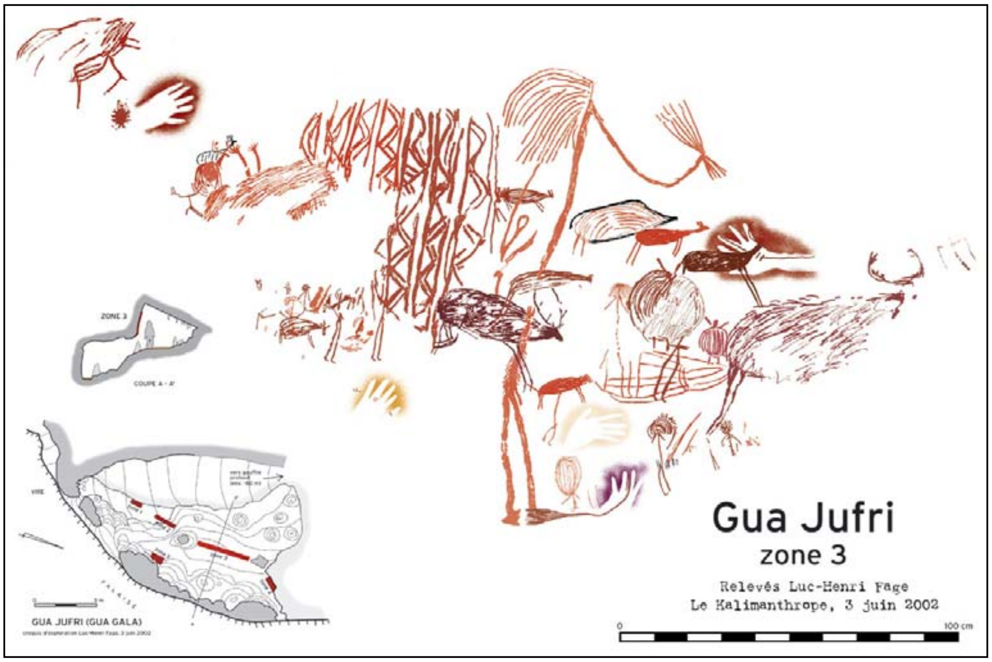
CHAPTER 6: TESTING AND APPLYING THE MODEL

J’ai vu des archipels sidéraux! et des îles
Dont les cieux délirants sont ouverts au vogueur:
- Est-ce en ces nuits sans fonds que tu dors et t’exiles,
Million d’oiseaux d’or, ô future Vigueur?

‘Le Bateau Ivre’
Arthur Rimbaud



Picture: Some of the exquisite cave drawings in Borneo. With permission from Luc-Henri Fage

6.1 MALAYAN SUN BEAR (URSUS (*HELARCTOS*) MALAYANUS) GENETICS AND MORPHOLOGY

Introduction

In Chapter 4, I discussed the phylogeny of Asian bears. The data suggest that the Ursinae originated about 4 Mya, and underwent rapid radiation between 3.5 and 2 Mya, leading to 4 ancestral bear lineages, including the lineage leading to *Ursus malayanus*. The fossil record suggests that the ancestor of *malayanus* occurred in an area between Hungary in the west and China during the lower Pleistocene or upper Pliocene. The species has also been described for the late Middle Pleistocene (300–200 Kya) in Vietnam (see Chapter 4.1, but see below in the Discussion). *U. malayanus* arrived on Java with the Middle–Late Pleistocene Punung fauna, which appeared to have migrated to Java from Sumatra at a time of warm and humid conditions. This suggests that it was part of Sumatra's fauna during the Middle Pleistocene. The species' late arrival on Java, despite earlier land connections between this island and the rest of Sundaland, would suggest that *malayanus* is a relatively recent arrival in southern Sundaland. I therefore hypothesize that the species evolved in Indochina, possibly east of the Mekong River, and found its way to Sundaland only during the Middle Pleistocene. If this is true one would expect to find relatively small differences between populations of *malayanus* in Sundaland, and slightly larger differences between Sundaland and Indochina. Here I will test this hypothesis by comparing measurements of Sun Bear skulls from different parts of its range.

Methods

I measured 81 Sun Bear skulls in the following museums: Zoological Museum Cibinong, Indonesia (n=17); National Museum of Natural History, Leiden, The Netherlands (n=14); Zoological Museum Amsterdam, The Netherlands (n=7); the Field Museum, Chicago, USA (n=3); the British Natural History Museum, London, England (n=22); Sarawak Museum, Kuching (n=8); Zoological Reference Collection, Singapore (n=9); and the Natural History Museum of Los Angeles County, USA (n=1). I measured another 9 skulls in different places in Kalimantan, while Colin Groves measured another skull in the Institute of Zoology, Beijing. Two skull were excluded from the study because their large size suggested that they had been misidentified; these were nr. 34.01 from the Sarawak Museum and nr. 2944 from the Cibinong collection. Both are more likely to be *Ursus thibetanus*.

I took measurements of 10 variables: greatest length (GTL); condylobasal length (CBL); palate length (PL); bizygomatic width (ZW); inter-orbital width (IO); post-orbital width (PO); width across mastoid processes (MAW); mandible length (ML); width across upper 3rd molars (MOW); and width across upper canines (CW). I made all measurements with an accuracy of 0.1 mm with a pair of Vernier callipers (precision 0.05 mm). For all skulls, I determined the age-class by assessing molar eruption and closure of the basilar suture, which is a standard technique: Adult = M^3 erupted and basilar suture fused; between Young Adult and Adult = M^3 erupted and basilar suture fusing; Young Adult= M^3 erupted and basilar suture open; Juvenile 2 = M^2 erupted, but not M^3; Juvenile 1= M^1 erupted, but not M^2 or M^3; and Infant = no permanent teeth erupted.

I analysed the measurements using multivariate statistical software (SPSS 11.0). I used Principal Component Analyses (PCA) to determine whether bear populations were craniometrically distinct. A PCA is often used in data reduction to identify a small number of factors that explain most of the variance observed in a much larger number of variables. Following this I used Discriminant Analyses (DA) to determine the nature of the differences between populations. A discriminant analysis is useful for situations where one wants to build a predictive model of group membership based on observed characteristics of each case. The procedure generates a set of discriminant functions based on linear combinations of the predictor variables that provide the best discrimination between the groups.

Results

Only 70 skulls were adult or young adult specimens, and because of significant differences between these and younger specimens I left all juvenile specimens out of the further analysis. As only 35 out 70 adult skulls were sexed, an ANOVA test was used to investigate the differences between males and females. GL and ZW differed significantly between the two sexes ($p<0.05$). Because males and females appeared to be equally distributed across the regional populations, I decided to initially lump together males and females.

A PCA of adult skulls showed little spatial structure in a plot of the first and second components (Fig. 6.1). The first component, which explained 79% of the total variance, correlated positively and equally with the 5 variables (GL, CBL, IO, ML, PO) included in the analysis, which indicated that the differences are mostly size, rather than shape-based. The second component, which explained 8% of the total variance, was positively correlated with PO (r^2=0.70), but less so with the other variables.

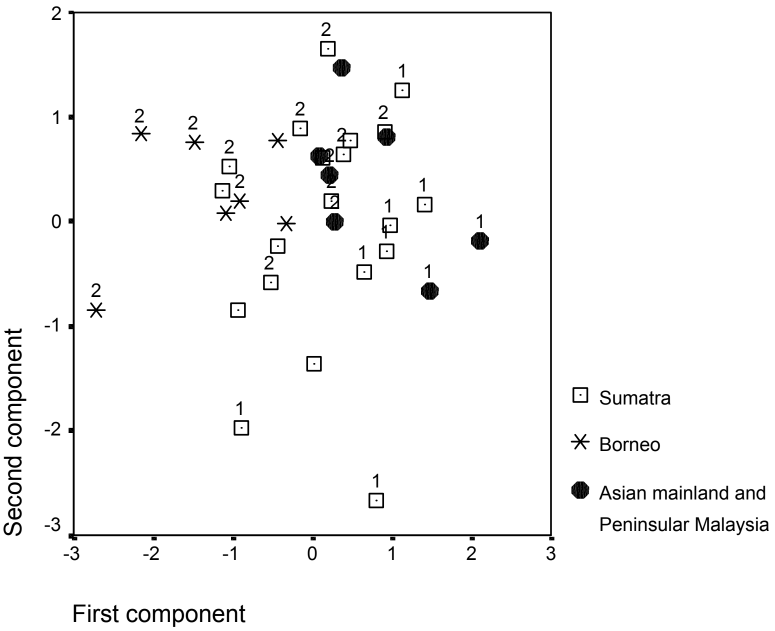
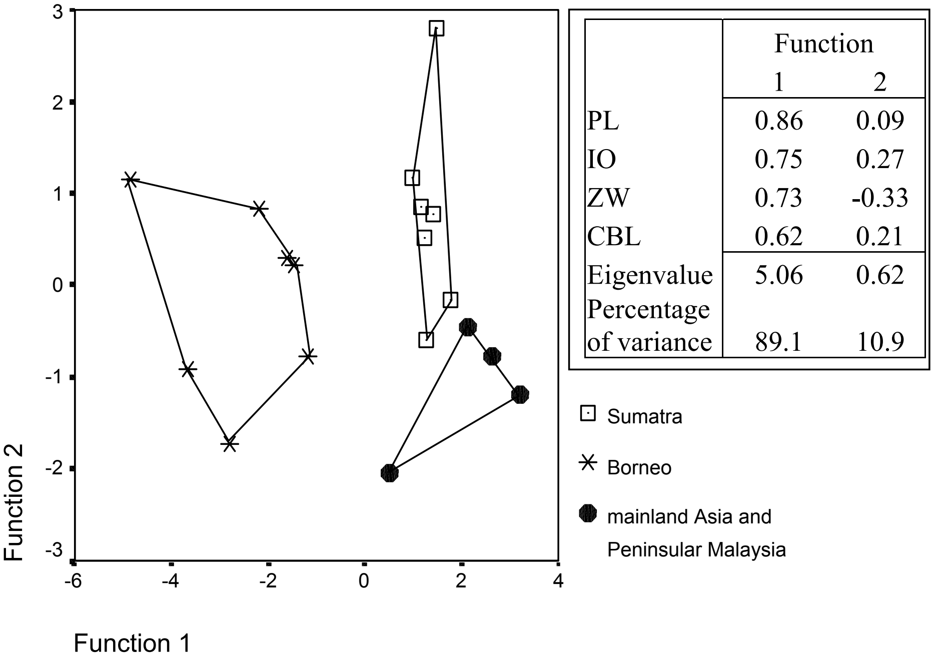


Figure 6.1. A PCA of adult Sun Bear specimens. Numbers refer to sex: 1=male; 2=female.

