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# What Is a Tiger? Biogeography, Morphology, and Taxonomy

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The tiger is certainly one of the most easily recognizable cats, with its distinctive and unique striped coat. It is also commonly believed to be the biggest cat species alive today, although this claim is questionable. The tiger shows considerable variation in its size, coloration and markings, reflecting the variety of habitats it occupies throughout its very wide geographical distribution from the temperate oak forests of the north to the humid tropical forests on the Equator. Understanding this variation is a key to its successful current and future conservation, but we are still uncertain of its significance. By going back through the tiger's two-million-year fossil history, we hope to provide a better overview of how and why today's variable tiger has evolved.

The tiger has always had a considerable impact on human cultures, especially where people and tigers have lived together and still do co-exist. Its large size and consequent need for large prey have brought it into conflict with people by preying on them and their livestock,

but it has also earned our respect and admiration for its power and prowess as a killer. The desire to wear its coat, or to create medicine from its bones and other body parts, continues today, with increasing detrimental impact even on supposedly protected populations; and the power of the tiger as a brand to help sell products throughout the world has never been stronger. With increasing human pressure on the remaining fragmented tiger populations, there has never been a better time to answer the question ‘What is a tiger?’ However, research on understanding geographical variation in tigers, including how many subspecies or even species survive, has produced conflicting results, which potentially undermine conservation efforts in the wild and in captivity. By knowing the tiger better, we may be able to be more certain what conservation efforts should be directed where, in order to save it and the landscapes it inhabits for future generations to respect and admire.

## TIGER MORPHOLOGY

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Like most felids, the tiger retains the basic cat body plan, but it represents one of two species that have reached the maximum size for this body plan for living felids today. There is much popular debate as to whether tigers are bigger than lions, but resolution of this discussion is difficult owing to a lack of reliable data. Big game hunters have always been prone to exaggerate the size of their lions and tigers, regardless of how they measure or weigh them, such as ‘over the curves’ or ‘between the pegs.’ It is also difficult to verify many ‘old’ measurements and weights. Data collected by field researchers, and relatively well-documented hunting records, show that the modern wild-living tiger probably has an average body weight (i.e., the estimated body weight excluding the stomach contents) of c. 160 kg for the adult male and c.115 kg for the adult female; whilst that for the average wild-living adult male lion is c.175 kg and c.120 kg for the adult female. We define ‘average’ as the simple average of all customarily recognized subspecies or local populations. However, as intraspecific size variation appears to be greater in the tiger than in the lion, the biggest tiger ‘individuals’ may be bigger than the biggest lion ‘individuals.’ If we use skull size (e.g., greatest length of skull) as a surrogate of body size, it is again clear that the biggest lions and tigers are about the same size unless the skull to body size ratio differs between these species—it has been suggested that the tiger may have a proportionally smaller head than the lion [1]. It may be safe to suggest that, on average, the lion can be said to be the biggest living cat, and taking into account the extinct massive American lion, *Panthera (leo) atrox*, the lion may even be the biggest felid ever known [2].

There is also continuing popular discussion as to whether Amur or Bengal tigers are bigger, but the biggest wild tiger ‘individual’ on record is a male Bengal tiger shot in 1967 in northern India [3], although this record needs to be verified. Although there are many claims of big wild Amur tiger individuals [4], it is impossible to verify these claims. It may be worth mentioning that the largest wild Amur tiger measured by V.G. Yudin was a 6-year-old male weighing 225 kg ( $n = 40$ , although it is not specified how many of these are adults [5]). On the other hand, from a sample of 15 adult and subadult male tigers captured in the Royal Chitwan National Park, Nepal, the heaviest tiger weighed 261 kg [6]. In both cases, it is unclear whether the individuals had full stomachs, which is crucial, especially for the Nepalese study, because of the capture technique they used. Therefore, the body weight of

the heaviest Nepalese male [6] could have been as low as c. 218 kg. The heaviest lion from a sample captured in the Kruger National Park, South Africa, had a body weight (standardized for stomach contents) of 225 kg ( $n = 41$  adult males [7]). Another sample recorded a male weighing 260 kg ( $n = 16$  males of  $>4$  years old [8]), although the body weight was not apparently standardized for stomach contents.

Despite a superficial similarity in skeletal morphology, there are interesting differences that may reflect the differing ecologies of these two big cats. Lion skulls are flatter and more concave in profile, perhaps reflecting the need to be able to stalk in open habitats and minimize their appearance to potential prey. The tiger's skull is more convex in profile, the posterior ends of the nasals extend further back than the posterior ends of the maxillae, and the mandible has a flat to concave ventral surface, so that it does not rock back and forth like that of the lion when put on a flat surface. A most surprising difference is in cranial volume [9]. Tiger skulls have relatively much larger cranial volumes, and hence presumably brain volumes, than those of lions (Table 4.1) [see reference 133]. For example, tiny adult Balinese tiger skulls have slightly larger cranial volumes than those of very much bigger lions from Kruger National Park, South Africa, despite the lions having skulls c. 20–30% longer than those of the Balinese tigers (Table 4.1). The lion's cranial volume: greatest skull length ratio is similar to that of its most closely related congeners, the jaguar, *P. onca*, and the leopard, *P. pardus*, whereas the tiger's is more than 22% greater (Table 4.1). Other authors have presented similar

**TABLE 4.1** Cranial volume, greatest length of skull, and their ratio of some tiger subspecies (Mean  $\pm$  Standard Error)

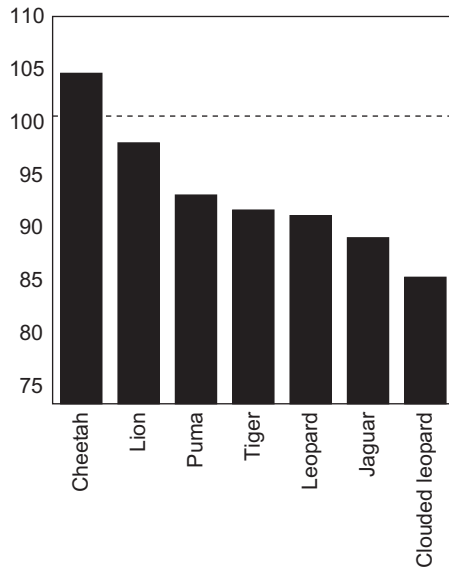
Species/subspecies		Greatest length of skull (sample size)	Cranial volume (sample size)
Bali	Male	296 $\pm$ 1.5 mm ( $n = 2$ )	296 $\pm$ 5.6 cm <sup>3</sup> ( $n = 2$ )
	Female	262 $\pm$ 2.0 mm ( $n = 6$ )	263 $\pm$ 6.6 cm <sup>3</sup> ( $n = 5$ )
India	Male	351 $\pm$ 2.5 mm ( $n = 37$ )	307 $\pm$ 4.4 cm <sup>3</sup> ( $n = 32$ )
	Female	293 $\pm$ 2.4 mm ( $n = 23$ )	264 $\pm$ 5.0 cm <sup>3</sup> ( $n = 18$ )
Kruger lion	Male	380 $\pm$ 3.9 mm ( $n = 15$ )	271 $\pm$ 7.1 cm <sup>3</sup> ( $n = 8$ )
	Female	314 $\pm$ 3.2 mm ( $n = 14$ )	228 $\pm$ 5.4 cm <sup>3</sup> ( $n = 6$ )
Cranial volume (cm <sup>3</sup> )/greatest length of skull (mm)			
Lion		0.75 $\pm$ 0.004 ( $n = 312$ )	
Jaguar		0.72 $\pm$ 0.012 ( $n = 22$ )	
Leopard		0.70 $\pm$ 0.008 ( $n = 36$ )	
Tiger		0.92 $\pm$ 0.005 ( $n = 193$ )	

Only adult specimens are included in the analyses.

Tigers from Bali Island are referred to as 'Bali,' and those from India and Nepal as 'India.'

Lions from the Kruger region, South Africa are referred to as 'Kruger lion.'

Source: Yamaguchi et al. 2009 [133]



**FIGURE 4.1** The brachial index (radius/humerus  $\times$  100) of big cats [15]. Cats with a higher index are usually more cursorial, but the lion is an exception, while the tiger is a typical forest cat.

data without comment [10–13]. It is unclear why this should be so and it may just reflect a phylogenetic difference.

Comparing limb bone lengths, it was found that the radius was significantly longer in the lion (about the same length as the humerus) compared with that of the tiger ( $<90\%$  humerus length), but both cats had forelimbs of overall similar length (Fig. 4.1) [14, 15]. The hind limb proportions of both lion and tiger are similar, but the relatively shorter forelimbs of the tiger compared with those of the lion suggest that the tiger is better at jumping and leaping. Therefore, the lion’s forelimb length is more than a mean of 90% of its hind limb length, whereas the tiger’s forelimb is only a mean of 86.5% of the hind limb length. However, overall the limb lengths and proportions of lion and tiger are very similar and typical for forest-dwelling cats.

### Fossil History

Molecular evidence suggests that the genus *Panthera* has its roots more than six million years ago [16–18] and, based on a cladistical analysis [19], it was proposed that the radiation of the genus *Panthera* occurred in eastern Asia, although there is fossil evidence suggesting a possible African origin for both the lion and leopard [20].

The fossil record of the tiger stretches back about two million years to the end of the Pliocene and beginning of the Pleistocene (Table 4.2). It has been estimated that the tiger evolved about 2.2 million years ago (MYA) based on a cladistical analysis [21], although molecular data from Johnson and colleagues in 2006 suggest a divergence of the tiger from other *Panthera* about 2.9–3.7 million years ago [18]. The earliest known tiger was *Panthera tigris palaeosinensis* from Anyan, Honan Province in northern China, which was about two million years old [22–25]. This tiger is believed to have survived in Japan until the late Pleistocene

TABLE 4.2 The fossil history of tigers

Geological epoch	Estimated age (MYA)	Locality	Synonym	References
late Pliocene/early Pleistocene	c.2	China, Honan, Anyan	<i>Felis palaeosinensis</i>	22, 23, 104
late Pliocene/early Pleistocene	1.3–2.1	Java, Gunung Butak (Jetis Beds)		20, 24, 32
early Pleistocene		China, Szechuan, Wanh sien		38, 106
middle to late Pleistocene	0.7–1.3	Java, Kendeng	<i>Felis groeneveldtii</i>	30
	1.0–1.2	Java, Ci Saat	?	107
	c. 1.0–1.2	Java, Kali Glagh complex	<i>Felis</i> sp. I	84
	0.7–1.3	Java, Trinil	<i>Felis trinilensis</i> <i>Feliopsis palaeojavanica</i> <i>Felis tigris soloensis</i>	30, 31, 105
	0.7–0.8	Java, Kedung Brubus	<i>Felis oxygnatha</i>	30, 107
middle Pleistocene		Java, Bangle		30, 31, 105
middle Pleistocene		Java, Jeruk		30, 31, 105
middle Pleistocene		Java, Kebon Duren		30, 31, 105
middle Pleistocene		Java, Teguan		30, 31, 105
	0.78	Sumatra, Padang Highlands		31, 108
	0.67–2.0	China, Yunnan, Yuanmou Basin		109
	0.8	China, Hubei, Yuanxian, Xuatangliangzi	<i>Panthera tigris</i>	110
	0.4–0.6	China, Choukoutien, Locality 1	<i>Felis acutidens</i> <i>Felis youngi</i> <i>Felis</i> cf. <i>tigris</i>	36, 84, 111, 112, 113, 114
	0.35	China, Jiangsu, Tangshan, Huludong	<i>Panthera tigris</i>	110
middle Pleistocene		China, West Hupei, Chinkiang		115
		China, Yunnan, Fuminhsien		116
		China, Kwangsi, Kweilin		117
	1.15–1.2	China, Shaanxi, Lantian, Gongwangling	<i>Felis</i> cf. <i>tigris</i>	110, 114, 118, 119
	0.65–0.8	China, Shaanxi, Lantian, Chenjiawo	<i>Felis</i> cf. <i>tigris</i>	110, 114, 119
middle to late Pleistocene	0.24	China, North Anhwei, Shihhung		114, 120
	0.06–0.12	Java, Sangiran, Punung	<i>Felis tigris soloensis</i>	20, 24, 32, 105, 107
late Pleistocene	0.027–0.053	Java, Ngangdong	<i>Felis soloensis</i>	31, 108
	0.03	China, Choukoutien		84

(Continued)

TABLE 4.2 (Continued)

Geological epoch	Estimated age (MYA)	Locality	Synonym	References
late Pleistocene		China, Inner Mongolia, Salawasu region		84
late Pleistocene		China, Heilongjiang		84
late Pleistocene		China, Jilin		84
late Pleistocene		China, Liaoning		84
late Pleistocene		China, Shandong		121
late Pleistocene		China, Harbin		37, 122
late Pleistocene		Japan, Mikkabi, Kuzuu, Tadaki		23
late Pleistocene		Japan, Yamaguti, Akiyoshi		123
late Pleistocene		Japan, Yamaguchi, Isa	<i>Felis youngi</i>	124
late Pleistocene		Japan, Gansuiji		125
late Pleistocene		Russia, Siberia, Bolschoj Lyachow I.; River Jana Basin		126
late Pleistocene		Russia, Altai, Tscharyisch River		34
late Pleistocene		Caucasus		127
late Pleistocene		Russia, East Beringia		27
late Pleistocene		India, Karnul Caves		35
late Pleistocene	0.0165	Sri Lanka, Kuruwita, Batadomba Cave		85
late Pleistocene		Sri Lanka, Ratnapura		85
Holocene	0.0138	Malaysia, Sarawak, Niah Caves		53
late Pleistocene	0.012	Philippines, Palawan, Ille Cave		54
Holocene		Java, Sampung		84
Holocene	0.003–0.0105	Malaysia, Sabah, Madai Cave		52

[22]. It was small, its skull being intermediate in size between that of a male Indian leopard and a female Sumatran tiger. Therefore, it is possible that *P.t. palaeosinensis* may not be a tiger at all and could be an ancestral big cat, which later gave rise to tigers, lions, leopards, and jaguars. A careful analysis of this putative tiger is long overdue [26]. Although as a consequence northern China is regarded as the evolutionary center of the tiger [19, 24, 27–29], this restricted center of origin is not necessary and fossil tigers from the Jetis Beds of Java are thought to be almost as old, ranging from 1.66 to 1.81 million years old [30–33]. This suggests a wide distribution of the ancestral tiger in eastern Asia by the beginning of the Pleistocene.

