

CRANIOMETRIC DIFFERENCES AMONG MALAYAN SUN BEARS (*URSUS MALAYANUS*); EVOLUTIONARY AND TAXONOMIC IMPLICATIONS

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ABSTRACT. – In this paper I use multivariate statistical analyses of Sun Bear (*Ursus malayanus*) skull measurements to investigate the differences between specimens from Borneo, Sumatra, the Malay Peninsula, and the Asian mainland. Specimens from Borneo were significantly smaller than those from elsewhere, but they had relatively long tooth rows. There were no significant differences between specimens from Sumatra, the Malay Peninsula and the Asian mainland. Based on these results, the interpretation of the fossil record, and some preliminary molecular work on the species, I hypothesize that *U. malayanus* originally evolved in the Sundaic Subregion some time during the Pliocene, and that soon after the species was split in a Malayan and a Bornean form. The Malayan form later dispersed to the Asian mainland and Sumatra. The observed morphological differentiation of the Bornean taxon from the others warrants its subspecific designation as *U. malayanus euryspilus*. I recommend assigning all remaining populations to the typical form *U. malayanus malayanus*. Although more research is needed, especially on the species' phylogeny, the results imply that the two subspecies should be independently dealt with in conservation management.

KEY WORDS. – bear, craniometrics, biogeography, evolution, fossil, South-East Asia, Ursidae.

INTRODUCTION

The Malayan Sun Bear (*Ursus (Helarctos) malayanus*) is a species of the tropical and subtropical parts of south and south-east Asia [note that I consider *Ursus* the more appropriate generic name for this species rather than *Helarctos* (see Meijaard 1999; 2003)]. Its historic range covered most of the south-east Asian mainland, as far west as Assam (Higgins, 1932), the upper Chitwan District in India (Wroughton, 1916) and Nepal (Hodgson, 1844), and as far north as Tibet and the Szechuan Province in China (Lydekker, 1906). The species has now apparently become extinct in China (Servheen, 1999; Fitzgerald & Krausman, 2002), and was thought to have disappeared from India, but Karanth et al. (2001) recently photographed a living Sun Bear in Anurachal Pradesh. The species also still occurs in parts of Burma, Laos, Thailand, Cambodia, Malaysia, but appears to have its stronghold on the islands of Sumatra and Borneo (Meijaard, 1999; Servheen, 1999).

The origin of the Ursinae (true bears), of which *U. malayanus* is a member, is placed in the Late Miocene, approximately seven million years ago (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 four Mya (see Fig. 1). This seems to fit data from the fossil record, because at about four 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 some time between 3.5 and two Mya, leading to four ancestral bear lineages (Waits et al., 1999). This included the lineage leading to the Asiatic Black Bear (*U. thibetanus*) and American Black Bear (*U. americanus*), the lineage of *U. malayanus*, and the lineage leading to the Brown Bear (*U. arctos*) and Polar Bear (*U. maritimus*).

Figure 1 coincides reasonably well with Mazza and Rustioni's (1994) phylogeny, which was based on the morphology of

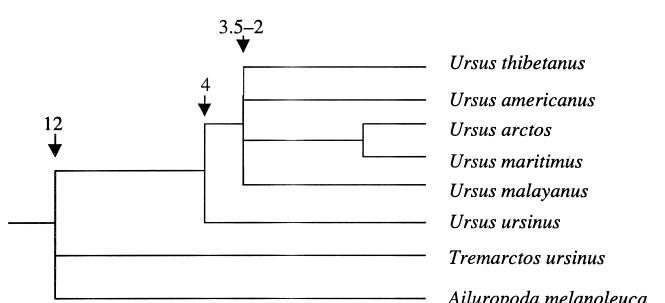


Fig. 1. The phylogenetic relationships between bears species (after Waits et al., 1999). Numbers refer to the estimated divergence times at each node.

bear fossils. 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 (Mazza & Rustioni, 1994; Morlo & Kudrat, 2001). 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 (Mazza & Rustioni, 1994). If indeed *U. thibetanus* originated 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, although sympatric or parapatric speciation cannot be excluded.

