

A REVIEW OF BEAR EVOLUTION

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Abstract: Ursidae is a young family, evolving from early canids during the late Oligocene and early Miocene, about 20-25 million years ago. The family has frequently been divided into subfamilies. Although debated, these often include: (1) Hemicyoninae, (2) Agriotheriinae, (3) Tremarctinae, (4) Ursinae, and (5) Ailuropodidae. Based on scattered literature published over the past century, we trace the evolutionary lineage of the various genera and species found in these subfamilies; most are extinct, 8 species remain. Many if not most of the relationships have been disputed for many years and we may be far from the definitive history. Speculated causes of extinction usually involved climate change and competition. Primitive man may have been the major competitor of some extinct species and modern man is definitely a major influence on bear evolution today.

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Members of the bear family, Ursidae, currently inhabit North America, Europe, Asia, and South America. Using generic names suggested by Hall (1981), Nowak and Paradiso (1983), Goldman et al. (1989), and Wayne et al. (1989), species found in Asia include the brown bear (*Ursus arctos*), Asiatic black bear (*U. thibetanus*), sun bear (*U. malayanus*), sloth bear (*U. ursinus*), and polar bear (*U. maritimus*). The taxonomic status of the sixth Asian member, the giant panda (*Ailuropoda melanoleuca*), remains in question, although most evidence suggests that it belongs to Ursidae. Brown bears and polar bears are found in Europe and these 2 species plus the American black bear (*Ursus americanus*) inhabit North America. The spectacled bear (*Tremarctos ornatus*) is the only member of Ursidae in South America.

Ursidae are placed in the order Carnivora but, except for the largely carnivorous polar bear, bears are omnivorous, feeding mostly on plant material, insects, fish, and mammals. They are generally large, stocky, and powerful animals. All bears are plantigrade, walking on their entire foot. The radius and ulna and the tibia and fibula are separate, which enables bears to rotate their limbs, improving their ability to dig and manipulate food, and facilitating climbing by some species. Bears' teeth reflect their omnivorous habits by lacking the carnassials common in other mammalian carnivores and having flattened molars adapted to crushing and grinding vegetation. Bears' premolars are reduced in size and utility, creating a gap between incisors and molars similar to that found in many herbivorous mammals.

Bears are a young family, evolving from early canids during the late Oligocene and early Miocene, about 20-25 million years before present (MYBP). So recent is this divergence that some taxonomists believe that canids and ursids should be considered as one family and dividing them is due to "custom of more than a century" (Simpson 1945). The majority of students,

however, have separated these 2 families but frequently disagree on where the line between canids and ursids, and many other taxonomic boundaries, should be drawn. Recently, the families Ursidae and Otariidae have been placed in the superfamily Ursoidea. These 2 families have been joined with members of the Canoidea superfamily, Canidae, Procyonidae, Mustelidae, and Phocidae, into the suborder Caniformia (Wozencraft 1989).

The purpose of this paper is not to create another view of bear evolution and resulting taxonomy. Rather, it is to summarize for the interest of biologists who work with extant species the large body of knowledge that has grown over the past century but is scattered in journals and papers that many of us rarely encounter.

SUBFAMILIES OF URSIDAE

Although 2 major contributors to bear taxonomy, Simpson (1945) and Erdbrink (1953), did not favor subfamily divisions as suggested by Kragavlich (1926), most systematians divide the bear family into 3 (Kragavlich 1926, Kurten 1966) or 4 (Pilgrim 1932, Thenius 1959) subfamilies without including Ailuropodidae, the subfamily that includes the giant panda. These authors generally disagree over the inclusion of the subfamily Hemicyoninae, or dog-like-bears (or bear-like-dogs), with either the canids or ursids. Hendey (1980) splits the bears into 5 subfamilies and 7 tribes; his groups include different genera than other students. We will include the giant panda as a bear and discuss 5 subfamilies (Fig. 1): (1) Hemicyoninae, (2) Agriotheriinae, (3) Tremarctinae, (4) Ursinae, and (5) Ailuropodidae.

SUBFAMILY HEMICYONINAE

It is believed that bears evolved from the canid line during the late Oligocene and early Miocene (Kurten

