

# 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

C. Richard Harington, Mario Cournoyer, Michel Chartier, Tara Lynn Fulton, and Beth Shapiro

**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 in-shore 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 (*Erigonathus 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). Walrus (*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

Received 9 December 2013. Accepted 4 March 2014.

Paper handled by Associate Editor Hans-Dieter Sues.

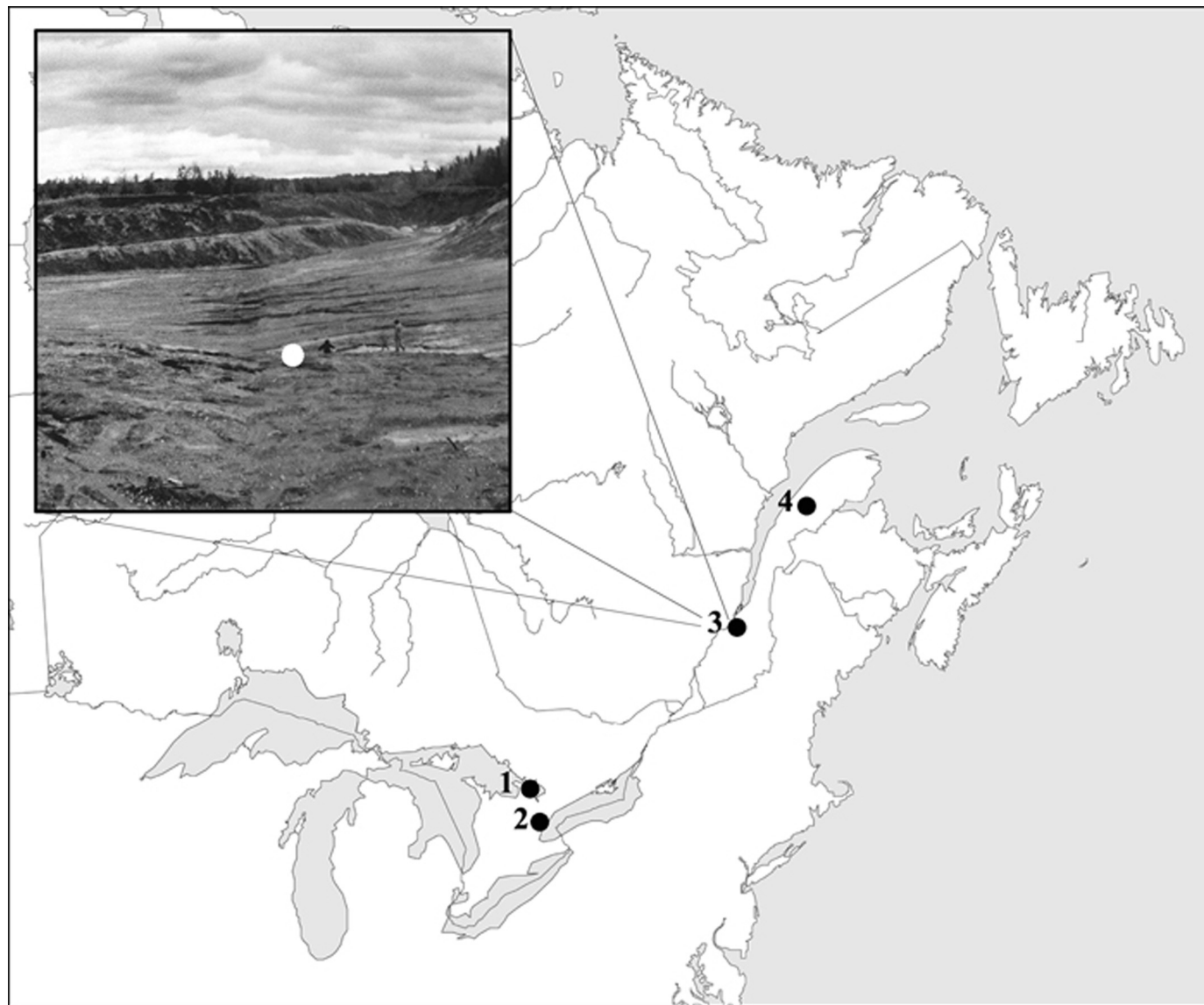
C.R. Harington. Canadian Museum of Nature (Paleobiology), P.O. Box 3443, Stn. D, Ottawa, ON K1P 6P4, Canada.

M. Cournoyer and M. Chartier. Musée de paléontologie et de l'évolution, 541 de la Congrégation, Montréal, QC H3K 2J1, Canada.

T.L. Fulton and B. Shapiro. Department of Biology, The Pennsylvania State University, 326 Mueller Lab, University Park, PA 16801, USA.

**Corresponding author:** Charles Harington (e-mail: dharington@mus-nature.ca).

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

<sup>a</sup>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.

### 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

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

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

<sup>a</sup>New addition to the Champlain Sea fauna (this paper).

