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Taxonomic issues in bears: impacts on conservation in zoos and the wild, and gaps in current knowledge

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Taxonomy is essential for underpinning conservation science and action, and the international and national implementation of protective legislation. However, many of the current scientific species and subspecies names for bears have a poor scientific basis. Poor understanding of ursid taxonomy could compromise conservation both in the wild and in captivity; all eight ursid species are listed on the Convention on International Trade of Endangered Species of Wild Fauna and Flora and 75% are Endangered or Vulnerable. Although there has been much molecular research on ursids in recent years, this has mainly focused on phylogenetic relationships, including resolution of whether the Giant panda *Ailuropoda melanoleuca* is an ursid. Some phylogeographical studies have provided new insights into geographical variation of some bear species, but these studies are often only regional, or lack sufficient samples, or use only mtDNA. There is an urgent need for integrated molecular and morphological studies of geographical variation of all bear species in order to establish a robust taxonomy for the Ursidae for enhanced conservation management and action.

Key-words: bears; conservation management; conservation science; taxonomy.

INTRODUCTION

Although taxonomy is often regarded as rather dull, it provides the essential underpinning of all conservation. If species and subspecies do not have scientific names, it is not possible to provide full legal protection for them under national or international law (e.g. O'Brien & Mayr, 1991). Therefore, it is fundamental for conservation science and action, as well as the implementation of national and international protective legislation, that the taxonomy of species and subspecies is accurate. If a widespread species

actually comprises two or more species, some of which are critically endangered, poor taxonomic research may inadvertently compromise the survival of those threatened populations. In captivity, hybridization may occur accidentally between unrecognized subspecies and even species, ultimately wasting huge amounts of resources as well as affecting the conservation of the species. Conversely, if too many species or subspecies are recognized, captive populations may suffer from inbreeding from small founder populations, when they would benefit from the mixing of needlessly separated captive gene pools. However, we must remember that taxonomy and systematics are fluid – they represent, to a greater or lesser extent, a consensus based on current evidence, and today's taxonomies will continue to change and, hopefully, improve as better evidence accumulates.

In this paper, I examine the taxonomic issues that currently affect the Ursidae. Most species are widespread, occurring in a wide variety of habitats, and some species, such as the Brown bear *Ursus arctos* and the American black bear *Ursus americanus*, show enormous phenotypic variation in size and coloration that has led to the recognition of very many species and subspecies in the past. For Brown bears, some 232 modern [of which 83 were described by C. Hart Merriam in North America (Hall, 1981)] and 39 fossil species and subspecies have been described (see Erdbrink, 1953), which Kurtén &

Anderson (1980) considered 'a waste of taxonomic effort, which, as far as we know, is unparalleled'. There are many problems that affect our understanding of the taxonomy of ursids and many other mammals. Firstly, the scientific names on which species and subspecies are based are poorly founded scientifically. These names date mainly from the 19th century when none, one or only a handful of specimens were examined to determine the diagnostic characteristics and differences from related species. It should be noted that normally there is a requirement for a holotype, which is the specimen that is selected as the voucher on which the scientific name is based (Mayr & Ashlock, 1991; Groves, 2001), but a wide range of specimens needs to be examined to determine which characters are diagnostic (i.e. typical or characteristic) for the taxon, and which are the result of individual or other kinds of variation in the population. Therefore, it is not surprising that these descriptions capture only a fraction of the normal range of individual variation within a species or subspecies. Where variation is clinal (i.e. changes gradually over a geographical range) it is easy to see how the analysis of a small number of samples distant from each other might result in several new species or subspecies being inadvertently recognized. Over time, this process has led inevitably to a proliferation of names, for which there is little or no scientific basis.

Normally taxonomic differences are based on diagnostic morphological characters, such as coloration, size, shape, presence/absence of characters, and combinations of measurements, particularly from skulls, but account must also be taken of sex, age, season, etc. (Pocock, 1941; Erdbrink, 1953). In recent years, new techniques and technologies have been developed which have greatly benefited taxonomy and systematics. New molecular techniques allow us to examine genetic variation over wide geographical areas regardless of sex, age and local phenotypic responses to the environment. These molecular studies compare the sequencing of base pairs of mitochondrial and nuclear DNA between individuals

and populations. Combining molecular and geographical data is known as phylogeography, and it has developed into a potent tool for examining geographical genetic variation and population subdivision. The analysis of ancient DNA (aDNA) even allows us to look back in time at the genetics of past populations and even extinct species, providing further insight into how the distribution of genetic variation has arisen today (Leonard *et al.*, 2000; Loreille *et al.*, 2001; Barnes *et al.*, 2002; Valdiosera *et al.*, 2007; Krause *et al.*, 2008). New morphometric techniques, such as geometric morphometrics, allow us to examine subtle differences in the shapes and sizes of skulls, the normal part of a skeleton that is the subject of taxonomic research, including removing and/or controlling for the influence of size, which often reflects a phenotypic response to the available local food resources. In other words, well-fed bears grow bigger! Sometimes the molecular and morphological approaches are in strong accord, in other cases they disagree, often because the old morphological taxonomy is poorly based in science. The best studies involve a combination of morphological and molecular techniques, without recourse to previous taxonomic arrangements, as checks against each approach.

However, whatever the approach, good taxonomic research requires statistically significant samples that cover the entire range of the species. Using current museum collections, this may be very hard to achieve. Inevitably there are collecting biases that reflect the interest and collecting activities of individuals, and the accessibility of the geographical range of a species. Opportunities to enhance the number of specimens available for all kinds of research must be taken in order to provide a better resource base for taxonomic and other research. In the meantime other complementary approaches, such as dynamic biogeographical modelling, should be considered to provide a framework against which we can examine our current knowledge of the geographical variation within each ursid species.

As is typical for many mammalian families, the bears suffer from numerous

taxonomic uncertainties. While the number of recognized species has remained stable over the last 140 years, our knowledge of the geographical variation in bears, given their phenotypic variation, is still very poor, although some recent studies have improved our understanding for some species or populations. In this article, I review the current taxonomic status of bear genera, species and subspecies, highlighting uncertainties and future areas for research. The impact that these uncertainties have on conservation in the wild and in captivity will also be examined.

