Introduction

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> I consider the mountainside a special place, a place with power, as I do certain other valleys and basins . . . where grizzlies still roam. I return to these places year after year, to keep track of the bears and to log my life. The bears provided a calendar for me when I got back from Vietnam, . . . I had trouble with a world whose idea of vitality was anything other than the naked authenticity of living or dying. The world paled, as did all that my life had been before, and I found myself estranged from my own time. Wild places and grizzly bears solved this problem.
> *Doug Peacock, 1990,* Grizzly Years

Bears have fascinated people since ancient times. The relationship between bears and humans dates back tens of thousands of years, during which time we have also competed with bears for shelter and food. Our strong link with bears is also attested to by the Neanderthal burial of "Le Regourdou," in France, where the skeleton of a Neanderthal in a fetal position was found under a funeral slab surrounded by the bones of a brown bear, probably sacrificed for the burial. Bears were also represented in rock paintings in caves inhabited by our ancestors in Europe. The bears depicted by our ancestors were cave bears, which roamed Eurasia until about 24,000 years ago when they became extinct during the Last Glacial Maximum. Recently, gene flow between extinct cave bears and brown bears has been discovered, providing direct evidence for ancestral hybridization between the two species which resulted in the modern *Ursus arctos* that we all know (Chapter 1).

In human culture, bears also represent an important figure in Native American mythologies. For example, the bear is a symbol of power and strength. In fact, warriors of some tribes wore necklaces of bear claws. Bears also play a major role in several religious ceremonies in many North American tribes, which used to have a bear dance as part of their tribal traditions, and they represent an important clan animal in some native cultures, for example in tribes such as the Cherokees, Creeks, Hurons, and Navajos. Furthermore, bears are often found carved on totem poles of several tribes of north-western North America.

Bears have also influenced the culture of many tribes in Asia. In fact, they are important animals for some tribes in Siberia, and the people of the Hokkaido and Ryukyu islands in Japan. For example, the Ainu people in Japan consider the bear as the "Spirit of the Mountains." In Russia, at a Fat'yanovo cultural site dated to around 1500 BC, necklaces made with bear teeth were found, and other Neolithic findings have been discovered as far north as Lake Ilmen, in the Russian oblast of Nóvgorod. Several bear claws with bronze mounting, dated between the ninth and eleventh centuries, were also discovered among a Finno-Ugrian group located along the River Tsna (a river in the Tambov and Ryazan oblasts of Russia), whereas another Finno-Ugrian group in the Urals venerated the bear as a symbol of heroism.

The images of bears in popular culture have helped them to become an icon that most people know and love. The most famous example is the teddy bear, which has been one of the most popular stuffed animals since the early 1900s and continues to be a favorite of children. Developed almost simultaneously by toymakers Morris Michtom in the US and Margarethe Steiff in Germany, and then named after US President Theodore "Teddy" Roosevelt, the teddy bear is an iconic children's toy celebrated in stories, songs, and films. More recently, Baloo from *The Jungle Book*, Winnie the Pooh, Yogi and Bubu, and Masha and the Bear tell us that the strong link between people and bears, which started more than 80,000 years ago, continues today.

At the present time eight bear species are recognized, from the very popular polar bear, giant panda, brown bear, and American black bear to the lesser-known Andean bear, sun bear, sloth bear, and Asiatic black bear. In Chapter 1, the authors follow a different taxonomy for sun bear (*Helarctos malayanus*) and Asiatic black bear (*Ursus thibetanus*), ascribing them to the genus *Melursus*. However, we recognize that further genetic and morphometric studies are still required in order to fully understand the taxonomy of these two bear species. Therefore, and pending further investigation on *Melursus* taxonomy, we will still refer in this book to the genus *Helarctos* for sun bear and *Ursus* for Asiatic black bear, acknowledging that they might deserve a different genus in future. The conservation issue facing some of these species is a big conservation challenge today. Human activities, population encroachment, and poaching in bear landscapes continue to represent serious threats for some bear species or populations. As an example, in more recent times, human–bear conflicts have been exacerbated by the increasing number of people sharing the same landscapes with bears. Such coexistence has engendered an increase in conflicts, such as damage to livestock, crops, and apiaries, as well as the fear of bear attacks (Chapters 15–17, 20, 28). Moreover, in some regions people continue to keep bears in terrible captive conditions to extract bile and other body parts, mainly in Asia where the trade in these kinds of products still flourishes (Chapter 26). For instance, in China and Vietnam, thousands of bears are kept in tiny cages and bred for their bile. Furthermore, an emerging threat to bear conservation is related to the effect of global warning. This is the case, for example, for polar bears, which are now more endangered than even a few decades ago due to the dramatic reduction of sea ice. In fact, polar bears depend on the ice shelf for feeding, breeding, and movement, and they can only persist where the temporal and spatial availability of sea ice provides adequate access to their marine mammal prey (Chapter 21). The panda, another iconic bear species, is also threatened by climate change. The panda is an extremely specialized species that relies on bamboo for 99% of its diet, occurs in a very restricted range, and has one of the lowest reproduction rates among bears (Chapters 6 and 21). The challenge that bear conservation and management represents around the world makes this book extremely important and timely because it provides informative and complete accounts of everything you want to know on bears to a broad audience. However, even if our general knowledge of bear ecology and behavior has significantly increased in the past decades, we still have a lot to learn about this group of species, and in particular tropical bears (Chapters 4, 7–10, 22, 24–28).

