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ARTICLE

Brown bear (*Ursus arctos*) (9880 ± 35 BP) from late-glacial Champlain Sea deposits at Saint-Nicolas, Quebec, Canada, and the dispersal history of brown bears

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Abstract: A bear third metatarsal was discovered in Champlain Sea deposits at the Saint-Nicolas site, Quebec. It is identified morphologically probably as a brown bear (*Ursus arctos*) based on the combination of morphology and ancient DNA. It is the first evidence of bears from Champlain Sea deposits. This bone was radiocarbon dated by accelerator mass spectrometry (AMS) to 9880 ± 35 BP (radiocarbon years BP, taken as 1950) — close to the end of the Champlain Sea phase in eastern North America. The specimen is considered in relation to other North American Quaternary brown bear remains, the dispersal history of the species, and the known Champlain Sea fauna from Saint-Nicolas, as well as stratigraphy at the site and paleoenvironment. Four major conclusions summarize the paper.

Résumé : Un troisième métatarsien d'ours a été découvert dans des dépôts de la mer de Champlain au site de Saint-Nicolas (Québec). À la lumière de sa morphologie et d'ADN ancien, il s'agirait probablement d'un os d'ours brun (*Ursus arctos*). L'os constitue la première preuve de la présence d'ours issue de dépôts de la mer de Champlain. La datation de l'os au radiocarbone par spectrométrie de masse par accélérateur (SMA) a donné un âge de 9880 ± 35 BP (années par datation au radiocarbone avant le présent, établi à 1950), soit vers la fin de la phase de la mer de Champlain dans l'est de l'Amérique du Nord. Le spécimen est examiné par rapport à d'autres restes d'ours bruns du Quaternaire de l'Amérique du Nord, à l'historique de dispersion de l'espèce et à la faune de la mer de Champlain révélée au site de Saint-Nicolas, ainsi qu'à la stratigraphie du site et qu'au paléomilieu. Quatre grandes conclusions sont présentées à la lumière des résultats. [Traduit par la Rédaction]

Introduction

The Champlain Sea was a major geographic feature in eastern North America near the close of the last (Wisconsinan) glaciation. It resulted from an inundation of the St. Lawrence Lowland by Atlantic waters that occurred between 13 000 and 9000 BP (Cronin et al. 2008). The weight of the Laurentide ice sheet as it melted back from the St. Lawrence Lowland depressed that region, causing Atlantic waters to flood in (with associated boreal flora and fauna). As the ice sheet melted back farther, the Lowland slowly rebounded, and the Champlain Sea waters drained back to the Atlantic Ocean (Harington et al. 2006). Based on our knowledge of their lives and habits of their modern counterparts, Champlain Sea vertebrates yield valuable clues to the paleoenvironment of the sea.

Several species of whale, particularly those adapted to cool inshore conditions, lived in the Champlain Sea. Approximately 80% of whale specimens recorded from Champlain Sea deposits are white whales (*Delphinapterus leucas*). Other whale species represented are humpback (*Megaptera novaeangliae*), bowhead (*Balaena mysticetus*), finback (*Balaenoptera physalus*), and harbor porpoise (*Phocoena phocoena*). Seals, particularly those adapted to breeding on pack ice, such as harp (*Pagophilus groenlandicus*) and bearded (*Erignathus barbatus*), and those adapted to breeding on land-fast ice, such as ringed (*Pusa hispida*), also lived in the Champlain Sea. An open coastal water species, the harbor seal (*Phoca vitulina*) has likewise been found near the southern margin of the sea (Harington 1981; Harington and Occhietti 1988). Walruses (*Odobenus rosmarus*), which tend to follow the pack-ice edge, have also been reported (Bouchard et al. 1993). These marine mammal fossils suggest the former presence of Arctic to boreal waters, with sea ice generally present.

Analysis of the ecological preferences of the 11 species of Champlain Sea fishes indicates the former existence of several freshwater and marine environments. Lake cisco (*Coregonus artedii*), lake charr (*Salvelinus namaycush*), deepwater sculpin (*Myoxocephalus thompsoni*), spoonhead sculpin (*Cottus ricei*), and longnose sucker (*Catostomus catostomus*) usually occupy deep, cold lakes. The rainbow smelt (*Osmerus mordax*), the *trachurus* form of the threespine stickleback (*Gasterosteus aculeatus*), and Atlantic tomcod (*Boreogadus tomcod*) are anadromous species. Capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*) and lumpfish (*Cyclopterus lumpus*) are more strictly marine fishes. The mean latitude of the ranges of these fishes is now southern Labrador, more than 8° farther north than during Champlain Sea time (McAllister et al. 1988).

Some comments on the appearance and habits of the brown bear, the species featured here, are warranted. Brown bears are mainly solitary, relatively large (males: 170–230 cm long, weighing 250–350 kg; females: 145–213 cm long, weighing 80–225 kg), having medium to dark brown fur, a dished head profile, distinctly high, muscle-filled humps powering the forelegs, long front claws, short round ears, and short tails. The largest, heaviest individuals in North America are from the Pacific Coast. They are a northern hemisphere species occurring in both Eurasia and

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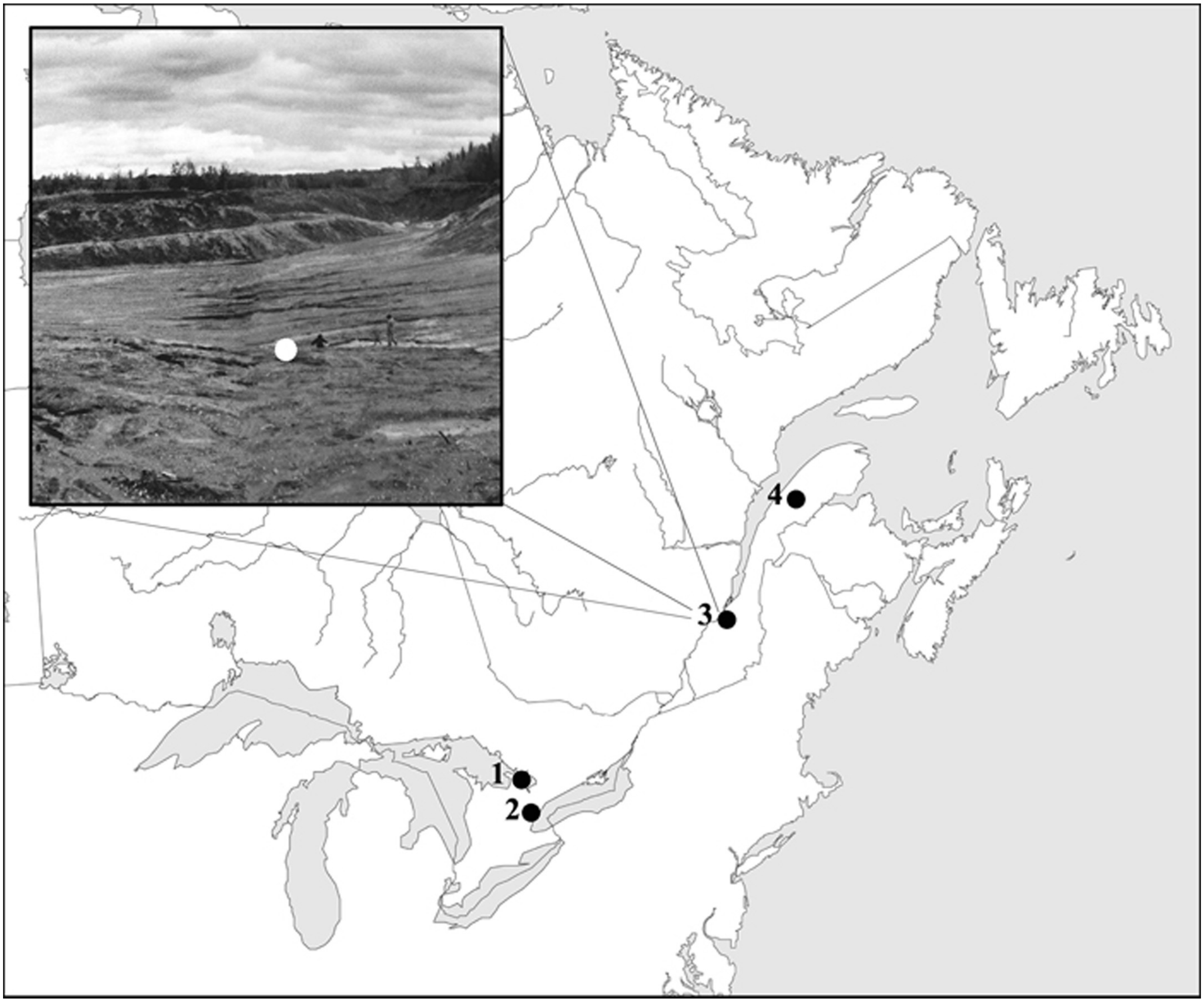
Fig. 1. Eastern Canada showing localities with brown bear fossils: 1, Orillia, Ontario (skull dated to 11 700 BP); 2, Woodbridge, Ontario (humerus estimated to be of Middle Wisconsinan age); 3, Saint-Nicolas, Quebec (third metatarsal dated to 9880 BP); 4, Trou Otis, Quebec (cranium estimated to be of Early Holocene age). Inset shows the site (white ring) where the fossil brown bear specimen was found in the Gosselin sandpit at Saint-Nicolas.