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 (de Vos & Long, 1993). *Ursus 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 (Meijaard, 2003). This suggests that it was part of Sumatra's fauna during the Middle–Late 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, and found its way to Sundaland only during the Middle Pleistocene. If this were true one would expect to find relatively small differences between populations of *malayanus* in Sundaland, and slightly larger differences between Sundaland and Indochina. Horsfield (1825), however, described two species of *U. (H.) malayanus* for Sundaland, i.e. *Helarctos malayanus* on Sumatra and *H. euryphilus* on Borneo (although this differentiation was based on one specimen from Borneo only), which would suggest that there are considerable differences among the Sundaic Sun Bears. Following this, Pocock (1932) dismissed the use of *euryphilus* 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. Further subspecific distinction was made for *annamiticus* (Heude, 1901) and *wardi* (Lydekker, 1906), although, according to Erdbrink (1953), 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*.

Here I will test the hypothesis that follows my assumption of an Indochinese origin of Sun Bears: the Sundaic Sun Bears differ more from the mainland Asian bears than they do from each other. I will do this by comparing measurements of Sun Bear skulls from different parts of its range.

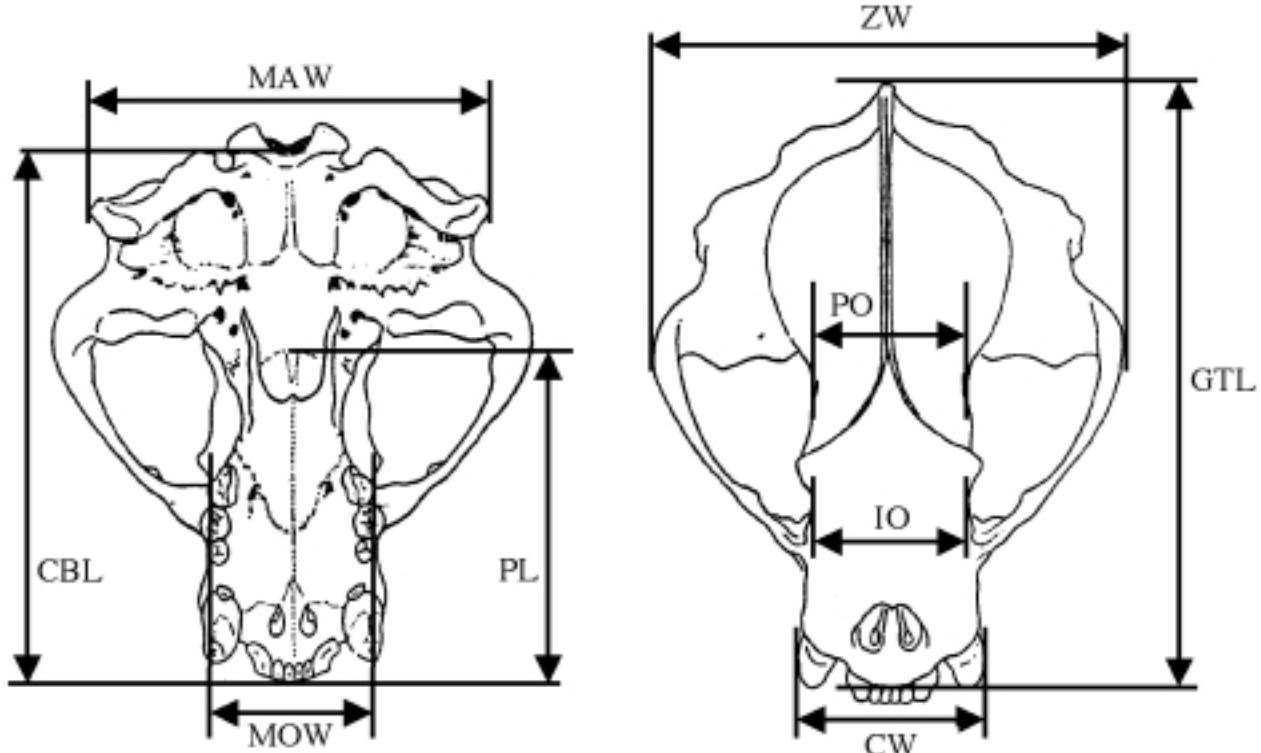


Fig. 2. Measurement details of *Ursus malayanus* skulls. Drawings from Pocock (1932).

Table 1. ANOVA test results for differences between adult male and female Sun Bears from Borneo, Sumatra, and Malaya/mainland Asia; only the variables with significant differences ($p < 0.05$) are shown. n=number of specimens; F=value for F-rest.