The idea to edit a major volume on the ecology and conservation of bears started in 2017 from the need to provide a comprehensive book on all the bear species that inhabit our planet, as well as a useful tool for both the general public and people more directly involved in the fields of animal ecology, behavior, and conservation such as researchers, wildlife managers, conservationists, stakeholders (such as farmers and hunters), and students. In our minds, this book would also been able to demonstrate why the study of human–bear interactions, and stakeholder perception and involvement, are crucial for bear conservation and management, with detailed examples and case studies from all the continents inhabited by bears. Such a book would also highlight the urgency of conservation actions that need to be put into practice in the different regions of the world, mainly for lesser-known bear species in developing countries. Additionally, and despite the long-term interest in bears, as well as the many groups working on bears for decades and the large literature on these species around the world, a comprehensive and very detailed book on all the bear species in the world had never been published before. To make this idea a reality, we started by contacting more than 250 people among the best bear biologists in the world. Many of them replied enthusiastically to our invitation, saying that such a book was very much welcomed and long overdue. Of course, this positive feedback gave us further motivation to move forward with this project, in which 200 authors ultimately participated, many of them having spent their entire lives studying bears. The authors come from 33 countries spread across five continents, and work at very diverse institutions, such as research centers, universities, IUCN SSC Bear Specialist Group and Polar Bear Specialist Group and IBA, and non-governmental organizations (NGOs). To give you an idea of the heterogeneity of the book's contributors, people involved in this project are from (in alphabetical order): Bhutan, Bolivia, Canada, China, Croatia, Denmark, Ecuador, Finland, France, Germany, Greece, Hungary, India, Iran, Italy, Japan, Malaysia, Mexico, Nepal, the Netherlands, Norway, Pakistan, Poland, Romania, Russia, Slovenia, Spain, Sri Lanka, Sweden, Turkey, UK, USA, and Venezuela.

Together with the most important information on the ecology and behavior of bear species, the volume also includes specific chapters on taxonomy, phylogeny and genetics, population status and trends, as well as conservation status, management, and climate changes. The book is composed of 28 chapters subdivided into four sections: Part I – Systematics, Ecology, and Behavior (Chapters 1–5); Part II – Species Accounts (Chapters 6–14); Part III – Human–Bear Coexistence (Chapters 15–19); and Part IV – Conservation and Management (Chapters 20–28).

We hope that you will enjoy this book at least as much as we have enjoyed its long preparation and our close collaboration with chapter contributors, and that the huge effort made by all the authors will be appreciated by the public and scientific community. We will consider that our work has achieved its goal if it is rewarded by an increase in the understanding of bears and their effective conservation. However, the future of bear species will depend on our capacity to find pragmatic solutions that should represent a trade-off between human growth and the needs of bears and their habitats. What bears, among the most charismatic creatures on the planet, do for people has an inestimable value for our most intimate life, and their loss will create a void impossible to fill. Being in a bear country captivates our minds and, at the same time, offers a lesson in humility by giving us the feeling that something more powerful than us is out there.

Part I Systematics, Ecology, and Behavior

Chapter 1

Systematics, Evolution, and Genetics of Bears

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Introduction

Bears, Family Ursidae, are among the largest of the Carnivora, but the Ursidae is among the least speciose carnivoran family with only eight extant species. Owing to the bears' widespread distribution in Eurasia, North America, and north-western South America, they occupy many habitats from the northern polar ice cap to tropical rainforests. Despite having few species, relationships between the Ursidae and other Carnivora and between ursid species (and indeed what constitutes an ursid) have been controversial. New molecular genetic techniques in recent years have allowed relationships to be explored in new ways, leading to some clarification, but debates continue owing to incomplete lineage sorting and ancient hybridization.

Bears are threatened by humans; conflict with human land uses and exploitation for fur and other body parts, coupled with habitat loss and extirpation through direct hunting, have led to fragmentation of populations of all species. Molecular genetics are key to understanding current and historical relationships between isolated populations, including species' colonization during glacial–interglacial cycles, to determine viability of local populations, needs for habitat corridors, and other aspects of population management, especially where bears are harvested for sport, etc. As natural habitats shrink, some bear species will inevitably require high levels of management, perhaps combining captive and wild populations following the IUCN's One Plan Approach. In this chapter we review the systematics of the Ursidae and its relationships with other Carnivora, the molecular phylogenetics of extant ursid species, the phylogeography of and morphological variation within each species, and the use of molecular genetics to monitor bear populations for management and conservation.

Systematics of the Ursidae

Wozencraft (1989) summarized the systematic history of the Carnivora, hence only a brief overview is given here. The classification of the Order Carnivora based on the morphology of the basicranium began with Turner (1848), was further developed by Flower (1869), and has since been refined, e.g. by Hunt (1974), who characterized the development and evolution of auditory bullae. The Carnivora is characterized by morphological characters, including carnassial teeth, i.e. the fourth upper premolar (P4) and first lower molar (m1), which form two shearing blades for slicing through body tissues, and the presence of three elements in the auditory bulla: the caudal and rostral entotympanic and ectotympanic bones (Hunt 1998; Wozencraft 1989).

Based on basicranial characteristics, the Carnivora comprises two suborders: the Feliformia (felids, viverrids, hyaenas, and related families) and the Caniformia (canids, ursids, pinnipeds, and musteloids). The Caniformia comprises two Infraorders, the Cynoidea (or Canoidea), including the Canidae, and the Arctoidea, including the remaining caniforms. Rose (2006) characterized the Arctoidea as having a suprameatal fossa (a hollow in the dorso-lateral wall of the middle-ear cavity) and loss of the third upper molar (M3), and that most arctoids have a single-chambered auditory bulla comprising mostly the ectotympanic bone. Some relationships within the Arctoidea remain controversial, although a consensus is growing. The main contentious areas include the relationship between the giant panda, *Ailuropoda melanoleuca*, the red panda, *Ailurus fulgens*, and the Ursidae (see below), whether the superfamily Pinnipedia is monophyletic, and the relationships between pinnipeds, the Ursidae, and Superfamily Musteloidea. Traditionally, the systematics of the Carnivora were based on morphological studies of extant and fossil taxa (e.g. Wozencraft 1989), but new molecular techniques have clarified many relationships, especially where homoplasy or convergence gave ambiguous or incorrect affinities between taxa. However, some relationships remain uncertain, owing to incomplete lineage sorting and ancient hybridization. The problematic systematics of the Arctoidea are discussed below.

The Superfamily Pinnipedia includes seals (Family Phocidae), walrus (Family Odobenidae), and sea lions and fur seals (Family Otariidae). Morphological studies since the nineteenth century suggested a sister relationship between the Ursidae and Otariidae/Odobenidae based, for example, on the structure of the auditory bulla, and between the Mustelidae and Phocidae, based, for example, on the absence of an alisphenoid canal, thereby supporting a diphyletic origin of the Pinnipedia. However, recent morphological studies demonstrated a monophyletic Pinnipedia (e.g. Berta et al. 2015, but see Koretsky et al. 2016).

Table 1.1 Classification of the extant Ursidae (Tedford 1976; Bryant 1996; Wagner 2010).