Fig. 6.1 also shows that most female specimens were situated in the upper left corner of the graph, suggesting that they are smaller than males and that they mask the geographic variation. I therefore decided to analyze males and females separately in discriminant analyses (DA). This reduced the analytical detail considerably, because of the reduced amount of specimens per regional population. Also, there were many missing values in the measurements which further reduced the number of valid cases that could be analysed.

A DA for adult males revealed little more than that Bornean specimens were smallest, Sumatran ones intermediate, and the mainland Asian and Peninsular Malaysian ones the largest. For female specimens on the other hand, there was more structure to the data (Fig. 6.2), with Bornean specimens separating clearly from the Sumatra/mainland Asia/Peninsular Malaysia specimens. The data in Fig. 6.2 indicate that Bornean specimens are differentiated from the Sumatran, Malayan, and Asian ones by their smaller size (see equally high correlation factors between the variables and first component). The Sumatran specimens appear to be separated from the Malayan/Asian mainland ones by their relatively narrow skulls (high value for ZW); the ratio between ZW and CBL for Sumatran female specimens ranges from 0.80–0.86 (n=10), whereas for Asian/Malayan skulls this ranged from 0.84–0.90 (n=5).



	Function	
	1	2
PL	0.86	0.09
IO	0.75	0.27
ZW	0.73	-0.33
CBL	0.62	0.21
Eigenvalue	5.06	0.62
Percentage of variance	89.1	10.9

Figure 6.2. A discriminant analysis of adult, female Sun Bear skulls, and the corresponding correlation matrix.

In an analysis of variance (ANOVA), the Bornean specimens were significantly smaller then the Asian and Sumatran specimens for all the variables (*p* < 0.001) (see Table 6.1 and Fig. 6.3). Figure 6.3 also indicates that Sumatran and Asian/Peninsular Malaysian specimens are similar in size and larger than the populations in SW, NW, and E Borneo.

		CBL	ZW	GL	IO	PO	PL	MAW	ML	MOW	CW
mainland	Mean	235.3	206.3	255.7	67.2	70.7	118.0	167.6	170.1	68.4	69.6
	n	9	11	10	10	9	7	7	8	6	5
	SD	12.1	10.8	16.4	3.8	3.0	9.5	7.2	12.7	6.0	15.6
Borneo	Mean	206.3	170.6	218.8	58.3	60.7	100.0	132.7	141.5	59.6	60.8
	n	17	22	19	22	14	21	21	10	12	12
	SD	13.9	12.1	14.0	3.9	3.8	8.0	10.6	9.9	2.6	4.8
Sumatra	Mean	227.3	191.2	246.0	65.2	65.5	114.5	152.0	159.8	65.2	71.0
	n	26	25	26	24	22	22	23	21	19	20
	SD	12.7	13.3	14.5	4.3	5.0	9.0	10.2	9.4	3.0	4.1

Table 6.1. The means and standard deviations (SD) of each of the measured variables for adult Sun Bears from Borneo, Sumatra, and Malaya/mainland Asia (males and females combined) .

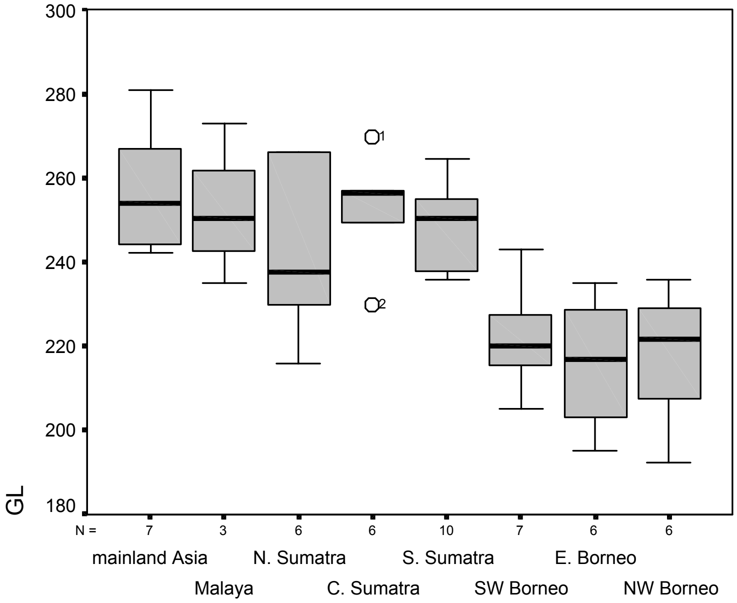


Figure 6.3. Means, standard deviations, range, and outliers of the greatest skull length for 8 subregions of the Sun Bear distribution range.

Discussion

Horsfield (1825) described two species within *Helarctos* for the southern part of the Sun Bear's range, i.e. *H. malayanus* on Sumatra and *H. euryspilus* on Borneo; this differentiation was, however, based on one specimen from Borneo only. The distinction between the two was based on the slightly smaller claws and smaller overall dimensions in *euryspilus*. Furthermore, 'the chief distinction of the Bornean species is the vivid and nearly orange anterior part of the neck', which, according to Horsfield (1825) differs in form from the Sumatran sub-species. Pocock (1932) dismissed the use of *euryspilus* and proposed it as a synonym for *malayanus*, because he regarded the differences found by Horsfield as mere individual variation. However, in 1941, Pocock (1941) stated that based on measurements by Lyon (1908; 1907 in Pocock 1941) he thought that because of the smaller size of the Bornean type of Sun Bear it was correct to regard it as a distinct sub-species. The significantly smaller skull size of the Bornean Sun Bear was also found in this research, which suggests the separation of the Bornean Sun Bear as a distinct taxon. Lyon (1908) also reported the relatively large maxillary teeth in Bornean Sun Bear, which were as big as the Sumatran ones, which was also confirmed in this research (Fig. 6.4). Elsewhere, I discussed the variation in size, shape, and colour of the ventral patch of Bornean and Sumatran Sun Bear (see Meijaard 1996; 1999b), but I found no consistent differences between these taxa.

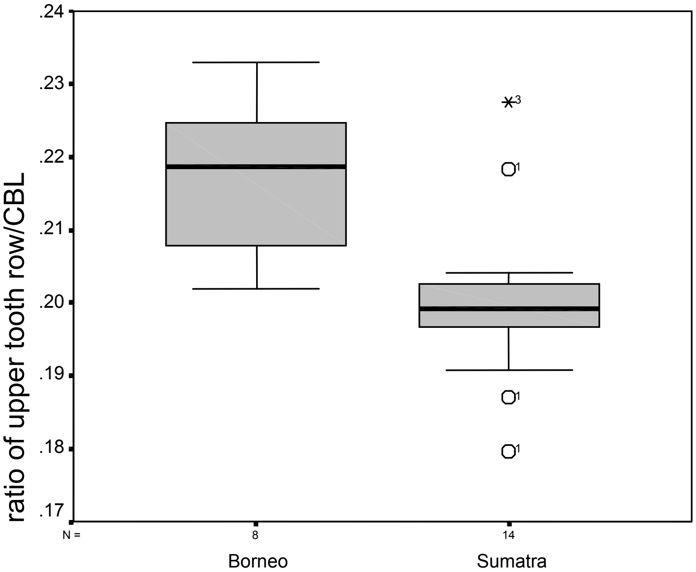


Figure 6.4. Means, standard deviations, range, and outliers of the ratio between the length of the upper tooth row and the condylo-basal length of adult Bornean and Sumatran Sun Bear specimens.

Further subspecific distinction was made for *annamiticus* Heude, 1901 and *wardi* Lydekker, 1906. Lydekker withdrew the latter as a new subspecies because there was a possibility that the hide on which its characters were based belonged to a specimen of the *U. thibetanus* (Erdbrink 1953). Heude (1901) differentiated *annamiticus* (from Vietnam) from *malayanus* (Sumatra) primarily based on its much smaller molars, and reduced canines. This was not confirmed in the present research, primarily because of the much wider range of values for molar length and length of tooth row in mainland Asian specimens compared to Bornean and Sumatran ones (Fig. 6.5); in fact, it appeared that the Asian specimens were differentiated into two distinct groups, although the sample size is too small to confirm this and it cannot be excluded that one aberrant point (see arrow) was caused by a measuring mistake.

Overall the Bornean Sun Bear specimens appear to be more different from the Sumatran, Malayan, and mainland Asian ones than these latter three populations from each other. If true, this could suggest that Bornean Sun Bears diverged from the other two populations before these became themselves separated. The general lack of morphological differentiation between the populations suggests that the divergence has been a relatively recent one, and probably occurred during the Middle or Late Pleistocene.

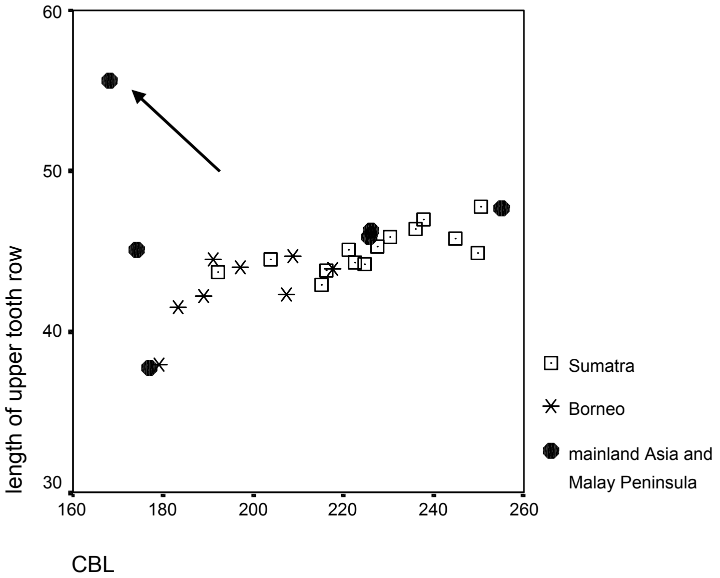


Figure 6.5. Graph of the condylo-basal length vs. length of upper tooth row for adult Sun Bear specimens (the arrow indicates the aberrant point mentioned in the text).