North America. Their dispersal history is discussed later. They prefer open areas such as alpine meadows, river valleys, and scrublands, and hibernate in winter where dens are usually located in mountainous or heavily forested areas often under tree roots, where snow cover is deep. Male home ranges are much larger than those of females. They are omnivorous, their diet being composed mainly of vegetative matter, but they also feed on fishes, small mammals, birds, and carrion (Naughton 2012). Their keen sense of smell and need to feed heavily before hibernation can draw them to shorelines where fishes, nesting birds, and washed-up marine mammal carcasses can be relatively abundant.

The purpose of this paper is to describe the bear fossil from the Saint-Nicolas site, Quebec, discuss its stratigraphic position, paleoenvironment, radiocarbon age, and identification through morphometric comparison with modern brown, polar, and black bear specimens, as well as analysis of its ancient DNA. The specimen is also considered in relation to the dispersal history of brown bears, and to the known Champlain Sea fauna from Saint-Nicolas.

Results

The Saint-Nicolas fauna and its paleoenvironment

The Saint-Nicolas (46°42′N, 71°23′W) site is a large sandpit located in the Saint-Nicolas ward of the city of Lévis, across the river from the city of Québec (Fig. 1) where tidal current sands of the Pleistocene–Holocene transition preserve an exceptional marine fossil fauna, including 38 kinds of invertebrates (Table 1), five fish species, five seabird species, four species of marine mammals, and one land mammal — the bear dealt with in this paper (Table 2). Radiocarbon ages of the fauna vary between 10 060 and 9810 BP. These sands are overlain by tidalites corresponding to the last phase of the Champlain Sea, until about 9750 BP. Lithological, geochemical, and paleontological data from the site suggest that sedimentation occurred in an archipelago at the entrance to the Champlain Sea that was subjected to tides of about 10 m (Occhietti et al. 2001). Faunal diversity is associated with marine productivity arising from the mixing of fresh and salt water. The

Table 1. Macroinvertebrates found in the Saint-Nicolas sandpits.

Macroinvertebrate	Description
Bryozoa	
Gen. et sp. indet. (encrusting form)	—
Gen. et sp. indet. (branching form)	—
Brachiopoda	
Hemithiris psittacea (Gmelin, 1790)	Parrot-beak lamp shell
Amphineura	
Gen. et sp. indet.[a]	—
Gastropoda	
Acirsa borealis (Lyell, 1841)	Chalky wentletrap
Boreotrophon truncatus (Strom, 1768)[a]	Bobtail trophon
Buccinum glaciale (?) Linnaeus, 1761	Glacial whelk
Buccinum plectrum Stimpson, 1865	Sinuous whelk
Buccinum scalariforme Moller, 1842 (*B. tenue* in Occhietti et al. 2001)	Ladder whelk
Buccinum undatum (?) Linnaeus, 1758	Waved whelk
Colus sp. (Mörch, 1786)[a]	Spindle shell
Boreoscala cf. *greenlandica* (Perry, 1811)	Greenland wentletrap
Haminoea solitaria (Say, 1822)	Solitary glassy-bubble
Lepeta caeca (Müller, 1776)	Northern blind limpet
Littorina cf. *L. saxatilis* (Olivi, 1792)	Rough periwinkle
Cryptonatica affinis (Gmelin, 1791) (*Natica clausa* in Occhietti et al. 2001)	Arctic moonsnail
Neptunea despecta (Linnaeus, 1758)	Common northern neptune
Oenopota sp. Mörch, 1852[a]	Lora
Puncturella cf. *P. noachina* (Linnaeus, 1771)[a]	Diluvian puncturella
Piliscus commodus (Middendorff, 1851)[a]	Widemouth lamellaria
Trichotropis borealis Broderip and G.B. Sowerby I., 1829	Boreal hairysnail
Velutina cf. *V. velutina* (Müller, 1776)	Smooth lamellaria
Volutopsius cf. *V. norwegicus* (Gmelin, 1791)[a]	Norway whelk
Pelecypoda	
Astarte montagui (Dillwyn, 1817)	Narrow-hinge astarte
Axinopsida orbiculata (G.O. Sars, 1878)[a]	Orbicular axinopsid
Chlamys islandica (Müller, 1776)	Iceland scallop
Crenella faba (Müller, 1776)[a]	Bean crenella
Hiatella arctica (Linnaeus, 1767)	Arctic hiatella
Macoma balthica (Linnaeus, 1758)	Baltic macoma
Macoma calcarea (Gmelin, 1791)	Chalky macoma
Mya arenaria Linnaeus, 1758	Softshell
Mya truncata Linnaeus, 1758	Truncate softshell
Mysella planulata (Stimpson, 1851)[a]	Plate mysella
Mytilus edulis Linnaeus, 1758	Blue mussel
Serripes groenlandicus (Mohr, 1786)	Greenland smoothcockle
Cirripedia	
Balanus crenatus Bruguière, 1789	Notched acorn barnacle
Chirona hameri (Ascanius, 1767) (*Balanus hameri* in Occhietti et al. 2001)	Turban barnacle
Echinoidea	
Stongylocentrotus sp.	Green sea urchin

[a]New addition to the Champlain Sea fauna (Mario Cournoyer, personal communication, 2010).

food web was composed of molluscs (abundant at low tide), fishes, birds (that may have nested on the small rocky islands or skerries), walrus, and seals (Occhietti et al. 2001), besides the bear.

Table 2. Vertebrates found in the Saint-Nicolas sandpits (see Cournoyer et al. 2006).