Class Mammalia Linnaeus, 1758; 1							
	Order Carnivora Bowdich, 1821; 33						
		Suborder Caniformia Kretzoi, 1943; 16, 194					
			Infraorder Arctoidea Flower, 1869; 15				
				Superfamily Ursoidea Batsch, 1788; 110			
					Family Ursidae Batsch, 1788; 110		
					Subfamily Ursinae Batsch, 1788; 110		
						Genus *Ursus* Linnaeus, 1758; 47	
							Ursus arctos Linnaeus, 1758; 47
							Ursus maritimus Phipps, 1774; 185
							Ursus americanus Pallas, 1780; 5
						Genus *Melursus* Meyer, 1793; 155	
							Melursus ursinus (Shaw, 1790; pls. 58–59)
							Melursus malayanus (Raffles, 1821; 254)
							Melursus thibetanus (G. Cuvier, 1823; 325)
					Subfamily Arctotheriinae F. Ameghino, 1902; 236		
						Genus *Tremarctos* Gervais, 1855; 20	
							Tremarctos ornatus (F. Cuvier, 1825)
					Subfamily Ailuropodinae Grevé, 1894; 217		
						Genus *Ailuropoda* Milne-Edwards, 1870; 342	
							Ailuropoda melanoleuca (David, 1869; 12–13)

There is still no consensus on the relationship between the Ursidae and other Arctoidea. Several studies showed a sister relationship between the Ursidae and the Pinnipedia, but excluded the Musteloidea (i.e. Mustelidae, Procyonidae, Ailuridae, and Mephitidae) (Luan et al. 2013), while in most others the Ursidae was basal with the Pinnipedia and the Musteloidea grouped together (Eizirik et al. 2010; Nyakatura & Bininda-Emonds 2012; Doronina et al. 2015) (Figure 1.1), or grouped the Ursidae with the Musteloidea (Luan et al. 2013).

The Ursidae comprises eight extant species, which many authors consider to form two subfamilies (Wozencraft 1989; Goswami 2010; Wagner 2010): the Ailuropodinae includes the basal and highly derived giant panda, *Ailuropoda melanoleuca*, which is adapted to feeding on bamboo; and the Ursinae, which comprises two tribes, the Tremarctini, including the Andean bear, *Tremarctos ornatus*, and the Ursini, comprising the remaining six ursid species. Hunt (1998) divided the Ursidae into four subfamilies: the Ursinae containing the extant bears; the Ailuropodinae containing the giant panda; and two extinct subfamilies, the Amphicynodontinae and the Hemicyoninae. He further divided the Ursinae into three tribes – Ursini, Tremarctini, and the ancestral Ursavini. Most recent authors place the Andean bear in the subfamily Tremarctinae (e.g. Soibelzon et al. 2005; Mitchell et al. 2016), but Wagner (2010) suggested that the Tremarctinae Merriam and Stock, 1925 is pre-dated by the Arctotheriinae Ameghino, 1903, but it actually dates to Ameghino (1902) (Table 1.1).

Currently, the extant Ursinae includes three genera: *Helarctos*, for the sun bear, *H. malayanus*; *Melursus*, for the sloth bear, *M. ursinus*; and *Ursus*, comprising the brown bear, *U. arctos*, polar bear, *U. maritimus*, Asian black bear, *U. thibetanus*, and American black bear, *U. americanus*. Previously, three genera were recognized for Asian bears, including *Melursus* (sloth bear), *Selenarctos* (Asian black bear), and *Helarctos* (sun bear). A recent molecular phylogenetic study by Kumar et al. (2017) showed that the sloth and sun bears are sister species in a clade with the Asian black bear, which is basal. This suggests that either all Ursinae should be in the genus *Ursus* as proposed previously (e.g. Wozencraft 1989; Hunt 1998) or that the three Asian bears may be in a separate genus, *Melursus*. Recently, Kitchener et al. (2017) employed Hennig's Rule, which discriminates genera if divergence times are *c*.5 million years or more. Using Hennig's Rule divides the Ursinae into *Melursus* for Asian bears and *Ursus* for the rest (Table 1.2).

The Ursidae has a primitive dental formula (I3/3 C1/1 PM4/4 M2/3) and a Type A auditory bulla (Hunt 1974), comprising mostly the ectotympanic but also rostral and two

Table 1.2 Classification of the Ursidae, including extinct taxa.

- Family Ursidae Batsch, 1788
- Subfamily Hemicyoninae Frick, 1926
  - Tribe Cephalogalini Bonis, 2013
    - *Adelpharctos* Bonis, 1971
    - *Cyonarctos* Bonis, 2013
    - *Phoberogale* Ginsburg & Morales, 1995
    - *Filholictis* Bonis, 2013
    - *Cephalogale* Jourdan, 1862
  - Tribe Phoberocyonini Ginsburg & Morales, 1995
    - *Plithocyon* Ginsburg, 1955
    - *Phoberocyon* Ginsburg, 1955
    - Tribe Hemicyonini Frick, 1926
    - *Zaragocyon* Ginsburg & Morales, 1995
    - *Dinocyon* Jourdan, 1861
    - *Hemicyon* Lartet, 1851
- Subfamily Ursavinae Hendey, 1980
    - *Ballusia* Ginsburg & Morales, 1998
    - *Ursavus* Schlosser, 1899
- Subfamily Agriotheriinae Kretzoi, 1929
    - *Agriotherium* Wagner, 1837
- Subfamily Ailuropodinae Grevé, 1894
  - Tribe Indarctini Abella et al., 2012
    - *Miomaci* Bonis et al., 2017
    - *Indarctos* Pilgrim, 1913
  - Tribe Ailuropodini Grevé, 1894
    - *Kretzoiarctos* Abella et al., 2012
    - *Agriarctos* Kretzoi, 1942
    - *Ailurarctos* Qi et al., 1989
    - *Ailuropoda* Milne-Edwards, 1870
- Subfamily Arctotheriinae Ameghino, 1903
    - *Plionarctos* Frick, 1926
    - *Arctodus* Leidy, 1854
    - *Arctotherium* Burmeister, 1879
    - *Tremarctos* Gervais, 1855
- Subfamily Ursinae Batsch, 1788
    - *Ursus* Linnaeus, 1758
    - *Melursus* Meyer, 1793

caudal entotympanic bones (Hunt 1998). The internal carotid artery loops inside the petrosal venous sinus, covered by the basioccipital, and may act as a countercurrent heat exchanger to cool the brain (Hunt 1998) (Figure 1.2).