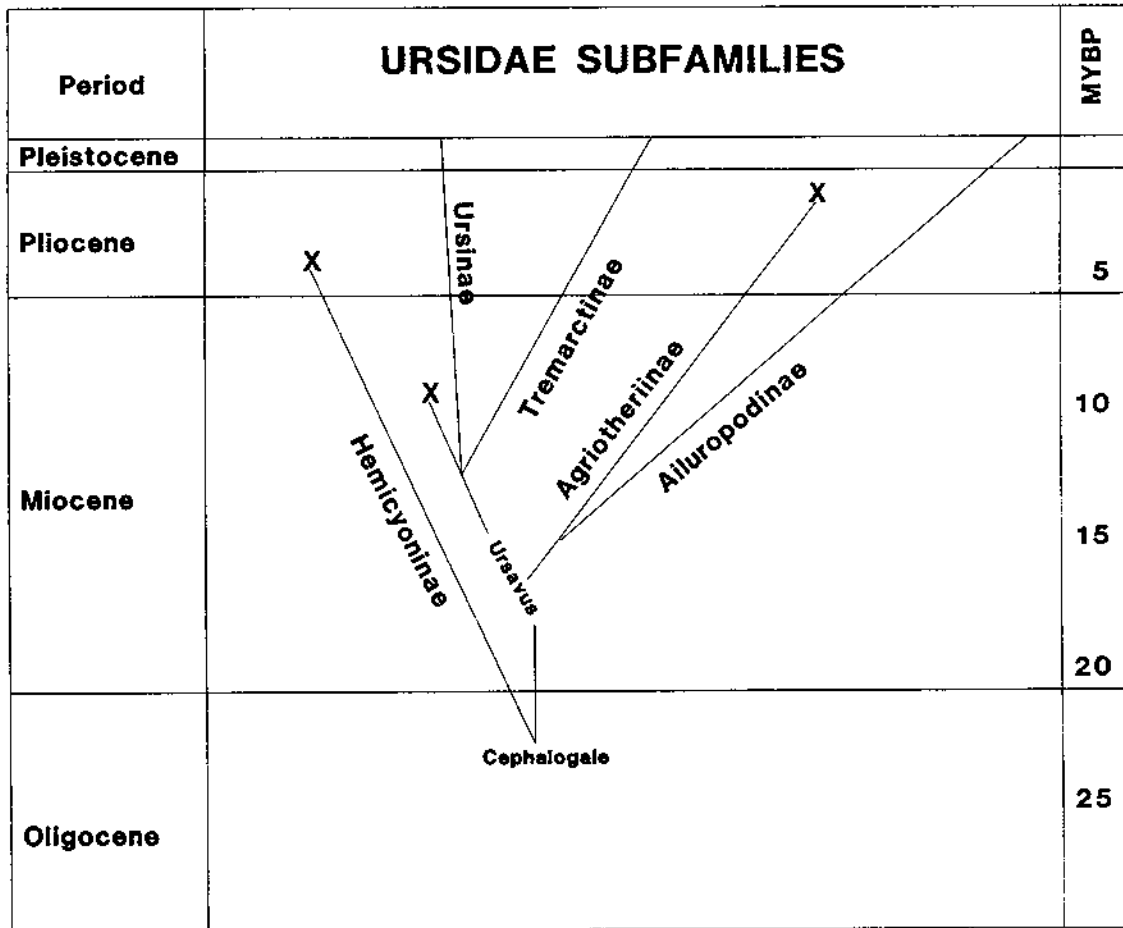


Fig. 1. A tentative phylogeny of Ursidae subfamilies. *Cephalogale* and *Ursavus* are base genera for these subfamilies.

1966). The change from canids to ursids left a fossil record relatively rich with intermediate genera and this has led to various opinions on where to differentiate the 2 families. Frick (1926) separated some intermediate forms from both the canids and ursids by creating the family Hemicyoninae, in which he included the genera *Hemicyon*, *Dinocyon*, *Hyaenarctos*, and *Ursavus* (since Matthew [1929] *Hyaenarctos* is considered to be *Agriotherium*). Frick (1926) specifically refrained from including this new family in the Ursidae, although Mitchell and Tedford (1973) thought that he had presented enough evidence that suggested it did belong with bears. Pilgrim (1932) placed Frick's family, Hemicyoninae, plus earlier genera, *Amphicyon* and *Cephalogale*, into Ursidae. This general division between canids and ursids was favored by many authors (Thenius 1959, Hendey 1972, Mitchell and Tedford 1973) although Kurten (1966) placed this group with the canids and considers the genus *Ursavus* to be the

first bears.

Several students (Erdbrink 1953, Kurten 1966, Mitchell and Tedford 1973, Thenius 1979) suggested that the evolutionary line between the canid subfamily Amphicyonodontinae and the ursid subfamily Hemicyoninae was through the genera *Cephalogale* and *Ursavus* (Fig. 2).

Members of Hemicyoninae were relatively small during their early history with *Cephalogale* being about the size of a raccoon. As was often the trend with Ursidae, however, they increased in size with time and some became the size of the largest modern bears. Hemicyoninae were largely carnivorous, but it appears that *Cephalogale* became increasing omnivorous, which is why it is considered to be the ancestor of all ursids.

Cephalogale occurred in Eurasia from the late Oligocene and North America from the early Miocene (Tedford et al. 1987). The much larger *Hemicyon* was confined to Eurasia during its early history but became