GENERA

The number of genera of bears has varied from one for each species to three in total (Table 1). There have been numerous studies of the phylogenetic relationships between modern bears based mainly on mitochondrial DNA (mtDNA) (Zhang & Ryder, 1994; Talbot & Shields, 1996a,b; Waits *et al.*, 1998, 1999; Yu *et al.*, 2007; Krause *et al.*, 2008) but until recently there had been none that used nuclear DNA or a combination of both (Yu *et al.*, 2004; Pagès *et al.*, 2008). All the phylogenetic trees show the Giant panda *Ailuropoda melanoleuca* as the most basal with a coalescence time varying between 12 and 22 million years ago (Ma), depending on the molecular method used. Then comes the Spectacled bear *Tremarctos ornatus* which diverged 6–15.6 Ma. The Giant panda has a distinctive adaptation, the pseudo-thumb or radial sesamoid, which has evolved a large

size to hold bamboo stems while feeding (Pocock, 1941; Salesa *et al.*, 2006b). Spectacled bears also have a small pseudo-thumb for grasping, which might suggest a close relationship, but basal arctoids, such as *Simo-cyon batalleri* (an ancestor of the Red panda *Ailurus fulgens*) from near Madrid, Spain, also had a well-developed radial sesamoid, which was apparently originally adapted for climbing (Salesa *et al.*, 2006a,b). Therefore, the pseudo-thumb is an ancestral feature or plesiomorphy, which cannot be used to infer that the Giant panda is an ursid. Thenius (1989) argued that while molecular data are good at establishing phylogenies, particularly where morphological specializations may confuse them, they should not dictate taxonomy. Thenius (1989) considered that the Giant panda should be placed in its own family, the Ailuropodidae, because it has a series of morphological and behavioural autapomorphies (derived features) that clearly distinguish it from the Ursidae.

Resolution of the phylogenetic relationships between the ursine bears is difficult, because they appear to have radiated rapidly about 5 million years ago (McLellan & Reinder, 1994; Yu *et al.*, 2007; Krause *et al.*, 2008; Pagès *et al.*, 2008). Most phylogenies show a close relationship between the Brown bear and Polar bear *Ursus maritimus*, while the Asian black bear *Ursus thibetanus* and American black bears are frequently shown as sister species, although the American black bear is sometimes shown to be closer to the Brown/Polar bears (Yu *et al.*, 2007; Krause

	EISENBERG (1981)	KRAUSE ET AL. (2008)	PAGÈS ET AL. (2008), WOZENCRAFT (2005); THIS PAPER
Brown bear	<i>Ursus arctos</i>	<i>Ursus arctos</i>	<i>Ursus arctos</i>
Polar bear	<i>Thalarctos maritimus</i>	<i>Ursus maritimus</i>	<i>Ursus maritimus</i>
American black bear	<i>Euarctos americanus</i>	<i>Ursus americanus</i>	<i>Ursus americanus</i>
Asian black bear	<i>Selenarctos thibetanus</i>	<i>Ursus thibetanus</i>	<i>Ursus thibetanus</i>
Sun bear	<i>Helarctos malayanus</i>	<i>Ursus malayanus</i>	<i>Helarctos malayanus</i>
Sloth bear	<i>Melursus ursinus</i>	<i>Ursus ursinus</i>	<i>Melursus ursinus</i>
Spectacled bear	<i>Tremarctos ornatus</i>	<i>Tremarctos ornatus</i>	<i>Tremarctos ornatus</i>
Giant panda	<i>Ailuropoda melanoleuca</i>	<i>Ailuropoda melanoleuca</i>	<i>Ailuropoda melanoleuca</i>

Table 1. The changing generic classification of bears.

et al., 2008; Pagès *et al.*, 2008). The greatest uncertainty remains with the phylogenetic placement and generic assignment of the Sloth bear *Melursus ursinus* and Sun bear *Helarctos malayanus*, each of which are variously shown as basal members of the Ursinae. The Sloth bear shows a number of distinct autapomorphies related to its adaptations for feeding on termites and ants, including only two pairs of upper incisors, a concave palate, well-developed lips and flanges on the nose, highly reduced molar and premolar dentition, and a low metabolic rate (Pocock, 1941; McNab, 1992). Some of the most recent phylogenies support the Sloth bear as basal to the rest of the ursines and its recognition as belonging to a monotypic genus, *Melursus* (Yu *et al.*, 2007; Krause *et al.*, 2008), while others are more uncertain (Pagès *et al.*, 2008). The Sun bear's status is

also uncertain, being alternately recognized as being in its own genus, *Helarctos*, or the most basal *Ursus*. Its skull and forelimb morphology seem to be different from those of other ursine bears and I would continue to support its recognition as *H. malayanus* until more evidence is available. In a molecular phylogeny, Pagès *et al.* (2008) distinguish *Helarctos* and *Melursus* because of the ability of *Ursus* spp to hibernate. Interestingly, there is a dramatic morphological convergence between the skulls of the Sun and Spectacled bears (Plate 1), which presumably relates to similarities in diet and foraging techniques.

But why is this generic discussion important? It has been suggested that the use of scarce conservation resources ought to be dictated partly or completely by the taxonomic and phylogenetic uniqueness of a species (e.g. Isaac *et al.*, 2007). Therefore, if

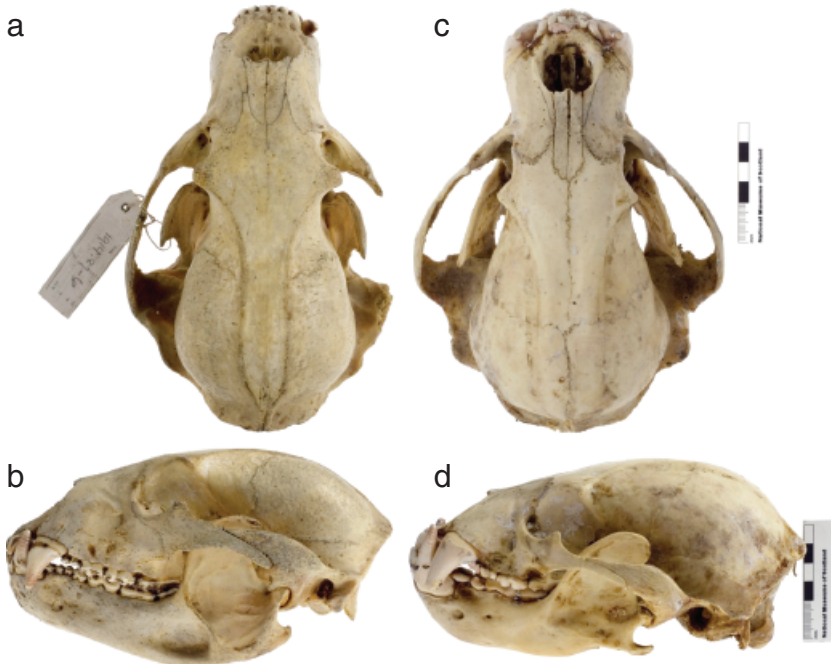


Plate 1. Dorsal and lateral views of skulls of the Sun bear *Helarctos malayanus* (right: c,d) and Spectacled bear *Tremarctos ornatus* (left: a,b) have a strikingly similar morphology, which may reflect convergent evolution owing to similarities in diet and foraging. © Neil McLean, National Museums Scotland.

the Sun and Sloth bears belong to their own genera, they would be regarded as being of greater conservation value than if they were in the genus *Ursus*. Therefore, better phylogenetic and taxonomic studies at the generic level are important not only for determining relationships between species but also they may be key to determining which species benefit from conservation action in the future.