Area	Variable	n	F	p
Borneo	ZW	14	17.0	0.01
	GL	12	14.2	0.00
	IO	13	7.3	0.02
	PL	12	22.4	0.00
	MW	11	8.3	0.02
Sumatra	CBL	18	5.8	0.03
	ZW	18	8.9	0.01
	GL	18	9.3	0.01
	ML	14	13.8	0.01
Asia	ZW	10	13.2	0.01
	GL	9	7.2	0.03
	PO	8	6.4	0.04
	ML	7	17.5	0.01
	MW	5	10.1	0.03

MATERIAL AND METHODS

I measured 81 Sun Bear skulls in the following museums: Zoological Museum Cibinong (MZB), Indonesia (n=17); National Museum of Natural History, Leiden (RML), The Netherlands (n=14); Zoological Museum Amsterdam (ZMA), The Netherlands (n=7); the Field Museum, Chicago (FMNH), USA (n=3); the British Natural History Museum, London (BMNH), (n=22); Sarawak Museum, Kuching (SM), Malaysia (n=8); Zoological Reference Collection, Singapore (ZRC) of the Raffles Museum of Biodiversity Research (n=9); and the Natural History Museum of Los Angeles County (LACM) (n=1). I measured another 9 skulls in different places in Kalimantan, while Colin Groves measured one skull, the type specimen of *H. annamiticus*, in the Institute of Zoology, Beijing. Measurements for an additional 18 skulls were obtained from the following literature sources: Lyon (1911); Pocock (1932); and Sody (1949). Two skulls 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 MZB collection. Both are more likely to be *U. thibetanus*.

I took measurements of 10 variables (cranial terminology after Navephap, 1999, for cranial measurements see Fig. 2): greatest length (GTL); condylobasal length (CBL); palate length (PL); bizygomatic width (ZW); inter-orbital width (IO); post-orbital width (PO); mastoid width = widest across the mastoid processes (MAW); molar width = palate width outside M3 (MOW); canine width = palate width outside upper canines (CW); and mandible length (not shown in Fig. 2) = from the centre of the condyloid process to the anteriormost end of the mandible (ML). 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 as follows: Adult = M3 erupted and basilar suture fused; between Young Adult and Adult = M3 erupted and basilar suture fusing; Young Adult = M3 erupted and basilar suture open; Juvenile 2 = M2 erupted, but not M3; Juvenile 1 = M1 erupted, but not M2 or M3; 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 and young specimens out of the analysis. I used analysis of variance (ANOVA) tests for specimens from Borneo, Sumatra, and the Asian mainland to investigate the differences between males and females (Table 1). Males and females were distributed as follows across the regional populations ($\text{♀} - \text{♂}$, Borneo 8–6; Sumatra 9–9; Asian mainland 4–6), and although I realized that the Borneo sample had relatively more females than males, and the Asian sample more males than females, I decided to initially lump together males and females to investigate geographical variation in the complete data set.

A PCA of adult skulls (n=34) showed little spatial structure in a plot of the first and second components (Fig. 3). The first component, which explained 79% of the total variance, correlated positively and equally with the five variables (GL, CBL, IO, ML, PO) included in the analysis, which indicated that the differences were mostly determined by size. Figure 3 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).

A DA for adult males only allowed the use of 3 variables because of the small sample size of the Asian group ($n=5$). It revealed little more than that Bornean specimens were smallest, Sumatran ones intermediate, and the mainland Asian and Peninsular Malaysian ones the largest. One specimen from Lao Fu Chay, Laos stood out for its relatively short, wide skull. For female specimens ($n=18$), there was more structure to the data (Fig. 4), with Bornean specimens separating clearly from the Sumatra/mainland Asia/Peninsular Malaysia specimens. The data in Fig. 4 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 (low correlation 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 ($n=5$).