Charting the fossil history of the tiger is fraught with difficulty, owing to the fragmentary nature of most of the remains, possible confusion with other big cats, uncertainties

over dating the contexts in which the fossils have been found, and possible taphonomic and geographical biases resulting from differences in excavation effort. However, fossil remains from China and Java dominate the evolutionary story thereafter. Many tiger fossils are known from the early middle to the late Pleistocene of China, Java, and Sumatra and many have been given chrono-subspecies status depending on their finding locality. However, tiger fossils have only been recorded since the end of the Pleistocene in India and the Altai of Russia [20, 24, 30–32, 34–38]. Herrington [27] also apparently recorded tiger skulls from eastern Beringia, but none have been found so far in North America to the south of the former Laurentide ice sheet that dominated the last glaciation. However, biogeographical analyses [39] suggest that Beringian tigers are unlikely and the identification of these specimens has been confirmed as that of lions from ancient DNA (see reference 83).

Groves [25] has summarized an evolutionary scheme for the tiger, although this may not be accurate any more, owing to advances in dating. Following *P.t. palaeosinensis* the jaw deepened posteriorly and the premolars and molars became narrow and high crowned to give rise to *P.t. oxygnatha* from Sangiran in Sumatra and Kedung Brubus in Java, which has been dated to about 1.66 million years old. The Trinil tiger *P.t. trinilensis* also from Java about 700,000 to 1.3 million years ago had a broader fourth lower premolar ( $P_4$ ) and the first lower molar ( $M_1$ ) was longer than  $P_4$ . *P.t. soloensis* from Punung and Ngangdong in Java was much larger, about the size of today's Bengal and Amur tigers, had an even longer  $M_1$ , which was broad, and a narrow  $P_4$ . It also had the typical narrow occiput of Javan tigers [32, 40] although it should be noted that this character occurs also in other putative tiger subspecies [26].

On the mainland a small primitive tiger, *P.t. acutidens*, with a long  $M_1$  equivalent to that of *P.t. trinilensis*, survived until 230,000–460,000 years ago at Zhoukoudian in China. This form increased dramatically in size and was found widely in Asia from Wanxien to Lyakhov Island and the Jana River, and has been dated to 65,000–80,000 years ago (although the origin of tigers at the latter two sites may have an alternative explanation; see below). In summary, Groves [25] suggested that tigers spread south into Java from two million years ago, where they changed and spread back into northern China, where they replaced the ancestral form. These tigers underwent more change before spreading southwards again 100,000 years ago to replace the old Javanese tigers. There is no evidence of multiregional differentiation of tigers, but a combination of local change, spread, and replacement, resulting in a very complex fossil history. During and since the Pleistocene tigers have evolved a smaller body [38] in common with many Pleistocene mammals [41, 42], which was probably caused by a reduction in seasonal productivity so that animals were unable to achieve their full growth potential [43, 44].

Tigers could and should be recorded from Borneo. The lowering of sea levels during glaciations revealed the Sunda shelf, which would have allowed free access to large mobile mammals like tigers. However, the evidence for Bornean tigers has been much debated, but includes skulls, teeth, skins, wall paintings and even a photograph of a live animal [45–51]. The Bisaya tribe hand down tiger canine teeth as a tradition going back 4–7 generations, which suggests that the tiger may have survived on Borneo until about 200 years ago [47]. Confirmation of the former presence of the tiger in Borneo has come from archaeological evidence from Niah Cave, Sarawak, including the crown of an upper canine from a young tiger dating from the Neolithic or more recently, and a fourth metacarpal from an adult female dating to about 13,745 years ago [49, 52, 53]. A navicular bone was also apparently recorded Madai Cave, Sabah, which could date from between 10,500 and 3,000 years ago [53]. It is



unclear why tigers are now extinct on Borneo. In 2008 Piper and colleagues reported on two phalangeal bones from a tiger which were found in a human-derived bone assemblage dating from about 12,000 years b.p. in Ille Cave, Northern Palawan in the Philippines [54], thus confirming the presence of the tiger on all larger islands west of Wallace’s Line.

Subspecies Taxonomy

For many years the consensus on the number of tiger subspecies was founded on the work of Mazák [28, 29] who recognized eight subspecies (Table 4.3). However, many specific and subspecific names have been proposed for tigers [29, 55], the most recent of which (see Luo *et al.*, Chapter 3), *Panthera tigris jacksoni*, is probably invalid (i.e., a *nomen nudum*, as no holotype was designated) [40, 56]. There is a common misperception that subspecies are based on sound scientific principles, but most of Mazák’s [28, 29] eight subspecies are based on a single specimen or a handful at most from their original descriptions. For example, Temminck [57] recognized two new tiger species, the Amur *Felis altaica* and the Javan *Felis sondaica*, on the basis of two specimens, for which the diagnostic character was the difference in the length of their fur. By the middle of the nineteenth century, four of the eight widely recognized subspecies had been described scientifically based on perhaps only three specimens (Table 4.3). Three further subspecies were described in the early twentieth century based on eight specimens, but the last of Mazák’s subspecies, which he described himself, was based on 25 specimens, which were compared with specimens of other putative tiger subspecies [58]. In the previous volume of this book published 20 years ago, Hemmer [24] questioned the need to draw clear geographical boundaries between tiger ‘subspecies’ as if they are static building blocks. We have started to understand that distinguishing between two or more tiger populations is possible, but whether they are biologically meaningful subspecies is much more difficult to ascertain (and would also be dependent on definitions of species and subspecies). Unfortunately, the traditional taxonomy of tigers appears to have focused on the former and paid relatively little attention to the latter.

TABLE 4.3 The eight classical subspecies of tigers\*

Common name	Subspecies	Authority	Number of specimens in type description	References
Bengal tiger	<i>Panthera tigris tigris</i>	(Linnaeus, 1758)	0	128
Caspian tiger	<i>Panthera tigris virgata</i>	(Illiger, 1815)	?1	129
Amur tiger	<i>Panthera tigris altaica</i>	(Temminck, 1844)	1	57
Javan tiger	<i>Panthera tigris sondaica</i>	(Temminck, 1844)	1	57
South Chinese tiger	<i>Panthera tigris amoyensis</i>	Hilzheimer, 1905	5	130
Balinese tiger	<i>Panthera tigris balica</i>	Schwarz, 1912	1	131
Sumatran tiger	<i>Panthera tigris sumatrae</i>	Pocock, 1929	2	46
Indochinese tiger	<i>Panthera tigris corbetti</i>	Mazák, 1968	25	58

\*See Refs 26, 28, 29.

## Geographical Variation in Tigers: Morphology

The characters used to diagnose each subspecies are also poorly defined, but include body size, fur length, coloration, striping (and spotting) pattern, and some skull characters, including the shape of the occipital region of the skull [26, 28, 29, 31, 46, 59]. However, other authors have also noted the wide variation in size, and pelage coloration and markings within putative subspecies [26, 31, 46, 60, 61–63], although Hooijer [38] suggested that most variation was clinal.

Therefore, the scientific basis for tiger subspecies is poor, being based on limited numbers of specimens, from which holotypes were selected, with no statistical evaluation of variation within and between putative subspecies. However, some authors have attempted to elucidate the geographical variation in tigers using statistical analyses of morphological and molecular data. For example, Herrington [27] carried out a multivariate statistical analysis of skull morphometrics to show that there were apparently distinctive differences between the skulls of six putative subspecies (the five extant ones and the Javan tiger) and also eight animals of unknown captive-origin. However, Herrington [27] first identified skull characteristics that seemed to distinguish those subspecies, and then she carried out the statistical tests on the basis of those characters. Therefore, it may not be possible to avoid considering her argument and subsequent analyses as being rather circular. However, there was some overlap in skull shape and size between Bengal and Indochinese tigers, and between Indochinese and Sumatran tigers, which was suggestive of clinal variation. In contrast, Chinese tigers were suggested to have very distinctive skulls, which were regarded as indicative of their putative ancestral status [27]. However, the results of Herrington's [27] study should be treated with caution, because sample sizes were often very small for each subspecies, and it is not clear whether samples were controlled for sex, age, and size (to examine shape variation).

Kitchener [26] carried out a preliminary analysis of geographical variation in tigers in order to examine the degree of variation between and within putative subspecies, in order to determine whether variation was clinal or discrete, or some combination of these [64–66]. Like Herrington's [27] study, some of the sample sizes were too small for some subspecies, so that his results should also be treated with caution. However, Kitchener's [26] analyses offer the first systematic approach to examining geographical variation in tigers. Below is a brief summary of his major findings.

### **Body Size**

It is well known that there is considerable variation in body size in tigers from large animals in the Russian Far East to small animals on the Sunda Islands [28, 29, 38]. However, this is not a simple cline, because tigers of equal or even greater body size are recorded from northern India and neighboring countries. On the other hand, casual examination of Mazák's [28] data shows that while female tigers, especially on the mainland, do not vary much in size, there is much variation in size between males of different putative subspecies. This would appear to suggest that sexual size dimorphism increases with increasing body size in male tigers. Kitchener [26] used greatest length of skull and upper carnassial ( $Pm^4$ ) length as surrogates for measures of body size. He found that for males, greatest length of skull increased with latitude, but carnassial length increased much more slowly. As expected, there were two peaks in the data at about 28°N (northern India, Nepal) and at about 45°N in

the Russian Far East (Fig. 4.2). However, within each putative subspecies there is considerable variation in size. Therefore, even though overall there was a significant difference in greatest skull length between putative subspecies, this was mostly not between neighboring subspecies, except between Balinese and Javan, and between Bengal, Chinese, and Amur, but it should be noted that for some of these subspecies, sample sizes were very small. There was no significant difference in male upper carnassial length between neighboring subspecies, suggesting that this varied clinally too (Fig. 4.3). Similar latitudinal variations in skull length are known in pumas [67].

Female greatest skull length showed less variation with latitude and upper carnassial length varied little between putative mainland subspecies (Figs 4.4 and 4.5). There was no significant difference in median greatest skull length between neighboring putative subspecies except between Javan and Balinese tigers, but sample sizes were very small for these. There was also no significant difference in female median upper carnassial lengths between neighboring subspecies. The female Sunda Island tigers did have significantly smaller upper carnassials than those of mainland animals. As expected from previous observations, sexual size dimorphism in greatest skull length did increase with latitude (Fig. 4.6), suggesting less overlap in prey size between the sexes at increasing latitudes or more competition between males for access to females in oestrus.

Coloration and Markings

The ground coloration of tigers varies from pale yellow to dark red [28, 29, 31, 46], which appears to reflect Gloger’s Rule [68], whereby darker tigers are found in humid tropical forests, whereas paler pelages are found in less humid temperate forests and grasslands. However, variation within populations may be considerable and may vary with season.