SPECIES

The number of species of bear has remained remarkably stable for 140 years, even though there has been considerable debate as to which genera they should belong and the interrelationships between species. Several different mtDNA clades have been identified among Brown bears. Currently, mtDNA data suggest that Brown bears are paraphyletic, because the Polar bear is derived from the same mtDNA clade (clade II) as the ABC (i.e. Admiralty, Baranof and Chichagof Islands) Brown bears (Taberlet & Bouvet, 1994; Talbot & Shields, 1996a,b; Waits *et al.*, 1999), and following conventional taxonomy, two or more Brown bear species ought to be recognized. However, Brown bears from two apparently distinct mtDNA clades, the western (clade I) and eastern (clade III) clades, do interbreed in contact zones in the wild and there are apparently no consistent morphological differences between the bears from these clades (Taberlet *et al.*, 1998). It is possible that the presence of Brown bear mtDNA in Polar bears may reflect an ancient hybridization event that may even have allowed the Polar bear to survive interglacials. As the climate warmed, Brown bears were able to move further north (see Doupě *et al.*, 2007) and Polar bears may have become stranded on land owing to lack of pack ice, so that opportunities for hybridization increased, resulting in more or less complete introgression. We know from stable isotope studies that some Polar bears had a terrestrial rather than a marine diet (Kitchener & Bonsall, 1997), supporting their land-locked existence. As the climate cooled, rapid natural

selection for the Polar bear phenotype would have occurred, perhaps coupled with genetic drift, and the populations would have diverged. On 16 April 2006, a Polar bear of unusual appearance was shot on Banks Island, Northwest Territories, Canada, which was found to be a Polar bear *U. maritimus* × Grizzly bear *U. arctos horribilis* hybrid (Doupě *et al.*, 2007) and there are increasing reports of Grizzly bears in this part of the Canadian Arctic, perhaps indicating a permanent range extension. It is possible that hybridization could occur increasingly frequently during the current global warming episode. However, it is unknown if clade IIb mtDNA is fixed in Polar bears, which could support this speculation of ancient hybridization and temporary introgression, so that further sampling is required over a wide geographical area (A. Cooper, pers. comm.).

Interestingly, using nuclear DNA, and in contrast to their mtDNA data, Pagès *et al.* (2008) found that Brown and Polar bears are reciprocally monophyletic, suggesting an ancient hybridization event (I. Barnes, pers. comm.).

SUBSPECIES

Polar bear *U. maritimus*

The Polar bear is regarded as a monotypic species. Although subspecies have been proposed in the past, none are recognized today. Wilson (1976) found that there was clinal variation in skull morphometrics across the Polar bear's North American range with the possible exception of a distinct population in South Alaska, which was proposed as a subspecies. A recent analysis of population genetics was unable to support the recognition of subspecies but it did recognize some geographical structuring of the global population (Paetkau *et al.*, 1999).

Brown bear *U. arctos*

With its widespread distribution in the northern hemisphere across a wide range of habitats, it is not surprising that the Brown bear shows a great deal of phenotypic variation.

This has led to the description of a plethora of subspecies based on morphological differences. Among those traditionally recognized are: Eurasian brown bear *Ursus arctos arctos*, Syrian bear *Ursus arctos syriacus*, the now-extinct Atlas bear *Ursus arctos crowtheri*, Isabelline or Red bear *Ursus arctos isabellinus*, Blue bear *Ursus arctos pruinosus*, Kamchatka bear *Ursus arctos beringianus*, Hairy-eared bear *Ursus arctos lasiotus*, Kodiak bear *Ursus arctos middendorffi*, Grizzly bears *Ursus arctos horribilis* and *Ursus arctos dalli*, etc. (Pocock, 1932a,b; Hall, 1981).

Morphological investigations have not been forthcoming in recent years [e.g. Erdbrink (1953) is one of the most recent], possibly owing to the difficulty of obtaining sufficiently large samples of a highly variable species, which now occupies a highly fragmented distribution in many parts of its range. However, molecular studies abound, although many of these are restricted to mtDNA analyses in particular range countries or regions (e.g. Saarma *et al.*, 2007), so that a clear picture of what genetic variation means taxonomically is not always possible. The lack of information from nuclear DNA has also led to misinterpretations of the meaning of mtDNA phylogenies. For example, Taberlet & Bouvet (1994) identified two main mtDNA lineages in Eurasian Brown bears; a western one, comprising two subclades, and an eastern one stretching from eastern Europe through northern Eurasia [see also Loreille *et al.* (2001) and Hofreiter *et al.* (2002) for relationships with the extinct Cave bear *Ursus spelaeus*]. Contact zones were found in Scandinavia and central Europe (Taberlet *et al.*, 1998). These subclades were assumed to have arisen in refugia in the Iberian, Italian and Balkan peninsulas when populations were thought to have been isolated during the Last Glacial Maximum (LGM), which was the peak of the last Ice Age about 20 000 years ago. However, Valdiosera *et al.* (2007) examined ancient mitochondrial DNA from Brown bear fossils in Europe, from Spain, France, Germany, Italy and Romania. Combined with existing aDNA data, they claimed that gene flow occurred between the

southern refugia of the western clade throughout the LGM, so that today's pattern of geographical variation is the result of a high degree of ♀ philopatry and a drastic reduction in geographical distribution during the late Holocene, probably owing to human-mediated habitat loss and hunting. This study emphasizes that today's phylogeographical patterns may not reflect those in deeper time and hence caution should be exercised in developing conservation management plans for bears based only on phylogeographies of mtDNA.

In Scandinavia, both western and eastern clades were found to be separated by more than 130 km with little evidence for contact between them (Taberlet & Bouvet, 1994; Taberlet *et al.*, 1998). The Scandinavian populations were originally subdivided into four management units based on mtDNA haplotypes but this was subsequently reduced to three by Manel *et al.* (2004). However, it should be noted that ♂-mediated gene flow occurs between these sub-populations, so that the pattern of mtDNA haplotypes we see today reflects a high degree of ♀ philopatry as a result of historical colonization patterns following the last glaciation and into the early Holocene (Taberlet *et al.*, 1995). Similar ♂-mediated gene flow is seen between North American Brown bear populations, despite ♀ philopatry reinforcing an apparent geographical separation between mtDNA clades (Paetkau *et al.*, 1998; Barnes *et al.*, 2002).

Overall five mtDNA clades were originally identified in the Brown bear (Waits *et al.*, 1999) (Table 2) but a recent analysis of aDNA has revealed a sixth basal clade, which was found in subfossil bones from two caves in Algeria and Morocco (Calvignac *et al.*, 2008). This study supports the view that the Atlas bear *U. a. crowtheri* was a distinct subspecies, although comparison with Middle Eastern bears *U. a. syriacus* would be required to confirm this. Other North African finds were from the European western clade (V), which suggests these Brown bears were imported to North Africa, possibly by the Romans.