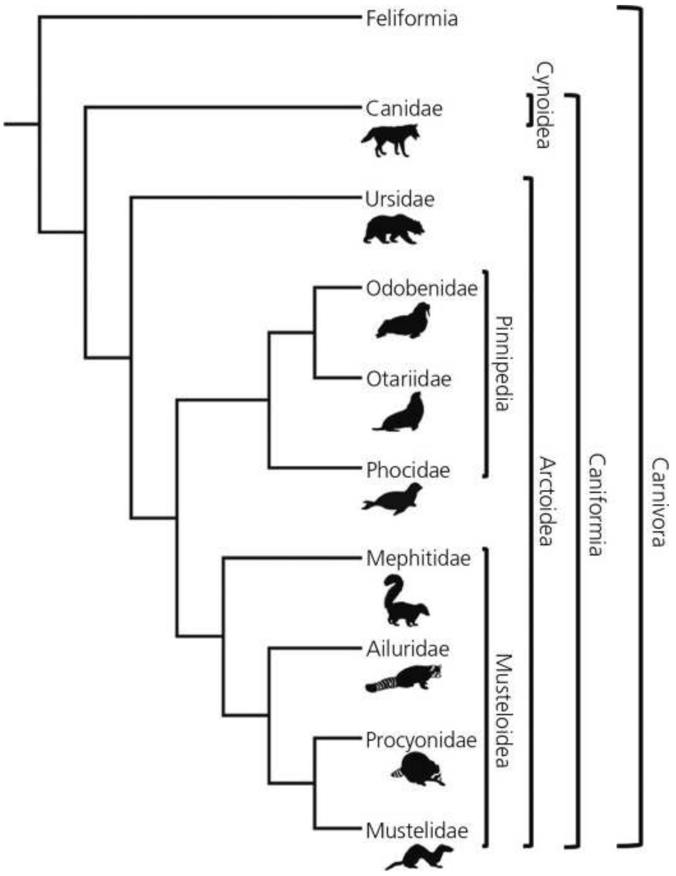

Figure 1.1 Phylogenetic tree showing a version of the relationships among the Arctoidea (Koepfli et al. 2017).

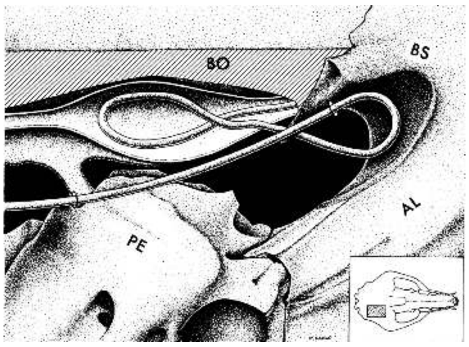

Figure 1.2 Dissected auditory region of a bear, showing the internal carotid artery looped within the inferior petrosal venous sinus on the lateral edge of the basioccipital bone. AL, alisphenoid; BO, basioccipital; BS, basisphenoid; PE, petrosal (Hunt 1977).

The Ursinae and Arctotheriinae share several morphological characters; a reduced lacrimal forming a vestigial bony rim around the naso-lacrimal foramen; a flat auditory bulla, which is much smaller than the mastoid, squamosal, and basioccipital processes; reduced premolars, whereby P4 has lost most of its shearing function; the upper and lower molars are quadrate (with four main cusps: paracone, metacone, protocone, and a large metaconule, which migrated to the postero-internal border to form the molars' oblong shape), and the rear border of M2 is greatly enlarged and elongated, forming a distinctive heel and making it the longest tooth in the maxilla (Wozencraft 1989; Hunt 1998).

The enamel on the surface of the talonid and trigonid basins of m2 of arctotheriines is tuberculated and forms a "z" pattern on the talonid (Hunt 1998). The skull is shorter than those of the Ursinae and there is a pre-masseteric fossa in the mandible in *Tremarctos* and *Arctodus*, but not *Plionarctos*. The diploid ($2n$) chromosome number is 52 biarmed autosomes in *Tremarctos* compared with $2n = 74$ mostly acrocentric chromosomes of the Ursinae, and $2n = 42$ mostly biarmed autosomes in the giant panda (Chorn & Hoffmann 1978).

The giant panda's classification was controversial since its description by David (1869), who regarded it as a bear, but Milne-Edwards (1870) classified it as a procyonid. Later authors proposed placing it in a family (Ailuridae) with the red panda, or in a monotypic family (Ailuropodidae). The controversy continued as different morphological features were presented for and against the two main hypotheses until molecular studies demonstrated unequivocally that the giant panda is basal to the Ursinae and Arctotheriinae. It is usually classified in the Ailuropodinae, although some still place it in its own family (although not recently, e.g. Thenius 1989), owing to its highly derived morphology and deep divergence time of *c.*12.5 million years ago (Ma) (Kutschera et al. 2014).

A key morphological character of the Ailuropodinae is a greatly enlarged radial sesamoid in the wrist, the so-called panda's thumb, which grasps stems, such as those of bamboo. In most other extant ursids the radial sesamoid is not enlarged, but recently the Andean bear's moderately enlarged radial sesamoid was described (Salesa et al. 2006). Therefore, enlarged radial sesamoids are either plesiomorphic (i.e. an ancestral character shared by two or more taxa), or they evolved independently in primarily herbivorous ursids. Other morphological characteristics of ailuropodines include the highly domed skull for attachment of massive jaw muscles, and enlarged molars and premolars for crushing tough bamboo stems and shoots.

Fossil History of the Ursidae

There is no agreement regarding quite what a bear is, because opinion differs as to which basal taxa should be included in the Ursidae. For any mammal group the deeper one descends into the fossil record, the more similar taxa become, until the origin of the group is reached. Today's bears differ greatly from those of the late Eocene and Oligocene (*c.*35–23 million years ago). Consequently, opinion differs as to which basal taxa should be included in the Ursidae (Table 1.2). A group of genera, including *Amphicynodon*, *Amphicticeps*, *Parictis*, *Kolponomos*, *Allocyon*, and *Pachycynodon*, distributed in Europe, Asia, and North America, constitute the amphicynodonts. This is either a paraphyletic stem lineage within the Ursidae or a monophyletic family Amphicynodontidae that may or may not be sister taxon to the Ursidae. The latter view point has gained credence in recent years, but without consensus. Here, we consider the amphicynodonts to constitute a distinct family and exclude them from further discussion.