In an ANOVA, the Bornean specimens (both sexes) were significantly smaller than the Asian and Sumatran specimens for all the variables ($p < 0.001$) (see Table 2 and Fig. 5), while Sumatran and Asian/Peninsular Malaysian specimens were similar in size. A similar ANOVA for females gave the same result with all Bornean specimens being significantly smaller ($p < 0.01$) than those from mainland Asia and Sumatra, and little difference between the latter two. For males, all variables but IO (Borneo vs. Asia: $p=0.11$; Borneo vs. Sumatra: $p=0.12$), PO (Borneo vs. Asia: $p=0.09$; Borneo vs. Sumatra: $p=0.81$), and PL (Borneo vs. Asia: $p=0.34$; Borneo vs. Sumatra: $p=0.20$), were again significantly smaller for Bornean specimens ($p < 0.05$). Because Lyon (1908) reported the relatively large maxillary teeth in Bornean Sun

Bear, which were as big as the Sumatran ones, I assessed the ratio between the length of the upper tooth row and CBL (Fig. 6). This showed that Bornean specimens stood out compared to Sumatran specimens because of their relatively long upper toothrow in relation to skull length.

I investigated whether some of the specimens for which the locality was unknown could be reliably allocated to any of the three main regions (Borneo, Sumatra, mainland Asia/Malay Peninsula). One skull (BMNH 1867.4.12.202) was marked 'Java' (where Sun Bears do not now occur), and in a DA of all adult skulls it was part of the distinct group of Bornean specimens. Other skulls of unknown origin grouped either with the Sumatra or the mainland Asia and Malay Peninsula groups, but because the separation between these groups is poorly defined the allocation of these unknown specimens to either of the groups is unjustified.

Finally, Heude (1901) differentiated *annamiticus* (from Vietnam) from *malayanus* (Sumatra) primarily based on the much smaller molars and reduced canines of *annamiticus*. 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. 7); in fact, it appeared that the Asian specimens were differentiated into two distinct groups, although the sample size is too small to confirm this. The specimen outside the range of the others (see arrow in Fig. 7) originated from the Garo Hills, in upper Assam, India (BMNH 1938.12.9.1). When I measured this skull, I noticed the very long M1 (21 mm) and M2 (13.2 mm) of this specimen, compared to the other mainland Asian specimens (mean M1=17.5, SD=0.52, $n=15$; mean M1=8, SD=0.4, $n=8$). Also, the palatine and mandible were relatively long, and the value for mastoid width low. It could be that this species was not *malayanus*, but instead a young *Melursus ursinus* or *U. thibetanus*.

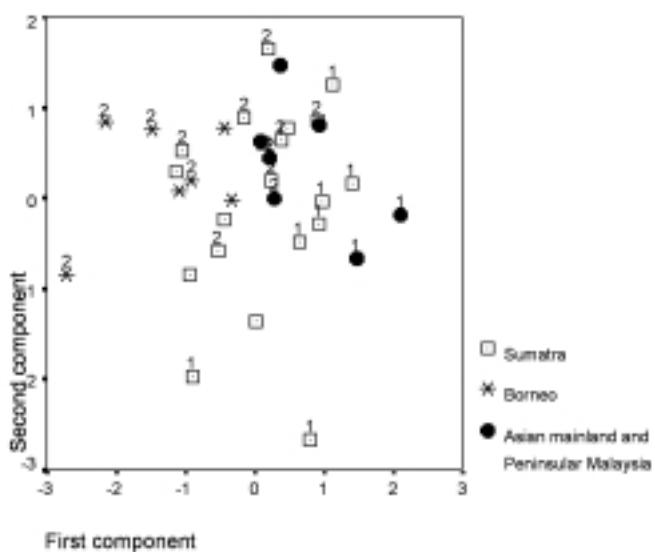


Fig. 3. A PCA of adult Sun Bear specimens. Numbers refer to sex: 1=male; 2=female.

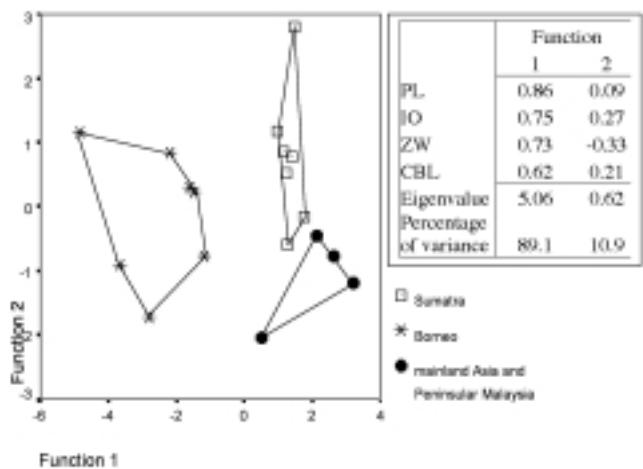


Fig. 4. A discriminant analysis of adult, female Sun Bear skulls, and the corresponding correlation matrix.