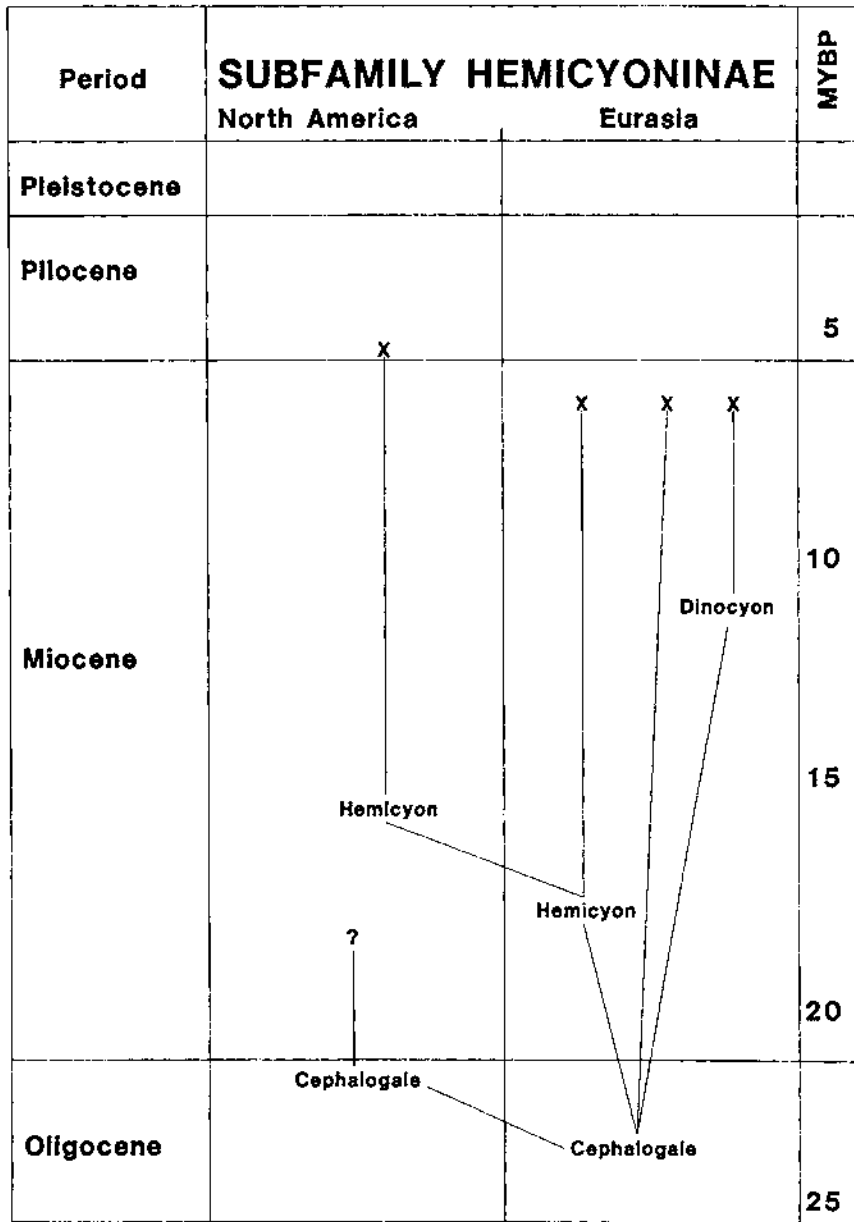


Fig. 2. A tentative phylogeny of the genera of the subfamily Hemicyoninae and approximate extinction dates.

very successful and spread to North America in the mid-Miocene (Hendey 1972, Tedford et al. 1987). Scott (1937) believed the bear-dogs were the dominant canid type in North America during the late Miocene and Pliocene. The extinction of Hemicyoninae has been related to the radiation of a more advanced subfamily of bears, Agriotheriinae (Hendey 1972, Kurten 1971), or possibly due to competition with large felids (Lydekker 1883, Frick 1926).

SUBFAMILY AGRIOTHERIINAE

The ursid subfamily Agriotheriinae as described by Thenius (1959) and Kurten (1966) include the genera *Ursavus*, *Indarctos*, and *Agriotherium*. The genus *Ursavus*, which is believed to have evolved in Europe from *Cephalogale*, appears to have given rise to its own subfamily Agriotheriinae plus the subfamilies Tremarctinae, Ursinae, and Ailuropodidae (Fig. 3). *Ursavus elmensis*, which was about the size of a fox, is

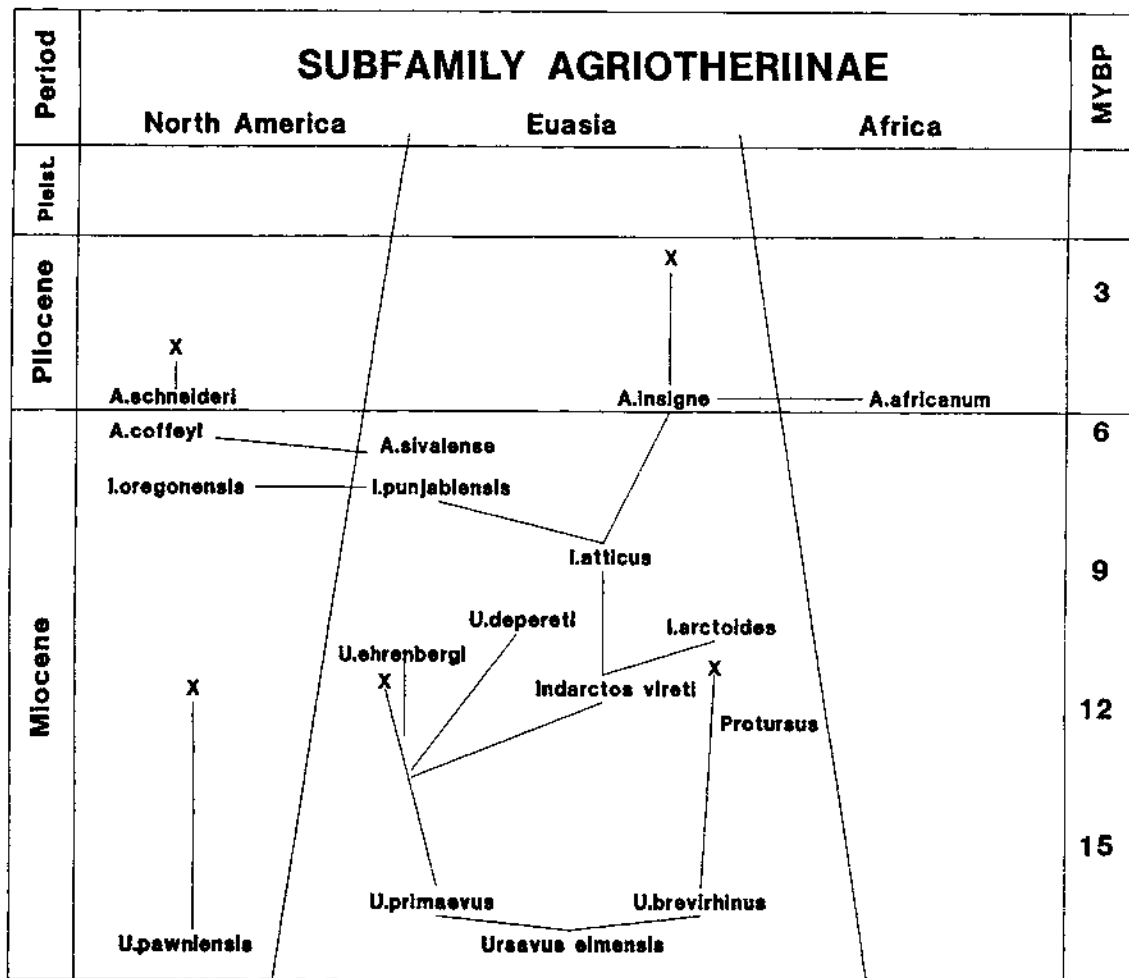


Fig. 3. A tentative phylogeny of the subfamily Agriotheriinae.