A small relict population of very small Brown bears from the inhospitable Gobi desert

CLADE	GEOGRAPHICAL DISTRIBUTION	NOMINAL SUBSPECIES/SPECIES
I	Western Europe, Balkans, southern Scandinavia	<i>arctos, marsicanus</i>
II	ABC Islands/Arctic	<i>horribilis/U. maritimus</i>
III	Eastern Alaska, northern Canada, eastern Siberia, Honshu, Japan	<i>horribilis</i>
IV	Southern Canada, northern USA	<i>horribilis</i>
V	Eastern Europe, northern Asia, Caucasus, ?Middle East, Tibet, China, Japan	<i>arctos, beringianus, syriacus, pruinosus, lasiotus, middendorffi, horribilis</i>
VI	Atlas Mountains, North Africa, ?Middle East	<i>crowtheri, ?syriacus</i>
VII	W Himalayas, Gobi	<i>isabellinus</i>

Table 2. Mitochondrial DNA clades of the Brown bear *Ursus arctos* (Waits *et al.*, 1999; Barnes *et al.*, 2002; Galbreath *et al.*, 2007; Calvignac *et al.*, 2008). It is unclear whether *syriacus* from the Middle East should be in clade V or VI because data are not available.

was identified by Schaller (1998) as probably belonging to the Isabelline bear *U. a. isabellinus*. A recent mtDNA study confirmed this identification but also showed that the Isabelline bear formed a distinct ancient (seventh) clade close to the Polar bears/ABC Brown bears of North America (Galbreath *et al.*, 2007). Moreover, this limited analysis confirmed that the blue bear *U. a. pruinosus* of Tibet, formed a subclade within the wider eastern Eurasian/North American clade (clade V).

In North America numerous species and subspecies names have been given to local populations of Brown bears, and mtDNA studies have identified three haplotypes that are geographically separated. These include the ABC Islands (which also share their mtDNA haplotype with Polar bears; clade II), the United States haplotype (clade IV) and the Alaskan/Canadian haplotype (clade III) (Talbot & Shields, 1996a,b).

It was originally assumed that the pattern of three allopatric haplotypes in North America reflected three different colonizations

via the Bering land bridge during the Pleistocene (Talbot & Shields, 1996a,b). However, an aDNA analysis of fossil Brown bear bones from Alaska has revealed that all three extant haplotypes occurred in Alaska and the Yukon 35 000–45 000 radiocarbon years ago (Leonard *et al.*, 2000). Therefore, today's phylogeographical pattern could only have occurred relatively recently. A more in-depth study with far larger numbers of samples confirmed that three haplotypes co-existed in Alaska before 35 000 BP, and two were found between 10 000 and 21 000 BP, before the present-day phylogeographical pattern was established (Barnes *et al.*, 2002). Brown bears were absent from Alaska during 21 000–35 000 BP and were only able to recolonize North America once the huge carnivorous Short-faced bear *Arctodus simus* was forced out by the spreading ice sheets of the Last Ice Age. This study concluded that the present phylogeographical pattern was established naturally after the end of the Last Ice Age or by the possible impact of human activities through megafaunal extinctions or later habitat loss and persecution.

Kurtén (1973) recognized three North American subspecies; *horribilis* in most of mainland North America, *dalli* representing the large coastal bears of British Columbia and Alaska and the huge *middendorffi* from Kodiak Island. Using microsatellites (nuclear DNA), Paetkau *et al.* (1998) found that despite their distinctive mtDNA, the ABC bears were not genetically isolated from mainland *horribilis* and the coastal grizzlies (*dalli*) were part of the contiguous continental Grizzly bear population. Only the Kodiak bear showed evidence of little or no genetic exchange with mainland populations. Therefore, it is inappropriate to use mtDNA alone, especially where ♀♀ are highly philopatric, in order to infer colonization patterns of Brown bears and hence to inform management of present populations.

American black bear *U. americanus*

Up to 16 subspecies of American black bear have been recognized (Hall, 1981) but this

would seem to be unlikely, given its former contiguous distribution. Recent phylogeographical studies have identified two mtDNA lineages; one in the west, mainly coastal in distribution, while the other seems to occupy the rest of the distribution (Wooding & Ward, 1997; Stone & Cook, 2000), but these lineages overlap in south-east Alaska. There is also evidence of recent contact and hybridization between them elsewhere (Wooding & Ward, 1997). Other studies are more localized. For example, a study of skull morphometrics in the eastern United States and Canada showed clinal variation in body size from large animals in the south (Louisiana and eastern Texas) to small animals in the north (Quebec), which appears to reflect differences in abundance of food (Kennedy *et al.*, 2002). Another study examined the subspecific status of black bears in the White River National Wildlife Refuge, Arkansas (Warrilow *et al.*, 2001). However, sampling has not been comprehensive enough from throughout the geographical distribution in any of the published studies carried out so far to answer the question as to how many subspecies there may be. It is possible that the two mtDNA lineages may represent subspecies, although without examining nuclear DNA and morphological data, this is mere speculation. It seems more likely that most variation in American black bears is clinal with no subspecies recognized.

Asian black bear *U. thibetanus*

There are no recent taxonomic or phylogeographical studies on the Asian black bear (e.g. Pocock, 1932a,b, 1941). Several subspecies have been described, including some on islands (Japan ssp *Ursus thibetanus japonicus*; Taiwan ssp *Ursus thibetanus formosanus*), which may be distinct. The Ussuri black bear *Ursus thibetanus ussuricus*, like the Amur tiger *Panthera tigris altaica*, is separated from the rest of its conspecifics by more than 1500 km (Servheen *et al.*, 1998). Although the Asian black bear's distribution was once contiguous from the Russian Far East to southern Asia, the loss of woodland

habitat since the beginning of the Neolithic era *c.* 9000 years ago and the exploitation of Asian black bears for traditional medicines by the early civilizations in northern China since at least the Shang dynasty *c.* 3500 years ago (Barnes, 1999; Ren, 2000), almost certainly led to the development of this disjunct distribution. Therefore, by default of their complete isolation Ussuri black bears should probably be treated as a distinct subspecies. Other subspecies are described from Pakistan in the west to south-east Asia but it is unclear whether these represent clinal variation or distinct geographical variation.

Sloth bear *M. ursinus*

The Sloth bear is usually regarded as having two subspecies; *Melursus ursinus ursinus* from the Indian peninsula and *Melursus ursinus inornatus* from Sri Lanka. They are apparently distinguishable on size [mean greatest lengths of skull: India (322 mm, $n = 6$), Sri Lanka (280 mm, $n = 4$): Pocock, 1941; Corbet & Hill, 1992]. However, I am not aware of any recent molecular studies and the sample sizes for the skull differences are very small. It is possible that there is clinal variation in skull size from larger animals in the north to smaller animals in the south but this has not been examined so far.

Sun bear *H. malayanus*

The Sun bear is also usually regarded as having two subspecies; *Helarctos malayanus malayanus* on the Asian mainland and Sumatra, and *Helarctos malayanus eurypilus* from Borneo (Chasen, 1940; Ellerman & Morrison-Scott, 1951; Corbet & Hill, 1992). A recent analysis of skull morphometrics by Meijaard (2004) has confirmed the distinctiveness of the Bornean population, which has a smaller skull size [mean condylobasal lengths of skull: Borneo (206.3 mm), Sumatra (227.3 mm), Asia (235.3 mm)] but a relatively longer upper tooththrow. However, there was no distinction between Sumatran and mainland samples. Meijaard (2004) referred also to a limited unpublished molecular study on 300 base pairs of mtDNA from

Sumatran and Bornean Sun bears by L. Waits, who found five clades, which did not fully accord with geography, suggesting that some gene flow may have occurred between the islands during the LGM. Further molecular and morphological research could help to confirm these tentative conclusions.