Vertebrate	Description
Fishes	
Acipenser sp.	Sturgeon
Cryptacanthodes sp.	Wrymouth
Lycodes sp.	Eelpout
Mallotus villosus	Capelin
Salmonidae indet.	Salmonid
Birds	
Clangula hyemalis	Long-tailed duck
Uria lomvia	Thick-billed murre
Somateria mollissima	Common eider
Sterna paradisaea	Arctic tern
Aves indet.	Unidentified bird
Mammals	
Pusa hispida	Ringed seal
Erignathus barbatus	Bearded seal
Odobenus rosmarus	Atlantic walrus
Delphinapterus leucas	White whale
Ursus arctos[a]	Brown bear

[a]New addition to the Champlain Sea fauna (this paper).

The Saint-Nicolas specimen and other brown bear remains from Eastern Canada

The bear specimen, reported here as representing a brown bear, was collected from the surface of late-glacial (latest Pleistocene to earliest Holocene) sands (presumably derived from the upper part of unit 2 as depicted in the composite section at Saint-Nicolas (Occhietti et al. 2001)), left over from previous excavations in the western part of the Saint-Nicolas sandpit (Fig. 1, inset), by the second author, Mario Cournoyer, in 2004, as part of a collecting program begun in 1995. Bear remains are rare in late-glacial deposits in Eastern Canada. No radiocarbon-dated black bear (*Ursus americanus*) or polar bear (*Ursus maritimus*) specimens of that age have been recorded for the region (Harington 2003), although black bear remains are reported from the upper infill (5742 ± 120 BP or younger) at Mine Cave located about 20 km northeast of Ottawa (Lauriol et al. 2003). Perhaps only two brown bear specimens approaching the age of the Saint-Nicolas bone are known: a well-preserved skull from a gravel pit near Orillia, Ontario, that yielded a radiocarbon age of 11 700 ± 250 BP (Peterson 1965*a*, 1965*b*; Tovell and Deane 1966); and most of a cranium thought to be of Early Holocene age from Trou Otis, a cave near La Rédemption, Quebec (Harington 1980*a*) (Fig. 1). It is also worth mentioning that a brown bear skull was excavated from an 18th century Labrador Inuit midden at Okak Island, Labrador, as well as data on the former presence of brown bears in historic time in northern Quebec – Labrador (Elton 1954; Spiess and Cox 1976; Pigott 1999; Loring and Spiess 2007).

Systematic paleontology

Order Carnivora Bowdich, 1821
Family Ursidae Fischer de Waldheim, 1817
Genus *Ursus* Linnaeus, 1758

Ursus arctos Linnaeus, 1758 (brown bear)

DESCRIPTION: The specimen is a right third metatarsal (MPEP (Musée de paléontologie et de l'évolution, Montréal) 82.1) that is broadly similar to those of brown (*Ursus arctos*), polar (*Ursus maritimus*), and black bears (*Ursus americanus*) in proportions of the proximal and distal articular end as well as shaft length (e.g., Fig. 2). Of bear third metatarsals to which the fossil was compared (Table 3), it is closest in size and shape to a brown bear (e.g., CMN (Canadian Museum of Nature) 41056, a 600 lb (272 kg) adult male from Banff, Alberta, albeit slightly smaller, rather than a much smaller black bear specimen (e.g., CMN 41055, a 480 lb (218 kg) adult male, likewise from Banff, Alberta)). Also, according to Table 2 data, it is clear that the fossil and brown bear specimens are generally larger, with no overlap, than those of the black bear. Unfortunately, only one polar bear third metatarsal (CMN 41090)

Fig. 2. Comparison of right third metatarsals from (*left*) modern black bear (*Ursus americanus*, CMN 41055, 480 lb (218 kg) adult male from Banff National Park, Alberta), (*center*) a Champlain Sea age (9880 ± 35 ^{14}C years BP (UCIAMS 71656)) brown bear (*Ursus arctos*, MPEP 82.1, old adult from Saint-Nicolas, Quebec), and (*right*) a modern brown bear (*Ursus arctos*, CMN 41056, 600 lb (272 kg) adult male from Banff National Park, Alberta). Note the rough patches of arthritic bone near the extremities of the fossil.

Table 3. Comparative measurements of a bear third metatarsal (MPEP 82.1) from Champlain Sea deposits at Saint-Nicolas, Quebec, with modern brown (*Ursus arctos*), polar (*Ursus maritimus*), and black (*Ursus americanus*) bear third metatarsals.

		Measurements (mm)[a]						
Specimens	Remarks	1	2	3	4	5	6	7
Ursus arctos (MPEP 82.1). Champlain Sea deposits, Saint-Nicolas, QC, Canada.	Old individual. Has arthritic growths near proximal and distal ends.	72.6	16.1	25.8	10.8	9.2	19.3	14.5
Ursus arctos (CMN 41056). Modern, Canada.	Old male. Has similar signs of arthritic growths to fossil.	79.0	18.6	26.0	13.5	9.4	18.9	15.8
Ursus arctos (CMN 2772). Modern, NWT, Canada.	Adult male	82.4	19.0	28.3	12.6	10.7	21.6	17.9
Ursus arctos (CMN 31187). Modern, NWT, Canada.	Probably adult male	84.0	19.9	25.9	13.0	10.0	20.5	18.7
Ursus maritimus (CMN 41090). Modern, Canada.	2 year old male	—	18.3	24.6	11.4e	—	—	—
Ursus americanus (CMN 41055). Modern, Canada.	Adult male	68.4	15.0	21.5	10.5	8.7	15.7	14.1
Ursus americanus (CMN 1583). Modern, BC, Canada.	Adult(?) male	66.5	14.8	24.6	9.6	8.6	15.4	14.1
Ursus americanus (CMN 75389). Modern, Canada.	Adult male	67.1	14.1	21.8	9.0	7.1	14.7	13.6
Ursus americanus (CMN 34109). Modern, YK, Canada.	Adult female	64.4	11.5	19.6	8.8	7.2	13.7	11.9
Ursus americanus (CMN 5009). Modern, QC, Canada.	Adult(?) female	61.1	12.2	18.1	8.3	6.5	12.2	11.8
Ursus americanus (CMN Z-162). Modern, Canada.	Adult female	57.6	10.6	18.2	8.7	7.1	12.3	12.0

[a]1, Maximum length; 2, maximum proximal width; 3, maximum proximal depth; 4, minimum shaft width; 5, minimum shaft depth; 6, maximum distal width; 7, maximum distal depth; e, estimated.

was available for comparison, and it was from a 2 year old male. Nevertheless, it is worth noting that CMN 41090 not only has proximal articular facets of nearly equal size, compared with the relatively much smaller posteromedial facets in black and brown bears, but the proximal articular surface is markedly broader relative to length in the polar bear compared with black and brown bears.

Apart from the reddish brown staining of the fossil (probably derived from its oxidized, sandy matrix), the only other significant feature is the rough surface — especially near the distal articular end — consistent with arthritis. Of four black bear skeletons examined by Greer et al. (1977, fig. 1*c*), one had marked arthritic changes, including bony growth around the articular facets of the metatarsals. Therefore, this pathology is common in older bears, and may support an older age for the individual in question.

In summary, morphologically, the third metatarsal from Saint-Nicolas is best referred to an old brown bear of perhaps 500 lb (227 kg). The full-fusion of the bone and the evidence for arthritis may support the old age of the individual. A three-dimensional model was made at CMN of the original, and digital images are available.