L. Waits (*in litt.*, 23 October 1999) calculated a phylogenetic tree for *malayanus* based on 300 base pairs of mtDNA sequence data (Fig. 6.6). She found that there were possibly 5 distinct clades (but sample size was low and no mainland Asian samples were included): 1. Sumatra + zoo animal; 2. Borneo; 3. mixed Borneo and Sumatra (although the Sumatran bear originated from a zoo and may possibly have been Bornean); 4. East Kalimantan; and 5. one sun bear of unknown origin. If the one Sumatran sample in the E. Kalimantan clade was misidentified, the Sun Bears would split clearly into a Sumatran and a Bornean group, confirming the morphological differentiation found here. If this is not the case, the phylogeny in Fig. 6.6 suggests incomplete lineage sorting with a 'Sumatran' mitochondrial DNA lineage remaining in Borneo.

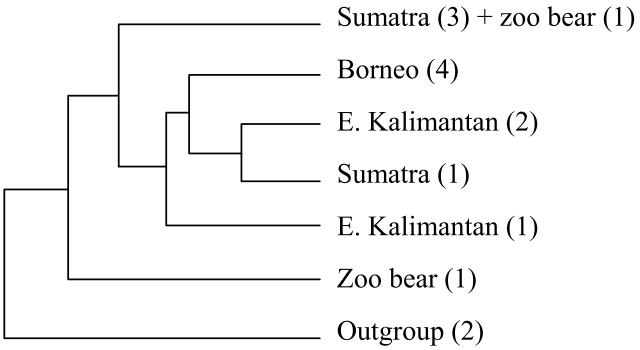


Figure 6.6. Phylogenetic neighbourjoining tree based on mtDNA sequence differences in Sun Bear samples (L. Waits, *in litt.*, 23 October 1999).

Having hypothesized on the relationships between the 3 main Sun Bear clades, I will now try to use the new biogeographic model to explain the patterns. We know that *malayanus* was present in Borneo (Medway 1964) and Sumatra (de Vos 1983) during the Late Pleistocene. It arrived before that on Java some 80–60 Kya, probably from Sumatra (as the Punung Fauna primarily consists of Sumatran rain forest species). Because Sun Bears are relatively large, robust animals, the absence from Java of older fossils of *malayanus* suggest that the species did indeed not occur on Java before the late Middle Pleistocene; otherwise one would expect to find the large fossil bones or teeth. Long et al. (1996) also claimed that Sun Bear fossils occurred in the Lang Trang Caves in Vietnam. The material had been identified by de Vos and Long (1993), but there were only 2 specimens as opposed to the much more common *Ursus thibetanus* fossils (n=33). *U. malayanus* has not been reported from any of the other fossil sites of mainland SE Asia (e.g. Tougard 2001), whereas *Ursus thibetanus* remains are common.

This almost complete absence of *malayanus* fossils from South China, Laos, Cambodia, Myanmar, and Thailand and their relatively common occurrence in Borneo, Sumatra, and Java suggests that the species evolved in Sundaland and later migrated to Indochina. The craniometric patterns found in this paper indicate that Sun Bears can be divided into 2 groups: Bornean and Sumatran/Malayan/mainland Asian. If we assume a Sundaic origin of the species than the morphological patterns can be best explained by assuming that the species evolved in Borneo, after which it crossed to Sumatra and the Asian mainland. Alternatively, the species evolved in Sumatra and then dispersed to Borneo and the Asian mainland, leading to a considerable size reduction in Bornean bears and a narrowing of the skulls in mainland Asian bears. For the time being, I lack the data to support either of these two hypotheses, but I reject the hypothesis in the Introduction that *malayanus* originated on the Asian mainland.

6.2 THE METABOLIC COSTS OF SWIMMING

Introduction

Many species radiations (ants, spiders, tortoises, geckos, skinks, rodents, primates) are reported to show transmarine migrations (see several authors in Raxworthy et al. 2002). However, many vicariantists have doubts about the importance of oceanic dispersals in explaining biogeographic and phylogenetic patterns (C. Groves, pers. comm., 25 March 2002). To find out which land mammals are likely to make intentional sea-crossings, Meijaard (2001, see Appendix 9) investigated and modelled their swimming capability over a range of body sizes. Although the model that I provided is based on simplified mathematical equations, the maximum swimming distances that it predicted were (somewhat surprisingly) in line with observed maximum swimming distances in several mammal species. The model suggests that maximum swimming distance increases with body size (see Table 1 in Appendix 9). This would mean that only animals above a certain body size would be able to swim, for instance, from Borneo to Sulawesi. Still small mammals are found on many isolated islands, and Kitchener et al. (1994b), for instance, reported the presence of one species of shrew on at least 9 islands. Another means of dispersal, such as floating on rafts of vegetation, could have been used, unless the dispersal can be traced back to a time when the islands were still physically connected to each other. Rafting as a means of dispersal was analysed by Houle (1998), who suggested that based on the survival limit to water deprivation successful dispersal on floating islands would be most plausible for small to medium-sized mammals and most land reptiles, especially those among them that were already preadapted to strong seasonal fluctuations in the availabity of food and water. Very large mammals are less likely to use such rafts, primarily because it would not be possible to support their weight or provide food and water during the crossing.

There are clearly other factors that influence the success of a sea crossing, the availability of suitable and empty ecological niches for a start. Still, the above hypothesis could mean that only animals of a certain body size, either large or small, would be successful cross-sea dispersers. Here, I test this hypothesis by investigating the ecology and body size of mammals from Sulawesi and comparing it to the mammals of continental islands (Borneo, Java) and the Asian mainland. Average genus body weights were used as reported in Payne et al. (1985) and Lekagul and McNeely (1977).

Results

Genus	nr of species	body weight (kg)	lifestyle	food
Crocidura	7	0.005–0.020	terrestrial	insectivorous
Haeromys	1	0.015–0.020	arboreal	seeds and figs
Crunomys	1	0.035–0.055	terrestrial	?
Maxomys	4	0.035–0.284	terrestrial	largely herbivorous
Melasmothrix	1	0.040–0.058	terrestrial	earthworms and larvae
Prosciurillus	3 or 4	0.050–0.10*	?	?
Margaretamys	3	0.050–0.10*	arboreal	?
Rattus	10	0.050–0.200	?	?
Bunomys	7	0.06–0.15	terrestrial	omnivorous
Tateomys	2	0.070–0.098	terrestrial, lower arboreal	only earthworms
Eropeplus	1	0.10–0.30*	?	?
Tarsius	6	0.108–0.134	terrestrial–lower arboreal	insectivorous
Hyosciurus	2	0.15–0.30*	mostly terrestrial	omnivorous
Taeromys	6	0.15–0.30*	mostly terrestrial	fruits, leaves, and insects
Rubrisciurus	1 or 1+	0.15-0.50	mostly arboreal	fruits, nuts etc.
Echiothrix	1	0.25–0.50*	?	?
Lenomys	1	0.30–0.60*	?	?
Paruromys	1	0.35–0.50	terrestrial	frugivorous
Macrogalidia	1	6–7	terrestrial	omnivorous
Macaca	6 or 7	6–15	terrestrial–lower arboreal	omnivorous
Sus	1	40–70	terrestrial	omnivorous
Babyrousa	2	40-100	terrestrial	omnivorous
Bubalus	2	150–300	terrestrial	herbivorous
Celebochoerus	1 or 2	ca 100 kg	terrestrial	?
Elephas	1 or 2	ca 100–1000	terrestrial	herbivorous
Stegodon	1 or 2	ca 100–1000	terrestrial	herbivorous

Table 6.2. Indigenous mammalian genera of Sulawesi, their body weight and ecology.

***bodyweight estimated from head-body and tail length. Sources used: Corbet and Hill (1992); C.P. Groves (pers. comm.); Macdonald (1993b; 1993a); Musser (1979; 1982a); Musser and Newcomb (1983); Musser et al. (1979); Rickart et al. (1998); Ruedi (1995); Smith and Jungers (1997); van Strien (2001); Whitten et al. (1987b); Wemmer and Watling (1986); Wemmer et al. (1983).**

If we have a closer look at the mammalian species that successfully crossed sea-barriers in our region, the following details are revealed. Table 6.2 shows Sulawesi's indigenous genera of Asian origin (excluding bats and cetaceans), and their ecological and morphological characteristics. Most authors now agree that Sulawesi has an endemic and insular mammal fauna, and that the island has not been connected to either Borneo or Java by a land bridge since the Oligocene (see Chapter 3.4). It can therefore be assumed that all of the island's present and past non-volant mammals had to cross a sea-barrier. Table 6.2 shows that 18 of the 26 genera on the island, which include 58 of the 72 species, have a bodyweight <1 kg, and are almost all terrestrial.