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 1965a, 1965b; 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 1980a) (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  | <i>Ursus</i> 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 ( $9880 \pm 35$   $^{14}\text{C}$  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.

| Specimens   | Remarks  | Measurements (mm) <sup>a</sup> |      |      |       |      |      |      |
|---|--|--------------------------------|------|------|-------|------|------|------|
|   |  | 1                              | 2    | 3    | 4     | 5    | 6    | 7    |
| <i>Ursus arctos</i> (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 |
| <i>Ursus arctos</i> (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 |
| <i>Ursus arctos</i> (CMN 2772). Modern, NWT, Canada.                                | Adult male   | 82.4                           | 19.0 | 28.3 | 12.6  | 10.7 | 21.6 | 17.9 |
| <i>Ursus arctos</i> (CMN 31187). Modern, NWT, Canada.                               | Probably adult male  | 84.0                           | 19.9 | 25.9 | 13.0  | 10.0 | 20.5 | 18.7 |
| <i>Ursus maritimus</i> (CMN 41090). Modern, Canada.                                 | 2 year old male  | —                              | 18.3 | 24.6 | 11.4e | —    | —    | —    |
| <i>Ursus americanus</i> (CMN 41055). Modern, Canada.                                | Adult male   | 68.4                           | 15.0 | 21.5 | 10.5  | 8.7  | 15.7 | 14.1 |
| <i>Ursus americanus</i> (CMN 1583). Modern, BC, Canada.                             | Adult(?) male  | 66.5                           | 14.8 | 24.6 | 9.6   | 8.6  | 15.4 | 14.1 |
| <i>Ursus americanus</i> (CMN 75389). Modern, Canada.                                | Adult male   | 67.1                           | 14.1 | 21.8 | 9.0   | 7.1  | 14.7 | 13.6 |
| <i>Ursus americanus</i> (CMN 34109). Modern, YK, Canada.                            | Adult female   | 64.4                           | 11.5 | 19.6 | 8.8   | 7.2  | 13.7 | 11.9 |
| <i>Ursus americanus</i> (CMN 5009). Modern, QC, Canada.                             | Adult(?) female  | 61.1                           | 12.2 | 18.1 | 8.3   | 6.5  | 12.2 | 11.8 |
| <i>Ursus americanus</i> (CMN Z-162). Modern, Canada.                                | Adult female   | 57.6                           | 10.6 | 18.2 | 8.7   | 7.1  | 12.3 | 12.0 |

<sup>a</sup>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. 1c), 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<sup>1</sup> and Table S1<sup>1</sup>) 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  $\mu$ L reaction comprising the following: 2 mg/mL rabbit serum albumin; 1 $\times$  Amplitaq Gold 360 buffer (Applied Biosystems Inc.); 1.2–5, SU Amplitaq Gold 360; 250  $\mu$ mol/L each dNTP; 2.5 mmol/L MgCl<sub>2</sub>; 1  $\mu$ mol/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 <sub>$\mu$ 96</sub> 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<sup>1</sup>). 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:  $\delta^{13}\text{C}$  (‰)  $-16.1 \pm 0.1$ ; fraction Modern  $0.2924 \pm 0.0012$ ;  $\text{D}^{14}\text{C}$  (‰)  $-707.6 \pm 1.2$ ;  $^{14}\text{C}$  age (BP)  $9880 \pm 35$ . Therefore, the AMS age of  $9880 \pm 35$  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  $9790 \pm 60$  BP (Beta-115199) (Occhietti et al. 2001; Harington 2003), suggesting that the brown bear and walrus were contemporary.