Ancient DNA description

DNA isolation, amplification, and sequencing

To confirm the identity of the third metatarsal (MPEP 82.1) and place it within a phylogenetic framework (Clade IV consisting of brown bears from southern Canada and the lower 48 states of the United States; Fig. 3; supplementary Fig. S1[1] and Table S1[1]) a 3 g sample of bone from the shaft was sent to the specialized ancient DNA facility at The Pennsylvania State University for mitochondrial DNA typing. DNA was extracted from the bone following Rohland and Hofreiter (2007). A segment of the mitochondrial control region was PCR (polymerase chain reaction) amplified in a 25 μL reaction comprising the following: 2 mg/mL rabbit serum albumin; 1× Amplitaq Gold 360 buffer (Applied Biosystems Inc.); 1.2–5, SU Amplitaq Gold 360; 250 μmol/L each dNTP; 2.5 mmol/L $MgCl_2$; 1 μmol/L each primer URSUSF1-136-156 (Valdiosera et al. 2007) and H16229 (Hanni et al. 1994). Cycling conditions were used according to the manufacturer's instructions, with a 58 °C annealing temperature. The PCR product was cleaned using a Millipore Multiscreen $PCR_{\mu 96}$ filter plate and directly sequenced using Big Dye v3.1 sequencing chemistry (Applied Biosystems) and the same primers as for amplification. Sequences were purified using ethanol precipitation and resolved using an Applied Biosystems 3730 xl capillary sequencer at the University Park Genomics Core Facility (Pennsylvania State University). Sequences were assembled in SeqMan (DNASTAR). The final sequence for specimen MPEP 82.1 was 275 base pairs long and has been entered into GenBank under accession number JQ364966.

Genetic analysis

NCBI BLAST was used to genetically identify the specimen as brown bear (*Ursus arctos*). The sequence was aligned manually in Se-al (Rambaut 2002) to other modern and ancient brown bear and polar bear (*Ursus maritimus*) control region sequences available on GenBank (supplementary Table S1[1]). The intraspecific relationship of the Saint-Nicolas specimen was determined using BEAST v1.5.3 (Drummond and Rambaut 2007). The HKY + G model of nucleotide substitution was selected using Model Test (Posada and Crandall 1998) and a flexible coalescent prior; the Bayesian skyline plot (Drummond et al. 2005) was used with 10 groups. Mean accelerator mass spectrometry (AMS) radiocarbon dates for ancient specimens were used to calibrate the clock. Two Markov chain Monte Carlo (MCMC) chains were run for 100 million generations each, subsampling every 10 000 generations and discarding the first 10% of samples as chain burn-in. Remaining samples were combined in LogCombiner. Effective sample sizes and MCMC convergence were assessed using Tracer v1.5 (Rambaut and Drummond 2007) and the maximum clade credibility tree (MCC tree; Fig. 3) was summarized using Tree Annotator.

In summary, the third metatarsal (MPEP 82.1) has been identified genetically as belonging to brown bear (*Ursus arctos*), with a top hit of 99% BLAST similarity to GenBank Accession U34271 (Paetkau and Strobeck 1996). For comparison, a BLAST search forced against the polar bear (*Ursus maritimus*) recovered a maximum identity of 92% similarity, and forced against black bear (*Ursus americanus*) received only 86% maximum identity. Therefore, the genetic analysis of bone from the bear third metatarsal (MPEP 82.1) supports the morphological identification.

Radiocarbon age

A 3.2 g sample of solid bone from the shaft of MPEP 82.1 was submitted to the Keck Carbon Cycle AMS Facility (Earth System Science Department, University of California, Irvine). Results were as follows: $\delta^{13}C$ (‰) –16.1 ± 0.1; fraction Modern 0.2924 ± 0.0012; $D^{14}C$ (‰) –707.6 ± 1.2; ^{14}C age (BP) 9880 ± 35. Therefore, the AMS age of 9880 ± 35 BP (UCIAMS 71656) lies near the close of the Champlain Sea episode (Occhietti et al. 2001; Cronin et al. 2008). This date is close to one on a walrus (*Odobenus rosmarus*) ilium from Saint-Nicolas of 9790 ± 60 BP (Beta-115199) (Occhietti et al. 2001; Harington 2003), suggesting that the brown bear and walrus were contemporary.

Discussion: the dispersal history of brown bears

It is worth discussing the Saint-Nicolas specimen in relation to the known dispersal history of brown bears. Brown bears probably arose from the Etruscan bear (*Ursus etruscus*) characteristic of the European Early Pleistocene (Kurtén and Anderson 1980). The earliest known brown bears from Middle Pleistocene (about 500 000 years) deposits in Choukoutien, China, are large. The species has a continuous record in East Asia from Middle Pleistocene to present time. It entered Europe later in the Middle Pleistocene — nearly 200 000 years ago, where it coexisted with the cave bear (*Ursus spelaeus*). From that time to the end of the Pleistocene, Britain remained a stronghold of the brown bear (Kurtén 1968). It had entered North America (Eastern Beringia) from Asia via the Bering Isthmus by Wisconsinan time (about 50 000 BP (Barnes et al. 2002; Harington 2003, p. 382); and see Table 4), and some had migrated south via the Ice-free Corridor east of the Cordillera at least as early as 27 000 BP (Edmonton, Alberta; Matheus et al. 2004). Therefore, brown bears ranged south of Eastern Beringia well before the Holocene and the coalescence of Laurentide and Cordilleran glaciers during the Last Glacial Maximum some 20 000 BP. A lower jaw fragment of a bear (*Ursus*) from Toronto interglacial (Sangamonian) deposits (Coleman 1913, 1933) cannot be identified specifically, since it cannot be located (K. Seymour, personal communication, 2014). It may represent an early black bear and is not germane to this discussion.

A brown bear humerus from Middle Wisconsinan deposits estimated to be between 50 000 and 40 000 BP at Woodbridge, Ontario (Fig. 1, locality 2), on the western outskirts of Toronto (Churcher and Morgan 1976 — but see Kurtén and Anderson 1980, who suggest that the specimen more likely represents a black bear. They state, "Wisconsin black bears were in many cases as large as present-day grizzlies and have, in fact, been mistaken for such, with the result that there are erroneous reports of Wisconsin *Ursus arctos* south of the ice (Churcher and Morgan 1976;

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjes-2013-0220.

Fig. 3. Molecular phylogeny of brown and polar bears from 50 ka to present, including the Saint-Nicolas Champlain Sea bear (MPEP 82.1) and the extinct Atlas and Syrian bears. Black circles mark clades that received Bayesian posterior probability support of 0.95 or higher. Clade IV, which includes the Saint-Nicolas Champlain Sea bear as indicated by the arrow, is enlarged in the inset box for increased detail. The phylogeny is a maximum clade credibility genealogy resulting from a Bayesian analysis in BEAST. The phylogeny including tip labels (the specific taxa that were used) is included as supplementary Fig. S1[1].