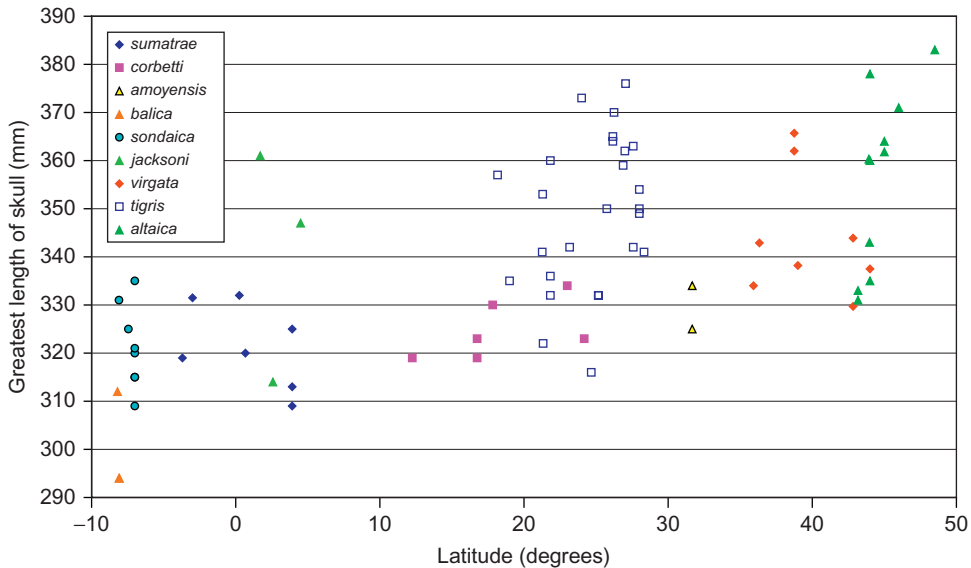
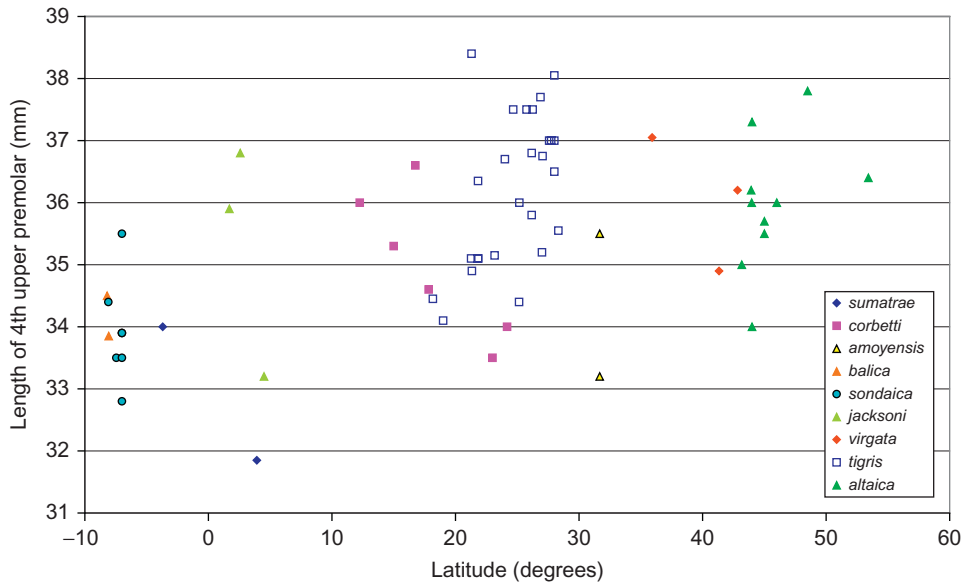
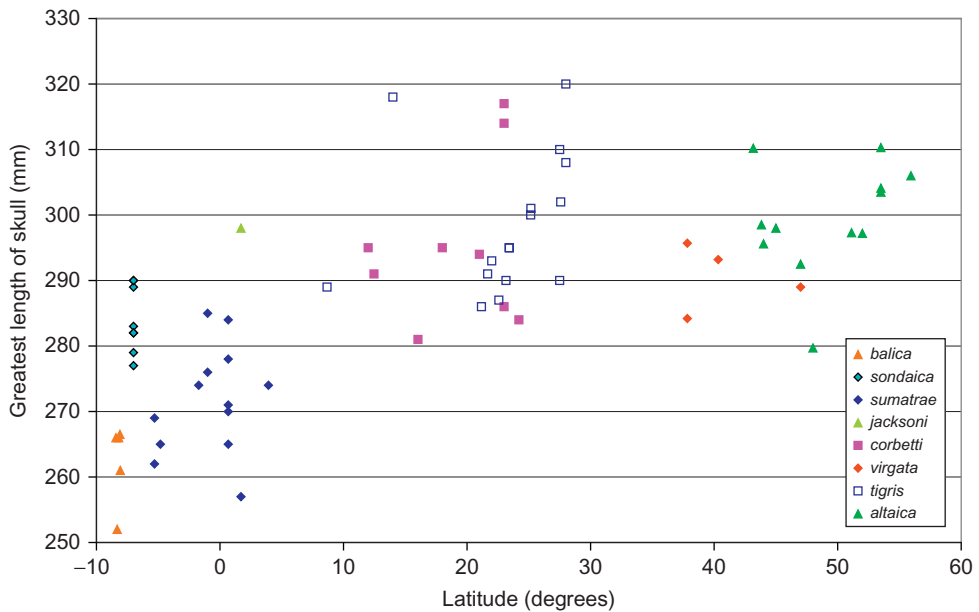


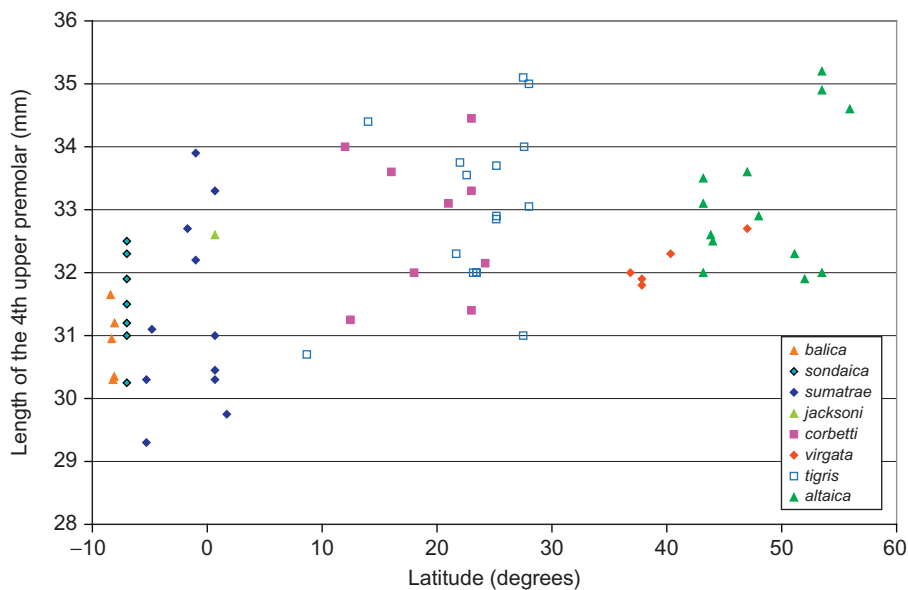
FIGURE 4.2 The relationship between greatest length of skull (mm) and latitude (°) in male tigers [26, 27, 132].



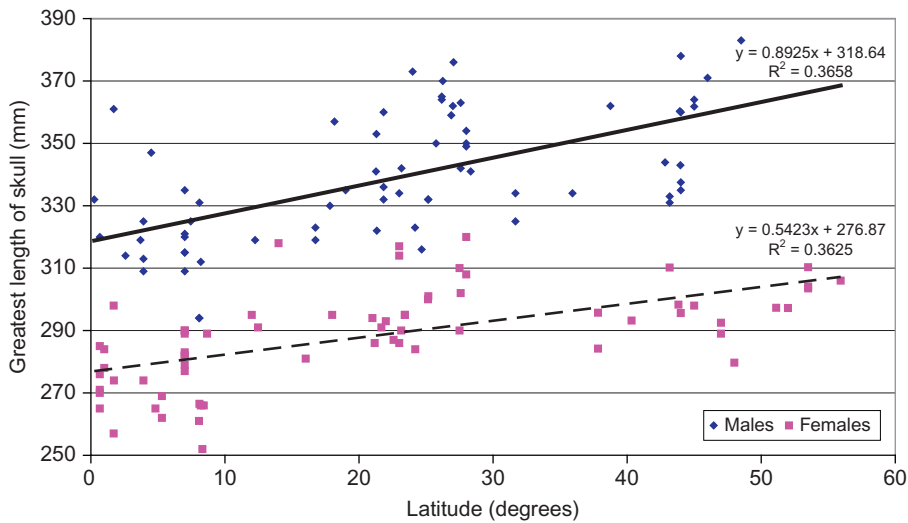
**FIGURE 4.3** The relationship between upper carnassial length (mm) and latitude ( $^{\circ}$ ) in male tigers [26, 29, 132].



**FIGURE 4.4** The relationship between greatest length of skull (mm) and latitude ( $^{\circ}$ ) in female tigers [26, 29, 132].

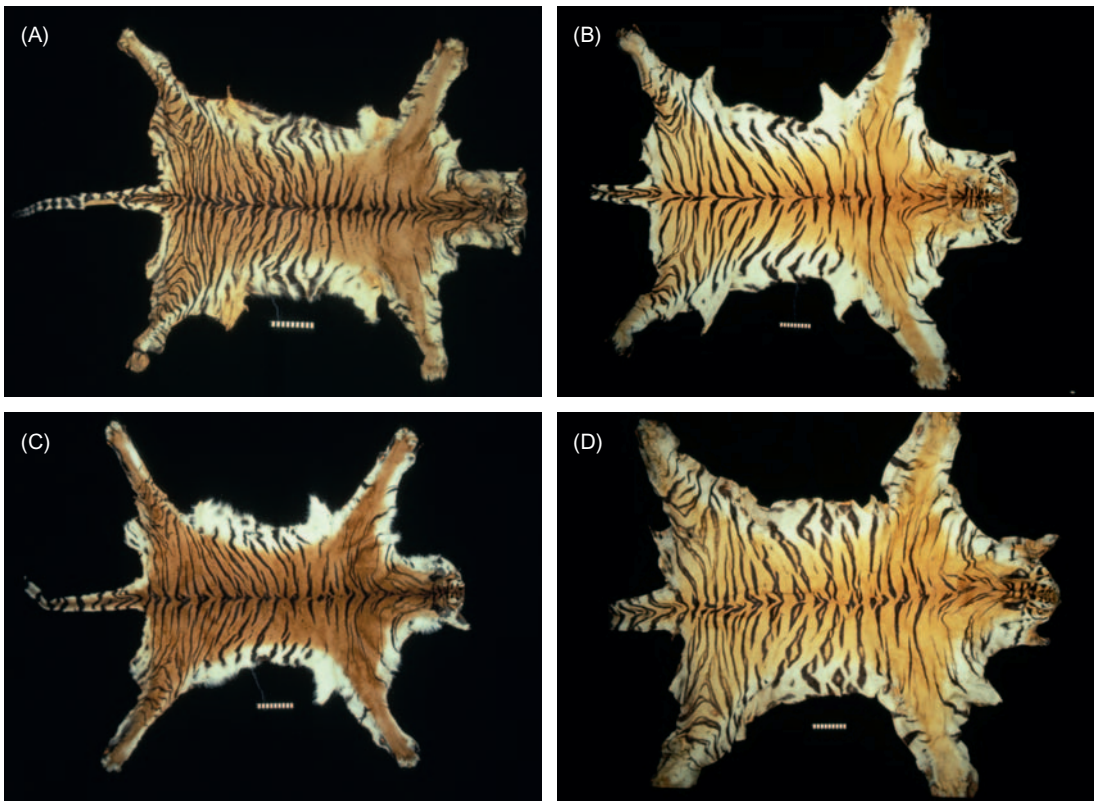


**FIGURE 4.5** The relationship between upper carnassial length (mm) and latitude (°) in female tigers [26, 29, 132].



**FIGURE 4.6** Sexual dimorphism in greatest length of skull (mm) in tigers with latitude (°) [26, 29, 132].

Mazák [69] reported a female Amur tiger with pelage coloration similar to that of a Sunda Island tiger, and other authors have noted that both Amur and Bengal tigers have widely varying pelage colorations [31, 46, 62]. Amur tigers tend to have darker fur when they molt into their shorter summer coat, and paler fur after the winter molt. However, it should also be borne in mind that the ground coloration of tigers will rapidly bleach in natural sunlight,



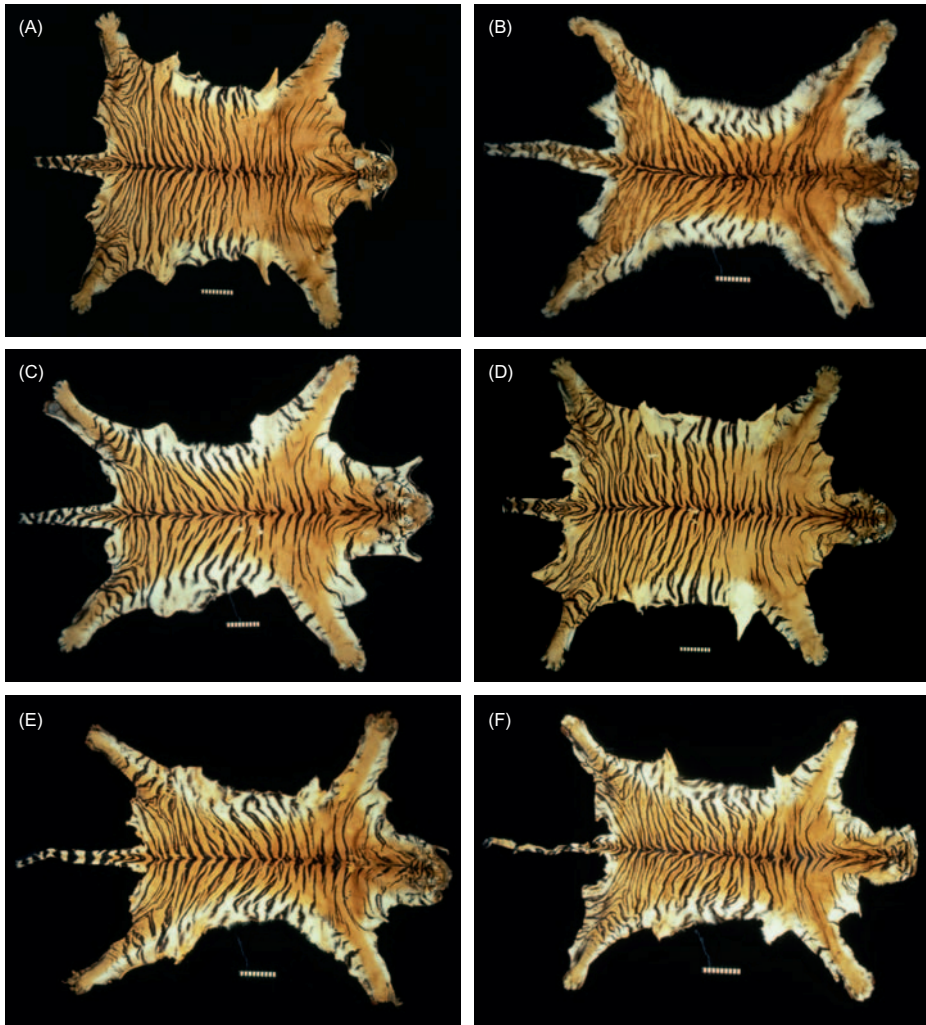
**FIGURE 4.7** Variation in coloration and markings of tiger pelages [26]. (A) Sumatra (BMNH 35.4.6.2), pelage score = 10; (B) India (BMNH 1983.307), pelage score 6–7; (C) Malaya (BMNH 37.1.2.1), pelage score = 10.5; (D) Bangladesh (BMNH 1882.12.10.1), pelage score = 7–8. (Photos © The Natural History Museum.)

so that openness of habitat, and latitude (and hence exposure to daylight hours in summer) may affect seasonal variation in ground coloration in individual tigers. For example, stripe coloration may be bleached from black to brown by exposure to sunlight [26].