The earliest Ursidae are from the earliest Oligocene. The family is subdivided into a number of subfamilies: Hemicyoninae, Ursavinae, Agriotheriinae, Ailuropodinae, Arctotheriinae, and Ursinae. The Hemicyoninae is the basal subfamily and encompasses about 10 genera in three tribes. Among these is the genus *Cephalogale*, often called "the earliest bear." This genus has recently been revised (de Bonis 2013), which showed that traditional "*Cephalogale*" is an assemblage of variably related, primitive Ursidae, within the tribe Cephalogalini, which now comprises five genera – *Cephalogale*, *Filholictis*, *Cyonarctos*, *Adelpharctos*, and *Phoberogale* – of jackal- to wolf-sized, rather canid-like animals. Cephalogalini is known from the earliest Oligocene (*c.*34 Ma) to the early Miocene (*c.*19 Ma). Their geographical range extended from Western Europe to the Midwestern United States, with *Cephalogale* and *Phoberogale* occurring on both continents. De Bonis (2013, p. 810) notes that no antecedents of Cephalogalini are known from the Eocene and surmises that they (and the Ursidae) may have had an Asian origin, where Cephalogalini are poorly known.

A second tribe of Hemicyoninae is the Phoberocyonini, revised by Ginsburg and Morales (1998). This tribe comprises *Phoberocyon* (not to be confused with *Phoberogale*) and *Plithocyon*, two genera with wide geographical ranges, both known from France to Florida. *Phoberocyon* is the older genus, with a stratigraphic range encompassing the late Oligocene to late middle Miocene (*c.*29–14 Ma), whereas *Plithocyon* is restricted to the middle Miocene (*c.*16–11.5 Ma). These two genera include larger, more derived species than the Cephalogalini, with the largest, e.g. *Phoberocyon aurelianensis*, within the size range of ursids today. Although phylogenetically close, *Phoberocyon* evolved toward hypercarnivory, with taller cusps on the lower carnassial and a narrow, trenchant talonid, whereas *Plithocyon* became more hypocarnivorous, with a low, wide carnassial. The reasons for this ecological divergence are debatable and complicated by the presence of both genera on multiple continents, each with different competitors. Nevertheless, the Ursidae would never be as hypercarnivorous again.

The Hemicyonini comprises two genera, *Hemicyon* and *Dinocyon*. *Hemicyon* includes generalized, medium- to large-sized hemicyonines of early and middle Miocene age with a broad geographical range from western Europe (where it is relatively common) to the midwestern United States, although Hunt (1998) suggests that the latter (*Hemicyon barbouri*) represents a distinct genus. *Hemicyon* is also recorded from Kenya by a single upper carnassial from the early Miocene (Schmidt-Kittler 1987). This tooth is the only record of a bear from Africa prior to *Agriotherium* in the latest Miocene (see below), despite decades of searching at productive localities, raising many presently unanswerable questions.

Dinocyon is much less common than *Hemicyon*. It is exclusively known from western Europe, in sediments dating from the middle Miocene to the earliest late Miocene (*c.*16–11 Ma). *Dinocyon* includes some of the largest bears of all time and, at least in tooth dimensions, rivaled giants such as *Agriotherium africanum* and *Arctotherium angustidens* (see below).

Closer to crown-group Ursidae, relationships between subfamilies are a little better understood (Abella et al. 2012), although the first, Ursavinae, is clearly a paraphyletic stem lineage. It comprises the genera *Ballusia* and *Ursavus*. The former is exclusively European from the early Miocene, whereas the latter comprises several species from the early to late Miocene of Eurasia and the middle Miocene of North America. *Ursavus* is traditionally considered ancestral to more derived bears. They are all small to medium-sized animals with generalized omnivore characteristics.

Following the Ursavinae is the subfamily Agriotheriinae, which includes only the genus *Agriotherium*. *A. africanum* is the first unequivocal bear to be described from sub-Saharan Africa, by Hendey (1980). Until that time, bears were only thought to have reached North Africa in the late Pleistocene, but never to have crossed the Sahara. *Agriotherium africanum* was considerably larger and more carnivorous than modern *Ursus*.

Crown-group Ursidae (the common ancestor of all living bears and all of its descendants) includes three subfamilies. The Arctotheriinae encompasses the South American ursid radiation, with *Tremarctos ornatus* as its surviving representative. The arctotheriines have antecedents in North America, where the ancestral taxon is *Plionarctos* of the late Miocene to Pliocene. *Tremarctos* also originated in North America, where *T. floridanus* overlapped in time with *Plionarctos*. However, most characteristic of the arctotheriine radiation are the short-faced bears, *Arctodus* (Pliocene of North America) and *Arctotherium* (Pleistocene of South America). Among the latter, *Arctotherium angustidens* may have been the largest bear (and carnivoran) of all time, with an estimated body mass of up to 1500 kg (Soibelzon & Schubert 2011). Curiously, the South American short-faced bear was more closely related to the living Andean bear (which is not short-faced) than it was to the North American short-faced bear. This is a striking example of convergence in size and morphology to ecological circumstance.

The Ursinae includes the extant genera *Melursus* and *Ursus*. The antecedents of *Melursus* are poorly known except for the Asian black bear. However, the genus *Ursus* is extremely well known in the fossil record, particularly the cave bear, *U. spelaeus*, which is studied from many thousands of specimens across large parts of western Eurasia, where it hibernated (and died) in caves. Numerous other species of *Ursus* have been described, including fossil relatives of the American black bear.

The final subfamily, the Ailuropodinae, includes the giant panda and relatives. The palaeontology of this subfamily has progressed greatly recently (Abella et al. 2012; de Bonis et al. 2017). The giant panda, once thought to be very isolated phylogenetically among the Ursidae, is now known to be among a large diversity of genera and species in the Ailuropodinae. Two tribes are recognized, the Indarctini and the Ailuropodini. The former includes the early genus *Miomaci* of the late Miocene in Europe and *Indarctos*, a genus known from the late Miocene of Eurasia and North America. The Ailuropodini comprises several genera, the oldest and most primitive of which are the European *Kretzoiarctos* and *Agriarctos* of late middle and early late Miocene age. Together with the Chinese *Ailurarctos*, these genera form a clade that is sister to *Ailuropoda*, culminating in the extant giant panda. This lineage shows a strong trend toward increased size and specialization to herbivory.