thought to be the most primitive species of this genus (Crusafont and Kurten 1976). It existed during the early Miocene, when the climate in Europe was relatively stable and sub-tropical.

From the small, primitive *U. elmensis*, 2 larger species appear to have evolved, *U. primaevus* and *U. brevirhinus* (Crusafont and Kurten 1976). Crusafont and Kurten believe that these 2 species were sympatric in Europe for a relatively long period and therefore deserve specific distinction, which Stromer (1940) and Thenius (1949, cited from Crusafont and Kurten 1976) did not give them. From *U. primaevus*, Crusafont and Kurten (1976) suggest that 2 larger species, *U. ehrenbergi* and *U. depereti* evolved. Thenius (1949) mentioned that *U. ehrenbergi* may have been close to the line leading to the subfamily Ursinae, though Crusafont and Kurten (1976) propose that the ursine bears probably arose from a line closer to the more

primitive *U. brevirhinus*. Members of the genera *Ursavus* were found in Eurasia for over 10 million years. It appears that *Ursavus*, perhaps the debated species *U. pawniensis*, was also in North America from the early to mid-Miocene (Tedford et al. 1987). Hende (1980) suggests the genus *Ursavus* should be their own subfamily, Ursavinae.

The transition from the genus *Ursavus* to *Indarctos* during the early Pliocene appears to follow an increase in body size (Hende 1972). Crusafont and Kurten (1976) proposed that the relatively lightly built *Indarctos vireti* was the most primitive species of this genus. The various species of *Indarctos* generally continued to increase in size and spread from Europe and Asia to North America, where the remains of *I. oregonensis*, a very large bear, was discovered in Oregon (Merriam et al. 1916) and Nebraska (Shultz and Martin 1975).

For many years there has been disagreement on the relationships of the third genus of the subfamily, *Agriotherium*. Recently, Thenius (1959) and Hendey (1972 and 1980) conclude that *Agriotherium* evolved from *Indarctos* and may even have been congeneric (Hendey 1980). Dalquest (1986), however, believes that the 2 are not closely related. The long-standing confusion over the evolutionary direction of the 2 species may be due to *Agriotherium* being more carnivorous than *Indarctos*, which is against the general trend of the Ursidae (Hendey 1980).

Remains of *Agriotherium* have been found in many parts of the world including Europe, Iran, India, South Africa, and North America (Hendey 1972). In North America, its known range extended from California to Florida and from Nebraska to southern Mexico (Dalquest 1986). In North America *Agriotherium* became larger than any extant species of bear (Scott 1937, Shultz and Martin 1975).

The extinction of *Agriotherium* due to competition with early Ursinae, as was a probable cause of extinction for other genera of Agriotheriinae, appears less plausible because *Agriotherium* was thought to be largely carnivorous. Competition with other carnivores may have been involved (Hendey 1972). Many carnivores had difficulties during the general extinction of the late Hemphillian near the Miocene/Pliocene boundary, when 60 mammalian genera disappeared from North America (Martin 1984). The last known representative of this subfamily, *A. insigne*, disappeared after the Villafranchian in Europe (Kurten 1968) as the climate began gradual cooling and warming oscillations, foreshadowing the ice age.

SUBFAMILY TREMARCTINAE

The subfamily Tremarctinae includes the genera *Plionarctos*, *Arctodus*, and *Tremarctos* (Thenius 1959, Kurten 1966). There is 1 extant species, *Tremarctos ornatus* of the South American Andes. Although the fossil evidence leading to Tremarctinae is poor, paleontologists suggest that *Ursavus* is likely the ancestral genus (Thenius 1959, 1976; Kurten 1966). Cytological and molecular methods indicate that *T. ornatus* diverged from the genus *Ursus* 10.5-15 MYBP (O'Brien et al. 1985, Goldman et al. 1989), when *Ursavus* sp. were common in Eurasia and apparently present in North America. Although there are several morphological and biochemical differences between Tremarctinae and Ursidae, including a different number of chromosomes (2n is 74 in *Ursus* and 52 in *Tremarctos*), the fact that *T. ornatus* and *U.*

thibetanus have crossed in captivity questions placing *Tremarctos* in its own subfamily (Mondolfi 1983).

The earliest Tremarctinae is *Plionarctos* and was found in the upper Pliocene of California (Frick 1926) although earlier roots in Asia are suspected (Kurten and Anderson 1980). This genus is likely the ancestor of the 2 other genera of the subfamily, *Tremarctos* and *Arctodus* (Fig. 4). These 2 genera made their first appearance in the Pleistocene of North and South America (Kurten 1966).

The early history of both *Arctodus* and *Tremarctos* is poorly recorded in the fossil record. Early students such as Merriam et al. (1916) and Frick (1926) and more recently Erdbrink (1953), believed *Arctodus* evolved from a line close to *Indarctos*. Thenius (1959) and Kurten (1966), however, believe that *Arctodus* was a Tremarctinae.

