanensis* was a very recent one, 0.5–0.3 Mya. But these dates are likely to be underestimates, as the origin of *Muntiacus* is more likely to be in the Late Miocene (e.g. Wang & Xu 1986), and an early date in much more in accord with the fossil record. Based on that information, I recalculated the approximate divergence times within *Muntiacus*.

Figure 4.20. Consensus tree of the phylogenetic relationships within the Muntiacinae



(after Wang & Xu 1986; Groves & Grubb 1990; Lan et al. 1995; Amato et al. 1999; Amato et al. 2000b; Wang & Lan 2000). The taxa "Subspecies from Burma" and "Subspecies from India" are those used by Amato et al. (2000b). The position and species status of *M. montanus* is largely hypothetical (after C.P. Groves, pers. comm.).

Groves and Grubb (1990) suggested that *M. atherodes* is the most primitive species of *Muntiacus*, which would indicate a probable divergence time in the Early Pliocene. If this is correct, the divergence between the Sundaic *atherodes* (and possibly *montanus*) and the Indochinese species may coincide with the hypothetical break up of the

Thai/Mala Peninsula in the Istmus of Kra area during PLIO 2 (e.g. Woodruff 2003, and see elsewhere in this thesis).

The research by Amato et al. (2000a) included the recently described muntjac species *M. truongsonensis*, *M. putaoensis*, and *M. rooseveltorum*, which in a phylogenetic analysis were grouped with *M. vuquangensis*. Unlike in the analysis by Wang and Lan (2000), this group did not form a monophyletic unit with *M. reevesi*, although overall relationships among the main lineages of muntjac were not well resolved. Amato et al. (1999) obtained similar results, which indicated a basal position for *M. reevesi*, while *M. crinifrons* and *M. gongshanensis* were considered so similar as to be one species. One area that was well resolved is the close relationship between *M. truongsonensis*, *M. putaoensis*, and *M. rooseveltorum*, for which it was remarked that all these species appear to be confined to old growth forests in mountains (respectively in Laos and Vietnam, North Burma, and Laos). *M. putaoensis* appears to be restricted to the mountainous area between the Mali Kha and Mai Kha Rivers, where it has been isolated from its closest relatives in the Annamite Mountains of Vietnam and Laos, at least since the LGM (Amato et al. 1999). Rabinowitz et al. (1999) hypothesized that these three species might be Pleistocene refugees from a time when climatic changes fragmented the wet evergreen forest of the region. As a consequence, the smallest muntjacs, which were probably least adapted to coping with the changing ecological conditions, became more restricted in their distribution. Species like the giant muntjac *M. vuquangensis* might have been able to compete more effectively with the common muntjacs in the lowlands, and thus maintain its wider distribution seen today. Also, *M. feae*, another small species, has been recorded only from a restricted mountainous area along the border between Thailand and Myanmar (Rabinowitz et al. 1999).

Finally, Geist (1998) suggested that in pockets of high resource density, where small, rich territories can be defended, “primitive”, aggressive morphs of muntjacs may have evolved from the ubiquitous *M. muntjak*, which is adapted to low resource density and large shared territories. He maintained that the scarcity and “spotty” distribution of the other muntjacs suggest this. The data presented here suggest a different scenario, with the rarer, restricted species being more primitive, and giving rise to the widely-distributed *M. muntjak* group.

Bovidae

Buntjer et al. (2002) reported that the reconstruction of the phylogeny of the Bovini has so far resisted traditional approaches. The only consistent outcome of comparisons of morphological or molecular characters is the early branching of the buffalo-like species (genera *Syncerus* and *Bubalus*), but the relationships among the remaining cattle species remain unclear. One of the reasons for this, according to Buntjer and colleagues, is the occurrence of hybridisation among cattle species leading to reticulated tree topologies, which are difficult to identify using standard techniques. Buntjer and his colleagues found that the phylogenetic relationships using amplified fragment length polymorphism fingerprinting are as in Fig. 4.21.

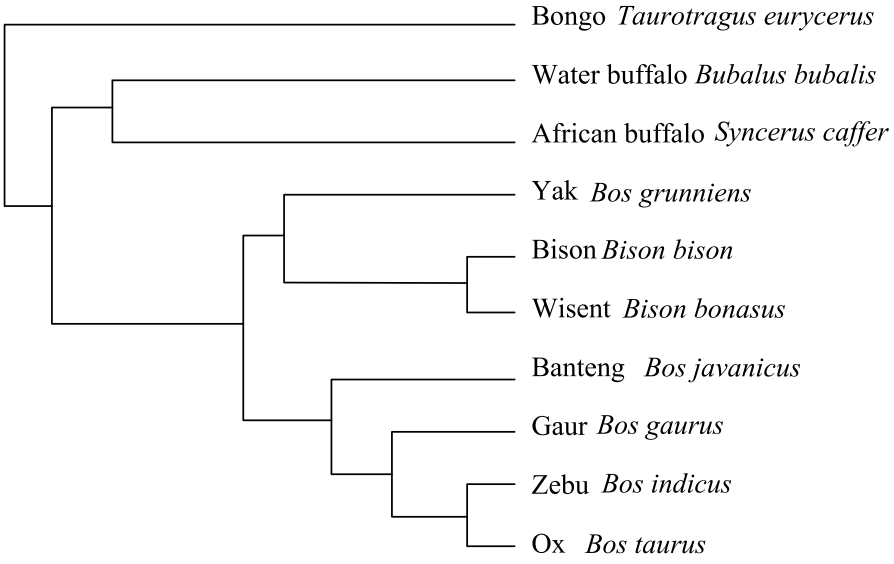


Figure 4.21. Phylogenetic relationship among the Bovinae (after Buntjer et al. 2002).