Table 2. The means and standard deviations (SD) of each of the measured variables for Sun Bears (both sexes) from Borneo, Sumatra, and Malaya/mainland Asia.

		CBL	ZW	GL	IO	PO	PL	MAW	ML	MOW	CW
Asia	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

DISCUSSION

The results show that skulls of the Bornean Sun Bear were significantly smaller than those from Sumatra and the Asian mainland, while its relatively large maxillary teeth further distinguished the Bornean from the Sumatran form. These results confirm Pocock's (1941) assignment of the Bornean form to a distinct taxon. Elsewhere, I discussed the variation in size, shape, and colour of the ventral patch of Bornean and Sumatran Sun Bear (see Meijaard, 1996; 1999), but I found no consistent differences between them. Those results also did not indicate any significant differences between the Sumatran Sun Bear and those from the Asian mainland and the Malay Peninsula.

The results suggest that the research hypothesis has to be rejected, because 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. This could suggest that Bornean Sun Bears diverged from the other two geographic groups before these diverged from each other. An alternative explanation is that the Bornean environment is different from that in Sumatra, mainland Asia, and the Malay Peninsula, which could have resulted in the morphological differentiation of the Bornean form from the others.

At present there are insufficient data to explain the observed morphometric relationships within *U. malayanus*. Still, there is a good fossil record that may assist in this. For instance, we know that *malayanus* was present in Borneo (Medway 1964) and Sumatra (de Vos 1983) during the Late Pleistocene, and may have occurred there before that time (there are hardly any records of mammal fossils from Borneo and Sumatra that predate the Late Pleistocene), and that it arrived on Java some

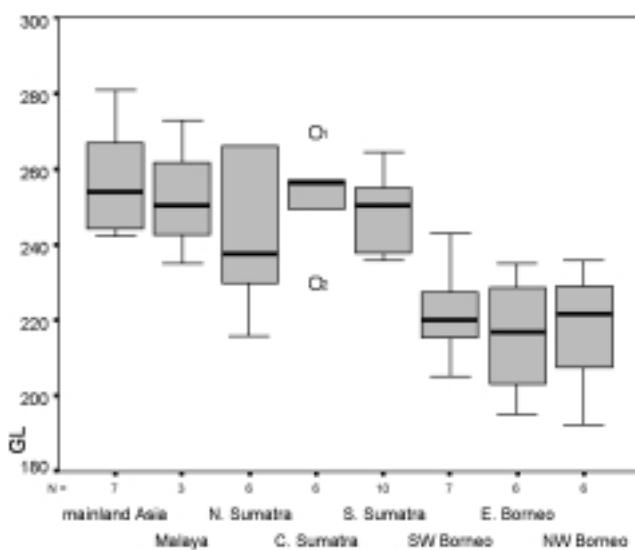


Fig. 5. Median, interquartile range, and outliers of the greatest skull length (both sexes combined) for 8 subregions of the Sun Bear distribution range.

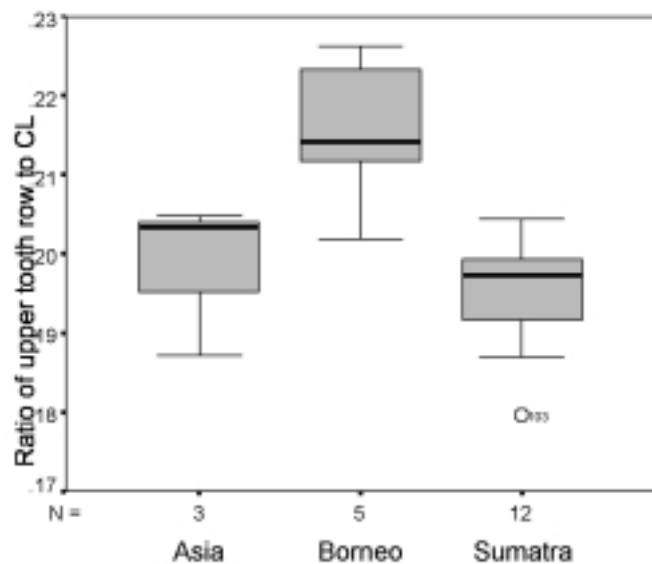


Fig. 6. Median, interquartile range, and outliers of the ratio between the length of the upper tooth row and the condylo-basal length of adult Bornean, Sumatran and mainland Asian Sun Bears (both sexes).