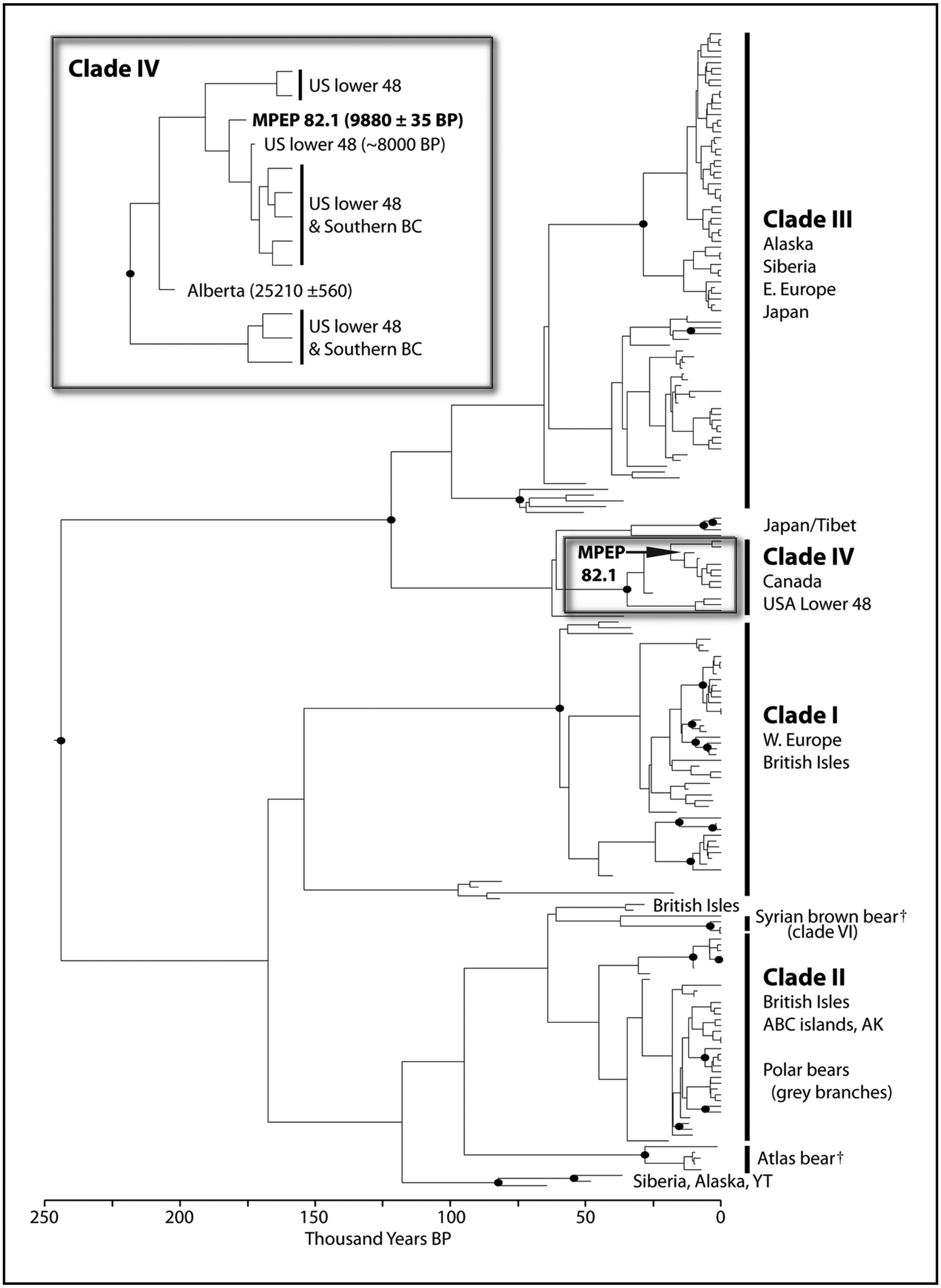


Table 4. Radiocarbon ages of Quaternary brown bears (*Ursus arctos*) bones from Western North America (oldest to latest)[a].

Localities	Material	Radiocarbon age	Lab No.	References and remarks
Colville River, Alaska	Bone	48 164±3224	AA-17510	P. Matheus, pers. comm. (1996)
Cripple Creek, Alaska	Ulna (FAM 95666)	47 100±3100	OxA-9260	A. Cooper, pers. comm. (2000)
Boliden Creek, Yukon	Cranium (CMN-42105)	>43 400	Beta-66923 CAMS-10527	C.R. Harington (unpublished)
Hunker Creek (Dawson Loc. 16), Yukon	Mandible (CMN 35965)	41 085±9050	Beta-16159	Harington (1977, 1978, 1980*b*, 1989, 1997)
Sixtymile Loc. 3, Yukon	Humerus (CMN 38279)	36 500±1150	Beta-16162	Harington (1989, 1997); Matheus (1995)
Fairbanks area, Alaska	Bone	36 400±1700	AA-1889	P. Matheus, pers. comm. (1996)
Cripple Creek, Fairbanks area, Alaska	Bone (FAM 95601)	36 137±783	AA-17509	P. Matheus, pers. comm. (1996)
On Your Knees Cave, Prince of Wales I., Alaska	Femur	35 365±800	AA-15227	Heaton (1995); Heaton et al. (1996; Heaton and Grady 1997)
Fairbanks area, Alaska	Bone	33 700±1100	AA-1887	P. Matheus, pers. comm. (1996)
Lower Goldstream, Alaska	Phalanx (FAM 30771)	20 080±160	OxA-9261	A. Cooper, pers. comm. (2000)
Probably Fairbanks area, Alaska	Bone (AMNH 30422)	19 027±132	AA-17507	P. Matheus, pers. comm. (1996)
Gold Hill, Alaska	Ulna (FAM 95670)	15 830±100	OxA-9263	A. Cooper, pers. comm. (2000)
Ester Creek, Alaska	Femur (FAM 95142)	14 150±90	OxA-9262	A. Cooper, pers. comm. (2000)
Goldstream Creek, Alaska	Bone (FAM 95595)	12 441±101	AA-17508	P. Matheus, pers. comm. (1996)
Pellucidar II Cave, BC	Bones	12 440±35	UCIAMS-41051	Steffen et al. (2008)
Pellucidar II Cave, BC	Bones	12 425±35	UCIAMS-41050	Steffen et al. (2008)
El Capitan Cave, Prince of Wales I., Alaska	Humerus	12 295±120	AA-10445	Heaton et al. (1996)
Enigma Cave, Dall I., Alaska	Humerus	11 715±120	AA-15226	Heaton et al. (1996)
Bumper Cave, Prince of Wales I., Alaska	Humerus	11 640±80	AA-15222	Heaton et al. (1996)
Bumper Cave, Prince of Wales I., Alaska	Humerus	11 225±110	AA-15223	Heaton et al. (1996)
Bumper Cave, Prince of Wales I., Alaska	Molar	10 970±85	AA-15225	Heaton et al. (1996)
Ester Creek, Alaska	Bone (FAM 95612)	10 015±62	AA-17506	P. Matheus, pers. comm. (1998)
Blowing in the Wind Cave, Prince of Wales I., Alaska	Skull (juvenile skeleton)	9995±95	AA10451	Heaton and Grady (1993; Heaton et al. 1996)
El Capitan Cave, Prince of Wales I., Alaska	Humerus (large)	9760±75	AA-7794	Heaton and Grady (1992)
Bumper Cave, Prince of Wales I., Alaska	Lower jaw	7205±65	AA-15224	Heaton et al. (1996); Heaton and Grady (1997)
Scaredy Cat Cave, Idaho	Bone	2600±60	Beta, number not given	E.C. Grimm, pers. comm. (2013)
South shore of Amundsen Gulf, NE corner of Pearce Point Harbor, NT	Humerus (CMC 1403)	1290±60 (1390±65)	S-3364	R.E. Morlan, CMC database (1999)

Note: I., island; pers. comm., personal communication.
[a]Most of these radiocarbon dates are listed in greater detail in Harington (2003, pp. 382–383).