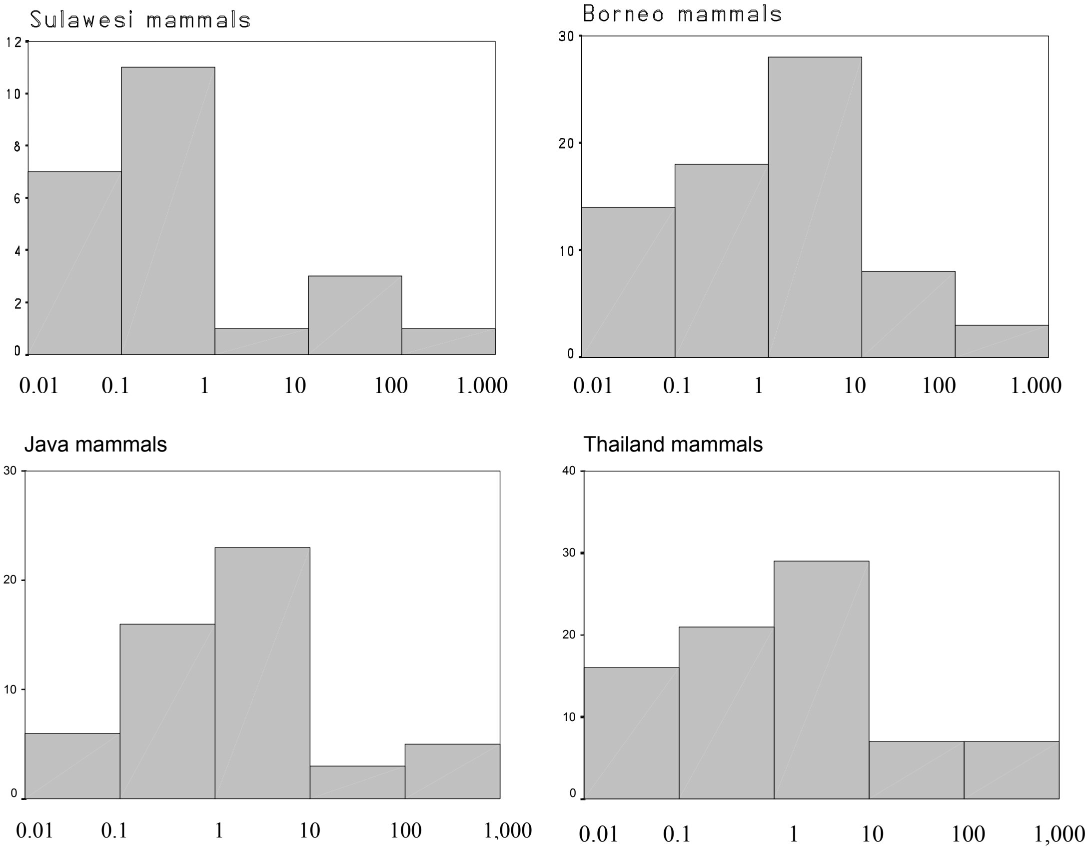


Figure 6.7. Log body weights frequencies of mammalian genera from Sulawesi, Borneo, Thailand, and Java.

The distribution of body weight frequency of Sulawesi mammals reveals that there are few mammal genera with bodyweights between 1 and 10 kg. This becomes even clearer when this fauna is compared with mammal genera from Thailand, Borneo and Java (see Figure 6.7). Compared to the other areas, Sulawesi lacks medium-sized carnivores and herbivores, and its fauna appears unbalanced.

Discussion

It is not immediately clear why medium-sized mammals are absent on Sulawesi. The phenomenon is not the result of either a size decrease or increase of originally medium-sized genera, as the middle-sized genera are completely missing from the fauna. Size increases in small mammals and size decreases in large mammals do occur on islands (see McNab 1994), but this does not explain the missing medium-sized species. A possible explanation might be that only small mammals could survive long enough on islands of floating vegetation, whereas only large mammals had sufficient bodymass and energy to cross sea-barriers by swimming. If this were true, medium-sized animals would not have been able to reach Sulawesi. However, the modelling of maximum survival times on floating islands predicts that, among mammals, resistance to water deprivation seems to increase proportionally with body weight (see Houle 1998), and medium-sized mammals should thus be more likely to survive on floating islands. On the other hand, considering that even a 210 g rodent was reported to survive without water for more than 13 days (Houle 1998), and that with good winds a floating island may reach Sulawesi from Borneo within a few days, bodymass itself may not be a good predictor for survival on floating islands. Possibly, the medium-sized carnivores and herbivores, which are generally good swimmers, would not stay on a floating island but choose to swim back to the shore.

Abegg and Thiery (2002) mentioned an additional factor that would determine the likelihood of a swimming or rafting animal establishing a viable population in a new land area. They point out that whenever newcomers were able to survive and gain access to food, they would quickly intermingle with populations of a different taxon. If the already established taxon was closely related to the newcomer, they would likely produce hybrids, and, as a consequence, the newcomer's genes would soon be absorbed by the considerably broader gene pool of the first settled taxon. This means that the likelihood of a successful dispersal across a sea barrier increases when fewer closely related taxa are already present in the new area. This is the case for new islands (or islands with newly established habitats) or islands that are rarely reached by rafters or swimmers. This may also be the reason why murid dispersal from Sundaland to Australia was largely uni-directional.

A further factor in successful sea-crossings was pointed out by Inger and Voris (2001), who suggested that several of the arboreal snakes of Sulawesi crossed from Borneo on floating trees swept on floods of the large rivers. Frogs, however, have been much less successful in crossing the Makassar Strait. Inger and Voris suggested that snakes are more likely to survive rafting than frogs as the former have a scaly epidermis protecting them from short contact with saline water, in sharp contrast to frogs, which are very vulnerable to saline water. Also, many female snakes store sperm prior to ovulation making it possible for one female to be the founder of a new population, wheras a new population of frogs requires an adult of both sexes. The data by Inger and Voris do suggest that at least some animals survived a rafting trip from Borneo to Sulawesi. Similarly, How et al. (1996) found that snakes from the Lesser Sunda Islands with arboreal habits were the best dispersers and showed least morphological variation between island populations.

Conclusion

There appears to be a trend in successful sea-crossings with smaller mammals and snakes using rafts of floating vegetation, whereas large mammals manage to swim across on their own account. These hypotheses require further testing, for instance by investigating reports of swimming mammals and animals found on rafts.

6.3 BANTENG (*BOS JAVANICUS*) MORPHOLOGY

Introduction

Wild Banteng presently occur in Java, the northern part of the Malay Peninsula, Burma, and Indochina, but not on Sumatra, while it remains unclear whether Bornean Banteng are feral or indeed a truly wild form. Originally, Lydekker (1898) distinguished three races of banteng: the Javan *Bos sondaicus* (= *javanicus*) *typicus*, the Burmese *B. s. birmanicus*, and the Manipur *B. s.* subsp. The last two were founded on differences in skin coloration. Lydekker also provisionally identified a fourth race from Borneo but he was unsure whether the differences in horn shape, which he had noticed in his early specimens, were a constant feature. By 1912 he had been able to examine further specimens and it seemed that the differences were indeed diagnostic: the Bornean form apparently has horns that are relatively stouter, are less curved, and have a more upright direction, giving them a smaller maximum span; the Bornean banteng is also characterized by the flatness of the forehead and the straight intercornual ridge. In Lydekker's opinion, these differences fully justified the right to racial distinction and he gave it the name *B. s. lowi* (Lydekker 1912). Of these named subspecies, 3 have come to be generally recognized: (1) *Bos javanicus javanicus* on Java, (2) *B. j. lowi* on Borneo, and (3) *B. j. birmanicus* on the Asian mainland. However, Groves and colleagues (unpublished data) examined banteng skulls and horns from Java, Borneo, and the Asian mainland and they suggested that, whereas the Bornean form was subspecifically separable as *B. j. lowi*, the Javan and mainland forms could not be clearly distinguished; and since *javanicus* has priority over *birmanicus* the Javan and mainland forms should both be referred to *B. j. javanicus*. Because banteng are the subject of one of my mammalian riddles I further investigate these issues here.

Methods

I analysed measurements of 136 adult male Banteng skulls that had kindly been made available by Colin Groves. To this I added horn measurements of 24 Bornean Banteng skulls that were reported by Hedges and Meijaard (1999). The measurements included greatest skull length (GTL); basal skull length (BL); bi-orbital breadth (BOB); post-orbital breadth (PO); greatest width of occipitals (GWO); least width of occipitals (LWO); breadth between the bases of the horns (BBH); breadth of the posterior end of the nasals (PNB); breadth of anterior end of the nasals (ANB); nasal length (NL); length of upper tooth row (TR); distance between horn tips (TIP); distance between horn base and tip (BASE); widest breadth of horn span (SPAN); diameter at the base of the horn sheath (DM); and the curve along the longest horn (HC). For further details on measuring methodology and statistical analysis refer to the *Ursus malayanus* research in section 6.1.

Results

Because of the many missing values in the data set, I decided to use a selected number of variables in the initial PCA. This resulted in a the separation of the Bornean specimens from mixed groups of Javan and mainland Asian specimens, both in a graph of the 1st and 2nd component and the 1st and 3rd component (Fig. 6.8)

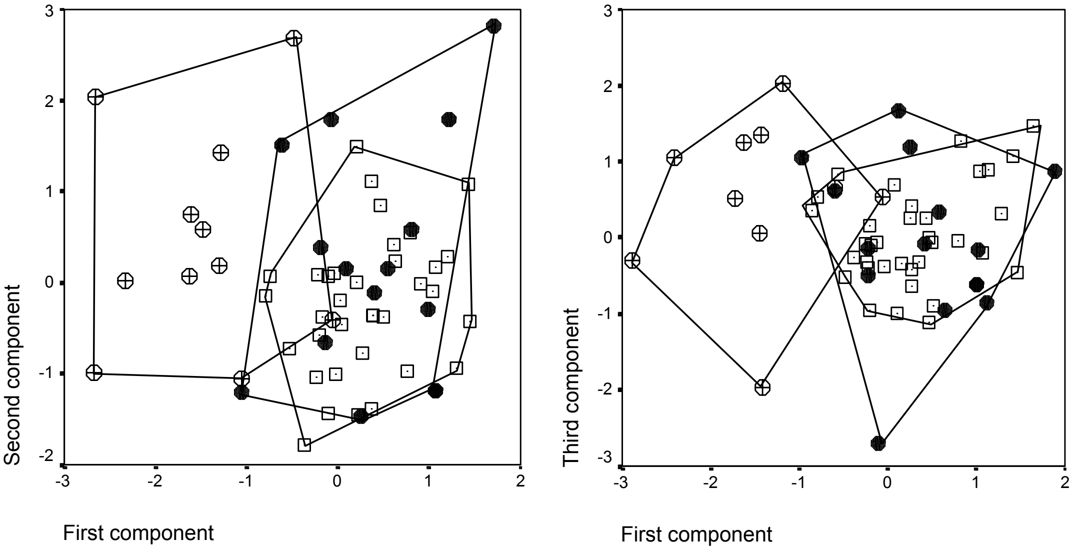


Figure 6.8. Principal component analysis for banteng skulls from Borneo (open circles with cross), Java (open squares), and mainland Asia (closed circles). Both the 1st vs 2nd component and 1st vs. 3rd component are shown. Correlation factors are shown in Table 6.3.

The data shown in the correlation matrix (Table 6.3) indicate that the difference between the Bornean and Asian/Javan samples is not primarily based on allometric size differences, because of the considerable variation in the correlation between the variables and the dominant first component. Bornean Banteng appear to be characterized by a relatively short tooth row and narrow horn span. Still for half of all variables (GTL, BL, BOB, GWO, NL, TIP, SPAN), the Bornean specimens are significantly smaller than the Javan and mainland Asian ones (ANOVA, $p<0.01$).