Molecular Phylogenies

The relationships among today's bear species have been unclear or contradictory depending on which methods were used. In particular, the relationships between the six ursine species remained unresolved until recently, because early molecular studies contradicted each other, mostly because of insufficient data (Talbot & Shields 1996; Yu et al. 2004). However, even larger molecular data sets that included nuclear genes did not confidently resolve the bears' phylogeny (Pages et al. 2008; Kutschera et al. 2014), resulting in a "forest of gene trees" with contradicting phylogenies. This suggested that bear evolution was either shaped by incomplete lineage sorting or that ancient hybridizations complicated phylogenetic reconstruction (Kutschera et al. 2014).

The first analyses of whole-genome data from all ursine and arctotheriine species have recently resolved relationships among bears (Figure 1.3; Kumar et al. 2017). Previously, the position of the American and Asian black bears with respect to their relatives was much debated (Pages et al. 2008; Kutschera et al. 2014). In the bifurcating tree (Figure 1.3), the American black bear is the sister species to polar and brown bears, while

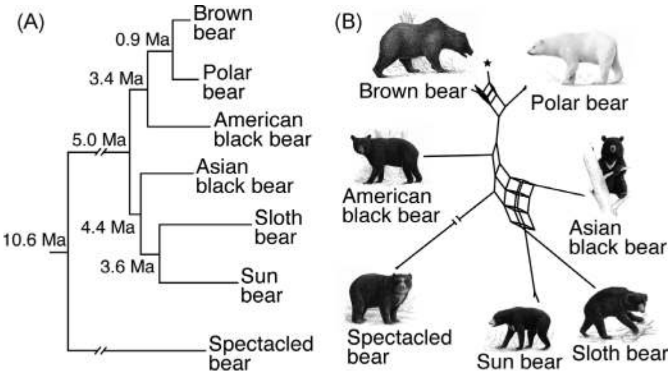

Figure 1.3 Phylogenomic analyses of 18,621 maximum likelihood trees estimated from non-overlapping 100-kb genome fragments from whole genome data of seven bear species (Kumar et al. 2017). (A) Schematic of coalescent species tree with 100% bootstrap support of all branches. Divergence time estimates in million years ago (Ma) from Kumar et al. (2017) were mapped onto the tree that was obtained from an analysis of 5.2 million bp coding sequences in MCMC tree (PAML) with multiple calibration points. (B) Split network analysis at a 7% threshold level. Ma, million years ago; ABC, brown bear from the Admiralty, Baranof, and Chichagof (ABC) Islands. Paintings by Jon Baldur Hlidberg (www.fauna.is). Modified from Kumar et al. (2017), figure 1.3, licensed under CC BY 4.0.

sun and sloth bears are grouped with the Asian black bear. The Arctotheriinae forms the sister group to all ursine bears. The giant panda was consistently placed as sister group to the Ursinae/Arctotheriinae in previous phylogenetic analyses (e.g. Kutschera et al. 2014).

However, analyses of bear genomes have shown that gene flow among species typifies the bears' evolutionary history (Kumar et al. 2017). Although harder to interpret, the bears' evolutionary radiation is actually a network, where signals from deviating phylogenetic trees become evident, with the American black bear placed between Asian bears and polar/brown bears (Figure 1.3B; Kumar et al. 2017). A brown bear from the Admiralty, Baranof, and Chichagof (ABC) Islands, off the western Canadian coast, is positioned between polar and brown bears, consistent with gene flow between ABC brown bears and polar bears (Miller et al. 2012; Cahill et al. 2015).

This network represents best the genome-wide evolutionary signal among extant ursids (Bapteste et al. 2013), because frequent hybridization among bears means their genomes are mosaics of evolutionary histories. A similar mosaic can result from incomplete lineage sorting, where ancestral gene lineages are randomly sorted along the species tree, and where phylogenetic signals may also differ from the species tree (Pamilo & Nei 1988). Only if all phylogenetic information in the evolutionary network is forced into one bifurcating tree is the more conventional view of bear evolution recovered (Figure 1.3A). While this tree may serve many purposes, such as taxonomy, conservation genetics, or molecular clock analyses, it provides an incomplete understanding of the bears' evolutionary history and it may also explain why some morphological characters are difficult to place on a simple, bifurcating tree.

Genetic differences among the bears can be converted into time, assuming that substitutions accumulate relatively constantly between species, as in a molecular clock (Zuckerkandl & Pauling 1962). Molecular divergence times among bears have been studied extensively (e.g. Kutschera et al. 2014; Kumar et al. 2017), with particular interest in the divergence of polar and brown bears (e.g. Hailer et al. 2012; Miller et al. 2012). Genome-wide estimates suggest the deepest split in the Ursinae (*Ursus* versus *Melursus*) was 5.0 (4.5–6.0) million years ago (Ma), and the divergence of polar and brown bears was 0.9 (0.6–1.1) Ma (Kumar et al. 2017).

Phylogenetic reconstruction of bears exemplifies the complications that gene flow creates for understanding evolutionary relationships. One of the first molecular studies on bear species used mitochondrial DNA (mtDNA) to study the relationship between polar and brown bears (Cronin et al. 1991). This analysis suggested that polar bears originated from brown bears from the ABC Islands, questioning their validity as a distinct species and leaving *Ursus arctos* paraphyletic. However, some 20 years later, a comprehensive analysis of nuclear gene loci demonstrated that polar bears are a separate, ancient lineage that diverged from the common ancestor of polar and brown bears about 600,000 years ago (ya) (Hailer et al. 2012). Therefore, the mtDNA of ABC Islands brown bears probably transferred to polar bears by hybridization, making it the first example of gene flow among bear species. For this transfer of mtDNA, female brown bears and male polar bears must have hybridized some 150,000 ya, coinciding with the penultimate glacial period (*c.*185,000–135,000 ya; Marine Isotope Stage 6; Margari et al. 2010). The brown bear mitochondrial haplotype has been identified in hundreds of polar bears studied for this locus so far (e.g. Cronin et al. 1991; Hailer et al. 2012). Under this scenario, the brown bear mitochondrial haplotype spread to all polar bears in a comparatively short time, also implying that brown bear mtDNA was selectively advantageous for polar bear survival, or the population bottleneck was very severe. An alternative explanation for high genetic similarity of polar and brown bear mtDNA is that gene flow occurred from polar bears into some brown bear populations (Cahill et al. 2013, 2018; Liu et al. 2014; Hassanin 2015). Indeed, gene flow between polar and brown bears was repeatedly detected in analyses of entire genomes (e.g. Miller et al. 2012; Cahill et al. 2015; Kumar et al. 2017). Up to 8.8% of the brown bear genome is of polar bear ancestry, but polar bear genomes harbor no significant genetic introgression from brown bears (Cahill et al. 2015). Cahill et al. (2018) suggested that brown bears carried some polar bear alleles away from where admixture occurred through male-dominated dispersal. It is unclear if this gene-flow asymmetry reflects continuing hybridization between the two species, is a remnant from the speciation event, or results from strong selection pressure on the highly specialized polar bear.