Of the 5 species of *Arctodus*, *A. pristinus*, and *A. simus* were in North America and *A. bonariensis*, *A. pamparus*, and *A. brasiliensis* were found in South America. Kurten (1967) suggested *A. pristinus* may represent a relatively primitive form. It was smaller, more lightly built, and probably less carnivorous than the other species and so far has only been found in the southeastern portion of North America.

More is known of *A. simus*, the great short-faced bear, than other Arctoid bears, because the fossil record is extensive in area, covering most of North America, and relatively complete. *A. simus* was a very large bear, with some individuals weighing at least 650 kg (Emslie and Czaplewski 1985). This bear had long legs and stood about 2 m at the shoulder, which suggests an adaptation for fast movement. Kurten (1967) thought that *A. simus* was not truly a cursorial predator, but may have been capable of bursts of speed exceeding those of *U. arctos*. Kurten (1967) suggested that its short but wide jaws demonstrated convergence with the great cats and indicated that it was largely carnivorous. According to Kurten's interpretation, *A. simus* was by far the most powerful predator during the Pleistocene and possibly preyed on contemporary species of bison, deer, horse, and ground sloth. Stirling and Derocher (1990) and McLellan (1993) suggested that co-existence with *A. simus* for or over 1 million years inflicted significant constraints on the evolution of *Ursus americanus*.

Emslie and Czaplewski (1985) disagree with the conclusions of Kurten (1967). Based on characteristics of the skull, body size, and relative lengths of distal and proximal limb segments, Emslie and Czaplewski (1985) suggest that *A. simus* was largely herbivorous.

A. simus disappeared at the end of the Wisconsin

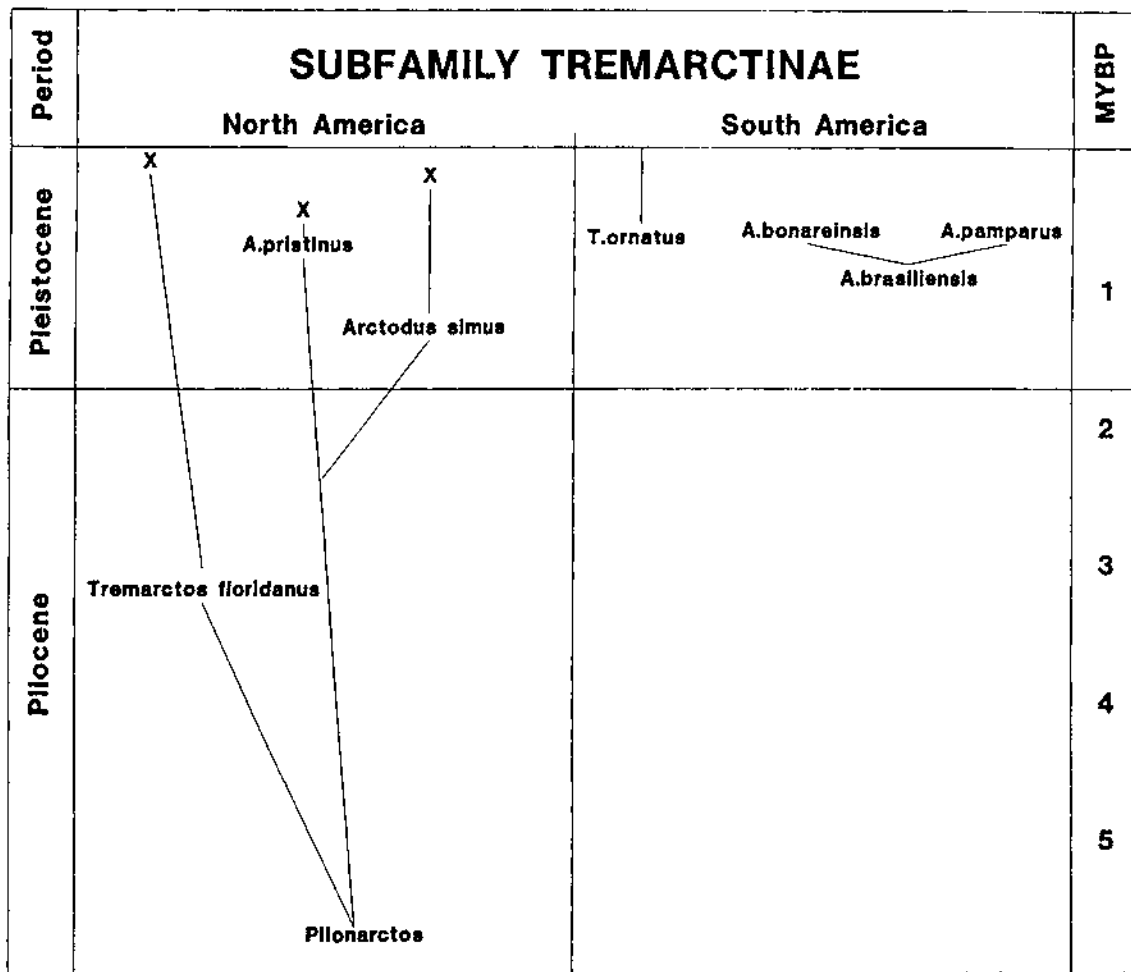


Fig. 4. A tentative phylogeny of the subfamily Tremarctinae.

glaciation, perhaps due to competition with *Ursus arctos* (Kurten and Anderson 1974). These 2 bears, however, apparently co-existed in Beringia for about 100,000 years, so if competition was the leading factor, other conditions must have changed. The close proximity in time between the disappearance of *A. simus* and the late Pleistocene extinction, when 57 of the 79 species of large mammal (>45 kg) in North America disappeared (Marten 1984), suggests a correlation, particularly if *A. simus* was largely carnivorous and much of its prey disappeared. The peak of this extinction was about 11,000 YBP (Martin 1984) whereas the last *A. simus* remains to be dated were more than 1,000 years older. This date, however, was obtained on an *Equus* bone found at the deepest level of a cave (Kurten and Anderson 1980) and the bear was likely younger, perhaps near the 10,000 years ago suggested by Harrington (1973). Two competing hypotheses

explaining the late Pleistocene extinction, which perhaps led to the extinction of *A. simus*, are overkill by Paleoindians of the Clovis culture, and climatic change that included a very dry period and a resulting reduction of habitat diversity.