It has been suggested that the striping pattern may also be diagnostic for some tiger subspecies. For example, Mazák [28] distinguished Sunda Island tigers from mainland tigers on the basis of a higher frequency of stripes, which tend to end in a line of spots (Fig. 4.7). Sumatran tigers are said to have thicker stripes than those of Javan and Balinese tigers, and Amur tigers are supposed to have thicker stripes than those of Bengal tigers [29, 31, 46, 70]. However, Heptner and Sludskii [63] showed that stripe thickness, pattern, and ground coloration varied considerably in both Amur and Caspian tigers.

Kitchener [26] used a simple character analysis to score the pelages of the different putative tiger species. Among the seven characters scored were the presence/absence of spots, thickness of stripes, stripe pattern on base of tail, frequency of striping on forequarters, presence/absence of loops within flank stripes, and darkness/lightness of ground coloration. Kitchener [26] found that there was much greater variation in total character scores for each





**FIGURE 4.8** The striping pattern of typical Sunda Island tigers is also found in other putative subspecies [26]. (A) Bali (BMNH 37.12.1.2), pelage score = 8.5; (B) Afghanistan (BMNH 1886.10.15.1), pelage score = 11; (C) India (BMNH 32.3.2.1), pelage score = 9–10; (D) Java (BMNH 37.12.1.1), pelage score = 9; (E) Annam (BMNH 33.4.1.204), pelage score = 8; (F) Sumatra (BMNH 35.4.6.3), pelage score = 9. (Photos © The Natural History Museum.)

pelage within subspecies than between them. Overall Sunda Island tigers tended to have darker well-striped pelages, whereas Bengal tigers had more variable and less well-striped pelages. The apparently diagnostic pelage characters identified by Mazák [28, 29] for Sunda Island tigers could also be found in Caspian, Indian, and Indochinese tigers (Fig. 4.8). There were no significant differences between median total pelage scores between putative tiger subspecies, although sample sizes were very low.

Kitchener [26] also scored the number of flank stripes on each pelage and found that, although there was a significant difference between median stripe frequency between putative

subspecies, this was not between neighboring ones, except between Javan and Balinese, which had very small sample sizes. Overall, there appeared to be a clinal variation in stripe frequency, which increased from north to south.

### **Skull Characters**

Several skull characters have been proposed to distinguish between tiger subspecies, including degree of development of the sagittal crest, dorsal convexity of the skull, and shape of the nasal bones and the occiput [24, 29, 46, 71]. Indeed, Hemmer [24] claimed to be able to identify the skulls of tigers to subspecies based on their skull characters.

There do appear to be some characters that distinguish skulls of some tiger ‘subspecies’ from each other. Adult male skulls of Amur and Caspian tigers possess very well developed sagittal crests, which are almost non-existent in any other subspecies. Caspian tigers often lack both upper 1st molars ( $M^1$ ) completely, including their alveoli, in almost complete contrast to all other putative subspecies. Javan and Balinese tigers often either lack one (or both) upper 2nd premolars ( $Pm^2$ ), or possess very small  $Pm^2$ s. This character occurs only rarely in the other subspecies. Most Sumatran tigers possess small round processes around the narrowest point between the orbits. This character occurs in some other subspecies (although not commonly), but is rare in both Javan and Balinese tigers. Male Bengal and Indochinese tiger skulls possess sagittal crests, which show a distinctive concave dorsal profile. Although some of these are useful in determining possible geographical origins of a skull, none occurs uniquely in any putative subspecies. Occipital shape, in particular, has been proposed as the main diagnostic character. In Javan and Balinese tigers it is said to be characteristically narrow, but in Caspian tigers it is said to be broad [26, 31, 40, 46, 59]. However, narrow occiputs have also been observed in Bengal and Indochinese tigers, so that their shape is not diagnostically distinct for the Javan tiger as claimed by Mazák and Groves (Fig. 4.9) [40].

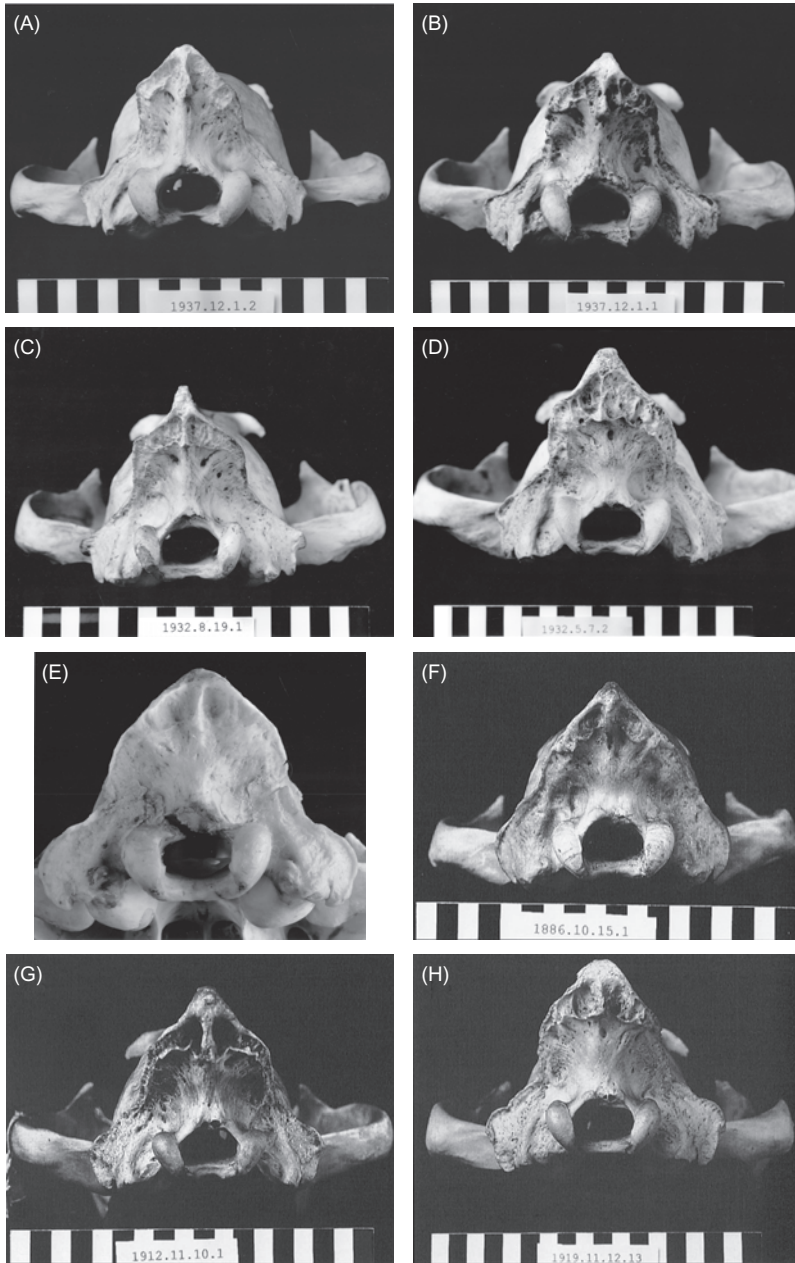
Kitchener [26] measured occipital height and width for skulls of all putative tiger subspecies and found that the occiputs of Javan tigers are no narrower than those of many Indian tigers when skull size is taken into account (Figs 4.10 and 4.11). Caspian and Amur tigers do indeed appear to have broader occiputs, perhaps indicating a close relationship, but this character was less able to differentiate between female tigers of different subspecies.

### **Why Do Tigers Vary in Size?**

Kitchener [26] reviewed the possible factors that may influence geographical variation in the body size of tigers. These included the following:

- **Bergmann’s Rule** [43]: Body size increases with latitude and hence decreasing temperature so that body surface area to volume ratios fall, and therefore in northern latitudes bigger tigers would lose less heat and need relatively less energy than smaller tigers.
- **Guthrie’s or Geist’s Rule** [41, 43]: Body size increases with increasing latitude, owing to an increase in the duration and amplitude of the seasonal productivity peak. In other words, when mammals are growing during the spring and summer, there is more food available so that they reach more of their growth potential. At very high latitudes, seasonal productivity falls and a reduction in body size would be expected, but tigers do not range so far north that this happens.





**FIGURE 4.9** Variation in occipital shape in tiger skulls [26]. The typical narrow occiput in Balinese (A: BMNH 37.12.1.2) and Javan (B: BMNH 37.12.1.1) tiger skulls occurs also in skulls from other populations, including Burma (C: BMNH 32.8.19.1) and India (D: BMNH 32.5.7.2). Other mainland tiger skulls show a variety of occipital shapes; Amur (E: NMS.Z. 1989.70.12), Caspian (F: BMNH 1886.10.15.1), Sumatran (G: BMNH 1912.11.10.1), and Sumatran (H: BMNH 1911.12.13). (Photos © National Museums Scotland (E) and Natural History Museum (rest).)

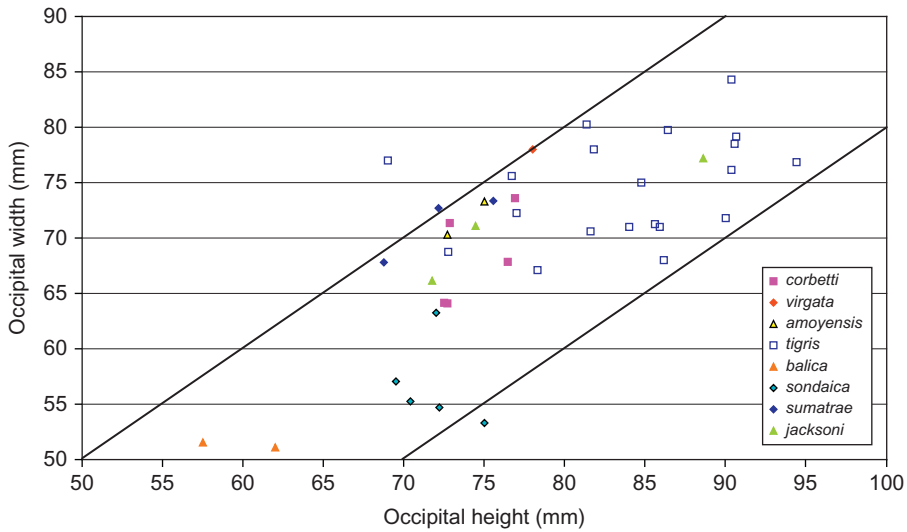


FIGURE 4.10 The relationship between occipital height (mm) and occipital width (mm) in male tigers [26].

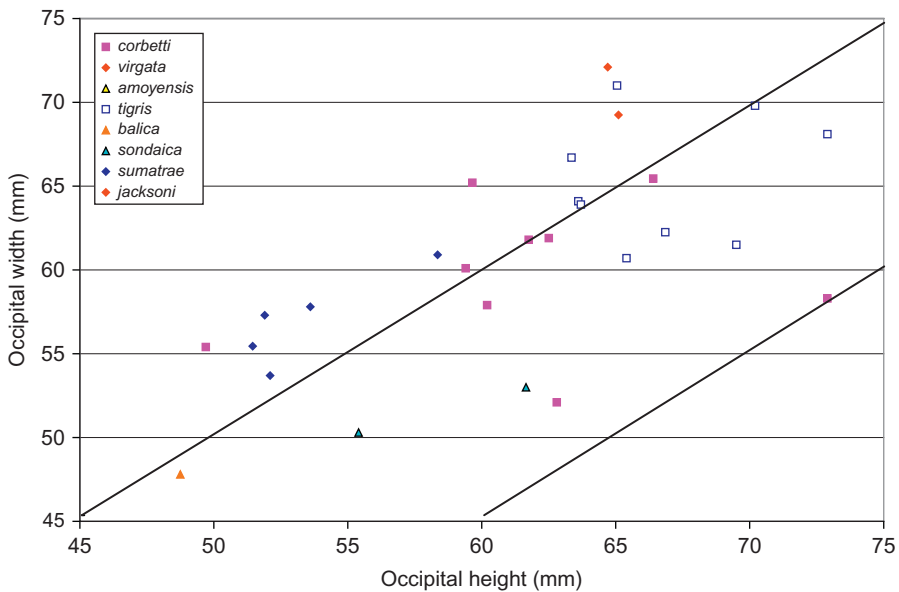


FIGURE 4.11 The relationship between occipital height (mm) and occipital width (mm) in female tigers [26].