Spectacled bear *T. ornatus*

The spectacled bear is treated as a monotypic species (e.g. Mondolfi, 1989), although there is considerable individual variation in facial markings. The Spectacled bear is the only survivor of the radiation of New World Short-faced bears, subfamily Tremarctinae, which included the formidable Short-faced bear *A. simus*, of North America (Kurtén & Anderson, 1980; Krause *et al.*, 2008).

Five other specific or subspecific names have been given to Spectacled bears based on differences in body proportions, claw length, facial markings, and skull sizes and proportions. For example, Hornaday (1911) gave the name *Ursus ornatus thomasi* to a Spectacled bear from the Andes of southern Colombia, which was living at the New York Zoological Gardens, USA, on the basis of a lack of white facial markings. However, this diagnostic character as with the others listed above are examples of individual variation.

Giant panda *A. melanoleuca*

Until recently the Giant panda was regarded as a monotypic species but a subspecies, *Ailuropoda melanoleuca qinlingensis*, from the Qinling Mountains, Shaanxi province, has been described based on genetic differences from Sichuan Giant pandas *Ailuropoda melanoleuca melanoleuca* (Wang *et al.*, 2003; Wan *et al.*, 2005). The proposed new subspecies differs morphologically, having a browner pelage and smaller skull with larger molars (Wan *et al.*, 2005).

DYNAMIC BIOGEOGRAPHY

Given the limitations of current samples, biogeographical modelling may offer ways of interpreting existing molecular and mor-

phological data, as well as providing a framework for focused future research. This approach has been taken for the Tiger *Panthera tigris*, which is traditionally regarded as having eight (or even nine) subspecies, apparently supported by molecular data (Kitchener, 1999; Luo *et al.*, 2004). However, morphological data suggest perhaps two lineages that derive from the Asian mainland and the Sunda islands (Kitchener, 1999; Mazák, in press). A biogeographical model by Kitchener & Dugmore (2000), which took into account changes in habitat since the LGM 20 000 years ago, supported both morphological and molecular analyses (Luo *et al.*, 2004; Mazák, in press), even though their conclusions as to subspecies were not in accord. This approach would be of great benefit to ursids, particularly the very widespread Brown, American black and Asian black bears. Indeed, the results from Kitchener & Dugmore (2000) are broadly applicable to the Asian black bear, which would suggest that perhaps only two subspecies would be recognized; the mainland *Ursus thibetanus thibetanus* and the Japanese black bear *U. t. japonicus*. It is likely that the Taiwanese black bear would have been contiguous with the mainland population when sea levels were lower during the LGM, and the Ussuri black bear would once have been in direct contact with Chinese populations and was derived from them following the end of the last Ice Age. The now complete isolation of the Ussuri black bear probably warrants its recognition as a distinct subspecies, *U. t. ussuricus*, even though the cause of its separation is likely to have been human activity. Molecular and morphological studies could test whether mainland variation is largely clinal and whether the Japanese black bear is distinctive.

CONSEQUENCES OF LACK OF KNOWLEDGE

Lack of a clear taxonomy for bears may have important consequences for conservation at the levels of species, subspecies and local populations, both in captivity and in the wild.

For example, the recognition of fewer monotypic genera (e.g. if the Sun bear were considered congeneric with other *Ursus* spp) could affect whether some species are considered for conservation action, especially if resources are limited. The current uniqueness of the Sun bear *H. malayanus* could disappear instantly if reclassified as *Ursus malayanus*, downgrading it in the conservation stakes (see differing points of view: Krause *et al.*, 2008; Pagès *et al.*, 2008). Clearly, we must take great care in whether to assign species to unique genera or not in the light of new data, and it is important to take all evidence into account rather than only short fragments of mtDNA.

Poor knowledge of subspecies often results in inadvertent hybridization in captivity so that conservation effort is wasted, and source stock may no longer be available from the wild or the remaining pure captive population may be too small to prevent high levels of inbreeding. A classic example was the discovery that the Association of Zoos and Aquariums (AZA) Asian lion *Panthera leo persica* Species Survival Plan[®] Program was totally compromised by unrecorded hybridization with African lions (O'Brien *et al.*, 1987); and the Amur leopard *Panthera pardus orientalis* captive-breeding programme will always be contaminated by the influence of a founder that was not an Amur leopard (Uphyrkina *et al.*, 2002). The decision by the AZA to allow hybridization of Sloth bear subspecies in North American zoos is surely insupportable if we want to maintain common standards and the integrity of *ex situ* conservation programmes. A huge proportion of enclosure space in European zoos is taken up by Brown bears (and Asian black bears) of unknown or mixed origin, and while many of these zoos will want to maintain 'local' Brown bears, much enclosure space could be freed up for bears of known threatened species and subspecies that desperately require extra holders (e.g. Sloth bears) for the establishment of viable captive populations.

Lack of recognition of subspecies in the wild may result in loss of unique populations, or the recognition of too many subspecies

may prevent mixing of depleted gene pools owing to local population bottlenecks. The recent confirmation of the Gobi bear as being effectively a malnourished Isabelline bear *U. a. isabellinus* (Galbreath *et al.*, 2007), may lead us to question whether conservation resources should be directed to a tiny population at the margin of the main subspecies range. In contrast the recent proposal of a new Giant panda subspecies (Wang *et al.*, 2003; Wan *et al.*, 2005) could have important consequences for the conservation of this species (if inadvertent hybridization has not already occurred), which would in theory require double the enclosure space to cater for two subspecies. Great care must be taken to be certain that new taxa really do exist before adding to the pile of scientific names that burden the bears.

Reintroductions may also suffer from lack of knowledge about the intraspecific taxonomy of a species. For example, following the discovery of two mtDNA subclades of Brown bears in Europe (Taberlet & Bouvet, 1994), the decision was made to reinforce the seriously threatened Pyrenean brown bear population (the western subclade Ia) by introductions of animals from Croatia (subclade Ib), which was widely criticized at the time because of the genetic mixing of two different subclades. However, later studies of fossil Brown bears showed that the current geographical distribution of these subclades could not be supported, so that they are an artefact of post-glacial colonization and/or human impact (Hofreiter *et al.*, 2004; Valdiosera *et al.*, 2007). Similarly, the isolation of the mtDNA haplotype II on the ABC Islands does not constitute the recognition of these bears as a unique subspecies, because ♂-mediated gene flow occurs at a relatively high level with mainland Grizzly bears (Paetkau *et al.*, 1998). We must take care that genetic evidence for colonization history is not confused with the unnecessary recognition of subspecies.