Relatively little is known of *Arctodus* in South America because few fossils have been found. *A. brasiliensis* was the smallest of the 3 species and, as it more closely resembled the North American species, may have been an intermediate. *A. pamparus* was also relatively small, whereas *A. bonariensis* was very large, rivaling *A. simus* in size (Kurten 1967). *A. bonariensis* had large canines and carnassials but short posterior molars, suggesting a carnivorous diet. Based on the structure of their molars, Kurten (1967) suggested the possibility of a mollusk-eating specialization for the other South American species.

The genus *Tremarctos* consists of 2 species,

Tremarctos floridanus and the extant spectacled bear, *T. ornatus*. As was the case with *Arctodus*, the ancestral genus to *Tremarctos* is believed to be *Plionarctos* (Kurten 1966; Thenius 1959, 1976). Fossils of the North American spectacled bear have been found most often in Florida and only rarely elsewhere (Kurten and Anderson 1980). *T. floridanus* seems to have been a slow-moving, heavily built, medium-sized bear with powerful forelimbs. Kurten (1966) suggested that *T. floridanus* filled a niche similar to that of the European cave bear, *Ursus spelaeus*, as a powerful, almost exclusively vegetarian bear. Reasons for the extinction of *T. floridanus* in the last 8,000 years are unclear, although competition with *U. americanus* has been suggested. These species, or at least early versions, co-existed in North America for about 3 million years, so if competition with *U. americanus* was the cause of extinction, an additional change, such as climate, must have precipitated it.

SUBFAMILY URSINAE

The subfamily Ursinae has been divided into many different phylogenetic groups in the past. Until recently, 5 genera, *Melursus* (sloth bear), *Helarctos* (sun bear), *Thalarchos* (polar bear), *Selenarctos* (Asiatic black bear), and *Ursus* (brown bear and American black bear) were recognized. Molecular and cytological methods (O'Brien et al. 1985, Goldman et al. 1989) plus successful crossing between several of the species in captivity (C. Servheen, U.S. Fish and Wildlife Service, pers. commun.) suggests that these bears are congeneric.

The evolution of Ursinae over the past 5 million years is well recorded in fossils of Europe. Early Ursinae likely evolved from *Ursavus* of the Miocene, perhaps through the genus *Protursus* of the mid-Miocene (Thenius 1959, Crusafont and Kurten 1976; Fig. 5). Climatic conditions in Europe during the late Miocene were dry, and savannahs and deserts were common. Such conditions were poor for bears, and their fossils are scarce until the Pliocene began, 5-6 MYBP.

Black Bears

Next to *Protursus*, the earliest member of the subfamily Ursinae is believed to be *Ursus minimus*, which has been found in many locations in Europe (Kurten 1968). *U. minimus* was a small, primitive species, that generally increased in size during its existence. It appears that *U. minimus* or a species similar to it radiated through Asia and was in North

America at least by the early Blancan, perhaps 3.5 MYBP (Kurten and Anderson 1980). In North America, this species is called *U. abstrusus*, but may be conspecific with *U. minimus*. This small early ursid likely gave rise to the Asiatic and American black bears. The timing of the divergence of *U. americanus* estimated from fossils is similar to the 4.4 MYBP derived through 2-dimensional electrophoresis (Goldman et al. 1989) and the 3.8 MYBP estimated from mitochondrial DNA divergence (Shields and Kocher 1991).

U. thibetanus ranged into Europe during in the mid-Pleistocene with remains being found in many countries (Kurten 1968). Why it was extirpated from Europe is unknown, but competition with the largely herbivorous cave bears may have been a factor. In North America, black bears are by far the most common fossil bears of the Pleistocene and have been found across most of the continent. As was the case with many species, late-Pleistocene black bears were much larger than they are today. Behavioral and morphological characteristics imposed on black bears by other ursids have been discussed by Herrero (1972), Stirling and Derocher (1990), and McLellan (1993).

Cave Bears

The small, primitive *U. minimus* gave rise to *U. etruscus*, which was also initially small but continued the trend towards a larger body size. This species radiated across Eurasia. In Europe, it gave rise to the cave bears and in Asia it was ancestral to brown bears.

Caves are a good environment for fossilization. Bears, with large, stocky bones, are especially well preserved. Thus cave bears, which often died in caves, have one of the best fossil records. The evolutionary lineage is so complete that delineating species has been difficult (Kurten 1968). In addition, the tens of thousands of individuals represented (an estimated 30,000-50,000 in 1 cave) has enabled the typical study of phylogeny and morphology plus studies of age and sex class structure, individual variation, and mortality rates.

Thenius (1959) recognizes 2 species of cave bear: *U. deningeri* and *U. spelaeus*, the giant cave bear of Europe. Kurten (1968) identifies another species, *U. savini*, between the etruscan bear and *U. deningeri*.