- **Island Dwarfing** [72]: Large mammals on islands often evolve a much smaller body size. The Balinese tiger was probably the smallest of contemporary tigers (but see Buzás and Farkas [73]) and the now-extinct Japanese tiger, which survived until the late Pleistocene [74], was even smaller, although apparently some larger individuals, based on canine size, have been recorded. Both probably evolved a small body size in response to the limited

availability of large mammal prey. Interestingly, Javan tiger males could achieve a larger body size than that of the neighboring Sumatran tiger, presumably because this large island retained a large mammal community similar to that of the mainland, which Sumatra does not.

- **Mean Weight of Vertebrate Prey Index (MWVP):** Island dwarfing may represent the extreme minimum case of mean vertebrate prey being correlated with predator body weight. MWVP index has been found to influence body size in both jaguars and pumas [75, 76]. Kitchener [26] found some evidence to support this; MWVP showed a high correlation with latitude in studies of scats where sample sizes were more than 50. However, in these field studies no account could be taken of differences in MWVP index between males and females. Increasing sexual size dimorphism may be due to female tigers preying on similar-sized prey throughout mainland Asia, but males feeding on larger prey with increasing latitude.

Although one or more of these factors may be important in determining the broad range of variation in size with latitude and seasonal productivity in different tiger populations, it still does not answer the question as to how many tiger subspecies there are and how significant this is for tiger conservation.

If we are to be able to recognize subspecies, it is usually proposed that we must be able to distinguish at least 75% of individuals of one putative subspecies from 100% of those of another neighboring one [65, 77]. Sometimes a false impression of subspecies may be apparent because of biased sampling at different places along a geographical cline. These points on the cline may well display statistically significant differences when sampled at a few points (a perfect recipe for justifying distinguishable 'subspecies'), but if we could sample along the whole cline, we would see that they grade imperceptibly from one into another. Although there are quite a few tiger specimens in museums, many have poor or no data, or they may not represent the full former geographical range of the tiger. For example, there may well be more than 200 Bengal tigers in museums, but only 10 Balinese tigers are so far known in all the world's museums [73, 78, A. Waalen, personal communication and N. Yamaguchi, unpublished]. One way of trying to resolve this problem of limited and biased sampling is to carry out biogeographical modeling of the current and former distribution of tigers based on ecological and/or environmental variables, and the biogeographical barriers that shape the geographical distribution of tigers.

## Biogeography of the Tiger

Palaeontological studies suggest that the tiger evolved in a more or less restricted area of eastern Asia and then subsequently colonized western Asia either via the Himalayan foothills or across central Asia, and via the land bridges to the Sunda Islands when sea levels reduced during the formation of glaciers. The tiger's entire evolutionary history has been dominated by glacial cycles. For example, oxygen isotope analyses of deep-sea sediments show that approximately 15 glacial/interglacial cycles have occurred in the last one million years [79–82]. During glacials or stadials, when global temperatures dropped and sea levels fell, exposing continental shelves, forests and woodlands declined to be replaced by open habitats such as grasslands and deserts. During interstadials or interglacials, when global temperatures rose,

islands were once again cut off by rising sea levels, forests expanded, and deserts and grasslands declined. The tiger is principally a forest species, because its main prey of deer, pigs, and cattle are also dependent on forests. Therefore, glacials restricted the tiger's geographical spread, but encouraged gene flow to the Sunda Islands, whereas interglacials prevented gene flow to islands, but encouraged more widespread mainland colonization.

Kitchener and Dugmore [39] developed two simple GIS models to reconstruct the original geographical distribution of the tiger before any human intervention. The first model (HTP; habitat, topography, precipitation) was based on a specimen and sighting locality map in Mazák [29]. By correlating the locality records with GIS environmental data, including habitat (from Biome 3), topography (height above sea level), and precipitation, probability of tiger occurrence was scored on a scale of 0–3, based on the proportion of each kind of environmental variable that the locality records coincided with in the total for Asia. Therefore, a score was calculated for each grid cell as the product of three scores of the environmental variables (i.e., up to a maximum of  $3 \times 3 \times 3 = 27$ ) and converted to a percentage which was then mapped. A second model (DDP; distribution data prediction) scored these environmental variables independently based on expert knowledge from literature references. Both these models offered transparent methods for reconstructing the tiger's former interglacial distribution and the results of both models were broadly similar (Figs 4.12 and 4.13), except that the HTP model predicted a broad distribution across northern Asia into Europe.

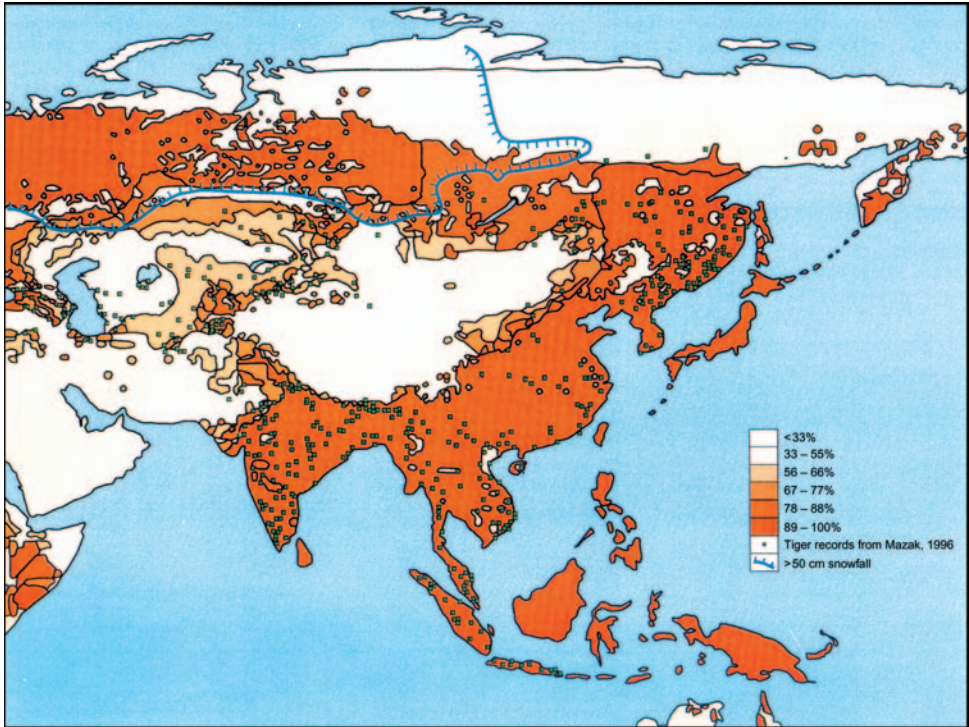
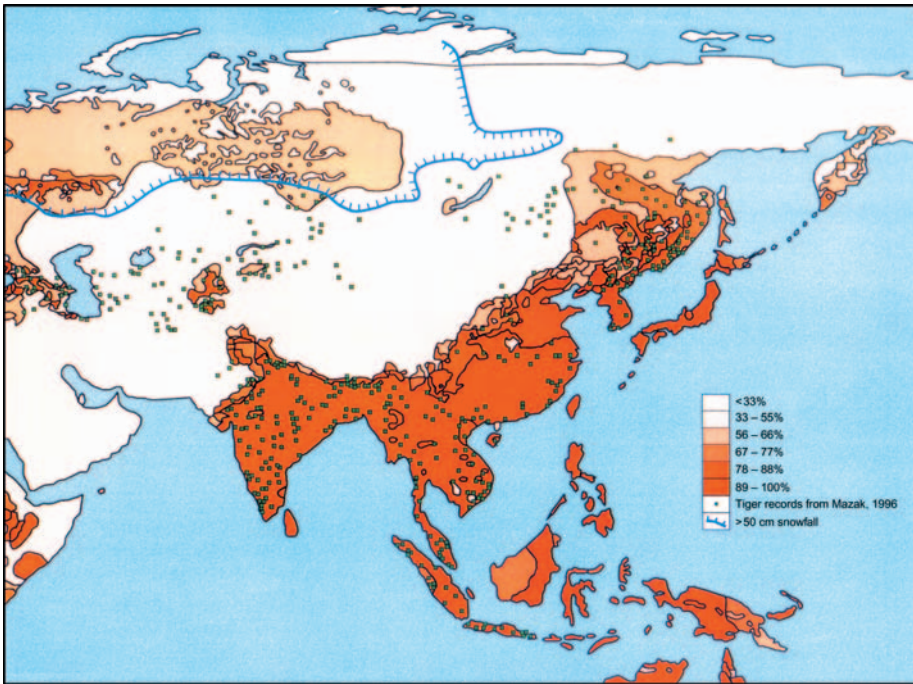


FIGURE 4.12 The maximum interglacial distribution of the tiger as predicted by the HTP model [39].

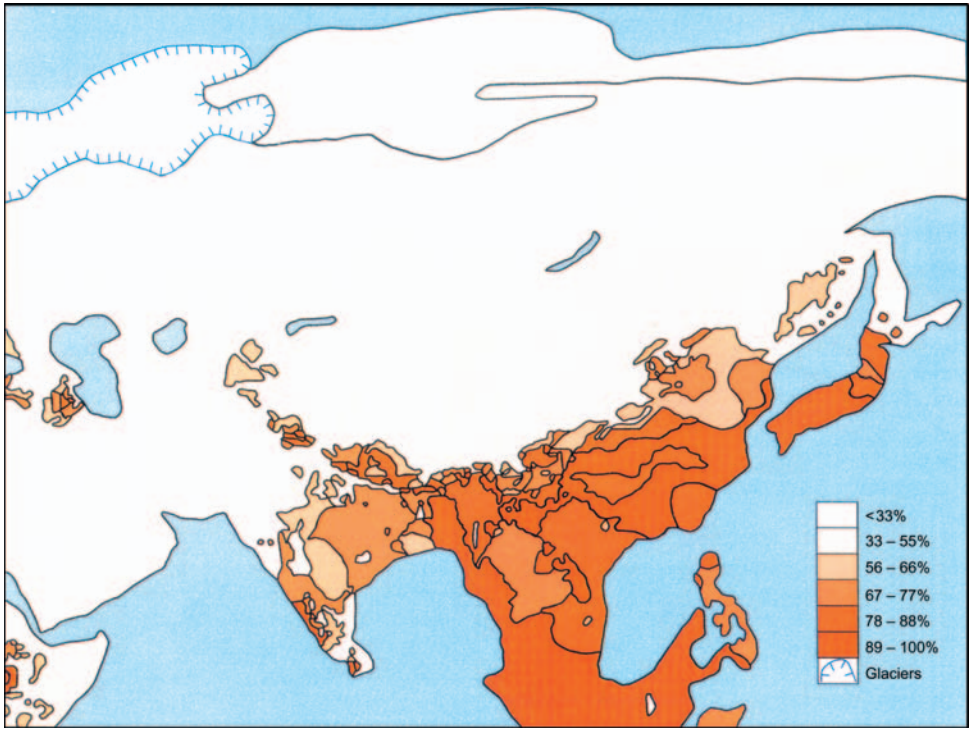




**FIGURE 4.13** The maximum interglacial distribution of the tiger as predicted by the DDP model [39].

However, by overlaying an isopleth indicating 0.5 metre depth of snow for 6 months' of the year, this effectively provided the boundary for all known northern tiger locality records. In other words, long periods of deep snow prevented tigers from hunting successfully and prevented their spread across northern Asia into Europe. Both models were poor at predicting the distribution of the Caspian tiger; it is quite likely that the tiger was tied closely to water sources, prey, and their adjacent tugai habitat of tall riparian vegetation. The models also suggest that northern Asia and Beringia were unsuitable for tigers. Perhaps tiger fossils found in the Jana River and the Lyakhov Islands are actually the remains of lions, or tiger remains carried there by northward-flowing rivers. The fossils found in these areas were consistent with molecular work using ancient DNA techniques suggesting Beringian 'tigers' were in fact lions [83].