Even though Polar bears are monotypic, there is some genetic substructuring (Paetkau *et al.*, 1999) and some big differences in size and shape of skulls (Wilson, 1976) within the

SPECIES	GENERIC STATUS	SPECIES STATUS	SUBSPECIES STATUS	REFERENCES
Brown/grizzly bear <i>Ursus arctos</i>	++	++	?? – very uncertain; distinct geographical variation, but lacking comprehensive global molecular and morphological study	Paetkau <i>et al.</i> (1998), Galbreath <i>et al.</i> (2007), Calvignac <i>et al.</i> (2008)
Polar bear <i>Ursus maritimus</i>	+++; formerly <i>Thalarctos</i>	++	++ – subspecies not usually recognized; geographical variation fairly well understood	Wilson (1976), Paetkau <i>et al.</i> (1999)
American black bear <i>Ursus americanus</i>	++, formerly <i>Euarctos</i>	++	?? – very uncertain; comprehensive morphological and molecular studies would be beneficial	Wooding & Ward (1997), Stone & Cook (2000), Kennedy <i>et al.</i> (2002)
Asian black bear <i>Ursus thibetanus</i>	++, formerly <i>Selenarctos</i>	++	? – uncertain, especially in China and South East Asia; requires comprehensive morphological and molecular studies	Pocock (1941)
Sloth bear <i>Melursus ursinus</i>	+, sometimes placed in <i>Ursus</i>	++	? – uncertain; two subspecies recognized, but requires confirmation from molecular and further morphological research	Corbet & Hill (1992)
Sun bear <i>Helarctos malayanus</i>	+, sometimes placed in <i>Ursus</i>	++	? – uncertain; two subspecies recognized, but requires confirmation from further morphological and molecular research	Meijaard (2004)
Spectacled bear <i>Temarcotus ornatus</i>	+++; subfamily Tremarctinae	++	+ – usually regarded as monotypic, but much individual pelage variation; molecular and morphological research recommended	Mondolfi (1989)
Giant panda <i>Ailuropoda melanoleuca</i>	+++; subfamily Ailuropodinae; sometimes placed in monotypic family, Ailuropodidae	++	? – recent molecular research suggests two subspecies, but further morphological and molecular research recommended	Thenius (1989), Wang <i>et al.</i> (2003), Wan <i>et al.</i> (2005)

Table 3. Current knowledge of the status of family, genera, species and subspecies of all ursid species: ++, high degree of stability and certainty; +, moderate certainty, but subject to change in the light of new evidence; ??, high degree of uncertainty; ?, moderate degree of uncertainty.

global population. Is this variation in morphology the result of phenotypic responses to different local food sources, or does it have a genetic component? Given that captive conservation of Polar bears is likely to become a vital component of their future survival during the current global warming episode, we must take care not to mix Polar bears from different local populations if their morphol-

ogy and genetics point to adaptation to the local environment.

Clearly we cannot wait until all taxonomic research is completed to a common level of scientific rigour, so informed decisions will have to be made in the short to medium term by bringing together specialists in genetics and morphology, as well as field workers and zoo managers in order to pool current

knowledge effectively. However, much taxonomic research still remains to be done.

WHAT NEXT?

There is clear stability over the number of ursid species but phylogenies continue to be refined and phylogeographical studies are increasing, although they remain focused largely on mtDNA. Table 3 reviews the current knowledge of genera, species and subspecies of all ursids and recommends further areas for research. It is clear that all species require urgently comprehensive studies of genetic (both mitochondrial and nuclear DNA) and morphological variation in order to ascertain which of the many described subspecies have taxonomic validity for ensuring the effectiveness of conservation action and implementation of national and international legislation. Every opportunity should be taken for the ethical and legal collection of samples for these studies to enhance those existing in museums and laboratories worldwide.

In conclusion taxonomic issues are just one important factor that is potentially compromising conservation of bears in captivity, along with issues relating to enhanced longevity, lack of opportunities for breeding and poor enclosure design and other welfare issues. In this paper I have tried to explain why it is important for both captive and wild conservation of bears that our knowledge of bear taxonomy is as good as it can be, so that we can ensure that scarce conservation resources are appropriately targeted without wasting effort through accidental hybridization or unnecessary splitting of populations. Molecular methods can be very powerful in looking at relationships between populations, but they are not a panacea and should be viewed critically in relation to other kinds of evidence. Zoo managers can assist advances in taxonomy by supplying samples for molecular research and ensuring that dead bears are preserved, whenever possible, in museum collections for morphological research. Zoos can themselves contribute basic information such as body measurements and weights, and

through basic photography, they can record seasonal and interannual changes in coat colour as fur is moulted and is subject to fading and wear through the year. These kinds of contributions from zoos are especially important for rare subspecies and/or bears with known geographical origin. All these data separately make tiny contributions to our overall knowledge, but without them we will never make progress and succeed in our mission to have effective conservation action in zoos and in the wild.

REFERENCES

- BARNES, G. L. (1999): *The rise of civilization in East Asia: the archaeology of China, Korea and Japan*. London: Thames & Hudson.
- BARNES, I., MATHEUS, P., SHAPIRO, B., JENSEN, D. & COOPER, A. (2002): Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* **295**: 2267–2270.
- CALVIGNAC, S., HUGHES, S., TOUGARD, C., MICHAUX, J., THEVENOT, M., PHILIPPE, M., HAMDINE, W. & HANNI, C. (2008): Ancient DNA evidence for the loss of a highly divergent brown bear clade during historical times. *Molecular Ecology* **17**: 1962–1970.
- CHASEN, F. N. (1940): A handlist of Malaysian mammals. *Bulletin of the Raffles Museum* No. 15: 1–209.
- CORBET, G. B. & HILL, J. E. (1992): *The mammals of the Indomalayan region: a systematic review*. London: Natural History Museum Publications, and Oxford: Oxford University Press.
- DOUPÉ, J. P., ENGLAND, J. H., FURZE, M. & PAETKAU, D. (2007): Most northerly observation of a grizzly bear (*Ursus arctos*) in Canada: photographic and DNA evidence from Melville Island, Northwest Territories. *Arctic* **60**(3): 271–276.
- EISENBERG, J. F. (1981): *The mammalian radiations*. Chicago, IL: Chicago University Press.
- ELLERMAN, J. R. & MORRISON-SCOTT, T. C. S. (1951): *Checklist of Palaearctic and Indian mammals 1758–1946*. London: Trustees of the British Museum.
- ERDBRINK, D. P. (1953): *A review of fossil and recent bears of the Old World with remarks on their phylogeny based on their dentition* **2**. Deventer, the Netherlands: Jan de Lange.
- GALBREATH, G. J., GROVES, C. P. & WAITS, L. P. (2007): Genetic resolution of composition and phylogenetic placement of the isabelline bear. *Ursus* **18**(1): 129–131.
- GROVES, C. P. (2001): *Primate taxonomy*. Washington, DC: Smithsonian Institution Press.
- HALL, E. R. (1981): *The mammals of North America II* (2nd edn). New York, NY: John Wiley.
- HOFREITER, M., CAPELLI, C., KRINGS, M., WAITS, L., CONARD, N., MÜNZEL, S., RABEDER, G., NAGEL, D., PAUNOVIC, M., JAMBRSIĆ, G., MEYER, S., WEISS, G. & PAABO, S. (2002): Ancient DNA analyses reveal high