Based on fossils, *U. spelaeus* appears to have been a large, stocky, mostly herbivorous bear. It had a relatively small geographic distribution, being found only in Europe and into the southwestern corner of Russia and the Ukraine. Such a small distribution

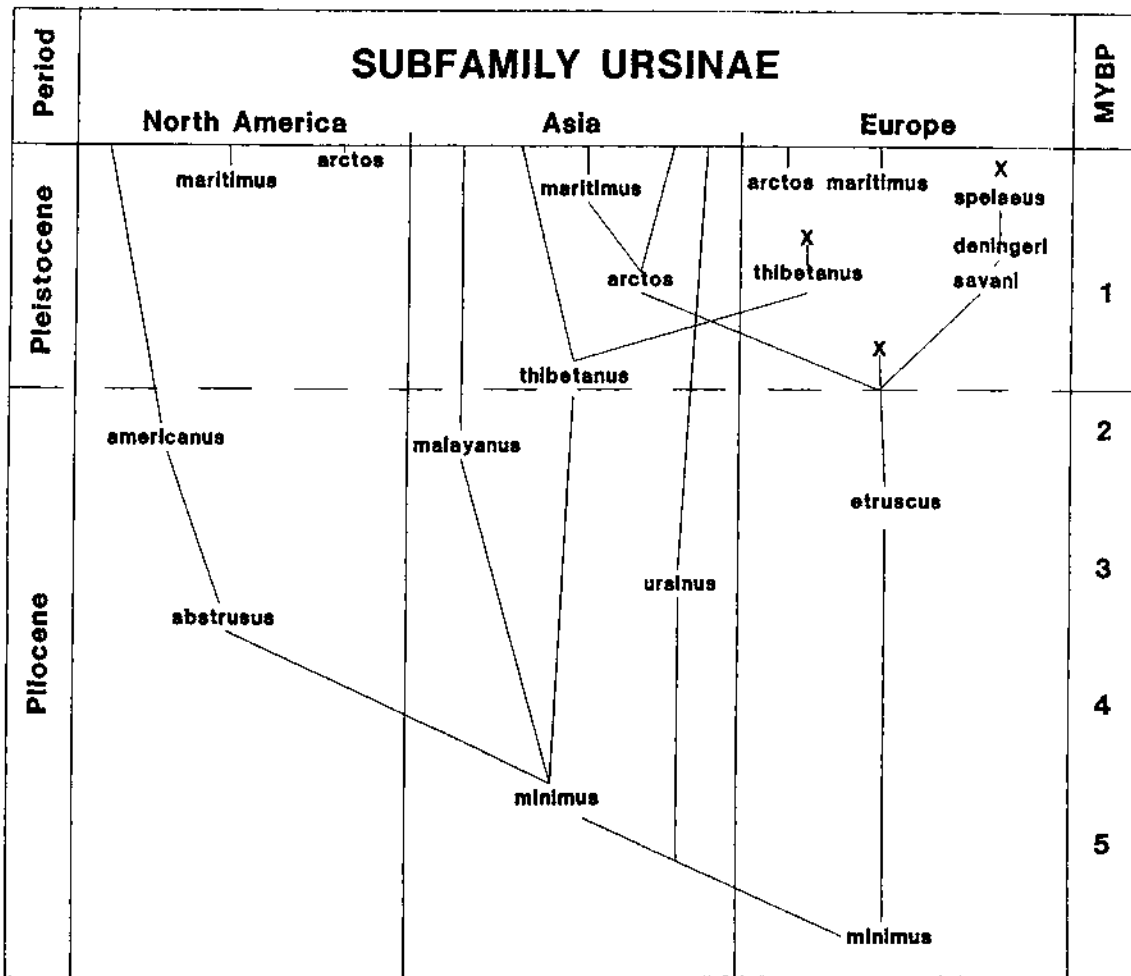


Fig. 5. A tentative phylogeny of the subfamily Ursinae.

suggests a dietary specialization or perhaps a dependence on caves or mountainous country where caves are found (Kurten 1976). Remains of *U. spelaeus* have not been found where caves are uncommon.

Many possible causes for the extinction of cave bears have been proposed. Kurten (1958) suggested that rapidly increasing numbers of humans may have settled caves during summer dispersal periods and thus excluded bears returning to hibernate in the early winter. Extant brown and black bears often hibernate in caves much too small for human occupation, so if this hypothesis is correct, then cave bears would have had different requirements than the extant species, or small caves were rare in their range. Competition with increasing numbers of humans and brown bears for caves and other resources plus climate change appear to be likely factors.

Brown Bears

The brown bear is believed to have evolved from *U. etruscus* in Asia. The oldest fossils were found in China from about 0.5 MYBP (Kurten 1968) and there has been a continuous record of *U. arctos* in Asia since then. *U. arctos* entered Europe about 0.25 MYBP and North Africa shortly after. Pleistocene remains of *U. arctos* are common in Great Britain and they may have contributed to the extirpation of the cave bear there.

U. arctos apparently entered Alaska about 100,000 YBP but did not move south until the late Wisconsin, about 13,000 YBP. Kurten and Anderson (1980) suggest the possibility of 2 independent migrations; narrow-skulled bears from northern Siberia through central Alaska to the rest of the continent becoming *U. a. horribilis*, and a southern migration of broad-skulled bears from Kamchatka to the Alaskan peninsula

becoming *U. a. middendorffi*. Fossils of brown bears in Ontario, Ohio, Kentucky (Guilday 1968), and Labrador (Spiess and Cox 1976) indicate they were once found much farther east than historical records show. Guilday (1968) suggested that immediately after the glacial retreat, a relatively boreal, parkland coniferous forest spread across the central and southern portions of the continent and with it, several western species, including brown bears.