Based on fossil finds, Gentry (1990) reported that the initial radiation between the Bovidae and Cervidae dates back to the Early Miocene, as evidenced by the most primitive bovid *Eotragus*. Based on divergence of bovine nucleotypes, the tribe Bovini started to diverge during the Middle Miocene, about 14.6–11.6 Mya, while the ancestor of the Sulawesi Anoas (*Bubalus* sp.) first diverged at about 12.4 Mya (Pitra et al. 1997). The timing of the Middle Miocene radiation of the Bovidae is well documented in the Siwaliks, where a transition to large mammal assemblages dominated by bovids is observed, as a result of a process of diversity increase occurring largely through immigration rather than through *in situ* speciation (Barry et al. 1991). Another phase of radiation occurred at the end of the Miocene and in the early Pliocene (MIO 4 – PLIO 1), when global climate change promoted the expansion of grasslands (Hassanin & Douzery 1999). The fossil record of the Bovinae [= Cattle-Bovini (*Bos*, *Bison*), Boselaphini, Tragelaphini, and Buffalo-Bovini (*Bubalus*, *Syncerus*)] suggests a common South Asian origin of this subfamily. The radiation of the Bovini, Boselaphini, and Tragelaphini indicates that the tragelaphines migrated to Africa from Asia during the Middle Miocene and the later separation between African and Asian buffaloes indicates a subsequent migration into Africa (Hassanin & Douzery 1999). Ritz et al. (2000) estimated that the Buffalo lineage diverged from the *Bos* lineage between 4.9 and 1.9 Mya, although the split between *Bos* and *Syncerus* was only half that time (2.6–1.0 Mya). They considered it unlikely that *Syncerus* was closer related to *Bos* than *Bubalus* to *Bos*, and suggested that the microsatellites techniques used in their research were increasingly inaccurate as evolutionary divergence increases. It is unclear how the divergence between the Buffalo lineage and *Bos* can be related to the new palaeogeographical and palaeoenvironmental model.

Pitra et al. (1997) found strong genetic evidence for a close phylogenetic proximity between the Anoas and the Indian Nilgai (*Boselaphus tragocamelus*). In apparent contradiction to this, Groves (1981b; 2001a) asserted that the Anoas are closely related to *Hemibos* from the Late Pliocene (3.2–1.8 Mya) Tatrot and Pinjor stages of the Siwaliks; the Anoa would therefore be derived much more recently than the estimate above. Also Janacek et al. (1996) suggested a more recent divergence for Anoa, and they reported that some 5 Mya the ancestor of the anoas of Sulawesi (*Bubalus depressicornis* and *B. quarlesi*) diverged from the ancestor of the African bovids, after which the ancestral Anoas must somehow have made it across to Sulawesi. This scenario was tentatively suggested to have happened as follows by Kakoi et al. (1994): 1. an ancestor of subgenus *Anoa* diverged from a common ancestor with the genus *Bubalus* outside Sulawesi, 2. one group of the ancestral *Anoa* first immigrated to Sulawesi and radiated all over the island. After that, they were separated from their outside group for a long term, until the secondary immigrants landed on the island. This isolation phase probably continued long enough to cause reproductive isolation between the first and the second immigrants, or to create the two species of the Anoa; the Mountain Anoa (*Bubalus quarlesi*) (the first immigrant) and the Lowland Anoa (*Bubalus depressicornis*) (the second immigrant), and 3. the ancestral lowland anoa, being bigger in body size, forced the smaller anoas to inhabit the higher altitude areas. Further genetic research by Schreiber et al. (1999) found that haplotype differentiations within Anoas approach the respective genetic distances which separate the three uncontested species of Asian buffalo (*B. depressicornis*, *B. arnee*, *B. mindorensis*). This may indicate that the Anoa haplotypes evolved independently for extended periods of time, estimated to be 1.25 Myr (Schreiber et al. 1999). It is yet unclear whether the divergence between the two Anoa species needs to be explained by a multiple migration model as suggested above by Kakoi, or whether Pleistocene environmental changes could account for the observed genetic variation.

Stremme (1911 in Hooijer 1958a) suggested that the Middle Pleistocene fossil species *Duboisia santeng* of Java and the Malay Peninsula was most closely related to the Nilgai and the Four-horned Antilope (*Tetracerus quadricornis*), although Hooijer's (1958a) data suggest a closer affinity of *Duboisia* to *Boselaphus* than to *Tetracerus. Boselaphus* and *Tetracerus* are species of the Indian Peninsula, and *Duboisa* might have been their Sundaic sisterspecies. This would then be similar to the biogeography of *Antilope*, of which a Middle Pleistocene form existed on Java (*Antilope saatensis*), while the only extant species in the genus occurs on the Indian Peninsula. Note, however, that Corbet and Hill (1992) indicated that few of the fossil *Antilope* species are likely to represent the genus as now understood.