Genome data from all bear species show that gene flow was much more common than assumed for mammalian genera (Kumar et al. 2017). Whether hybridization is current or ancestral among bears, different parts of their genomes have different evolutionary histories. This complicates our understanding of bear evolution. For example, some parts of the American black bear's genome support a close relationship with the polar and brown bears, while other parts place the American black bear closest to the Asian black bear (Figure 1.3B). Phylogenetic reconstruction among the Asian bears is even more complicated and consistent with natural hybridization between Asian black bears and sun bears (Galbreath et al. 2008). Technical advances in analyses of ancient DNA allow studies of entire genomes of extinct species. Recently, a study found gene flow from extinct cave bears, *Ursus spelaeus*, into brown bears (Barlow et al. 2018), providing direct evidence for ancestral hybridization. Such interspecific gene flow might have been advantageous for adapting to changing environments.

Phylogeography and Intraspecific Taxonomy

Although relationships between species are now better understood, relationships between populations within species and the taxonomic status of those populations are often unresolved in

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the Ursidae despite descriptions of many different subspecies and even species. For example, 232 recent and 39 fossil species and subspecies of today's *Ursus arctos* have been described (see Erdbrink 1953; Hall 1981), which Kurtén and Anderson (1980) considered "a waste of taxonomic effort, which, as far as we know, is unparalleled." Phylogeographical studies allow better understanding of how populations are related to each other, where refugia existed during glaciations, and how species have recolonized continental ranges. However, lack of genetic and morphological data and their frequent apparent incongruence, along with high intraspecific variability, have led to poor resolution of intraspecific taxonomy and relationships in some species. For example, polar and Andean bears are considered monotypic, despite geographical variation in size and some genetic structuring of populations, although ESUs (evolutionary significant units) or MUs (management units) are recognized owing to genetically discrete populations, which occupy different habitats or experience different climatic conditions. In contrast, 8–12 extant brown bear subspecies are described; some are historically and widely recognized, but recent ones are not fully accepted, and for some, their geographical ranges are poorly known. Below, we briefly review the phylogeography and current status of subspecies within each bear species.

Ailuropoda melanoleuca

The giant panda was widely regarded as monotypic until Wan et al. (2003) described *A. m. qinlingensis*, from the Qinling Mountains, Shaanxi Province, based on genetic differentiation from *A. m. melanoleuca* in Sichuan. This proposed new subspecies appears to have a browner pelage and smaller skull with larger molars (Wan et al. 2005). However, the distribution gap between the two putative subspecies is caused by human impacts, so genetic differences may represent genetic drift in now separate populations or clinal variation in a previously continuous range.

The giant panda's phylogeography shows a mismatch between mitochondrial and nuclear genetic studies. Early studies of short mtDNA sequences showed no haplogroups, even using longer sequence lengths up to 680 base pairs (bp) (Zhang et al. 2007; Hu et al. 2010a), which distinguish brown bear subclades. Recent studies, using complete mitochondrial genomes, revealed at least three extant and two extinct clades in giant pandas (Barlow et al. 2019). However, although mitochondrial clades are well defined and calibrated, they are not restricted to any population and show no geographical subdivision. In contrast, nuclear DNA reveals quite finely resolved geographical patterns with the Qinling Mountains, home to the most divergent population (Zhao et al. 2013), and Xiaoxiangling as a probable refugium (Chen et al. 2013). This discordance in genetic markers probably results from female-biased dispersal (Hu et al. 2010b). Also, considering drastic range decreases and population fragmentation, it is probable that many other genetic lineages are extinct, which could have highlighted the species' history and phylogeography.

Tremarctos ornatus

Although subspecies were proposed previously (García-Rangel 2012), today the Andean bear is regarded as monotypic. However, genetic studies show that Andean bears comprise two ESUs: the Northern Andean clade (NAC; Venezuela, Colombia, Ecuador, and north-central Peru) and the Southern Andean clade (SAC; southern Peru and the northern and central Bolivian Andes), which split around 500,000 ya (Ruiz-García 2013; Ruiz-García et al. 2020a). Additionally, in Bolivia, some Andean bears from Santa Cruz Department were more related to the NAC than the SAC. These results and the slightly higher-level genetic diversity in the SAC show that the latter was the ancestral Andean bear population, contradicting palaeontological finds, which support the most northern Andean bear population as ancestral. Haplotypes vary in how they spread through the Colombian Andean Cordilleras. Gene-flow estimates were relatively high; therefore, geographical barriers have not prevented dispersal of Andean bears there. However, significant genetic heterogeneity was found in northern Colombian populations, with significant spatial autocorrelation for the Andean bear in Colombia (Ruiz-García et al. 2020b). In contrast, no genetic differentiation was found between different Cordillera Provinces, and northern–southern regions in Ecuador (Ruiz-García et al. 2020c).

The first molecular genetic studies of Andean bears used nuclear markers (microsatellites; Ruiz-García 2003, 2007; Ruiz-García et al. 2005) and estimated low to medium genetic diversities. However, mitochondrial markers yielded high levels of genetic diversity. This paradox is probably explained by "ascertainment bias" (Ellegren et al. 1995), whereby the species for which microsatellites were developed shows higher genetic diversity than that of the non-target species. In this case, the microsatellites used for Andean bears were originally designed for American black bears (Kumar et al. 2017).