Polar Bear

The Polar bear is a recent offshoot of *U. arctos*. Indications of a recent divergence include the rarity of fully fossilized polar bear remains (Kurten 1964) whereas subfossils are common, and that these species produce fertile hybrids in captivity (Kowalska 1965). Mitochondrial DNA divergence (Shields and Kocher 1991) and 2-dimensional electrophoresis (Goldman et al. 1989) also suggest a recent split. Polar bears are repeating the trend that was seen with *Agriotherium* and *Arctodus* by becoming carnivores; this time specializing on marine mammals. The apparent morphological and behavioral differences between polar bears and brown bears indicate that polar bears are rapidly evolving as they exploit a new niche.

Sun and Sloth Bears

The fossil records of south Asian bears, the sun (*Ursus malayanus*) and sloth bears (*U. ursinus*) are poor, and their origins more speculative than for other species (Kurten 1966). *U. malayanus* is first found in the late Pliocene and *U. ursinus* in the Pleistocene. Thenius (1959) thought they separated from the other Ursinae even before *Protursus*, whereas Hendey (1972) speculated that the split was after *Protursus* but before *U. minimus*. Electrophoretic analysis indicates a more recent split, not significantly different from that of other extant members of the subfamily except the polar bear (Goldman et al. 1989). Recent analyses of mitochondrial DNA suggest that the 6 ursine species originated sequentially during the past 6 million years, beginning with *U. ursinus* and ending with the polar bear (Waits et al. unpubl. data, submitted). It is becoming increasingly evident that *U. ursinus*, *malayanus*, *thibetanus*, *americanus*, and *etruscus* all branched from the primitive *U. minimus* or *U. abstrusus* that radiated through Eurasia near the Miocene/Pliocene boundary and into North America shortly after. The great morphological differences between *U. malayanus*, *U. ursinus*, and other bears is likely due to recent adaptive change as the south Asian

bears exploited new niches.

SUBFAMILY AILUROPODIDAE

The phylogeny of the giant panda has been disputed since 1870, when Milne-Edwards placed Ailuropoda into the family Procyonidae, while David had called it an ursid the previous year (O'Brien et al. 1985). Some recent authors (Tagle et al. 1986) linked *Ailuropoda* closer to the lesser panda (*Ailurus fulgens*) than to the bears, but there has been an overwhelming number of papers placing *Ailuropoda* not close, but closer to bears than to the lesser panda (Kurten 1985, O'Brien et al. 1985, Mayr 1986, Ramsay and Dunbrack 1987, Goldman et al. 1989). These papers were based on 6 independent molecular and genetic measures, fossil evidence, and reproductive characteristics. These recent reports plus the comparative anatomical work of Davis (1964), earlier protein evolution work of Sarich (1973), and the synthesis of Thenius (1979) indicate the giant panda should be placed into its own subfamily, Ailuropodidae, of the family Ursidae.

The earliest evidence of *Ailuropoda* was during the late Pliocene, about 3 MYBP (Schaller et al. 1985). Wang (1974) divides *Ailuropoda* into 2 species: *A. microta* was a smaller, primitive species that became extinct during the mid-Pleistocene. *A. melanoleuca* was once larger than it is today and then ranged south of the Yangtze river at least to Burma. The decrease in the panda's range has been attributed to climatic changes during the Pleistocene and, like almost all extant species, man's activities during the postglacial (Schaller et al. 1985).

The fossil record leading to *Ailuropoda* is poor and evolutionary links speculative at best. Matthew and Granger (1923), Davis (1964), Hendey (1972), and Wolff (1978) believed the panda evolved from *Indarctos* of the subfamily Agriotheriinae. Thenius (1979) however, identified a possible ancestor, *Agriarctos*, from the late Miocene of Hungary, and suggested it was a descendant of *Ursavus* from the mid-Miocene (Fig. 6). After re-evaluation, Hendey (1980) concluded that *Ursavus depereti* was more likely to be the ancestor of the pandas than was *Indarctos*. The divergence between bears and the giant panda has been estimated to be 18-22 MYBP (Goldman et al. 1989), and thus, separation from an early *Ursavus*, either via *Indarctos* or not, is possible. The panda has a specialized niche and, like other species that diverged from the omnivorous trend, likely went through a period of rapid evolution, which accounts for their morphological and behavioral differences from other bears.

Period	SUBFAMILY AILUROPODIDAE	MYBP
Pleistocene	A. melanoleuca	
Pliocene	Ailuropoda microta	5
Miocene	Agriarctos	10
	U. deperetti	15
	Ursavus primaevus	20
Oligocene		25

Fig. 6. A tentative phylogeny of the subfamily Ailuropodidae.

CONCLUSIONS

The Ursidae is a young family consisting of 5 subfamilies: Ursinae, Tremarctinae, Agriotheriinae, Ailuropodidae, and Hemicyoninae. The distinction and inclusion of the later 2 subfamilies in the family Ursidae is probably not settled.

Patterns of extinction and evolution within the Ursidae reflect some of the adaptive zones for carnivores that disappear and then reappear (Martin 1989). From the highly adaptable omnivorous base,

more specialized forms evolved. Several species, such as *Arctodus simus*, *Agriotherium insigne*, and *Ursus maritimus*, appear to have filled a more carnivorous niche. Others, such as *Ursus spelaeus*, *Tremarctos floridanus*, and *Ailuropoda melanoleuca*, became more herbivorous. The importance of climatic change and interspecific competition is repeated often by students who speculate on the causation of bear extinction.

Three species, *U. thibetanus*, *U. americanus*, and *U. arctos* still have wide geographic ranges and exploit a

variety of niches from deserts to rain forests. These species are likely candidates for future speciation of the family Ursinae. The recent explosion in human numbers and resulting selective pressures and genetic isolation is obviously driving bear evolution today.

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