	Component		
	1	2	3
BOB	0.81	-0.40	0.05
TIP	0.83	0.40	-0.25
BASE	0.30	0.87	0.13
SPAN	0.85	0.24	-0.12
GWO	0.78	-0.43	0.20
NL	0.69	-0.23	-0.32
TR	0.33	0.05	0.90
Eigenvalue	3.3	1.4	1.0
percentage of variance	47.8	19.7	14.9

Table 6.3. Correlation matrix between the principal components in Fig. 6.8 and the variables.

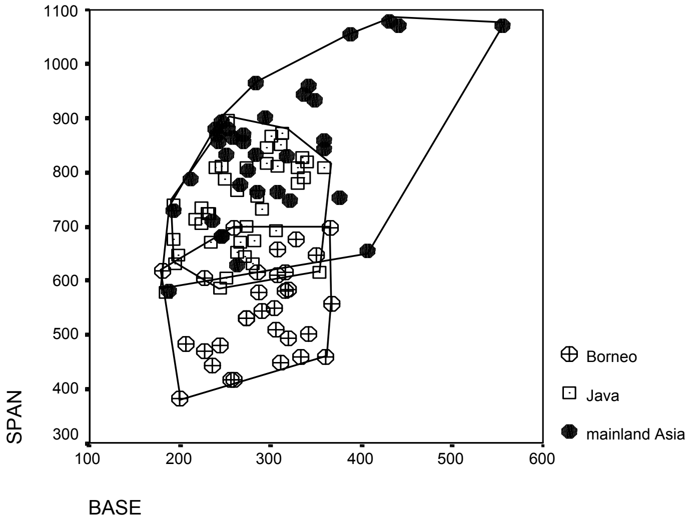


Figure 6.9. Bi-variate diagram of banteng horn length (BASE) vs. horn span (SPAN)

A discriminant analysis of these 3 groups showed that Bornean banteng are a relatively distinct from the Javan and mainland Asian banteng with all the Bornean specimens classified as belonging to that group. As in the PCA, Bornean specimens were differentiated from the other groups by relatively low values for SPAN and high values for TR; both the first and second discriminant functions were significant. The groups of Asian mainland and Javan specimens on the other hand showed considerable overlap, and they were distinguished from each other primarily by the relatively high value for GWO of the Javan specimens. The differences between Bornean specimens and Asian/Javan ones are also clear in a bi-variate graph that shows the relatively low SPAN-value for Borneo skulls (Figs. 6.9).

Discussion

The results show that Bornean Banteng are a distinct taxon compared to the Javan and Asian mainland taxa. They are smaller and have relatively upright horns (low SPAN value). Also they have relatively long toothrows for their comparatively short skulls. Further differences were obscured by the many missing values in the analysis. The Javan and Asian mainland specimens seem to be almost indistinguishable, apart from the much longer horns in the Asian mainland specimens (Fig. 6.9 and Table 6.3). Phyogenetically this would suggest that the Javan and mainland Asian Banteng are sister taxa that together form a sister group to Bornean Banteng. How could such a pattern arise? One would expect the geographically close Bornean and Javan populations to be similar, especially because the two islands were connected to each other during the LGM and open grassland areas were probably common at that time in the area between the islands (see Appendix 1). The following scenarios are possible:

1. The ancestral Banteng migrated to Java in the Middle Pleistocene, as a result of which they diverged from their nearest relative the Gaur (*Bos gaurus*). During a period of low sea-level in the Middle or Late Pleistocene, they dispersed to Borneo and from there to the Asian mainland, bypassing Sumatra where the species does not now occur (but may have done so in the Late Pleistocene).
2. The dispersal from Java to Borneo happened first, and at a later stage Banteng migrated to mainland Asia via Sumatra or a land bridge connecting Java to the Malay Peninsula; dispersal via Sumatra would mean that later this population became extinct, as suggested by Hooijer (1958b)
3. Banteng originally evolved in Borneo from where it spread to Java and mainland Asia in the Middle Pleistocene.
4. Banteng evolved on the Asian mainland from where it dispersed first to Borneo and then to Java. Because of the fossil record this must have happened before the arrival of Banteng of Java, i.e. pre-900 Kya.

5. The ancestral Banteng migrated from the Asian mainland to Java and Borneo (or only to Java), after which the Javan and Bornean populations diverged. The Asian mainland Banteng was only recently introduced from Java.

Bos palaeosondaicus, the likely ancestor to *Bos javanicus* (Hooijer 1958a, b) occurred on Java from the Middle Pleistocene onward (ca. 900 Kya). Among the many Pleistocene fossil sites of the Asian mainland, however, there is only one for which fossils of *Bos javanicus* were recorded, i.e. Thum Wiman Nakin, a late Middle Pleistocene site in Thailand, and another with what is recorded as *B. j. palaesondaicus* in Thum Khai Phet, Thailand (Tougard et al. 1996; Tougard 2001). Fossils of other bovid species have been reported much more frequently on the SE Asian mainland, e.g., *Bos gaurus* from Thâm Hang, Laos (Fromaget, 1936 in Drawhorn 1994); Thâm P'a Loi, Laos (Fromaget and Saurin, 1936 in Drawhorn 1994); Thâm Khuyen, Thailand (Cuong, 1985 in Drawhorn 1994); Keo Leng, Vietnam (Solheim, 1980 in Drawhorn 1994); and Hang Hum, Vietnam (*Bibos gaurus* cf. *grangeri*) (Kahlke and Nghiå, 1965 in Drawhorn 1994). Interestingly, the bovids from Thum Wiman Nakin were initially identified as *B. gaurus* by Ginsburg and colleagues (1982 in Drawhorn 1994), and presumably reidentified as *B. javanicus* by Tougard. Because I have not studied the fossil material myself it is impossible to judge the accuracy of Tougard's taxonomic assessment. If indeed the Thum Wiman Nakin specimen is *B. gaurus* then it becomes conceivable that Banteng are not native to the Asian mainland. This becomes even more plausible if one recalls that Tougard et al. (1996) claimed that the Late Pleistocene Lang Trang fauna in Indochina does not contain Banteng. Assuming the correctness of this assumption scenarios 3 and 4 become unlikely.

The craniometric similarities between Javan and mainland Asian Banteng preclude scenario 1, because it would probably have resulted in a greater similarity between the mainland Asian and Bornean Banteng. Also, scenario 2 is rather unlikely as it requires the occurrence of two independent dispersal events from Java (one to Borneo and one to the mainland), with the added requirement that Sumatra was either bypassed or that the population became extinct. Scenario 5 appears to be the most parsimonious with the available data, and it is thus most likely that the Asian Banteng was introduced from Java. This would explain the similarity between Javan and mainland Asian skulls and the absence of Banteng fossils from the Asian mainland.

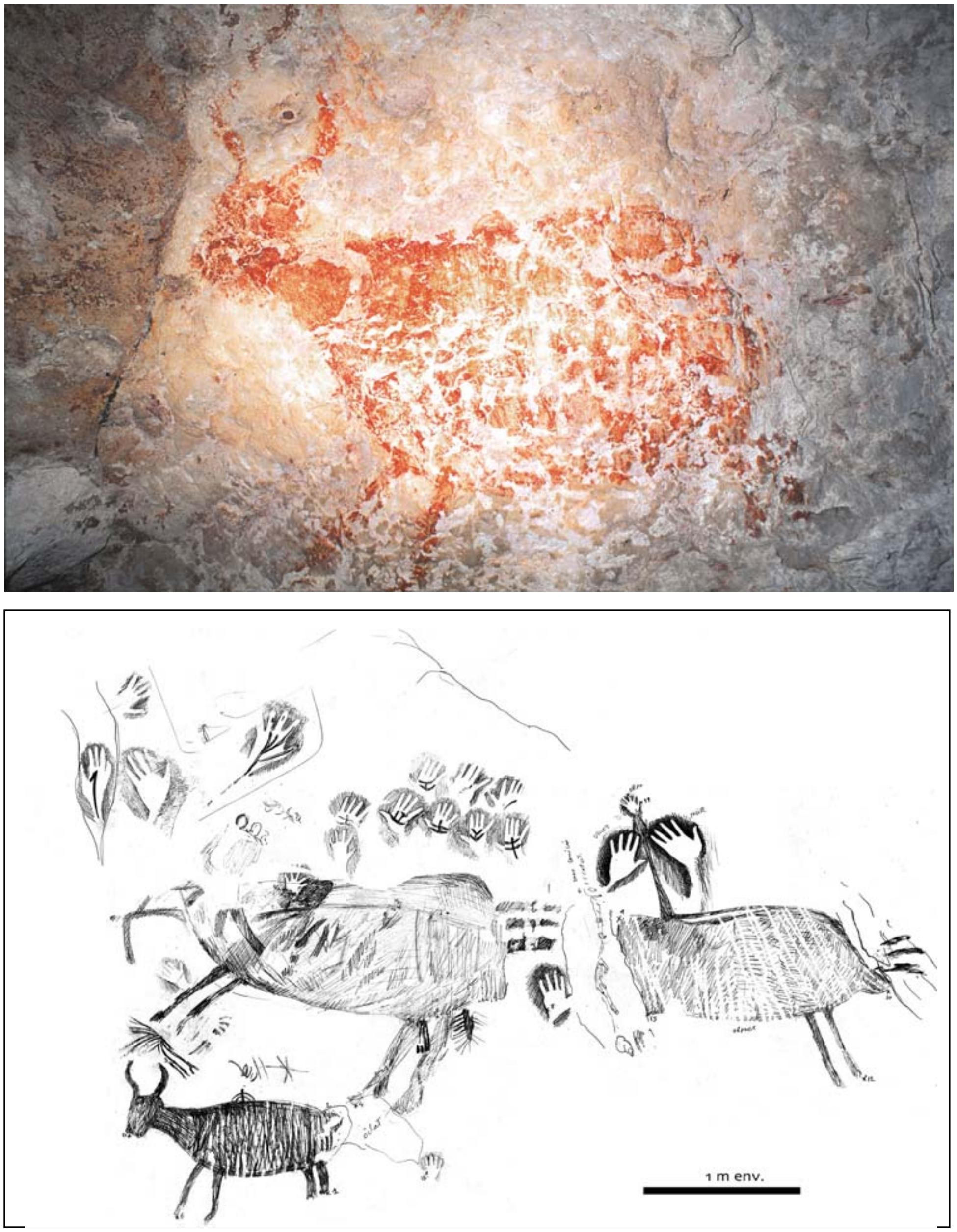


Figure 6.10. Cave drawings, presumably of banteng, from Ilas Kenceng on the Mangkalihat Peninsula, East Kalimantan (with permission from Luc-Henri Fage).