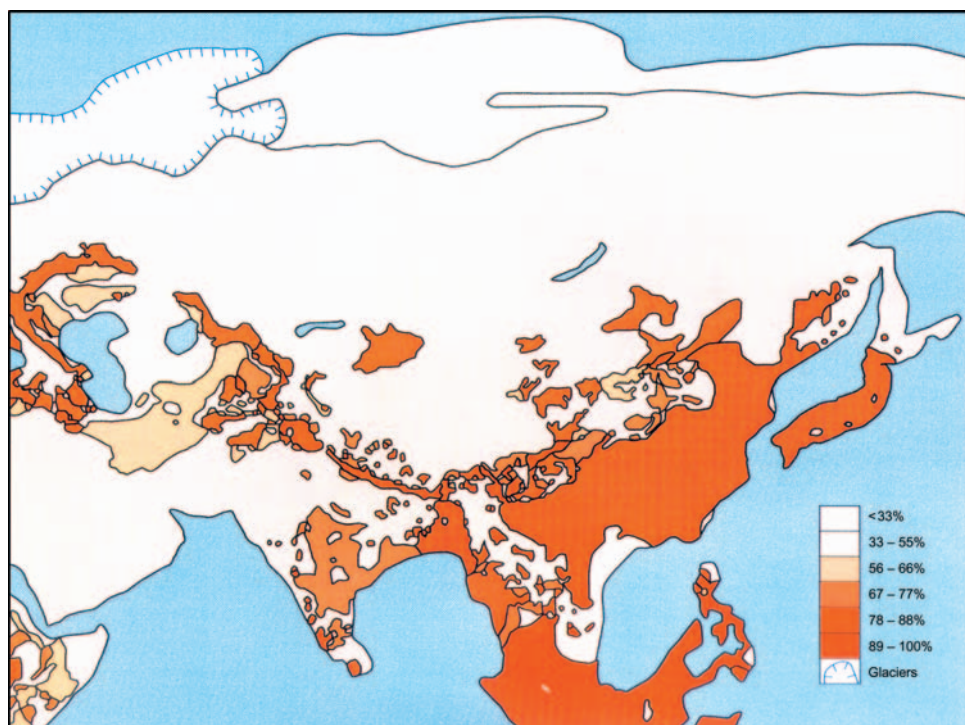
Kitchener and Dugmore [39] also used BIOME3 and knowledge of the exposed continental shelves during the last glacial maximum (LGM) approximately 20,000 years ago to see what effect this extreme environmental situation would have on the geographical distribution of the tiger using both HTP and DDP models. The palaeontological history of the tiger is dominated by glacial cycles, so that the extremes of the LGM and the present interglacial provide an indication of the repeated cyclicity in facilitation and prevention of gene flow between different tiger populations. Both models showed that tiger distribution became more restricted and was pushed southwards (Figs 4.14 and 4.15). There was contiguous tiger distribution between the Southeast Asian mainland and the three main Sunda Islands, including Sumatra, Java, and Borneo. India was mostly unsuitable for the tiger, and



**FIGURE 4.14** The distribution of the tiger at the last glacial maximum (approximately 20,000 years b.p.) as predicted by the HTP model [39].

may have been a stronghold of the lion during this period, although there was a suggestion that the tiger could have colonized its western Asian distribution via the Himalayan foothills rather than via Central Asia or the so-called Gansu Corridor [29, 63], although this has been disputed by others [84]. The absence of tigers in India until the Holocene (when rising sea levels would have cut off Sri Lanka), may explain why the tiger is also now absent from that island. The discovery of a  $M_1$  and a right middle phalanx (toe bone) from a big cat, with morphological characteristics resembling those of the tiger rather than the lion, implies that the tiger may have once inhabited Sri Lanka [85]. This suggests that the model should be revisited, although it did predict suitable habitat in Sri Lanka and in the western Ghats of India during glacials. In contrast, the model predicted that Japan would be suitable for tigers throughout glacial cycles, but indicated no possible route for colonization. This is suggestive that the small Japanese tigers of the late Pleistocene [74] were isolated for a considerable period of time and probably represented a distinct species.

In theory, one might expect smaller Sunda Island tigers to be found on the Malay Peninsula. However, the Toba eruption in northern Sumatra c.75,000 years ago devastated a huge area of natural habitat in northern Sumatra and the Malay Peninsula. Today the mammalian fauna north-west of Toba is mostly of mainland origin, including the orang-utan, *Pongo abelii*, but the more mobile and adaptable tigers there are probably all of Sundaic origin, while



**FIGURE 4.15** The distribution of the tiger at the last glacial maximum (approximately 20,000 years b.p.) as predicted by the DDP model [39].

the Malayan tigers are mainland in origin. This is supported by recent phylogeographical research [56].

Overall, the biogeographical approach coupled with a limited morphological review of geographical variation in tigers supported a hypothesis that there are perhaps three tiger subspecies:

1. Mainland tiger, *Panthera tigris tigris*.
2. Caspian tiger, *P.t. virgata*—although it is possible that the Caspian tiger may be part of the mainland tiger subspecies as their ranges appear to have been separated recently mainly by distance, thereby reducing the number of subspecies to only two. This appears to have been confirmed by recent genetic work, which shows that Caspian tiger mt DNA differs by only a single nucleotide from that of the Amur tiger [86].
3. Sunda Island tiger, *P.t. sondaica*—it is possible that Sumatran tigers may be a natural hybrid between mainland and Sunda Island tigers, but this needs to be tested genetically [26, 40]. Mazák's [87] craniometric study appears to suggest that Sumatran tigers are probably hybrids between the mainland and Sunda Island lineages.

We are fully aware that many populations were originally (or have become) distinguishable owing to natural or human-induced population fragmentation (morphologically and/or genetically) within each of those subspecies (see morphological variation in Bengal tigers

in Sankhala [88, p. 183]). However, we consider that the tiger may be evolutionarily sorted into the two or three 'subspecies' proposed above on the basis of the deduced recent evolutionary history of the species. Kitchener and Dugmore [39] suggested that their model provided a more flexible approach to tiger conservation, because the number of subspecies was reduced. Therefore, at face value conservationists may interpret that it would be possible to reinforce critically endangered populations of tigers in southern China with animals from Indochina and even India. However, firstly, colonization events on an evolutionary timescale should not be confused with population management plans over a few years, and secondly, Kitchener and Dugmore [39] also recognized the clinal nature of variation in tigers and that locally there may well be co-adapted gene complexes that have important evolutionary value and potential. Therefore, they suggested that reinforcement of tiger populations should not occur if source animals originated further away than the maximum dispersal distance known for wild tigers (which is more than 1000 km), taking into account natural barriers such as mountain ranges, very large rivers, and the sea (N.B. tigers have been known to swim up to 29 km across rivers and 12 km across the sea [26]). The Amur tiger population would, therefore, by default have to be managed separately from other mainland populations.

## Molecular and Morphological Research

There have been several molecular studies of tigers, which have often arrived at conflicting conclusions. Cracraft *et al.* [89] claimed to have identified a genetic marker for the Sumatran tiger, which using the phylogenetic species concept (PSC) [90], would mean that it would have to be recognized as a distinct species. However, the status of mainland tigers was not resolved and no analysis was carried out of extinct forms. Wenzel *et al.* [91] carried out a broader study of the genetics of tigers, but failed to find differences between populations that would be consistent with subspecies, although they did find markers for each putative subspecies population, which have been used extensively by the zoo community to determine whether individuals are 'hybrids' or 'pure-bred' subspecies. Therefore, Wenzel *et al.*'s [91] molecular results were in broad agreement with the morphological results of Kitchener [26] and the biogeography of Kitchener and Dugmore [39]. Later, Hendrickson *et al.* [92] examined MHC polymorphism within captive and wild-living Amur, Sumatran, and Bengal tigers and, although they found the Sumatran tiger to be basal, there was no clear separation between putative subspecies.

Other research has claimed that two free-ranging Indian tigers in Dhudhwa Tiger Preserve in northern India showed evidence of possible hybridization with Amur tigers in the past [93, 94]. Although we do not reject the possibility of apparent hybridization, in terms of the actual results we cannot be certain that the animals from Darjeeling Zoo used in this study were really Amur tigers, because no global studbook numbers were given. Also, the very successful extraction of nuclear microsatellites from museum skins 50–125 years old, using the ancient DNA techniques available in 1990s, is remarkable and more likely to have arisen from contamination. Contamination may also have resulted in the equally remarkable 42 base-pair substitutions recorded between the mtDNA D-loops of Bengal and Amur tigers [94].



In 2004, Luo *et al.* [56] carried out the most comprehensive molecular phylogeographical research ever on extant tiger populations (see also Luo *et al.*, Chapter 3), and claimed to have found phylogeographical evidence for distinguishing genetically between the surviving putative tiger subspecies, if doing so were necessary. They proposed the recognition of a new subspecies, *Panthera tigris jacksoni*, from the Malay Peninsula, which had been isolated by the narrow Isthmus of Kra, which is an important biogeographical barrier between species and subspecies in Southeast Asia. However, genetic differences between putative subspecies were very small. One of the supposed subspecies was clearly diphyletic (e.g., Indochinese tigers, excluding the Malay Peninsula). Some did not show the expected adjacent geographical relationship to each other (e.g., adjacency of Sumatran and Bengal tigers). Some showed genetic substructuring that could not be interpreted geographically. In one case examples of one putative subspecies of presumably known studbook animals were reassigned to another on the basis of their genetics rather than by considering their morphology. Interestingly, the extant tigers were suggested to share a common ancestor only very recently (72,000–108,000 years ago) in comparison with the modern leopard (470,000–825,000 years ago [95]). Luo *et al.* [56] suggested that the Toba eruption of about 75,000 years ago could have been responsible for this recent coalescence time for extant tiger populations.

It has also been shown that the mtDNA of the extinct Caspian tiger differs from that of the Amur tiger by a single nucleotide [85]. This strongly suggests that morphological similarities in striping patterns, and occipital and sagittal crests of skulls, are the result of common ancestry, and implies that tigers were able to move across central Asia to colonize both the Caspian and Amur regions when the environment was more equable. This study is in contradiction to the biogeographical model of Kitchener and Dugmore [39].

However, we must take care in assuming that phylogeographical genetic patterns seen today are consistent over time, particularly if a species has undergone dramatic reduction in and fragmentation of geographical ranges recently, and coupled with local population recoveries in some areas. For example, the contemporary phylogeography of the North American brown bear, *Ursus arctos*, was interpreted such that the three surviving geographically separated haplotype clades, all of which had an eastern Asian origin, may have been the result of separate colonizations via the Bering land bridge around the LGM [96]. This would have resulted in a proposal for separate management of these populations as Evolutionarily Significant Units (ESU) based on their perceived haplotype differences [96]. However, an ancient DNA (aDNA) study of fossil brown bear remains from North America showed that all three haplotypes occurred at the same time and in the same place in Alaska more than c. 35,000 years ago. This study also showed that the pattern of haplotypes was established in the late Pleistocene, so that today's distribution is the result of either founding populations in each region being comprised of individuals from each different clade or genetic drift following population fragmentation [97, 98]. Although one cannot make a direct comparison of phylogeographical patterns between different species [96], this may provide a possible interpretation for genetically distinguishable tiger populations, such as ones suggested by Luo *et al.* [56]. For example, the Malay Peninsula population may have originated from Indochinese tigers following the Toba eruption 75,000 b.p., when the vegetation of northern Sumatra and the Malay Peninsula were almost certainly obliterated, or as a result of very recent isolation since the LGM. In this context, it will be interesting to see whether the haplotype for the Malay Peninsula tigers is eventually recorded elsewhere

in Southeast Asia, suggesting that its current predominance in Malaya is owing to a possible combination of founder effects and genetic drift in a small fragmented population within historic times. Also, phylogeographical patterns of mtDNA variants in the absence of obvious physical barriers may represent an intermediate state of a spontaneous diffusion process after the removal of barriers [99]. In this context, we need to gather more information before concluding that apparently genetically distinguishable populations at present make biological sense based on the species' recent evolutionary history. Sadly, however, any chance of detecting key scientific evidence to tease out the evolutionary history of the tiger may be lost forever as tiger populations continue to decline in the region, although museum specimens may prove an invaluable genetic archive over the last 100 or so years.

In 2006, Mazák and Groves [40] carried out a multivariate statistical analysis of skull measurements of tigers from the Sunda Islands and Southeast Asia. Based on this study they recognized three phylogenetic species of tiger, namely the extinct Javan tiger, *Panthera sondaica*, with the Balinese tiger as a subspecies, and the Sumatran tiger, *P. sumatrae*, which are distinct on the basis of skull characters (e.g., occipital and nasal shape) from mainland tigers, *P. tigris*. Our concern about this study is that it has only examined a small part of the tiger's geographical variation and it is unclear how distinct these putative species are when compared to all mainland forms. Secondly, some of the characters that define, for example, the Javan tiger, can also be seen in other tigers, including those on the mainland. Finally, the basic striping patterns of these tigers can be seen in all putative traditional subspecies. The clear morphological and genetic distinctions seen between mainland and Sunda Island clouded leopards, *Neofelis nebulosa* and *N. diardi* [100, 101] are not seen between putative phylogenetic species of tiger. Is the current phylogeographical pattern seen in tigers the result of historical accident or does it reflect important biogeographical processes? At this time, we are unable to answer this question.

A craniometric study on all tigers by Mazák [87] suggests that there are two main lineages: a mainland one and a Sunda island one, with Sumatran tigers probably being of hybrid origin. Mainland tigers varied clinally, although Amur tiger skulls were most distinct. These results are in close agreement with previous recent morphological and biogeographical studies [26, 39].

## Conservation Significance

Research on geographical variation in tigers is suggesting two possible models, which have enormous significance for future tiger conservation. The more conservative model, based both on molecular and morphological research (e.g. see Refs 40, 56 and 86), suggests that eight or more subspecies, some of which may even be distinct phylogenetic species, should be recognized. This would require very little change in the way that conservation strategies for the tiger are pursued. Captive populations are already defined in these terms and the fragmentation of wild populations means that most can be classified accordingly or their affinity can be determined through non-harmful genetic testing (e.g. from scats).

An alternative model, also based on biogeographical and different molecular and morphological research, suggests that much of the variation in tigers is clinal and that some apparent distinctions between populations may be the result of genetic drift in recently fragmented

populations [26, 39, 88, 91]. This model could have enormous significance for the conservation of the tiger; for example, it recognizes that the tiger is a large mobile adaptable species that could easily result in gene exchange between local populations more than 1,000 km apart, which is the maximum known dispersal distance of the tiger [63]. Therefore, a more dynamic approach to tiger conservation could be followed. This would allow the reinforcement of critically endangered regional populations such as that of the South Chinese tiger. It is difficult to see what geographical barrier formerly prevented Indochinese and even Bengal tigers from having effective gene flows with these tigers in the past when populations were contiguous. Human intervention could help restore the genetic basis for captive (and any surviving wild) South Chinese tigers, which might form the basis for future reintroductions. This approach could also see the restoration of tigers to the Caspian region, owing to morphological and genetic similarities with the Amur tiger [86]—a single nucleotide difference in mtDNA suggests that these tigers are the same.

In contrast, Amur tigers are isolated several thousand kilometres away from the nearest surviving tigers elsewhere in Asia and, even if they were to represent one end of a cline, their adaptation to a temperate ecosystem must surely make them ecologically distinct.