Lagomorphs

Leporidae

Two wild leporids occur in Indonesia; the Sumatran *Nesolagus netscheri*, which only exists on some mountains; and *Lepus nigricollis*. The relationships of *Nesolagus* with other leporids is distant and the species is regarded as a primitive form with no close relationships (Flux 1990). Based on the enamel patterns of premolars, Patnaik (2002) presented a generalized phylogeny for the Old World Leporidae (see Fig. 4.22), which suggests that the *Nesolagus* lineage diverged from its nearest relatives during the Late Miocene (at least 8 Mya). Similarly, Chapman and Flux (1990) estimated the divergence time of the *Nesolagus* line from the one leading to the other rabbits as "Miocene". A relative of *Nesolagus netscheri* was recently found in Annamite Mountains in Laos and Vietnam (*N. timminsi*), and it was estimated that this species diverged from the Sumatran rabbit some 8 Mya (Surridge et al. 1999). If these estimates are accurate, the ancestral species to *Nesolagus netscheri* diverged from its mainland Asian relative shortly after the divergence of this lineage, which Patnaik (2002) combined with the fossil genus *Alilepus*.

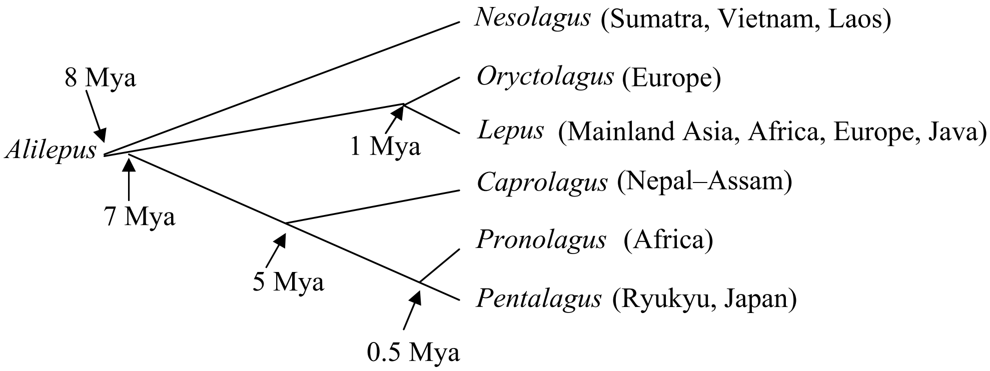


Figure 4.22. Generalized phylogeny for Old World leporid genera based on P3 morphology (after Patnaik 2002).

Unfortunately, the phylogeny in Fig. 4.22 has little in common with another phylogeny based on P_3 morphology by Averianov (1999). He suggested that *Pronolagus* and *Pentalagus* were part of a group what diverged in the Late Miocene rather than Late Pleistocene as suggested by Patnaik. Also, Averianov created one monophyletic group in which *Nesolagus* was sisterspecies to a clade with *Caprolagus* and *Poelagus* and another clade with *Oryctolagus*, *Indolagus*, and *Lepus*. Until more consistent phylogenies are established, the true relationships within the Leporidae will remain unknown and cannot be related to the palaeogeographical model.

Another rabbit lineage, *Caprolagus* is considered to be of Middle Pleistocene origin (Chapman & Flux 1990) (note that according to Patnaik's phylogeny the genus *Caprolagus* diverged in the Pleistocene from a fossil ancestor *Pliosiwalagus*; these intermediate fossil genera are not shown in Fig. 4.22). Fossil remains of this genus (*Caprolagus lapis*) have been found in Java (Dawson 1971). Dawson (1971) suggested that in the early Middle Pleistocene 3 or 4 species of *Caprolagus* occurred on Java, although probably not all at the same time. The only extant species of the genus, *Caprolagus hispidus*, survives in its tall grassland habitat in northern India and southern Nepal (Bell et al. 1990).

Finally, the Indian hare (*Lepus nigricollis*), which occurs on the Indian subcontinent, is also found on Java (Corbet & Hill 1992; Melisch 1992). Melisch (1992) and Corbet and Hill (1992) suggested that the species had been introduced to Java, primarily because of its disjunct distribution pattern. Also Dammerman (1931 in van Strien 2001) reported that the species had been introduced by the Dutch Governor Daendels between 1807 and 1811, although there is no historical evidence to confirm this (van Strien 2001). Dawson (1971), however, reporting on Late Pleistocene finds of leporid fossils, suggest that a species like *Lepus nigricollis* (*Lepus* cf. *L. nigricollis*) existed on Java at the time of the LGM. Interestingly enough, neither *Caprolagus* nor *Lepus* have been found on Sumatra, either as extant or as fossil species (Dawson 1971).