Chasen (1940) and Hooijer's (1958b) suggestion that the typical Banteng occurred in a truly wild state only on Java would support its introduction to mainland Asia, but not the true wild character of the Bornean Banteng. That Banteng are also indigenous to Borneo is suggested by recent findings of cave drawings in East Kalimantan depicting the species (Fig. 6.10). These drawings have been dated at a minimum of 9.9 Kya, but could be older (Fage et al. 2002; Plagnes et al. in press), and this seems to be evidence for the presence of banteng on Borneo at least since the LGM.

Whether the hypothesized introduction of Banteng from Java to mainland Asia involved domesticated or wild Banteng remains unclear, although considering the problems of transporting several wild Banteng on a small ship it is more likely that the animals were (semi-)domesticated. Banteng were domesticated on Bali and Sumatra by at least 500 AD (early Holocene Banteng remains from Sumatra indicate that the species did exist on the island, but became extinct, see Hooijer 1958a) while evidence from Java dates back to 800 AD (Meijer 1962). In the 14th century Javanese ode 'Nagarakrtagama' it is mentioned that Bali cattle were traded from Bali to Java, while elephants, camels, and donkeys were also transported by ship to Java. The introduction could thus have happened some time after 500 AD, although an earlier date is not impossible. Such introductions may also have occurred to Sumatra. Prehistoric (sub-fossil) remains have been found in the Padang highlands of West Sumatra (Hooijer 1958a). These are somewhat larger in size than modern banteng (as were the remains found in the Niah caves in Sarawak).

Interestingly, one of the characters that differentiate Bornean from Javan Banteng (the straighter horns) also differentiates fossil Banteng (*Bibos palaeosondaicus*) from present-day Javan Banteng. It is therefore possible that after the Bornean split from the Javan Banteng it retained the narrow horn span, while the Javan form developed more curved horns. Even if Bornean Banteng are indigenous to the island and have been so since the Middle Pleistocene, this still does not answer the question about their genetic purity. Hoogerwerf (1970) refers to several reports dating from the 1930s and 1940s which mentioned that many groups of banteng in Kalimantan—and particularly East Kalimantan—were no longer pure-bred having interbred with stray domestic cattle. Furthermore, Schneeberger (1945) mentioned domestic cattle that were left behind by villagers in the Krayan-Kelabit highlands of northern East Kalimantan. In addition, the 'banteng' which have in recent times lived in and around the grasslands of south-eastern Kalimantan may be the descendants of feral 'Bali cattle' (domestic Banteng) because in the early 20th century they were described as 'cattle' (they were kept under a system of free-range husbandry and only rounded up when needed for meat but they were not wild Banteng) (Brookfield 1997).

Further molecular research is needed to test the above hypothesis on banteng evolution. If correct it should show considerable sequence differences between Bornean and Javan Banteng, whereas the mainland Asian Banteng would be similar to the Javan ones. Also, the effects of a genetic bottleneck should still be detectable in Asian Banteng, because the introduction hypothesis suggests that only a few founder animals initially made it to Asia. Some preliminary molecular work has already been done which suggested (rather cryptically) that gene flow had occurred between Javan and Asian Banteng (Read 1998). If Bornean feral cattle were derived from Bornean wild Banteng then it should also be possible to differentiate between two different feral cattle lineages, one originating from Bornean, and one from Javan Banteng, although mixing of these lineages may now obscure the differences.

6.4 MOUSE-DEER (TRAGULUS SP.) MORPHOLOGY

The results of the research on the *Tragulus* genus was separately published by Meijaard and Groves (in press-c, and Appendix 5). Although the study revealed much about the taxonomy of the genus, including the resurrection of a very distinct species, *T. versicolor* from coastal Vietnam, it did not tell us much about the evolution of mouse-deer. This is mostly because there is a complete lack of supporting data on the phylogenetic relationships within *Tragulus* (although one study by Forstner et al. on that subject will soon be published). Still, it is useful to reiterate some of the findings of the craniometric study and attempt to link them to the new biogeographic model.

Firstly, the distinctness of *T. versicolor*, a mouse-deer species in the area east of the Mekong River, suggests that at some stage the genus was split into three groups: 1. east of the Mekong (*T. versicolor*); 2. Indochina and Sundaland, including Java (*T. javanicus*, but note that Meijaard and Groves suggested splitting this into *T. javanicus*; Java, and *T. kanchil*; elsewhere); and 3. primarily Sundaland (*T. napu*). I do not know the divergence sequence nor divergence time among these species groups, but the existence of a distinct species of mouse-deer related to the *T. napu* group on Balabac Island (near Palawan) could suggest that this species became established in the Middle Pleistocene, because at that time a land bridge probably existed between Borneo and Palawan (see Chapter 5.2). Because Balabac is closer to Borneo it cannot be excluded that this species (*T. nigricans*) became established on Balabac at a later stage, although its morphological distinctness suggests an isolation history of at least several hundred Kyr. If correct, this would give the *T. napu* species group at least a Middle Pleistocene age and probably older. Unfortunately the fossil record of *Tragulus* is poor with only a small number of Late Pleistocene finds on Java and Borneo and a late Middle Pleistocene find in Thum Wiman Nakin in Thailand (Tougard et al. 1996). It is therefore impossible to further interpret the evolutionary history of this group until new data become available.

The skull morphology analysis of *T. javanicus* indicates a phylogenetic pattern that conforms with the geographic relationship between the groups, i.e. a central group consisting of the Sundaland islands, Sumatra, Indochina and the Malay Peninsula, with the Borneo group in the east, the West Malay islands in the west, and Java and the possibly distinct Cirebon group in the south (see Appendix 5). This suggests a divergence process congruent with the present geographical and ecological lay-out of the region, which indicates that the groups were separated relatively recently, and very likely, just after the post-LGM, rising sea-levels isolated the groups from each other.

The grouping of *T. kanchil* from the small Sundaland islands with Sumatra, Indochina and the Malay Peninsula suggest that during the LGM the island specimens migrated from the west onto the exposed Sundaland area, where they were separated from Borneo-derived animals by the Molengraaff River. If this hypothesis is correct, then it would be expected that the specimens from east of the Molengraaff River are more similar to the Borneo specimens than to those from the Sundaland islands, a finding that was confirmed by the close morphological similarity between *T. kanchil* from Subi Island (see Fig. 18 in Appendix 5) and those from Borneo. Also, in *T. napu* this can be found, because the form from Serasan (or Sirhassen) Island is indistinguishable from the Bornean *T. napu*. Other interesting zoogeographic patterns in *T. kanchil/javanicus* include:

1. The similarity between *T. k. pallidus* from Laut Island, north of Natuna, to the Asian mainland form of *T. kanchil* might suggest that this tentative subspecies became established on Laut during the LGM. Because of the location of the delta of the Siam River, it would have probably migrated there from the Thailand/Cambodia area.

2. The apparent similarity of one form of *T. javanicus* from Java with *T. kanchil* from Bangka might indicate that during the LGM a Bangka/Sumatra form migrated to Java and mixed with the existing population. Rumours about the apparent existence of two distinct forms of mouse-deer on Java may be related to that event.

The Discriminant Analysis patterns found in *T. napu* are less easily explained than those in *T. javanicus*. In *T. napu* the Borneo, Sumatra, and Malay Peninsula specimens group together, but they are considerably different from the Sundaland islands group. This would indicate that when the Sundaland island populations were separated from the others, they underwent considerable morphological change. Van Dort (1986) described this and referred to it as character-displacement, although in fact it appears to be the opposite. In Appendix 5, we showed that on the Sundaland islands *T. javanicus* and *T. napu* converge towards rather than diverge away from each other, as would be expected in character-displacement. The fact that Borneo, Sumatra, and the Malay Peninsula group together quite tightly (see Fig. 5, Appendix 5) would suggest that there have either been high levels of gene flow within that region, or that the species was isolated in any of the three regions until relatively recently and that when the land masses were connected populations dispersed to the other areas. At present it is not yet possible to find out to which area *T. napu* was restricted before the LGM (if indeed this was the case).

One of the remarkable patterns found in the Discriminant Analysis of both *T. napu* and *T. javanicus* is the grouping together of specimens from the Terutau or west Malay islands. These islands presently lie less than 20 km off the coast of the Malay Peninsula and I would have expected them to having been connected to the mainland when sea-levels were low during the LGM. The patterns found for both *Tragulus* species suggest genetic isolation of the Terutau specimens for a longer time than, for instance, those found on the Sundaland islands. This could indicate that there was either geographical or ecological isolation of the island area from the mainland; the latter is unlikely as both islands are separated from the mainland by seas less than 20 m deep and would have been connected to the Malay peninsula for most of the LGM.

It is surprising to see that the specimens from western Borneo were generally smaller than those from the east and north-east. Considering how similar the Bornean specimens are to the Sumatran specimens, I would have expected to find that those on the western side of Borneo, nearest to Sumatra, would have been larger than those from east and north-east Borneo. It is possible that the populations in these parts of Borneo and Sumatra were interbreeding during the last glacial period when the Sundashelf area was emergent, and that therefore they are more closely related to each other than to the presently adjacent populations in west and north Sumatra, and east and north-east Borneo. I could, however, not find such relationships in the skull dimensions.

6.5 CERVINE MORPHOLOGY AND GENETICS

In a paper on the phylogenetic relationships among Asian deer (Meijaard & Groves in prep., Appendix 7), we investigated the sequence of divergence events with the genera *Axis*, *Cervus*, and *Elaphurus*. Based on craniometric analysis, molecular data, and the fossil record we hypothesized the following:

The subgenus *Hyelaphus* with the 3 species *kuhli*, *calamianensis*, and *porcinus* is distinct from *Axis*, and subgeneric separation should be maintained. *Hyelaphus* separated from other deer during the Early Pliocene, which could suggest that this group with primarily Sundaic affinities diverged from the subgenus *Axis* that is mostly found on the Asian mainland during the Early–Middle Pliocene highstand. The species *kuhli* (which is very similar to the Javan fossil endemic *Axis lydekkeri*) is now restricted to Bawean Island, while *calamianensis* only occurs on some small islands offshore Palawan. This indicates the occurrence of centrifugal evolution with more progressive species pushing the more primitive forms to the periphery of the group's distribution range.