Stovall and Johnston 1935)". However, this view is not supported by critical comments on the Ontario specimen itself that can override Churcher's and Morgan's conclusion, which had been peer reviewed. Therefore, we choose to accept the conclusion of Churcher and Morgan (1976)), indicating that the species was able to spread rapidly eastward once it had penetrated the heartland of North America. Further complicating this matter is a study by Karrow et al. (2001) who considered that the humerus should be identified as *Ursus* sp. Brown bears also spread southwestward between about 40 000 and 10 000 BP to the western United States (Maricopa, California; Labor-of-Love Cave, Nevada; Jaguar Cave, Idaho; and Little Box Elder Cave, Wyoming) — well within the historic and recent range of the species (Faunmap Working Group 1994, p. 416). According to Graham (1991) this group of brown bears should include a cranial fragment of "*Ursus optimus*" from McKittrick, California, formerly thought to be a black bear (Kurtén and Anderson 1980, p. 183), as well as another eastward-moving brown bear "*Ursus procerus*", a skull from Ohio with badly worn teeth. Remains dated between 15 000 and 10 000 BP are from Jaguar Cave, Idaho, Porcupine Cave, Utah, and the more easterly locality of Welsh Cave, Kentucky. Remains dated to Middle Holocene time (8000–4000 BP) are all located in western United States — well within the historic and modern range of the brown bear, except for Schulze Cave, Texas, which is marginally eastward of that range. Late Holocene (5000–4000 BP) remains are located in the western United States, except for one from McKinstry, Minnesota — close to the Canadian border. Other late-glacial and Holocene brown bear remains from Eastern Canada, including the Saint-Nicolas specimen from Champlain Sea deposits, have been mentioned earlier (Fig. 1).

Conclusions

1. A third metatarsal from a sandpit located at Saint-Nicolas, within the city of Lévis, Quebec, identified by morphological and ancient DNA analysis proved to be that of a brown bear (*Ursus arctos*). It is the first bear fossil identified from Champlain Sea deposits, in addition to being the first Champlain Sea vertebrate fossil from which DNA has been successfully extracted for identification purposes. Morphological and pathological evidence suggest the specimen was from an old bear, and iron staining indicates the specimen came from a layer of oxidized sand.
2. Collagen from the bone was AMS dated to 9880 ± 35 BP, indicating that brown bears reached the margins of the Champlain Sea during its final phase, perhaps to scavenge washed-up carcasses of marine mammals. This date is close to that of a walrus (*Odobenus rosmarus*) ilium (dated to 9780 ± 60 BP) from sands at Saint-Nicolas, indicating that brown bears and walruses were contemporary there.
3. Tidal-current sands of the Pleistocene–Holocene transition at Saint-Nicolas, now across the Saint Lawrence River from the city of Québec, preserve an exceptional marine fossil fauna including 38 kinds of invertebrates, five fish species, five seabird species, and five mammal species (four of them marine). This faunal diversity is associated with high marine productiv-

ity arising from mixing of salt and fresh water. Radiocarbon ages for the fauna range from about 10 060 to 9810 BP. Sediments at the site were deposited in an archipelago at the entrance to the Champlain Sea that was subjected to tides of about 10 m.

4. Brown bears probably arose from Etruscan bears (*Ursus etruscus*) characteristic of Early Pleistocene Europe. The earliest known brown bears are from Middle Pleistocene deposits of Choukoutien, China, and the species has a continuous record in East Asia from then to the present time. The species entered Europe later in the Middle Pleistocene, and had entered North America via the Bering Isthmus by Wisconsinan time — about 50 000 BP. Some migrated south to the heartland of North America via the Ice-free Corridor east of the Cordillera, reaching the southwestern part of its historic range in western United States and Eastern Canada (probably Woodbridge, near Toronto) shortly after. Perhaps only two brown bear specimens approaching the age of that from Saint-Nicolas are known from Eastern Canada: a skull from a gravel pit near Orillia, Ontario, dated to about 11 700 BP, and most of a cranium from Trou Otis, a cave near La Rédemption, Quebec, thought to be Early Holocene in age. Brown bears probably died out in Eastern Canada (Quebec and Labrador) in historic time.

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EU400181_southernEurope_valdegoba_80000_stratDated75to90
AB010728_Gobi_gobi_0_ 0
DQ914409_Asia_Pakistan_0_ 0
DQ914410_Asia_Pakistan_0_ 0
DQ914408_Asia_Iran_0_ 0
JF900165_B11_britishIsles_Ireland_32430_67 0
JF900173_B21_Ireland_2b_28390_17 7
EF033712.10_Alaska_ABCislands_0_ 0
EF033710.9_Alaska_ABCislands_0_ 0
EF033706.8_Alaska_ABCislands_0_ 0
EF033720.11_Alaska_ABCislands_0_ 0
EF033719.11_Alaska_ABCislands_0_ 0
AY082844.AK374V8_Alaska_PrinceOfWales_9995_9 5
JF900161_B07_britishIsles_Ireland_26340_32 0
JF900162_B08_britishIsles_Ireland_26340_32 0
UM.EF033727_polarBear_Canada_0_ 0
JF900169_B17_britishIsles_Ireland_8719_4 8
JF900172_B20_britishIsles_Ireland_9946_5 3
UM.JF900123_TF22_polarBear_HenrietteIsland_50_ 0
UM.JF900126_TF25_polarBear_FranzJosephLandEastCoastNovayaZemlya_50_ 0
UM.JF900127_TF27_polarBear_HenrietteIsland_50_ 0
UM.JF900128_TF28_polarBear_NewSiberianIslandsBolshoyLyakhovskiyZimovyeMaloe_50_ 0
UM.TF32_polarBear_TaimyrChelyuskinCape_50_ 0
UM.EF033728_polarBear_Norway_0_ 0
UM.JF900125_TF24_polarBear_TaimyrChelyuskinCapePolarStation_50_ 0
UM.JF900115_TF14_polarBear_NuiqVillageAK_0_ 0
UM.EF033729_polarBear_Norway_0_ 0
UM.JF900117_TF16_polarBear_SavoVillageAK_0_ 0
UM.JF900108_TF2_polarBear_BarrVillageAK_0_ 0
UM.JF900105_Polar1_polarBear_WrangelIsland_0_ 0
UM.EF033730_polarBear_ WRussia_0_ 0
UM.JF900116_TF15_polarBear_PrudVillageAK_0_ 0
UM.JF900114_TF12_polarBear_GambVillageAK_0_ 0
UM.JF900152_TF103_polarBear_1290_4 0
UM.JF900130_TF30_polarBear_VilkitskiyIsland_50_ 0
UM.JF900122_TF21_polarBear_NewSiberian IslandNovayaSibir IslandWCoast_50_ 0
UM.JF900124_TF23_polarBear_HenrietteIsland_50_ 0
UM.JF900129_TF29_polarBear_AnabarBaySeaCoast_50_ 0
JF900168_B16_britishIsles_Ireland_11460_5 7
JF900160_B03_britishIsles_Ireland_11920_8 5
JF900159_B02_britishIsles_Ireland_10650_10 0
JF900170_B18_britishIsles_Ireland_10495_5 1
AY082840.FAM95657_Alaska_Fairbanks_19360_14 0
AM411399_northAfrica_Morocco_1285_3 0
AM411400_northAfrica_Algeria_9620_20 0
AM411402_northAfrica_Algeria_7650_4 0
AM411401_northAfrica_Algeria_9620_20 0
AM411403_northAfrica_Algeria_7345_4 0
AY082842.CMN38279_Alaska_SixtyMile_36500_115 0
AY082841_Alaska_ColvilleRiver_48164_322 4
AY082843_Siberia_DuvannyYar_undate d