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## DISCUSSION

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Despite the flurry of research on tiger geographical variation, using both molecular and morphological techniques, more questions remain today about how many tiger species or even subspecies remain. Part of this problem arises from the complex evolutionary history of the tiger with its apparently frequent (re)colonizations and replacements of former populations as sea levels and habitats fluctuated, owing to continuing climatic change over the last 2 million years or so. Part of the problem also arises from poor historic sampling, including the recording of basic data, from contemporary populations, so that for some populations very few specimens survive which allow for poor genetic or morphological characterization or comparison with other populations. This is exacerbated by historical population fragmentation over the past decade or so and possible genetic drift, which may not provide a true picture of original geographical variation and its distribution.

So where do we go from here? Above we have outlined two basic models for understanding geographical variation in tigers and their possible consequences for tiger conservation. Both are supported by peer-reviewed research, but neither currently allows a resolution of what we should be doing today, because they come to different conclusions about 'What is a tiger?' In 1997, Dinerstein et al. [102] proposed a habitat-based approach to tiger conservation that was not dependent on an understanding of tiger geographical variation or intraspecific taxonomy. By identifying 161 tiger conservation units (TCUs) that covered the full range of habitats used by tigers—and with a goal of perpetuating tigers in as many of these as possible to cover the full adaptive potential of the tiger—it was hoped that an easy-to-use basis for future tiger conservation strategies at both the local and global levels could be provided. However, many TCUs (61%) were under threat even then and even some safe tiger habitats, including protected areas, are no longer able to support viable populations. Increasing poverty coupled with phenomenal economic development is resulting in even more habitat loss and poaching of tigers for their skins and for use in traditional Chinese medicines to an

ever-growing and affluent market in China, Korea, and Japan. In 2006, Dinerstein et al. [103] revised their estimates of tiger landscape units (TCLs = TCUs) and recorded a 40% decline in the tiger's geographical distribution in the previous ten years to about 7% of its historical distribution (see also Sanderson et al., Chapter 9; Wikramanayake et al., Chapter 40). Only 76 TCLs now survive. Captive tiger populations are managed on a taxonomic basis. However, within the next 50 years it will be likely that there will be more genetic interchange between captivity and the wild in order to maintain the genetic integrity of both populations, since large areas to support genetically viable populations may well be doomed at the present rate of loss of habitat. Data presented by Dinerstein et al. [103] emphasize that this is a likely outcome given current rates of habitat loss and population fragmentation.

Therefore, it is essential that we come to a consensus as soon as possible so that effective conservation management in the wild and captivity can proceed on the basis of sound science. What has been missing up to now is an integrated research program involving molecular and morphological methods, and which uses contemporary, historical and fossil specimens, and is coupled with more sophisticated biogeographical analyses. We have too many snapshots and not enough big pictures to solve the puzzle of tiger geographical variation. This need is urgent as we hear news of the Bengal tiger population plummeting to perhaps only 1300–1500 individuals in 2007 [104]. We are eager to join with our colleagues in solving this problem to the best of our techniques and abilities.

## WHAT IS A TIGER, 2009?

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In 1987, when the first edition of *Tigers of the World* was published, there was a great deal of certainty. We knew there were eight subspecies, two or three of which were sadly extinct. For some tiger subspecies the future was relatively assured, such as the burgeoning populations of Bengal tigers, a recovering population of Amur tigers, and still goodish populations of Sumatran and Indochinese tigers, for which some long-term conservation strategy was surely just around the corner.

Today, that certainty has been replaced by uncertainty. The security of wild populations of the tiger has been put into doubt, except perhaps for the Amur tiger, although its future may be more uncertain owing to what global climate change may do to the remaining viable habitats and the prey on which it is dependent. Increasing economic development, coupled with grinding poverty, have significantly worsened the fate of the tiger over the last few decades. However, saddest of all is that we are even more uncertain of 'What is a tiger?' because new techniques and studies have questioned the traditional classification, which was the bedrock of global conservation efforts.

Therefore, we rapidly need to work together in order to resolve this fundamental issue as soon as possible. Because if we do not really know what the tiger is, how can we hope to save it for future generations?

## References

1. Hemmer H. Körperproportionsunterschiede bei Pantherkatzen (Pantherinae). *Säugetierkund Mitt.* 1974;22:233–236.
2. Turner A, Anton M. *Fossil Cats and Their Living Relatives*. New York: Columbia University Press; 1997.

3. Wood GL. *The Guinness Book of Animal Facts and Feats*. 3rd ed. Middlesex: Guinness Superlatives Ltd; 1982.
4. Baikov NA. *Manchurian Tiger* (in Russian). Harbin: Society of the Study of Manchurian Krai; 1925.
5. Katou K. *Panthera tigris and Panthera leo*. Tokyo: Chyoeisha; 2000.
6. Smith JLD, Sunquist ME, Tamang KM, Rai PB. A technique for capturing and immobilising tigers. *J Wildl Manage*. 1983;47:255–259.
7. Smuts GL, Robinson GA, Whyte IJ. Comparative growth of wild male and female lions (*Panthera leo*). *J Zool*. 1980;190:365–373.
8. Orford HJL, Perrin MR, Berry HH. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). *J Zool*. 1988;216:717–733.
9. Yamaguchi N, Kitchener AC, Gilissen E, Macdonald DW. unpublished data.
10. Hemmer H. Socialization by intelligence. Social behaviour in carnivores as a function of relative brain size and environment. *Carnivore*. 1978;1(1):102–105.
11. Eisenberg JF. *The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation and Behaviour*. Chicago: Chicago University Press; 1981.
12. Gittleman JL. Carnivore brain size, behavioural ecology, and phylogeny. *J Mammal*. 1986;67:23–36.
13. Gittleman JL. Female brain size and parental care in carnivores. *Proc Natl Acad Sci U S A*. 1994;91:5495–5497.
14. Gonyea WJ. Adaptive differences in the body proportions of large felids. *Acta Anat*. 1976;96:81–96.
15. Werdelin L, Lewis ME. A revision of the genus *Dinofelis* (Mammalia, Felidae). *Zool J Linn Soc*. 2001;132:147–258.
16. Collier GE, O'Brien SJ. A molecular phylogeny of the Felidae immunological distance. *Evolution*. 1985;39:473–487.
17. Wayne RK, Benveniste RE, Janczewski N, O'Brien SJ. Molecular and biochemical evolution of the Carnivora. In: Gittleman JL, ed. *Carnivore Behaviour, Ecology and Evolution*. London: Chapman and Hall; 1989:465–494.
18. Johnson WE, Eizirik E, Pecon-Slattery J, et al. The late miocene radiation of modern felidae: a genetic assessment. *Science*. 2006;311:73–77.
19. Hemmer H. Die Evolution der Pantherkatzen Modell zur Überprüfung der Brauchbarkeit der Hennigschen Prinzipien der Phylogenetischen Systematik für wirbeltierpaläontologische Studien. *Paläontologische Z*. 1981;55:109–116.
20. Hemmer H. Fossil history of the living Felidae. In: Eaton RL, ed. *The World's Cats*; vol. III (2) Seattle: The University of Washington; 1976:1–14.
21. Bininda-Emonds ORP, Gittleman JL, Purvis A. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora. *Biol Rev*. 1999;74:143–175.
22. Zdansky O. Jungtertiäre Carnivoren. *Palaeontologia Sinica C*. 1924;2(1):1–145.
23. Hemmer H. Wohin gehört 'Felis' palaeosinensis Zdansky 1924 in systematischer Hinsicht? *Neues Jahrb Geol P–A*. 1967;129:83–96.
24. Hemmer H. The phylogeny of the tiger (*Panthera tigris*). In: Tilson RL, Seal US, eds. *Tigers of the World. The Biology, Biopolitics, Management and Conservation of an Endangered Species*. Park Ridge, NJ: Noyes Publications; 1987:28–35.
25. Groves CP. How old are subspecies? A tiger's eye-view of human evolution. *Archaeol Oceania*. 1992;27:153–160.
26. Kitchener AC. Tiger distribution, phenotypic variation and conservation issues. In: Seidensticker J, Christie S, Jackson P, eds. *Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes*. Cambridge: Cambridge University Press; 1999:19–39.
27. Herrington SJ. Subspecies and the conservation of *Panthera tigris*: preserving genetic heterogeneity. In: Tilson RL, Seal US, eds. *Tigers of the World: The Biology, Biopolitics, Management and Conservation of an Endangered Species*. Park Ridge, New Jersey: Noyes Publications; 1987:51–63.
28. Mazák VJ. *Panthera tigris*. *Mamm Species*. 1981;152:1–8.
29. Mazák VJ. *Der Tiger*. Magdeburg: Westarp Wissenschaften (reprint of 1983 edition, 1996).
30. Dubois E. Das geologische Alter der Kendeng- oder Trinil-Fauna. *Tijdschr Ned Aardrijkskundig Genootschap 2 Series*. 1908;24:1235–1271.
31. Brongersma LD. Notes on some recent and fossil cats, chiefly from the Malay Archipelago. *Zool Meded*. 1935;18:1–89.
32. Hemmer H. Fossil mammals of Java. II. Zur Fossilgeschichte des Tigers (*Panthera tigris* (L.)) in Java. *K Ned Akad Wet*. 1971;74:35–52.
33. Swisher CC III, Curtis GH, Jacob T, et al. Age of the earliest known hominids in Java, Indonesia. *Science*. 1994;263:1118–1121.



34. Brandt F. Neue Untersuchungen über die in den alataischen Höhlen aufgefundenen Säugethierreste, ein Beitrag zur quaternären Faune des Russischen Reiches. *Bull Acad Impériale St. Petersbourg*. 1871;15:147–202.
35. Lydekker R. Preliminary notes on the Mammalia of the Karnul Caves. *Rec Geol Surv India*. 1886;19:120–122.
36. Zdansky O. Die Säugetiere der Quartärfauna von Chou-K'ou-Tien. *Palaeontologia Sinica C*. 1928;5(4):1–146.
37. Loukashkin AS. Some observations on the remains of a Pleistocene fauna and of the Palaeolithic age. In: MacCurdy GG, ed. *Northern Manchuria in Early Man*. Freeport: Books for Libraries Press; 1937:327–340.
38. Hooijer DA. Pleistocene remains of *Panthera tigris* (Linnaeus) subspecies from Wanh sien, Szechuan, China, compared with fossil and recent tigers from other localities. *Am Mus Novit*. 1947;1346:1–17.
39. Kitchener AC, Dugmore AJ. Biogeographical change in the tiger. *Anim Conserv*. 2000;3:113–124.
40. Mazák JH, Groves CP. A taxonomic revision of the tigers (*Panthera tigris*) of southeast Asia. *Z Säugetierkunde*. 2006;71:268–287.
41. Guthrie RD. Mosaics, allelochemicals and nutrients. In: Martin PS, Klein RG, eds. *Pleistocene Extinctions*. Tuscon: University of Arizona Press; 1984:259–298.
42. Kurtén B. *The Pleistocene Mammals of Europe*. London: Weidenfeld and Nicolson; 1967.
43. Geist V. Bergmann's rule is invalid. *Can J Zool*. 1987;65:1035–1038.
44. Geist V. On the evolution and adaptations of *Alces*. *Swed Wildl Res Suppl*. 1987;1:11–13.
45. Hose C, McDougall W. *The Pagan Tribes of Borneo*. London: Macmillan; 1912.
46. Pocock RI. Tigers. *J Bombay Nat Hist Soc*. 1929;33:505–541.
47. Peranio R. Animal teeth and oath taking among the Bisaya. *Sarawak Mus J*. 1960;9:6–13.
48. Gersi D. *Dans la jungle de Borneo (Kalimantan)*. Paris: Editions GP; 1975.
49. Lord M. *Mammals of Borneo*. Kuala Lumpur: Malaysian Branch of the Royal Asiatic Society; 1977.
50. Yasuma S. *An Invitation to the Mammals of East Kalimantan* PUSREHUT Special Publication 3: Republic of Indonesia, Japan International Cooperation Agency and Directorate General of Higher Education; 1994.
51. Meijaard E. The Bornean tiger; speculation on its existence. *Cat News*. 1999;30:12–15.
52. Piper PJ, Cranbrook Earl of, Rabett RJ. Confirmation of the presence of the tiger *Panthera tigris* (L.) in late Pleistocene and Holocene Borneo. *Malay Nat J*. 2007;59(3):259–267.
53. Hooijer DA. Further 'Hell' mammals from Niah. *Sarawak Mus J*. 1963;11:196–200.
54. Piper PJ, Ochoa J, Lewis H, et al. The first evidence for the past presence of the tiger *Panthera tigris* (L.) on the island of Palawan, Philippines: extinction in an island population. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2008;264:123–127.
55. Corbet GB, Hill JE. *The Mammals of the Indomalayan Region*. London and Oxford: The Natural History Museum and Oxford University Press; 1992.
56. Luo SJ, Kim JH, Johnson WE, et al. Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *PLoS Biol*. 2004;2:2275–2293.
57. Temminck CJ. Aperçu général et spécifique sur les mammifères qui habitent le Japon et les Iles qui en dépendent. pls 11–20. In: von Siebold PT, ed. *Fauna Japonica*. Amsterdam: Müller; 1844:25–59.
58. Mazák V. Nouvelle sous-espece de tigre provenant de l'Asie due Sud-Est. *Mammalia*. 1968;32:104–112.
59. Hemmer H. Zur Stellung des Tigers (*Panthera tigris*) der Insel Bali. *Z Säugetierkunde*. 1969;34:216–223.
60. Mazák V. Notes on Siberian long-haired tiger, *Panthera tigris altaica* (Temminck, 1844), with a remark on Temminck's mammal volume of the Fauna Japonica. *Mammalia*. 1967;31:537–573.
61. Weigel I. Das Fellmuster der wildlebenden Katzenarten und der hauskatzen in vergleichender und stammesgeschichtlicher Hinsicht. *Säugetierkundliche Mitt*. 1961;9:1–120.
62. Schroeter W. Über Färbung, Farbabweichungen, Streifenverminderungen und Farbaufhellungen beim Tiger, *Panthera tigris* (Linné, 1758). *Säugetierkundliche Mitteilungen*. 1981;29(4):1–8.
63. Heptner VH, Sludskii AA. *Mammals of the Soviet Union*. Vol. II, Part 2. Carnivores (Feloidea). Leiden: Brill; 1992.
64. Corbet GB. *The Terrestrial Mammals of Western Europe*. London: Foulis; 1966.
65. Corbet GB. Patterns of subspecific variation. *Symp Zool Soc Lond*. 1970;26:105–116.
66. Corbet GB. The species in mammals. In: Claridge MF, Dawah HA, Wilson MR, eds. *The Units of Biodiversity*. London: Chapman and Hall; 1997:341–356.
67. Kurtén B. Fossil puma (Mammalia: Felidae) in North America. *Neth J Zool*. 1976;26:502–534.
68. Ortolani A, Caro TM. The adaptive significance of colour patterns in carnivores. In: Gittleman JL, ed. *Ithaca: Cornell University Press; 1996:132–188. Carnivore Behaviour, Ecology and Evolution; vol. 2.*
69. Mazák V. On the Bali tiger, *Panthera tigris balica* (Schwarz, 1912). *V\_sntník\_eskoslovenské Spole\_nosti Zoologické*. 1976;40:179–195.