The Philippine deer, *C. mariannus* and *C. alfredi* probably diverged from the other deer during the Pliocene lowstand (between 4 and 3.2 Mya, also see Chapter 5.2, Palawan section). We hypothesized that the ancestors to these species migrated via Borneo, Palawan and Mindoro to the rest of the Philippine islands.

The relationships between the remaining deer remain unclear and depend on the analytical technique (mtDNA, nuclear DNA, enzymes, craniometrics, behavioural studies). Still it appears that *Axis*, *Cervus*, and *Dama* diverged rapidly during the Late Miocene–Early Pliocene, when in Asia there was a change from generally humid and warm conditions to drier and cooler ones. The resulting replacement on the Asian mainland of tropical closed forest by more open, deciduous forests and grassland may have been an important factor in the rapid radiation of cervids.

6.6 SE ASIAN PIGS

During the earlier Tertiary, SE Asia had a rich suid community, with several pig species from different tribes co-occurring in Yunnan, China, during the Late–Middle Miocene (see for instance van der Made and Defen 1994). These included *Yunnanochoerus lufengensis* (Tayassuidae, Palaeochoerinae) and the suids *Propotamochoerus wui*, *P. hyotherioides* (Suinae, Dicoryphochoerini), and *Chleustochoerus* sp. (Hyotheriinae). This shows how diverse suids were at that time, and also that apparently several species from different tribes co-existed, which appears to be in contrast with the present-day situation in SE Asia in which never more than 2 pig species from 2 tribes (Babyrousini and Suini) co-occur (taxonomy after van der Made 1997). This decline in pig diversity, probably at both species and higher taxonomic levels, may be due to the increasing climatic fluctuations during the Pliocene and Pleistocene and generally lower temperatures and humidity. The highest diversity now remains in the Asian tropics where between 11 and 14 species exist (depending on species definitions): *S. scrofa*, *S. salvanius*, *S. bucculentus*, *S. verrucosus*, *S. barbatus*, *S. celebensis*, *S. philippensis*, *S. cebifrons*, *S. ahoenobarbus*, *S. oliveri*, and either 1 or 4 species of *Babyrousa* (see Meijaard & Groves 2002), while further species in the Philippines remain to be described (Oliver 2001).

As part of the present research I investigated the craniometrics of SE Asian pig species. The findings were combined with research on mtDNA sequence differences between SE Asian pig species (Lucchini et al. in prep., see Appendix 8), which revealed some surprising results. It appears that we need to rethink the grouping of SE Asian pig species into 3 groups (1. *verrucosus*—consisting of *S. verrucosus*, *S. barbatus* (including *ahoenobarbus*), possibly *S. bucculentus*, *Sus celebensis*, and *S. cebifrons*; 2. *philippensis*—consisting of that species; and 3. *scrofa*—consisting of *S. scrofa* and *S. salvanius*), as proposed by Groves (1981). Instead there appear to be 2 or 3 different groups:

1. A group of pigs from the Philippines and Sulawesi that retains characters that are plesiomorphic compared to the other groups, and from which the Sulawesi species has diverged most.

2a. The *S. barbatus*, among which little morphological differentiation was found, but which separated into a Sumatran group and a Malaysian/Bornean group based on different DNA sequences.

2b. A group consisting of *S. scrofa*, *S. verrucosus*, and *S.* cf. *barbatus ahoenobarbus*, in which especially the former two appear to be morphometrically similar. The molecular analysis grouped *ahoenobarbus* with group 1 (*S. cebifrons*), but *verrucosus* was not used in the analysis.

In the paper we discuss the divergence sequence of the SE Asian pig species, but because not all pig species have yet been incorporated a complete picture of pig evolution during the Quaternary is still lacking. A possible evolutionary scenario for the SE Asian pigs would be as follows: Some time during the Pliocene an ancestral pig species crossed from Sundaland to the Philippines. This could either have happened via Sulawesi or via Palawan, but much more likely the latter; the source population in either case would have been in what is now Borneo. The morphometric distinctness of Palawan's *ahoenobarbus* (and its basal position in a phenetic species tree, see Fig. 11, Appendix 8) indicates that this dispersal went via Palawan to the Philippines, while *celebensis* crossed into Sulawesi. The presence of two more genera of suids in Sulawesi (*Celebochoerus* and *Babyrousa*), which split off from the main stock of Suidae at much earlier times (Thenius 1970; Hooijer 1975), is indicative of several invasions of ancestral suid types to Sulawesi over a considerable length of time. Fossils of two *Celebochoerus* species occur in Late Pliocene (ca. 2.5 Mya) and Middle Pleistocene (ca. 0.8 Mya) deposits in Sulawesi (van den Bergh 1999), but *S. celebensis* fossils have so far only been found in Holocene sites (Cranbrook (Earl of) 1981). This suggests that *celebensis* crossed into Sulawesi at some time during the Pleistocene, and possibly even led to the demise of *Celebochoerus*.

The dispersal event to Palawan and on to the rest of the Philippines is most likely to have taken place during a period of low sea levels, because Sundaland is separated from both the Philippine and Sulawesi areas by deep seas, and the land areas were considerably closer to each other when sea levels were much lower than at present. Such major drops in sea level occurred in the Early Pliocene (ca. 5.2 Mya) and Early–Middle Pliocene (3.6 Mya), while sea levels became very low at around 2.7 Mya (Haq et al. 1987; Mitchum et al. 1993). Further low sea levels occurred during the Late Pliocene and Pleistocene, especially after 0.8 Mya, but we expect that the cross-over from Sundaland to Sulawesi and the Philippines occurred during one of the earlier Pliocene sea level lowstands.

After the dispersal events to Sulawesi and the Philippines, the *verrucosus* and *barbatus* lineages diverged. Considering that the former is restricted to Java and the latter to Borneo/Sumatra/Malay Peninsula, the divergence would have happened as the result of Java's separation from the rest of Sundaland. It is unclear whether the split between *scrofa* and *verrucosus* happened before or after the *verrucosus/barbatus* split. Aimi (1989) suggested that *S. stremmi*, an Early Pleistocene pig species from Java, was ancestral to *S. verrucosus*, which would indicate that this lineage reached Java some 2 Mya. My palaeogeographical reconstructions suggest that this is the first time that mammal species were able to reach Java (apart from an Early Pliocene episode when some mammals may have occurred in western Java). During the Pleistocene, however, there were several periods when Java was connected by land to the rest of Sundaland, and it is possible that *barbatus* reached Java at some stage, as suggested by Hardjasamita (1987), or that *verrucosus* dispersed to northern Sundaland. Ecologically the species differ considerably; *barbatus* is adapted to life in dense rainforest where supra-annual mast fruiting events largely determine the population demographics (Caldecott 1991; Caldecott et al. 1993), but *S. verrucosus* is restricted to secondary forests at low altitude, and expanses of grass and bush land, and rarely occurs in primary rainforest, although it is unclear to what extent this may be caused by competition from *S. scrofa* (Blouch 1983). *S. verrucosus* evolved in the generally drier climate of Java and its more open vegetation types, and would probably not survive in Sundaland's rainforest. Differences in habitat preference would therefore have provided a significant barrier between the *verrucosus* and *barbatus* lineages.

Finally, as suggested by the molecular work, there appears to be a clear split within *S. barbatus*, with the Bornean and Peninsular Malaysian populations in one group and the Sumatran in another. The hard polytomy found between the three *barbatus* populations suggests that rapid radiation occurred between them. Considering the lack of morphological differentiation between the populations, I think that the divergence between them happened relatively recently, very likely during the Late Pleistocene. During the last glacial maximum (LGM), evergreen forest areas in Sundaland were probably restricted to several refuges and *barbatus* could have been separated into different populations (see Fig. 13, Appendix 8). If indeed, the Peninsular Malaysian population is more closely related to the Bornean than to the Sumatran one, the population of Peninsular Malaysia may have gone extinct during the LGM and reinvaded the peninsula from Borneo when climatic conditions became wetter once more, but before rising sea levels separated Borneo from Peninsular Malaysia. In relation to this it should also be mentioned that *barbatus* is absent from northern Sumatra, which suggests that the Sumatran population was restricted to the southern part of Sumatra, and did not reinvade the northern parts after the LGM.

6.7 BORNEO'S PRIMATES: A BIOGEOGRAPHICAL AND EVOLUTIONARY MODEL

This chapter refers to the paper by Meijaard and Nijman (2003, see Appendix 2). In that paper we mapped the distribution ranges of Borneo's primate species based on 1414 presence records for the 13 species. We overlaid these distribution ranges in a GIS to investigate patterns of sympatry and species richness.

The results showed that two areas in Borneo had the highest number of co-occurring primate species, a large area in lowland East Kalimantan, and a smaller area in southeast Sabah. It is interesting to speculate why these particular areas in northeast Borneo are rich in primate species. Brandon-Jones (1996a; 1998; 2001) suggested that northern Sabah, and particularly Mt. Kinabalu, was a major focus of biodiversity because of a glacial rainforest refugium in this area, but this may be disputed. There is now considerable evidence that much of Borneo remained covered in rainforest, even during the last glacial maximum (LGM), although there are indications of an extension of grasses, and evergreen rainforest may have been somewhat reduced (see various sources in this thesis). Drier conditions may have occurred in East and South Kalimantan where data suggest a more open vegetation type (Caratini and Tissot, 1988). It is therefore hard to link the primate-rich areas of East Kalimantan to a hypothesized LGM rainforest refugium in that area. Such a refugium may, however, have existed much earlier in the Pleistocene, which could have led to isolation and later renewed expansion of species. Recent mtDNA data (Warren et al. 2001) of orang-utan seem to point in that direction. A phylogenetic tree of the Bornean orang-utan suggests a basal position for the Sabah population, dating back to approximately 1.1 Mya. The populations of East Kalimantan, north West Kalimantan and Sarawak, and south West and Central Kalimantan later descended from the Sabah population. This scenario of Middle Pleistocene refugias in northern Borneo could to some extent explain the concentration of primate species in northeast Borneo.