Melursus malayanus

Usually two subspecies of sun bears are recognized: *M. m. malayanus* on the Asian mainland and Sumatra, and *M. m. euryspilus* from Borneo (Corbet & Hill 1992). Meijaard (2004) analyzed skull morphometrics of sun bears and confirmed that the Bornean population, which has a smaller skull and relatively longer upper tooth row, is distinct from Sumatran and mainland populations.

Very little is known about sun bear genetics. Meijaard (2004) cited an unpublished mtDNA study by L. Waits on sun bears from Sumatra and Borneo that yielded five clades with no geographical structure, suggesting some gene flow between islands during the Last Glacial Maximum (LGM). From published data, two mtDNA lineages are reported from Borneo (divergence 5.6 ± 1.9 base pairs (bp)), but no geographical separation (Onuma et al. 2006). Yu et al. (2007) and Krause et al. (2008) obtained mtDNA sequences from three putative continental Asian sun bears that could represent another subspecies, and which yielded two additional

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haplotypes that diverged from the two Bornean lineages by 14.39 ± 3.39 bp and 16.26 ± 3.57 bp, respectively. The differences between these mtDNA clades suggest a robust structure exists, dividing continental and island bears, but this is not yet fully resolved.

Melursus ursinus

Usually two subspecies of sloth bear are recognized: *M. u. ursinus* from peninsular India and *M. u. inornatus*, which has a smaller skull, from Sri Lanka (Corbet & Hill 1992). However, sample sizes for cranial lengths were very small. There may be clinal variation in skull size with latitude from larger northern animals to smaller southern animals, but this has not yet been studied.

The sloth bear's phylogeography has not been studied. However, in GenBank there are seven sequences of mtDNA fragments, including Zhang and Ryder 1993 (captive); Yu et al. 2007 (no locality); Talbot and Shields 1996 (captive); Mohan et al. unpublished (India); and Krause et al. 2008 (no locality). Not all these sequences could be aligned, although a comparison reveals at least three highly divergent haplogroups, lacking any geographical information.

Melursus thibetanus

Asian black bears are widely distributed in southern and eastern Asia; several subspecies are usually recognized, including *M. t. thibetanus* from Nepal to SE Asia, *M. t. japonicus* from Japan, *M. t. formosanus* from Taiwan, *M. t. gedrosianus* from Pakistan, *M. t. ussuricus* from the Russian Far East, Korea and northern China, *M. t. mupinensis* from southern and central China, and *M. t. laniger* from Kashmir and Punjab (Ellerman & Morrison-Scott 1953).

The Asian black bear's phylogeographical structure, based on mtDNA, is robust, but not yet fully resolved. It includes several haplogroups roughly congruent with seven putative subspecies (Hwang et al. 2008; Kadariya et al. 2018). The Japanese subspecies forms a distinct basal mitochondrial clade (Wu et al. 2015; Kadariya et al. 2018), which probably colonized Japan in the Middle Pleistocene, and is further substructured among the Honshu bears (Ohnishi et al. 2009; Kim et al. 2011). The mainland Asian clade probably represents a latitudinal cline, with increasing adaptation to more tropical climates from north to south, including the Taiwanese population, but the exact phylogenetic order of the matrilines is uncertain (Ohnishi et al. 2009; Kim et al. 2011; Wu et al. 2015; Kadariya et al. 2018). Recently, Kadariya et al. (2018) showed that the Himalayan population is a distinct basal lineage to mainland Asian populations. This suggests that three subspecies are recognizable: *M. t. thibetanus* from mainland Asia, *M. t. laniger* from the Himalayas, and *M. t. japonicus* from Japan. This species' phylogeographical structure is consistent with female philopatry and it seems very likely that it was influenced by the Pleistocene and Holocene glaciations throughout its range.

Although the Ussuri black bear (known as *M. t. ussuricus*) is separated by more than 1500 km from other populations, it is not genetically distinct. The Ussuri population arose very recently, separating *c.*20,000 years ago (peak LGM), and adapting to colder climates. The distribution gap, cf. the tiger, *Panthera tigris*, arose even later, owing to forest loss since the early Neolithic, *c.*9000 years ago, and the exploitation of bears for traditional medicines by early civilizations in northern China since at least the Shang dynasty *c.*3500 years ago (Barnes 1999; Ren 2000). Owing to its ecological distinctiveness and geographical isolation, the Ussuri population should be considered as a separate MU.

Ursus americanus

Owing to its widespread distribution, coupled with polychromatism (Rounds 1987), many subspecies of *U. americanus* (16 listed by Hall 1981) were recognized, with *U. a. americanus* occupying most of the species range.

For American black bears phylogeographical structures are described for both mitochondrial and nuclear DNA (Wooding & Ward 1997; Pelletier et al 2011; Puckett et al. 2015). Analysis of mtDNA revealed two lineages; the continental lineage is subdivided into eastern and western subclades, while the coastal lineage has a much simpler structure along the Pacific coast of North America. Nuclear SNP (single nucleotide polymorphism) data also showed quite clear geographical structure, including three main continental nuclear clusters (Alaska, Eastern, and Western), which were divided into nine subdivisions (Puckett et al. 2015). However, nuclear and mitochondrial clusters mostly did not coincide. The current phylogeographical structure is believed to have originated before the LGM [31–67 kya (thousand years ago) for nuclear clusters and 169 kya to 1.07 Ma for the mitochondrial ones] in several refugia in northern and southern North America, including Beringia, the north-west Pacific, the Southwest, and the Southeast (Puckett et al. 2015).

Neither mitochondrial nor nuclear structures match subspecies delineation very well (Puckett et al. 2015). Indeed, it is difficult to discern subspecies owing to complex admixture following expansion from these refugia, although Puckett et al. (2015) suggested that the nine subclusters could be associated with subspecies, which still seems too many for a highly mobile species showing extensive admixture. Perhaps the three mtDNA clusters, which appear mostly geographically discrete, would be better recognized as subspecies, including *U. a. americanus* (clade A-east) in the east, *U. a. emmonsii* in the west (clade B) and *U. a. cinnamomum* (clade A-west) from the central range.

Ursus maritimus

The polar bear is a monotypic species, although subspecies were previously proposed. Wilson (1976) found clinal variation in skull morphometrics across North America, with the possible exception of a distinct population in South Alaska,