70. Pocock RI. *The Fauna of British India, including Ceylon and Burma. Mammalia – Vol. I. Primates and Carnivora (in part), Families Felidae and Viverridae*. London: Taylor and Francis; 1939.
71. Pocock RI. The panthers and ounces of Asia. *J Bombay Nat Hist Soc*. 1931;34:64–82.
72. Lister A, Bahn P. *Mammoths*. London: Boxtree; 1994.
73. Buzás B, Farkas B. An additional skull of the Bali tiger, *Panthera tigris balica* (Schwarz) in the Hungarian Natural History Museum. *Miscellanea Zoologica Hungarica*. 1997;11:101–105.
74. Hemmer H. Der Tiger, *Panthera tigris palaeosinensis* (Zdansky, 1924) im Jungpleistozän Japans. *Neues Jahrb Geol P M*. 1968;10:610–618.
75. Iriarte JA, Franklin WL, Johnson WE, Redford KH. Biogeographic variation of food habits and body size of the American puma. *Oecologia*. 1990;85:185–190.
76. Hoogesteijn R, Mondolfi E. Body mass and skull measurements in four jaguar populations and observations on their prey base. *Bull Fla Mus Nat Hist*. 1996;39:195–219.
77. Mayr E, Ashlock PD. *Principles of Systematic Zoology*. 2nd ed. New York: McGraw-Hill; 1991.
78. Mazák V, Groves CP, van Bree PJH. On a skin and skull of the Bali tiger, and a list of preserved specimens of *Panthera tigris balica* (Schwarz, 1912). *Z Säugetierkunde*. 1978;43:108–113.
79. Denton GH. Cenozoic climate change. In: *African Biogeography, Climate Change, & Human Evolution*. Oxford: Oxford University Press; 1999:94–114.
80. Mannion AM. *Natural Environmental Change*. London: Routledge; 1999.
81. Nesje A, Dahl SO. *Glaciers and Environmental Change*. London: Arnold; 2000.
82. Stringer C, Gamble C. *In Search of the Neanderthals*. New York: Thames and Hudson; 1993.
83. Barnett R, Shapiro B, Barnes I, et al. Phylogeography of lions (*Panthera leo*) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Mol Ecol*. 2009;18:1668–1677.
84. Springhorn RA. Skull of the Caspian tiger (*Panthera tigris virgata* (Illiger, 1815)) from the estate of the Russian scholar Constantin von Scharnhorst (1846–1908) in the collection of the Lippisches Landesmuseum Detmold, research history and a review of the subspecies' extinction. *Lipp Mitt Gesch Landeskd*. 2004;73:323–350.
85. Manamendra-Arachchi K, Pethiyagoda R, Dissanayake R, Meegaskumbura M. A second extinct big cat from the Late Quaternary of Sri Lanka. *Raffles Bull Zool Suppl*. 2005;12:423–434.
86. Driscoll CA, Yamaguchi N, Bar-Gal GK, et al. Mitochondrial phylogeography illuminates the origin of the extinct Caspian tiger and its relationship to the Amur tiger. *PLoS ONE* 4(1): e4125.
87. Mazák J. Craniometric variation in the tiger (*Panthera tigris*): implications for patterns of diversity, taxonomy and conservation. *Mamm Biol*. 2008. doi:10.1016/j.mambio.2008.06.003.
88. Sankhala K. *Tiger*. New York: Simon and Schuster; 1977.
89. Cracraft J, Felsenstein J, Vaughn J, Helm-Bychowski K. Sorting out tigers (*Panthera tigris*): mitochondrial sequences, nuclear inserts, systematics, and conservation genetics. *Anim Conserv*. 1998;1:139–150.
90. Cracraft J. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: Otte D, Endler JA, eds. *Speciation and Its Consequences*. Sunderland: Sinauer Associates; 1989:28–59.
91. Wentzel J, Stephens JC, Johnson W, et al. Subspecies of tigers: molecular assessment using 'voucher specimens' of geographically traceable individuals. In: Seidensticker J, Christie S, Jackson P, eds. *Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes*. Cambridge: Cambridge University Press; 1999:20–49.
92. Hendrickson SL, Mayer GC, Wallen EP, Quigley K. Genetic variability and geographic structure of three subspecies of tigers (*Panthera tigris*) based on MHC class I variation. *Anim Conserv*. 2000;3:135–143.
93. Shankaranayanan P, Banerjee M, Kacker RK, et al. Genetic variation in Asiatic lions and Indian tigers. *Electrophoresis*. 1997;18:1693–1700.
94. Shankaranayanan P, Singh L. Mitochondrial DNA. sequence divergence among big cats and their hybrids. *Curr Sci*. 1998;75:919–923.
95. Uphyrkina O, Johnson WE, Quigley H, et al. Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. *Mol Ecol*. 2001;10(11):2617–2633.
96. Waits LP, Talbot SL, Ward RH, Shields GF. Mitochondrial DNA phylogeography of North American brown bear and implication for conservation. *Conserv Biol*. 1998;12:408–417.
97. Leonard JA, Wayne RK, Cooper A. Population genetics of Ice Age brown bears. *Proc Natl Acad Sci U S A*. 2000;97:1561–1565.

98. Barnes I, Matheus P, Shapiro B, Cooper A. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science*. 2002;295:2267–2270.
99. Hofreiter M, Serre D, Rohland N, et al. Lack of phylogeography in European mammals before the last glaciation. *Proc Natl Acad Sci U S A*. 2004;101:12963–12968.
100. Kitchener AC, Beaumont MA, Richardson D. Geographical variation in the clouded leopard, *Neofelis nebulosa*, reveals two species instead of one. *Curr Biol*. 2006;16:2377–2383.
101. Buckley-Beason VA, Johnson WE, Nash W, et al. Molecular evidence for species-level distinction in modern clouded leopards (*Neofelis nebulosa*). *Curr Biol*. 2006;16:2371–2376.
102. Dinerstein E, Wikramanayake E, Robinson J, et al. *A Framework for Identifying High Priority Areas and Actions for the Conservation of Tigers in the Wild*. Washington DC: World Wildlife Fund-US and Wildlife Conservation Society; 1997.
103. Dinerstein E, Loucks C, Heydlauff A, et al. *Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005–2015*. The technical assessment. Washington DC and New York: WWF, WCS, Smithsonian Institution and NFWF-STF; 2006.
104. Anonymous. Govt admits only 1,300–1,500 tigers left. *Times India*. 4 August, 2007.
105. von Koenigswald GHR. Beitrag zur Kenntnis der fossilen Wirbeltiere Javas. *Wet Meded: Dienst Mijnbouw Nederlandsch Oost-Indie*. 1933;1(23):1–184.
106. Young CC. New fossils from Wanhsien (Szechuan). *Bull Geol Soc China*. 1939;19:317–331.
107. van de Bergh GD, de Vos J, Sondaar PY. The Late Quaternary palaeogeography of mammal evolution in the Indonesian archipelago. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2001;171:385–408.
108. Swisher CC, Rink WJ, Anton SC, et al. Latest *Homo erectus* of Java: Potential contemporaneity with *Homo sapiens* in southeast Asia. *Science*. 1996;274:1870–1872.
109. Zhu RX, An Z, Potts R, Hoffman KA. Magnetostratigraphic dating of early humans in China. *Earth Sci Rev*. 2003;61:341–359.
110. Dong W, Jin C-z, Xu Q-q, Liu J-y, et al. A comparative analysis on the mammalian faunas associated with *Homo erectus* in China. *Acta Anthropol Sin*. 2000;19(Supplement):246–256.
111. Pei WC. On the Carnivora from Locality 1 of Choukoutien. *Palaeontologia Sin C*. 1934;8(1):1–217.
112. Pei WC. On the mammalian remains from Locality 3 at Choukoutien. *Palaeontologia Sin C*. 1936;7(5):1–121.
113. Teilhard de Chardin P. Fossil mammals from Locality 9 of Choukoutien. *Paleontologia Sin C*. 1936;7(4):1–71.
114. Groves CPA *Theory of Human and Primate Evolution*. Oxford: Clarendon Press; 1989.
115. Chiu C-l, Chang Y-p, Tung Y-s. Pleistocene mammalian fossils from Chinkiang District, W. Hupei. *Vertebrat Palasiatic*. 1960;4:157–158.
116. Young CC. On some fossil mammals from Yunnan. *Bull Geol Soc China*. 1932;11:383–393.
117. Pei WC. Fossil mammals from the Kwangsi Caves. *Bull Geol Soc China*. 1935;14:413–425.
118. Chow M. Mammals of 'Lantian man' locality at Lantian, Shensi. *Vertebrat Palasiatic*. 1964;8:301–307.
119. Wu X-z, Yuan Z-x, Han D-f, et al. Report of the excavation at Lantian man locality of Gongwangling in 1965. *Vertebrat Palasiatic*. 1966;10:23–29.
120. Young CC, Chow MM. Pleistocene stratigraphy and new fossil localities of Shihhung and Wuho, northern Anhwei. *Acta Palaeontol Sin*. 1955;3(1):43–53.
121. Zulu Z. The first discovery of *Panthera tigris* fossils in Shandong Province and its significance. *Mar Geol Quaternary Geol*. 1994;14:69–74.
122. Loukashkin AS. The manchurian tiger. *China J Shanghai*. 1938;28:127–133.
123. Shikama T, Okafuji G. Quaternary cave and fissure deposits and their fossils in Akiyoshi District, Yamaguti Prefecture. *Sci Rep Yokohama Natl Univ 2 Biol Geol Sci*. 1958;7:43–103.
124. Shikama T, Okafuji G. On some Choukoutien mammals from Isa, Yamaguchi Prefecture, Japan. *Sci Rep Yokohama Natl Univ 2 Biol Geol Sci*. 1963;9:51–58.
125. Takai F, Hasegawa Y. Vertebrate fossils from the Gansuiji Formation. *J Anthropol Soc Nippon*. 1966;74:155–167.
126. Tscherski JD. Wissenschaftliche Resultate der von der Kaiserliche Akademie der Wissenschaften zur Erforschung des Janalandes und der neusibirischen Inseln in den Jahren 1885 und 1886 ausgesandten Expedition. Abt. IV. Beschreibung der Sammlung posttertiärer Säugethiere. *Mémoires Acad Impériale Sci St.-Petersbourg, VII<sup>e</sup> Série*. 1892;40:1–511.



127. Vereshchagin NK. *The Mammals of the Caucasus: A History of the Evolution of the Fauna*. Nauka, Moscow. Jerusalem: Engl. transl. by Israel Program for Scientific Translations; 1967.
128. Linnaeus C. *Systema Naturae per Regna Tria Naturae*. 10th ed. vol. 1. Uppsala: Laurentii Salvii; 1758.
129. Illiger C. Ueberblick der Säugethiere nach ihrer Vertheilung über die Welttheile. *Abh Physikalischen Kl Königlich-Preussischen Akad Wiss Jahren 1804–1811*. 1815:39–159.
130. Hilzheimer H. Über einige Tigerschädel aus der Strassburger Zoologischen Sammlung. *Zool Anz*. 1905;28:594–599.
131. Schwarz E. Notes on Malay tigers, with description of a new form from Bali. *Ann Mag Natl Hist* 8. 1912;10: 324–326.
132. Ognev SI. *Mammals of the USSR and Adjacent Countries, Vol. III Carnivora (Fissipedia and Pinnipedia)*. Jerusalem, Jerusalem: Israel Program for Scientific Translations; 1962.
133. Yamaguchi N, Kitchener AC, Gilissen E, Macdonald DW. Brain size of the lion (*Panthera leo*) and the tiger (*Panthera tigris*): implications for intrageneric phylogeny, intraspecific differences and the effects of captivity. *Biol J Linn Soc*. 2009; 98: 85–93.