- mitochondrial DNA sequence diversity and parallel morphological evolution of late Pleistocene cave bears. *Molecular Biology and Evolution* **19**: 1244–1250.
- HOFREITER, M., SERRE, D., ROHLAND, N., RABEDER, G., NAGEL, D., CONARD, N., MÜNZEL, S. & PÄÄBO, S. (2004): Lack of phylogeography in European mammals before the last glaciation. *Proceedings of the National Academy of Sciences USA* **101**: 12963–12968.
- HORNADAY, W. T. (1911): The spectacled bear. *Bulletin of the New York Zoological Society* No. 45: 747–748.
- ISAAC, N. B., TURVEY, S. T., COLLEN, B., WATERMAN, C. & BAILLIE, J. E. M. (2007): Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE* **2**(3): e296. DOI: 10.1371/journal.pone.0000296. Available at <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0000296>.
- KENNEDY, M. L., KENNEDY, P. K., BOGAN, M. A. & WAITS, J. L. (2002): Geographic variation in the black bear (*Ursus americanus*) in the eastern United States and Canada. *The Southwestern Naturalist* **47**: 257–266.
- KITCHENER, A. C. (1999): Tiger distribution, phenotypic variation and conservation issues. In *Riding the tiger. Tiger conservation in human-dominated landscapes*: 19–39. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge: Cambridge University Press.
- KITCHENER, A. C. & BONSALE, C. (1997): AMS radiocarbon dates for some extinct Scottish mammals. *Quaternary Newsletter*. No. 83: 1–11.
- KITCHENER, A. C. & DUGMORE, A. J. (2000): Biogeographical change in the tiger, *Panthera tigris*. *Animal Conservation* **3**: 113–124.
- KRAUSE, J., UNGER, T., NOËON, A., MALASPINAS, A.-S., KOLOKTRONIS, S.-O., STILLER, M., SOIBELZON, L., SPRIGGS, H., DEAR, P. H., BRIGGS, A. W., BRAY, S. C. E., O'BRIEN, S. J., RABEDER, G., MATHEUS, P., COOPER, A., SLATKIN, M., PÄÄBO, S. & HOFREITER, M. (2008): Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene–Pliocene boundary. *BMC Evolutionary Biology* **8**: 220–232.
- KURTÉN, B. (1973): Transberingian relationships of *Ursus arctos* Linné (brown and grizzly bears). *Commentationes Biologicae* **65**: 1–10.
- KURTÉN, B. & ANDERSON, E. (1980): *Pleistocene mammals of North America*. New York, NY: Columbia University Press.
- LEONARD, J. A., WAYNE, R. K. & COOPER, A. (2000): Population genetics of Ice Age brown bears. *Proceedings of the National Academy of Sciences USA* **97**: 1651–1654.
- LOREILLE, O., ORLANDO, L., PATOU-MATHIS, M., PHILIPPE, M., TABERLET, P. & HÄNNI, C. (2001): Ancient DNA analysis reveals divergence of cave bear, *Ursus spelaeus*, and brown bear, *Ursus arctos*, lineages. *Current Biology* **11**: 200–203.
- LUO, S. J., KIM, J. H., JOHNSON, W. E., VAN DER WALT, J., MARTENSON, J., YUKHI, N., MIQUELLE, D. G., UPHYRINKA, O., GOODRICH, J. M., QUIGLEY, H. B., TILSON, R., BRADY, G., MARTELLI, P., SUBRAMANIAM, V., MCDUGAL, C., HEAN, S., HUANG, S. Q., PAN, W., KARANTH, U. K., SUNQUIST, M., SMITH, J. L. & O'BRIEN, S. J. (2004): Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *PLoS Biology* **2**: 2275–2293. Available at <http://biology.plosjournals.org/perlserv/?request=get-document&doi=10.1371%2Fjournal.pbio.0020442>.
- McLELLAN, B. & REINDER, D. C. (1994): A review of bear evolution. *International Conference on Bear Research and Management* **9**(1): 85–96.
- McNAB, B. K. (1992): Rate of metabolism in the termite-eating sloth bear (*Ursus ursinus*). *Journal of Mammalogy* **73**: 168–172.
- MANEL, S., BELLEMAIN, E., SWENSON, J. E. & FRANÉIS, O. (2004): Assumed and inferred spatial structure of populations: the Scandinavian brown bears revisited. *Molecular Ecology* **13**: 1327–1331.
- MAYR, E. & ASHLOCK, P. D. (1991): *Principles of systematic biology*. New York, NY: McGraw-Hill.
- MAZÁK, J. (In press): Craniometric variation in the tiger (*Panthera tigris*): implications for patterns of diversity, taxonomy and conservation. *Mammalian Biology*. DOI: 10.1016/j.mambio.2008.06.003.
- MEIJAARD, E. (2004): Craniometric differences among Malayan sun bears (*Ursus malayanus*): evolutionary and taxonomic implications. *The Raffles Bulletin of Zoology* **52**(2): 665–672.
- MONDOLFI, E. (1989): Notes on the distribution, habitat, food habits, status and conservation of the spectacled bear (*Tremarctos ornatus* Cuvier) in Venezuela. *Mammalia* **53**: 525–544.
- O'BRIEN, S. J. & MAYR, E. (1991): Bureaucratic mischief: recognizing endangered species and subspecies. *Science* **251**: 1187–1188.
- O'BRIEN, S. J., JOSLIN, P., SMITH III, G. L., WOLFE, R., SCHAFER, N., HEATH, E., OTT-JOSLIN, J., RAWAL, P. P., BHATTACHARJEE, K. K. & MARTENSON, J. S. (1987): Evidence for African origins of founders of the Asiatic lion species survival plan. *Zoo Biology* **6**: 99–116.
- PAETKAU, D., SHIELDS, G. F. & STROBECK, C. (1998): Gene flow between insular, coastal and interior populations of brown bears in Alaska. *Molecular Ecology* **7**: 1283–1292.
- PAETKAU, D., AMSTRUP, S. C., BORN, E. W., CALVERT, W., DEROCHE, A. E., GARNER, G. W., MESSIER, F., STIRLING, I., TAYLOR, M. K., WIIG, Ø. & STROBECK, C. (1999): Genetic structure of the world's polar bear populations. *Molecular Ecology* **8**: 1571–1584.
- PAGÈS, M., CALVIGNAC, S., KLEIN, C., PARIS, M., HUGHES, S. & HÄNNI, C. (2008): Combined analysis of fourteen nuclear genes refines the Ursidae phylogeny. *Molecular Phylogenetics and Evolution* **47**: 73–83.
- POCOCK, R. I. (1932a): The black and brown bears of Europe and Asia. *Journal of the Bombay Natural History Society* **35**: 771–823.
- POCOCK, R. I. (1932b): The black and brown bears of Europe and Asia. *Journal of the Bombay Natural History Society* **36**: 101–138.
- POCOCK, R. I. (1941): *The fauna of British India including Ceylon and Burma. Mammalia vol. II Carnivora (continued from vol. I). Suborders Aeluroidea (part) and Arctoidea*. London: Taylor and Francis.
- REN, G. (2000): Decline of the mid- to late Holocene forests in China: climatic change or human impact? *Journal of Quaternary Science* **15**: 273–281.