80–60 Kya, probably from Sumatra (as the Punung Fauna primarily consists of Sumatran rainforest species, see Meijaard, 2003). Because Sun Bears are relatively large, robust animals, the absence from Java—where a good fossil record exists dating back to 5 million years ago—of older fossils of *malayanus* suggests that the species did indeed not occur on Java before the late Middle Pleistocene; otherwise one would expect that fossil bones or teeth had been found somewhere. Long et al. (1996) claimed that Sun Bear fossils occurred in the Lang Trang Caves in Vietnam. The material was identified by de Vos & Long (1993), but there were only two *malayanus* specimens as opposed to the much more common *U. thibetanus* fossils (n=33). *Ursus malayanus* has not been reported from any of the other fossil sites of mainland SE Asia (e.g. Tougaard, 2001), whereas *U. 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 could suggest that *malayanus* used to be more common in the Sundaic Subregion, possibly because it was better adapted to the tropical forest of Sundaland than to the drier forest types of the Asian mainland. Also, on the Asian mainland, *malayanus* occurs sympatrically with the generally more common *thibetanus*, and the former may be competitively excluded by the latter, which may also explain why their fossils are rarely found together.

In conclusion, I tentatively suggest a Sundaic origin for *malayanus*, which according to molecular data split from its nearest relative *thibetanus* or possibly *U. arctos* (see Fitzgerald & Krausman, 2002) some time during the Pliocene. Between ca. 4.5 and 3.5 Mya, the Sundaic fauna may have been separated from the Indo-Chinese fauna by high sea-levels that for about 1 Myr physically separated the two faunas on either side of the Isthmus of Kra (Meijaard, 2003; Woodruff, 2003) (Fig. 8). I hypothesize that this provided the underlying mechanism for the divergence of *malayanus*

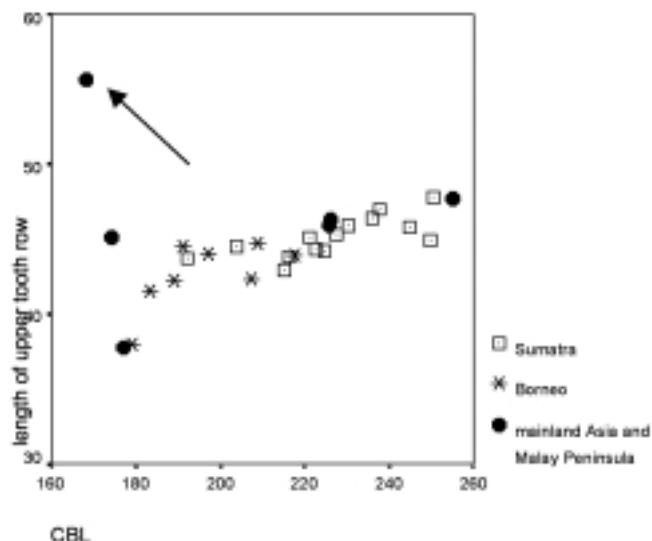


Fig. 7. Graph of the condylo-basal length vs. length of upper tooth row for adult Sun Bear specimens (n=28; the arrow indicates the aberrant point mentioned in the text).

from its mainland Asian relative. Figure 8 suggests that Sun Bears would then initially have evolved in the areas that are now Peninsular Malaysia and Borneo, and that there were no connections to Sumatra. Borneo split from the Malay Peninsula later in the Pliocene (Meijaard, 2003), and this could have been the time when the two morphological forms identified in this research diverged. The Malayan form could then have dispersed to Sumatra and the Asian mainland sometime during the Late Pliocene or Pleistocene.