Genbank Accession Number	Lab number (this study)	Assigned Location	Location details	Specimen Age	Reference
JQ364966	MPEP 82.1 (TF106)	Quebec	Champlain Sea	9880±35	This study
EF033706		Alaska	ABC islands	modern	Waits et al 1998
EF033710		Alaska	ABC islands	modern	Waits et al 1998
EF033712		Alaska	ABC islands	modern	Waits et al 1998
EF033719		Alaska	ABC islands	modern	Waits et al 1998
EF033720		Alaska	ABC islands	modern	Waits et al 1998
EF033731		Alaska	Alaska Range	modern	Waits et al 1998
EF033874		Alaska	Anderson	modern	Waits et al 1998
EF033862		Alaska	Arctic Natl Wildlife Refuge	modern	Waits et al 1998
DQ914404		Alaska	British Columbia	modern	Waits et al 1998
DQ914401		Alaska	British Columbia	modern	Waits et al 1998
AY082841		Alaska	Colville River	48164±3224	Barnes et al 2002
AY082816		Alaska	Fairbanks	10015±62	Barnes et al 2002
AY082812		Alaska	Fairbanks	11940±100	Barnes et al 2002
AY082822		Alaska	Fairbanks	12310±65	Barnes et al 2002
AY082824		Alaska	Fairbanks	12320±90	Barnes et al 2002
AY082827		Alaska	Fairbanks	12441±75D	Barnes et al 2002
AY082814		Alaska	Fairbanks	13415±74	Barnes et al 2002
AY082819		Alaska	Fairbanks	13760±50	Barnes et al 2002
AY082815		Alaska	Fairbanks	14150±90	Barnes et al 2002
AY082813		Alaska	Fairbanks	14310±100	Barnes et al 2002
AY082820		Alaska	Fairbanks	14810±80	Barnes et al 2002
AY082821		Alaska	Fairbanks	14980±60	Barnes et al 2002
AY082828		Alaska	Fairbanks	15370±60	Barnes et al 2002
AY082823		Alaska	Fairbanks	15830±100	Barnes et al 2002
AY082825		Alaska	Fairbanks	19027±130	Barnes et al 2002
AY082840		Alaska	Fairbanks	19360±140	Barnes et al 2002
AY082810		Alaska	Fairbanks	20080±160	Barnes et al 2002
AY082829		Alaska	Fairbanks	20820±120	Barnes et al 2002
AY082832		Alaska	Fairbanks	36137±783	Barnes et al 2002
AY082836		Alaska	Fairbanks	41787±212	Barnes et al 2002
AY082837		Alaska	Fairbanks	42600±850	Barnes et al 2002
AY082833		Alaska	Fairbanks	47100±3100D	Barnes et al 2002
AY082830		Alaska	Fairbanks	50800±1900	Barnes et al 2002
AY082817		Alaska	Fairbanks	9535±75	Barnes et al 2002
EF033733		Alaska	Interior Alaska	modern	Waits et al 1998
EF033737		Alaska	Interior Alaska	modern	Waits et al 1998
EF033845		Alaska	Izembeck	modern	Waits et al 1998
EF033826		Alaska	Katmai	modern	Waits et al 1998

EU574910	Alaska	Kenai	modern	Jackson et al 2008
EU574911	Alaska	Kenai	modern	Jackson et al 2008
EF033895	Alaska	Kluane	modern	Waits et al 1998
EF033896	Alaska	Kluane	modern	Waits et al 1998
EF033773	Alaska	Kodiak	modern	Waits et al 1998
AY08283	Alaska	Old	35970±660	Barnes et al 2002
9	Alaska	Crow	modern	Miller et al 1998
EF033872	Alaska	Paulatuk	9995±95	Barnes et al 2002
AY08284	Alaska	Prince of Wales Island	36500±1150	Barnes et al 2002
4	Alaska	SixtyMile	modern	Miller et al 1998
DQ914408	Asia	Iran	modern	Miller et al 2006
DQ914409	Asia	Pakistan	modern	Miller et al 2006
DQ914410	Asia	Pakistan	modern	Miller et al 2006
DQ914407	Asia	Tibet	modern	Miller et al 2006
X75862	Central Europe	Appenine	modern	Taberlet & Bouvet 1994
AJ809334	Central Europe	Austria	40020±1000	Hofreiter et al 2004
AJ809333	Central Europe	Austria	47500±0inf	Hofreiter et al 2004
X75864	Central Europe	Balkan	modern	Taberlet & Bouvet 1994
X75870	Central Europe	Balkan	modern	Taberlet & Bouvet 1994
X75877	Central Europe	Bosnia	modern	Taberlet & Bouvet 1994
X75867	Central Europe	Croatia	modern	Taberlet & Bouvet 1994
EF488501	Central Europe	Germany	1665±35	Valdiosera et al 2007
EF488498	Central Europe	Germany	1770±35	Valdiosera et al 2007
EF488499	Central Europe	Germany	5210±35	Valdiosera et al 2007
EF488500	Central Europe	Germany	750±150	Valdiosera et al 2007
EF488488	Central Europe	Italy	16440±65	Valdiosera et al 2007
X75874	Central Europe	Netherlands	modern	Taberlet & Bouvet 1994
EF488506	Central Europe	Romania	2250±50	Valdiosera et al 2007
EF488507	Central Europe	Romania	2250±50	Valdiosera et al 2007
X75872	Central Europe	Romania	modern	Taberlet & Bouvet 1994
X75873	Central Europe	Romania	modern	Taberlet & Bouvet 1994
X75875	Central Europe	Slovakia	modern	Taberlet & Bouvet 1994
X75876	Central Europe	Slovakia	modern	Taberlet & Bouvet 1994
AY331273	Eastern Europe	Estonia	modern	Saarma et al 2008
X75869	Eastern Europe	Estonia	modern	Taberlet & Bouvet 1994
AY331263	Eastern Europe	Finland	modern	Saarma et al 2008
AY331270	Eastern Europe	Finland	modern	Saarma et al 2008
AY331272	Eastern Europe	Finland	modern	Saarma et al 2008
AY331275	Eastern Europe	Finland	modern	Saarma et al 2008
AY331262	Eastern Europe	Finland & Russia	modern	Saarma et al 2008
AY331265	Eastern Europe	Finland & Russia	modern	Saarma et al 2008
AY331267	Eastern Europe	Finland & Russia	modern	Saarma et al 2008
AY331271	Eastern Europe	Finland & Russia	modern	Saarma et al 2008
AY331268	Eastern Europe	Western Russia	modern	Saarma et al 2008
AB010728	Gobi	Gobi Desert	modern	Masuda et al 1998