6.8 EVOLUTION OF *PRESBYTIS*

In Meijaard and Groves (in press-a, see Appendix 3) we applied the palaeoenvironmental and palaeogeographical model to explain the phylogenetic relationships and sequence of species divergence within the genus *Presbytis*. The results are discussed in detail in that paper; here I highlight some of the aspects.

The reconstructions start with the split between *Nasalis* and *Presbytis*, which occurred in the Late Miocene, according to Sarich (1970) and Zain (2001). Presumably, this split occurred in Sundaland, whereas the mainland Asian colobines diverged in another center of radiation (Zhang et al. 1993b). If the *Presbytis* group indeed entered Sundaland at the end of the Miocene or in the Early Pliocene they would have followed a route along the Malay Peninsula into what is now Borneo, and possibly Sumatra (see reconstructions in Chapter 5). Java became disconnected from this landmass after the Early Pliocene, and dispersal to Java could only have occurred across sea water (until the island became reconnected to the rest of Sundaland during the Early–Middle Pliocene).

Considering the early divergence of *potenziani*, hypothesized by Brandon-Jones and supported by our craniometric data, the ancestral *potenziani* probably entered Sumatra across the Asahan Arch (Figure 3, Appendix 3), which shortly afterwards became submerged, cutting off connections between Malaya/Borneo and Sumatra. Presumably, *P. potenziani* evolved on Sumatra and spread to the Mentawai Islands during the Pliocene–Pleistocene. Why the species became extinct on mainland Sumatra is unclear. It may either have been displaced by a later *Presbytis* species, or, maybe, its habitat temporarily disappeared during one of the Pleistocene glacials. None of the phylogenetic reconstructions supports a sister species relationship between *potenziani* and *thomasi*, although Wilson and Wilson (1977), who compared *Presbytis* vocalizations, suggested that the two may be subspecifically related. Still, it is unlikely that *potenziani* and *thomasi* arose vicariantly when the Mentawai Islands and Sumatra became disconnected.

In Borneo/Malaya, several Myr later, a split probably occurred between *sabana* (with or without the other species from the *hosei*-group) and *frontata*. I hypothesized that this split happened at the start of the Pleistocene and was caused by the development of the Mahakam River; it may, however, be more likely the result of the severe Late Pliocene glacial that occurred ca. 2.4 Mya. This could have significantly restricted evergreen rainforests on Borneo.

Sometime during the Pliocene the separation of Borneo from the Malay Peninsula would have provided a mechanism for the divergence between the *siamensis/femoralis/melalophos/chrysomelas* group and the remaining Bornean *Presbytis* species. *P. comata* would subsequently have migrated to Java across an Early–Middle Pleistocene land bridge, but it is unclear whether this land bridge was only connected to the Malay Peninsula or whether there was also a direct link to Borneo. Zain's (2001) data and our craniometrical analysis support a close relationship between the Javan *comata* and the Bornean *rubicunda*. Although there is limited concordance between the 3 phylogenetic models regarding the relationships between *thomasi*, *comata*, and *rubicunda*, Zain's data strongly suggest that the 3 species form a monophyletic clade. We speculated that an ancestral species on the southern Malay Peninsula, or on the peninsula's extension along the Riau/Lingga Archipelagos and Bangka and Belitung Islands, crossed to Sumatra, Java, and Borneo during an Early-Middle Pleistocene glacial period. It remains unclear where and for how long these land connections between Malaya, Java, Sumatra, and Borneo existed. During the Early–Middle Pleistocene, the following situation may have existed: 1. In northern Borneo, the *hosei*-group occurred, separated by the Kapuas and Mahakam Rivers from the *frontata*-ancestor; 2.. In southwest Borneo, *rubicunda* lived; 3. On Java, *comata* occurred; 4. On most of Sumatra, *thomasi—potenziani* occurred; the latter had by then been isolated on the Mentawai Islands; and 5. The *melalophos*-group (including *siamensis*, *femoralis*, and *natunae*) occurred on the Malay Peninsula and its southern extension to the Riau, Lingga, Bangka, and Belitung areas (see Figure 6, Appendix 3).

Assuming that Zain's (2001) divergence times are approximately correct, speciation in the *melalophos*-group happened during the Middle Pleistocene, sometime between 1.4 and 0.8 Mya. At that time minimum sea levels dropped to 80 m below the present-day levels, and these much lower sea-levels could have provided opportunities for dispersal of the *melalophos*-group into Borneo and Sumatra, which, after sea-levels rose, would have isolated them in those areas (Figure 7, Appendix 3).

The 3 phylogenetic models do not agree on the relationships between *melalophos*, *femoralis*, *siamensis*, and *natunae*, and the speciation model for this group remains unclear. Considering that *melalophos* occurs exclusively on Sumatra, evidently its evolution was the direct result of the dispersal of its ancestor from Malaya to Sumatra during a period of low sea-levels, after which it was isolated again when sea-levels rose. On Sumatra, *melalophos* would have encountered *thomasi*, unless the latter species was already isolated in north Sumatra (north of the Sibolga area), which I think may have been an island for much of the Pleistocene.

Figure 8 in Appendix 3 provides an explanation for the curious distribution patterns of *P. f. percura*, *P. s. paenulata*, and *P. s. cana* (see Figure 1, Appendix 3). Because of the existence of drier vegetation types during the LGM that were unsuitable for *Presbytis*, species would have retreated into wet forest refugia. Figure 8 shows that such a refugium existed near the mouth of the Molengraaff River (hereafter named Bunguran refugium) and on the west side of the mountains of Malaya (west Malay refugium). If we assume that *femoralis* retreated to the Bunguran refugium, and *siamensis* to the west Malay one, then after the climatic amelioration, when sea-levels started to rise, *femoralis* could have migrated west following the courses of the main rivers, which would have led them northwest towards central Malaya and southern Thailand, and west-southwest towards their present-day Sumatran ranges. *P. siamensis*, on the other hand, could have stayed in the west Malay refugium, but presumably found an opportunity to reach eastern Sumatra, directly opposite its Malayan range. *P. femoralis*, on its return to Sumatra, drove a wedge in the *siamensis* population. Zain's (2001) data show that this may not be the full story, as he found that *P. femoralis femoralis* and *P. f. robinsoni* diverged during the Middle Pleistocene, ca. 750 Kyr before the LGM, while also suggesting that *femoralis* is not monophyletic relative to *melalophos* and *siamensis*. This could mean that *P. f. robinsoni*, from the northern Malay Peninsula, is specifically distinct from *P. femoralis femoralis* and *P. f. percura*. Further taxonomic and phylogenetic work is needed before we can really test the above hypothesis.

For *P. chrysomelas*, a similar scenario can be developed, with the species retreating towards the Bunguran refugium during the LGM (note that there are no pre-Holocene fossils of this species on mainland Borneo), after which it reinvaded Borneo from the west. *P. chrysomelas* largely displaces both *frontata* and *rubicunda* in the lowlands of Sarawak (Banks, 1931; Nijman and Meijaard, in preparation), whereas in east Borneo, where *chrysomelas* is absent, *frontata* and *rubicunda* are found at low elevations. This suggests that *chrysomelas* occupied the exposed Sunda Shelf during the LGM, and when sea-levels started to rise it moved into western Borneo, thereby displacing *frontata* and *rubicunda*, especially in swamp areas.

6.9 LEOPARD (PANTHERA PARDUS) MORPHOLOGY

I answered the main question on how leopards managed to reach Java without leaving any traces on Sumatra or Borneo in Meijaard (in press, see Appendix 4). In that paper I showed that Javan Leopards are morphologically distinct from other leopards which indicates that they have evolved in isolation for a considerable length of time. I suggested that leopards reached Java from the Malay Peninsula during the Early–Middle Pleistocene, which fits the molecular clock-based divergence time between the Javan leopard and its closest relatives, the mainland Asian leopards. At that time a landbridge existed between Java and the Asian mainland that bypassed Sumatra (see Chapter 5.2), which could explain why the species did not become established on Sumatra. After this period Java probably remained isolated from Sumatra until the two islands became connected again during the late Middle Pleistocene. I argued that the ecological conditions on Sumatra and Borneo were such that insufficient prey biomass was available for the co-existence of several large predators; this hypothesis was supported by prey biomass and large carnivore occurrence data from different parts of Asia. It therefore appears that the Javan leopard arrived on Java and was unable to colonize Borneo or Sumatra during times of lowered sea levels because of insufficient prey density and competition from Tiger on Sumatra and Clouded Leopard on both islands. If leopards did reach Sumatra and Borneo they presumably became extinct because of the aforementioned ecological constraints.

The hypothesis regarding Javan leopard is supported by the biogeographical model presented in the dissertation. The arrival of the leopard on Java during stages PLEI 3 and PLEI 4, as suggested by the fossil record, fits the palaeogeographies at that time, while it’s isolation on Java is supported by both molecular research and the palaeogeography during PLEI 4 – PLEI 5, when the land bridge between Java and the rest of Sundaland disappeared. Still, further testing is required to prove that indeed Javan leopards reached the island in the Early–Middle Pleistocene. To investigate whether ecological characteristics of leopards can explain its absence from Sumatra and Borneo it is probably best to study interactions between Tiger and Leopard in a tropical environment similar to Sumatra and Borneo; the co-existing large predator populations of Peninsular Malaysia would be ideal.

6.10 MAMMALIAN ISLAND SPECIES AS PALAEOENVIRONMENTAL INDICATORS

Work on this paper (Meijaard 2003, also see Appendix 1) started when I was working on Mouse-Deer populations. I realized that these forest-dependent species (especially *T. napu*) would only have been able to survive on islands if there had been forest since these islands were isolated by rising sea-levels. Not only did this apply to Mouse-Deer, but also to other forest-dependent species. I realized that, in fact, the ecology of island faunas provided valuable information about the type of forest that existed at the end of the LGM when these islands came into being. This provided a valuable tool for modelling Late Pleistocene environments throughout Sundaland.

The results indicate that during the LGM several areas remained covered in evergreen tropical forest, i.e. the Mentawai Islands, the Natuna Islands, the area west of the Malay Peninsula, and Palawan, while in the following areas drier vegetation types probably existed: the southern Java Sea, east Borneo, the area east of the Malay Peninsula, and the Gulf of Thailand. This paper has therefore provided some very useful insights in the palaeoenvironments during the LGM, including support for the existence of tropical forest refugia during the LGM.