The above is clearly not the full story. L. Waits (in litt., 23 October 1999) calculated a phylogenetic tree for Bornean and Sumatran Sun Bears based on 300 base pairs of mtDNA sequence data. She found that there were possibly five distinct clades that were discordant with the geography of the species, which could either suggest incomplete lineage sorting or that gene flow occurred between Sumatran and Bornean populations, possibly during the last glacial maximum. The possible mixing of lineages will make it even harder to unravel the evolutionary history of this species.

Finally, the craniometric patterns found in this paper indicate that Sun Bears can be divided into two groups: Borneo and Sumatra/Malaya/mainland Asia. This suggests that at least the Bornean subspecies is valid and its name, *euryspilus*, should be maintained. Heude (1901) named *annamiticus* based on three skulls from Annam which he claimed as distinct from the typical Sumatran form in the steeper slope of the muzzle and in some dental differences. Pocock (1941) stated that the slope of the muzzle is a very variable character, depending on the development of 'air cells' in the frontals; he also found no differences between the teeth of *annamiticus* and *malayanus*. Based on this, Pocock suggested that *annamiticus* should be considered as a race of *malayanus* (from Sumatra). This research has largely confirmed the overall similarity between skulls from Sumatra, the Malay Peninsula, and the Asian mainland (with the possible

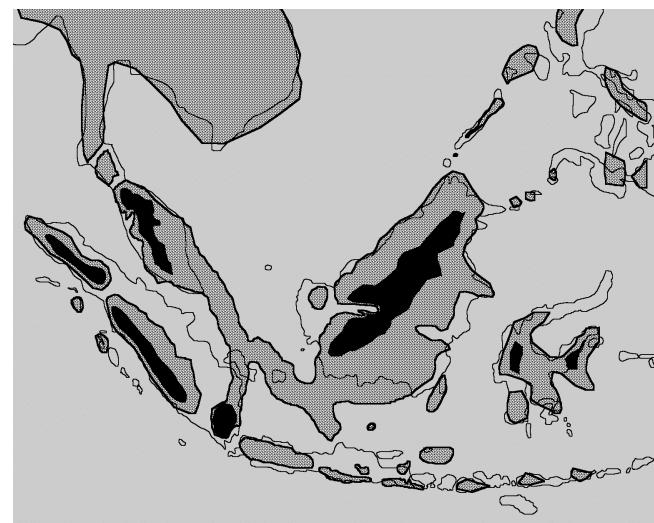


Fig. 8. Palaeoenvironmental reconstruction for the Early–Middle Pliocene highstand. The grey areas show the land area at this time in relation to the present-day shape of the region, black areas are uplands (after Meijaard, 2003).

exception of the specimen from upper Assam), and until further evidence becomes available I suggest to maintain the two subspecies; *U. m. malayanus* for Sumatra, the Malay Peninsula, and the Asian mainland, and *U. m. euryspilus* for Borneo.

The differences between two taxa from these islands demonstrated in this research have implications for conservation management. Insufficient information is presently available to assess whether the morphological and genetic differences between *U. m. malayanus* and *U. m. euryspilus* have also resulted in ecological and behavioural differentiation. Still, we should be cautious in applying ecological information from one taxon to the other, for instance in population and habitat viability assessments. In the light of this, I recommend different conservation strategies for these taxa, especially in ex situ breeding management.

COMPARATIVE MATERIAL

Below I present a list of all museum specimens with known localities used in this research:

Mainland Asia and Malaysia – 6 females, - BMNH 0204, Chin Hills, Burma, coll. "JMM". - BMNH 1860.5.4.67, Wellesley Prov., Malay Peninsula, coll. Capt. Boscawen, 1860. - BMNH 1898.5.19.1, Malacca, Malay Peninsula, coll. Zool. Soc., 1898. - BMNH 1915.12.1.9, Sai Yoke, Siam, coll. K.G. Gairdner, 1915. - BMNH 1926.10.4.77, Zuantri, Annam (=Luantan, Annam, Vietnam), coll. Delacour & Lowe, 4 Oct. 1926. - BMNH 1938.12.9.1, Garo Hills, upper Assam, India, coll. "H.W.W.", 1938; 3 males - BMNH 1927.12.1.98, Hué, Annam (=Vietnam), coll. Delacour & Lowe, 1927. - BMNH 3.2.6.90, Bukit Besar, Malay Peninsula, coll. H.C. Robinson & K. Annandale, 1903. - BMNH 91.11.26.2, Tonghoo, Burma, coll. E.W. Oates, 1891; 6 ex., - BMNH 79.11.21.198, India, coll. Dr. Martell, 1879. - BMNH 88.4.11.1, Cochin China (=Vietnam), coll. Boncard, 1888. - FMNH 31796, Laos, Lao Fu Chay, coll. Coolidge, 1929. - FMNH 53931, Malaysia, Perak. - Heude 1039, Type *H. annamiticus*. - MCZ 671, Pegu, Burma.