JF900158	B01	Britain & Ireland	England	12143±46	Edwards et al 2011
JF900159	B02	Britain & Ireland	Ireland	10650±100	Edwards et al 2011
JF900162	B08	Britain & Ireland	Ireland	26340±32	Edwards et al 2011
JF900163	B09	Britain & Ireland	Ireland	33310±770	Edwards et al 2011
JF900164	B10	Britain & Ireland	Ireland	37870±1270	Edwards et al 2011
JF900165	B11	Britain & Ireland	Ireland	32430±670	Edwards et al 2011
JF900166	B13	Britain & Ireland	Ireland	4520±37	Edwards et al 2011
JF900167	B14	Britain & Ireland	Ireland	3517±31	Edwards et al 2011
JF900168	B16	Britain & Ireland	Ireland	11460±57	Edwards et al 2011
JF900169	B17	Britain & Ireland	Ireland	8719±48	Edwards et al 2011
JF900170	B18	Britain & Ireland	Ireland	10495±51	Edwards et al 2011
JF900171	B19	Britain & Ireland	Ireland	32648±245	Edwards et al 2011
JF900172	B20	Britain & Ireland	Ireland	9946±53	Edwards et al 2011
JS900174	B23	Britain & Ireland	Ireland	4136±37	Edwards et al 2011
JF900175	B24	Britain & Ireland	Ireland	2956±33	Edwards et al 2011
AY08284		Britain & Ireland	Scotland	ca 8000	Barnes et al 2002
AB013046		Japan	Japan	modern	Matsuhashi et al 1999
AB013047		Japan	Japan	modern	Matsuhashi et al 1999
AB013050		Japan	Japan	modern	Matsuhashi et al 2000
AB013054		Japan	Japan	modern	Matsuhashi et al 2000
AB013055		Japan	Japan	modern	Matsuhashi et al 2000
AB013056		Japan	Japan	modern	Matsuhashi et al 2000
AB013058		Japan	Japan	modern	Matsuhashi et al 2000
AB013061		Japan	Japan	modern	Matsuhashi et al 2000
AB013063		Japan	Japan	modern	Matsuhashi et al 2000
AB013065		Japan	Japan	modern	Matsuhashi et al 2000
AY796010		Lower 48 United States	Alberta	25210±560	Matheus et al 2004
DQ914389		Lower 48 United States	California	modern	Miller et al 2006
AY082838		Lower 48 United States	Montana	ca 8000	Barnes et al 2002
DQ914298		Lower 48 United States	northwestern USA	modern	Miller et al 2006
DQ914329		Lower 48 United States	northwestern USA	modern	Miller et al 2006
DQ914332		Lower 48 United States	northwestern USA	modern	Miller et al 2006
DQ914339		Lower 48 United States	northwestern USA	modern	Miller et al 2006
DQ914349		Lower 48 United States	northwestern USA	modern	Miller et al 2006
EF033998		Lower 48 United States	northwestern USA	modern	Miller et al 1998
DQ914293		Lower 48 United States	southern British Columbia	modern	Miller et al 2006
DQ914294		Lower 48 United States	southern British Columbia	modern	Miller et al 2006
DQ914355		Lower 48 United States	southwestern USA	modern	Miller et al 2006
AM411398		North Africa	Algeria	1550±40	Calvignac et al 2008
AM411397		North Africa	Algeria	1679±35	Calvignac et al 2008
AM411403		North Africa	Algeria	7345±40	Calvignac et al 2008
AM411402		North Africa	Algeria	7650±40	Calvignac et al 2008
AM411400		North Africa	Algeria	9620±200	Calvignac et al 2008
AM411401		North Africa	Algeria	9620±200	Calvignac et al 2008
AM411399		North Africa	Morocco	1285±30	Calvignac et al 2008

JF900105	Polar1	Polar Bear	Wrangel Island	modern	Edwards et al 2011
JF900114	TF12	Polar Bear	Alaska	modern	Edwards et al 2011
JF900115	TF14	Polar Bear	Nuiq Village, Alaska	modern	Edwards et al 2011
JF900116	TF15	Polar Bear	Prudoe Village, Alaska	modern	Edwards et al 2011
JF900117	TF16	Polar Bear	Savo Village, Alaska	modern	Edwards et al 2011
JF900108	TF2	Polar Bear	Barr Village, Alaska	modern	Edwards et al 2011
JF900122	TF21	Polar Bear	New Siberian Islands	1932*	Edwards et al 2011
JF900123	TF22	Polar Bear	Henriette Island	1932*	Edwards et al 2011
JF900124	TF23	Polar Bear	Henriette Island	1932*	Edwards et al 2011
JF900125	TF24	Polar Bear	Taimyr; Chelyuskin Cape Polar Station	1932*	Edwards et al 2011
JF900126	TF25	Polar Bear	Novaya Zemlya	1932*	Edwards et al 2011
JF900127	TF27	Polar Bear	Henriette Island New	1932*	Edwards et al 2011
JF900128	TF28	Polar Bear	Siberian Islands	1932*	Edwards et al 2011
JF900129	TF29	Polar Bear	Anabar Bay	1932*	Edwards et al 2011
JF900130	TF30	Polar Bear	Vilkitski Island	1932*	Edwards et al 2011
ident. to JF900125	TF32	Polar Bear	Taimyr Chelyuskin Cape	1932*	Edwards et al 2011
EF033727		Polar Bear	Canada	modern	Waits et al 1998
EF033728		Polar Bear	Norway	modern	Waits et al 1998
X75871		Scandinavia	Norway	modern	Taberlet & Bouvet 1994
L38271		Scandinavia	Sweden	modern	Kohn et al 1995
L38273		Scandinavia	Sweden	modern	Kohn et al 1995
X75868		Scandinavia	Sweden	modern	Taberlet & Bouvet 1994
AY082843		Siberia	Duvanny Yar, eastern Siberia	Pleistocene	Barnes et al 2002
DQ914406		Siberia	far eastern Russia	modern	Miller et al 2006
X75873		Siberia	far eastern Russia	modern	Taberlet & Bouvet 1994; Miller et al 2006
X75874		Siberia	OkhotskSea	modern	Taberlet & Bouvet 1994; Miller et al 2006
EF488495		Southern Europe	France	1570±35	Valdiosera et al 2007
EF488493		Southern Europe	France	1750±30	Valdiosera et al 2007
EF488491		Southern Europe	France	1790±55	Valdiosera et al 2007
EF488505		Southern Europe	France	3445±40	Valdiosera et al 2007
EF488492		Southern Europe	France	3845±40	Valdiosera et al 2007
EF488496		Southern Europe	France	4645±40	Valdiosera et al 2007
EF488494		Southern Europe	France	6525±50	Valdiosera et al 2007
X75878		Southern Europe	France	modern	Taberlet & Bouvet 1994
EF488504		Southern Europe	Spain	17440±425	Valdiosera et al 2007
EF488497		Southern Europe	Spain	350±40	Valdiosera et al 2007
EU400207		Southern Europe	Spain	40±0	Valdiosera et al 2008
EF488490		Southern Europe	Spain	5380±45	Valdiosera et al 2007
EU400179		Southern Europe	Spain	6325±50	Valdiosera et al 2008
EF488487		Southern Europe	Spain	7500±55	Valdiosera et al 2007
EU400184		Southern Europe	Spain	modern	Valdiosera et al 2008
EU400198		Southern Europe	Spain	modern	Valdiosera et al 2008
EU400201		Southern Europe	Spain	modern	Valdiosera et al 2008
EU400202		Southern Europe	Spain	modern	Valdiosera et al 2008

EU400203	Southern Europe	Spain	modern	Valdiosera et al 2008
EU400206	Southern Europe	Spain	modern	Valdiosera et al 2008
X75865	Southern Europe	Spain	modern	Taberlet & Bouvet 1994
X75866	Southern Europe	Spain	modern	Taberlet & Bouvet 1994
EU400181	Southern Europe	Valdegoba Cave, Spain	75-90 ka	Valdiosera et al 2008
EU400182	Southern Europe	Valdegoba Cave, Spain	75-90 ka	Valdiosera et al 2008
EU400183	Southern Europe	Valdegoba Cave, Spain	75-90 ka	Valdiosera et al 2008
EU526804	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526793	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526803	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526797	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526805	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526806	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU52680	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526814	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526811	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526809	Kamchatka	Kamchatka	modern	Korsten et al 2009
EU526812	Kamchatka	Kamchatka	modern	Korsten et al 2009

*sample isolation date