- SAARMA, U., HO, S. Y. W., PYBUS, O. G., KALJUSTE, M., TUMANOV, I. L., KOJOLA, I., VOROBIEV, A. A., MARKOV, N. I., SAVELJEV, A. P., VALDMANN, H., LYAPUNOVA, E. A., ABRAMOV, A. V., MÄNNIL, P., PUTCHKOVSKIY, S. V. & RÖKOV, A. M. (2007): Mitogenetic structure of brown bears (*Ursus arctos* L.) in northeastern Europe and a new time frame for the formation of European brown bear lineages. *Molecular Ecology* **16**: 401–413.
- SALESA, M. J., ANTÖN, M., PEIGNÉ, S. & MORALES, J. (2006a): Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proceedings of the National Academy of Sciences USA* **103**: 379–382.
- SALESA, M. J., SILICEO, G., ANTÖN, M., ABELLA, J., MONTAÑA, P. & MORALES, J. (2006b): “Anatomy of the ‘false thumb’ of *Temarcos ornatus* (Carnivora, Ursidae, Temarctinae): phylogenetic and functional implications. *Estudios Geológicos* **62**: 389–394.
- SCHALLER, G. B. (1998): *Wildlife of the Tibetan steppe*. Chicago, IL: Chicago University Press.
- SERVHEEN, C., HERRERO, S. & PEYTON, B. (Eds) (1998): *Bears. Status survey and conservation action plan*. Gland, Switzerland: IUCN.
- SHIELDS, G. F., ADAMS, D., GARNER, G., LABELLE, M., PIETSCH, J., RAMSAY, M., SCHWARTZ, C., TITUS, K. & WILLIAMSON, S. (2000): Phylogeography of mitochondrial DNA variation in brown bears and polar bears. *Molecular Phylogenetics and Evolution* **15**: 319–326.
- STONE, K. D. & COOK, J. A. (2000): Phylogeography of black bears (*Ursus americanus*) of the Pacific Northwest. *Canadian Journal of Zoology* **78**: 1218–1223.
- TABERLET, P. & BOUVET, J. (1994): Mitochondrial DNA polymorphism, phylogeography, and conservation genetics of the brown bear *Ursus arctos* in Europe. *Proceedings of the Royal Society London B* **255**: 195–200.
- TABERLET, P., SWENSON, J. E., SANDEGREN, F. & BJÄRVALL, A. (1995): Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear *Ursus arctos* in Scandinavia. *Conservation Biology* **9**: 1255–1261.
- TABERLET, P., FUMAGALLI, L., WUST-SAUCY, A.-G. & COSSON, J.-F. (1998): Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* **7**: 453–464.
- TALBOT, S. L. & SHIELDS, G. F. (1996a): Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecular Phylogenetics and Evolution* **5**: 477–494.
- TALBOT, S. L. & SHIELDS, G. F. (1996b): A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes. *Molecular Phylogenetics and Evolution* **5**: 567–575.
- THENIUS, E. (1989): Molekulare und “adaptive” Evolution, Kladistik und Stammesgeschichte. Ergänzungen zu einer Arbeitshypothese. *Zeitschrift für Zoologische Evolutionsforschung* **27**: 94–105.
- UPHYRKINA, O., MIQUELLE, D., QUIGLEY, H., DRISCOLL, C. & O'BRIEN, S. J. (2002): Conservation genetics of the Far Eastern leopard (*Panthera pardus orientalis*). *The Journal of Heredity* **93**: 303–311.
- VALDIOSERA, C. E., GARCÍA, N., ANDERUNG, C., DALÉN, L., CRÉGUT-BONNOURE, E., KAHLKE, R.-D., STILLER, M., BRANDSTRÖM, M., THOMAS, M. G., ARSUAGA, J. L., GÖTHERSTRÖM, A. & BARNES, I. (2007): Staying out in the cold: glacial refugia and mitochondrial DNA phylogeography in ancient European brown bears. *Molecular Ecology* **16**: 5140–5148.
- WAITS, L., PAETKAU, D. & STROBECK, C. (1998): Genetics of the bears of the world. In *Bears. Status survey and conservation action plan*: 25–32. Servheen, C., Herrero, S. & Peyton, B. (Eds). Gland, Switzerland: IUCN.
- WAITS, L. P., SULLIVAN, J., O'BRIEN, S. J. & WARD, R. H. (1999): Rapid radiation events in the family Ursidae indicated by likelihood phylogenetic estimation from multiple fragments of mtDNA. *Molecular Phylogenetics and Evolution* **13**: 82–92.
- WAN, Q.-H., WU, H. & FANG, S.-G. (2005): A new subspecies of giant panda (*Ailuropoda melanoleuca*) from Shaanxi, China. *Journal of Mammalogy* **86**: 397–402.
- WANG, Q.-H., FANG, S.-G., WU, H. & FUJIHARA, T. (2003): Genetic differentiation and subspecies development of the giant panda as revealed by DNA fingerprinting. *Electrophoresis* **24**: 1353–1359.
- WARRILLOW, J., CULVER, M., HALLERMAN, E. & VAUGHAN, M. (2001): Subspecific affinity of black bears in the White River National Wildlife Refuge. *The American Genetics Association* **92**: 226–233.
- WILSON, D. E. (1976): Cranial variation in polar bears. In *Bears: their biology and management. A selection of papers from the third international conference on bears*: 447–453. Pelton, M. R., Lentfer, J. W. & Folk, G. E. (Eds). Morges, Switzerland: IUCN.
- WOODING, S. & WARD, R. (1997): Phylogeography and Pleistocene evolution in the North American black bear. *Molecular Biology and Evolution* **14**: 1096–1105.
- WOZENCRAFT, W. C. (2005): Order Carnivora. In *Mammal species of the world. A taxonomic and geographic reference* (3rd edn): 532–628. Wilson, D. E. & Reeder, D. M. (Eds). Baltimore, MD: The Johns Hopkins University Press.
- YU, L., LI, Q., RYDER, O. A. & ZHANG, Y. (2004): Phylogeny of the bears (Ursidae) based on nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* **32**: 480–494.
- YU, L., LI, Y.-W., RYDER, O. A. & ZHANG, Y.-P. (2007): Analysis of complete mitochondrial genome sequences increases phylogenetic resolution of bears (Ursidae), a mammalian family that experienced rapid speciation. *BMC Evolutionary Biology* **7**: 198–209.
- ZHANG, Y. & RYDER, O. (1994): Phylogenetic relationships of bears (the Ursidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **3**: 351–359.

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