Borneo – 6 females, - MZB 2943, Z. O. Borneo. - MZB 6737, Borneo, Sampit, coll. J.J. Menken, 16 Jun. 1935. - RML 679, Balikpapan, , 19 May 1915. - RML 907, Balikpapan, , 9 May 1914. - ZRC.4.1242, Sarawak. - ZRC.4.1247, ? (Mal/Br. Borneo); 3 males, - BMNH 1908.7.17.14, British N. Borneo, 1908. - MZB 6739, Parit Tjempaga, Sampit, Borneo. - SM 0618/4, Ng. Tahalit, S. Mengiong, Balleh, Kapit; 11 ex., - BMNH 1856.9.27.10, Sarawak, coll. Wallace, 1856. - BMNH 1910.4.5.134, Karaginton, Martapoera, S. Borneo, coll. O. Thomas & G.C. Gairdner, 1910. - BMNH 1955.734, Sarawak, coll. H.C. Robinson, 1955. - RML 4879, Sampit, Borneo, coll. Westenenk, 13 Jul. 1929. - RML, no nr., Borneo. - SM 50.19; 50.120, 50.123, 50.125, 50.126, and 1 no number – all of presumed Sarawak origin.

Sumatra – 15 females, - BMNH 1938.11.30.70, Ranto Panjang, Acheen, Sumatra, coll. W.J. Frost, 3 Mar. 1938. -

MZB 3316, Lampung, Sumatra. - MZB 3317, Pedada Bay, Lampung, Sumatra. - MZB 6734, Palembang, Sumatra, coll. Soekarno, 30 Apr. 1933. - MZB 6735, Kotabumi, Lampung, Sumatra, 2 Feb. 1939. - RML 252, Pangkalan Benteng, 24 km from Palembang, Dec. 1941. - RML 4880, Boea, Padangsche Bovenlanden, Sumatra, coll. Dubois. - ZMA 1029, Sumatra, S. Silau, Asahan, Sum. E.coast. - ZMA 1030, Deli, Sumatra. - ZMA 9085, Palembang. - ZRC.4.1237, Gn. Tampin, Negri Sembilan. - ZRC.4.1238 and 4.1239, Siak, Sumatra. - ZRC.4.1240, Palembang, Sumatra. - ZRC.4.1245, Sumatra; 11 males, - BMNH 1938.11.30.69, Ranto Panjang, Acheen, Sumatra, coll. W.J. Frost, 3 Mar. 1938. - FMNH 14801, Sumatra, Telok Betong. - MZB 3318, G. Padjabadja, Z. O. Lampung, Sumatra. - MZB 6736, Palembang. - MZB 6741, Fort vd Capellen, Sumatra, west coast. - MZB 763, Fort vd Capellen, Sumatra, west coast. - RML 4878, Loeboek, G. Meraksa, Batang Ugan Oeloe, Palembang, coll. L. Coomans de Ruiter, 11 Jul. 1928. - RML coll Sody no. 1, Lampoengs, Z. Sumatra, coll. Giestings. - ZMA 1028, Telok Betung, Indonesia. - ZMA 1031, "Wisaran" Deli, Sumatra. - ZRC.4.1241, Palembang, Sumatra; 8 ex., - BMNH 1919.11.12.12, Sungai Kurubang, Sumatra, coll. H.C. Robinson & C.B. Kloss, 1919. - BMNH 1947.451, Sumatra, coll. E. Bernard, 1947. - BMNH 1947.452, Sumatra, coll. E. Bernard, 1947. - MZB 980, Bangka, Jambi, Sumatra. - RML 11976, Sumatra, coll. van Son. - RML 3320, Sumatra, coll. W. Groeneveldt, 3 Feb. 1938. - RML 3321, Sumatra, coll. W. Groeneveldt. - RML coll Sody no. 2, Perlak, Atjeh, N. Sumatra.

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