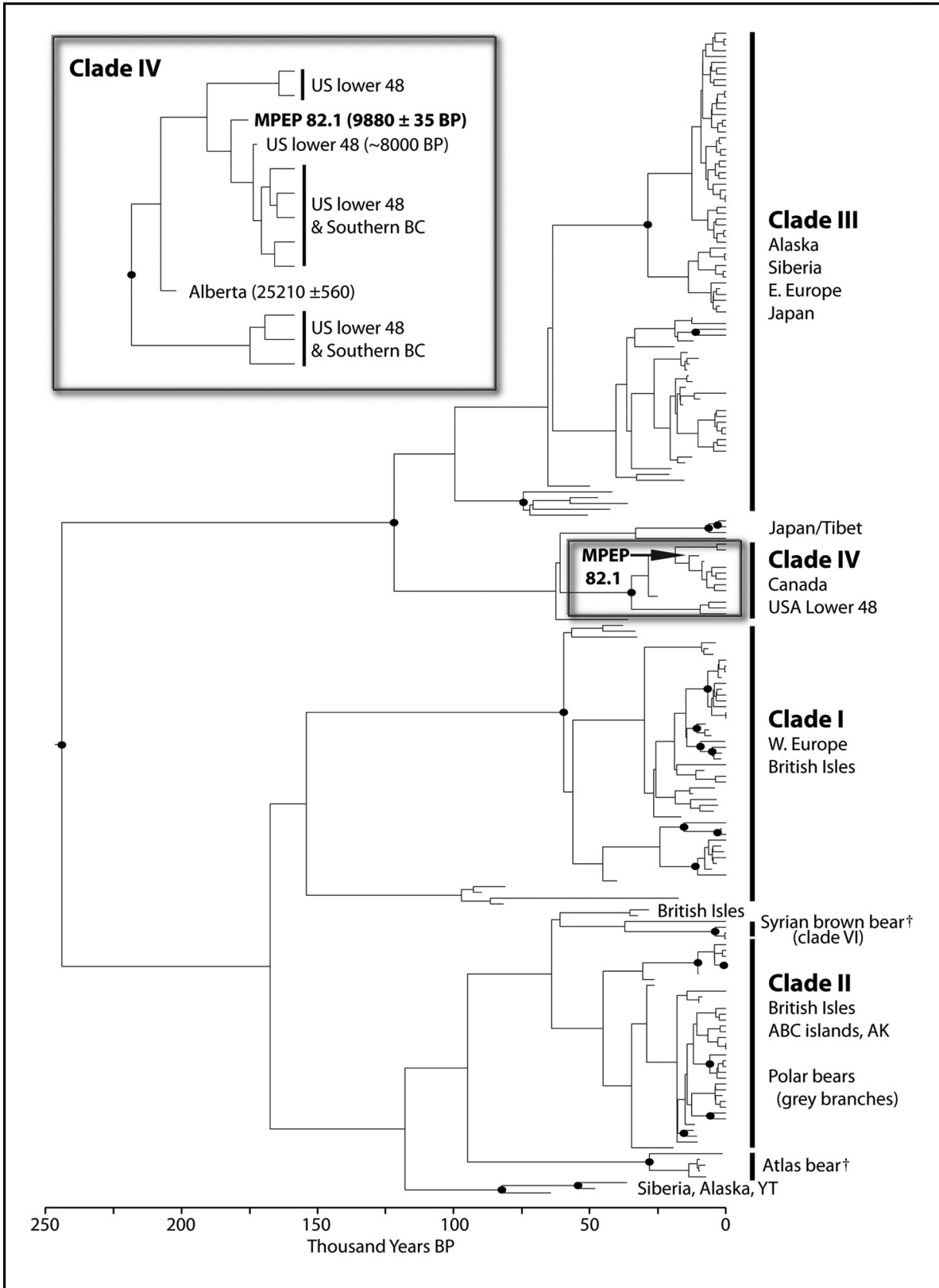
### Discussion: the dispersal history of brown bears

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 Wisconsinian 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 Wisconsinian 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;

<sup>1</sup>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<sup>1</sup>.



Can. J. Earth Sci. Downloaded from www.nrcresearchpress.com by Santa Cruz (UCSC) on 06/26/14  
 For personal use only.

**Table 4.** Radiocarbon ages of Quaternary brown bears (*Ursus arctos*) bones from Western North America (oldest to latest)<sup>a</sup>.

| 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<br>CAMS-10527 | C.R. Harington (unpublished)                                    |
| Hunker Creek (Dawson Loc. 16), Yukon                               | Mandible (CMN 35965)      | 41 085±9050       | Beta-16159               | Harington (1977, 1978, 1980b, 1989, 1997)                       |
| Sixtymile Loc. 3, Yukon  | Humerus (CMN 38279)       | 36 500±1150       | Beta-16162               | Harington (1989, 1997);<br>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);<br>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);<br>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);<br>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.

<sup>a</sup>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 Can-

ada, 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 walrus 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.

## Acknowledgements

We wish to acknowledge the help of Kevin Seymour (Royal Ontario Museum) for first noting at the 2006 Canadian Paleontology Conference that the Saint-Nicolas bone represented a land mammal, maybe a bear, rather than a marine mammal; Steve Cumbaa (Canadian Museum of Nature) for help with the initial identification of the specimen to genus; Musée de paléontologie et de l'évolution in Montréal, Quebec, for covering the cost of the radiocarbon date; Eric Grimm (Illinois State Museum) and Russ Graham (The Pennsylvania State Museum) for advice on FAUNMAP dates on brown bears; Margaret Currie (Canadian Museum of Nature) for assembling the modern comparative bear specimens; Gail Harington for word-processing the manuscript. We also thank Kevin Seymour; the Journal's Associate Editor Hans-Dieter Sues; and an anonymous reviewer for helping us to improve the manuscript.

## References

- Barnes, I., Matheus, P., Shapiro, B., Jensen, D., and Cooper, A. 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science*, **295**: 2267–2270. doi:10.1126/science.1067814. PMID:11910112.
- Bouchard, M.A., Harington, C.R., and Guilbault, J.-P. 1993. First evidence of a walrus (*Odobenus rosmarus* L.) in Late Pleistocene Champlain Sea sediments, Québec. *Canadian Journal of Earth Sciences*, **30**(8): 1715–1719. doi:10.1139/e93-150.
- Bowdich, T.E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith, Paris, 115 pp.
- Churcher, C.S., and Morgan, A.V. 1976. A grizzly bear from the Middle Wisconsinan of Woodbridge, Ontario. *Canadian Journal of Earth Sciences*, **13**(2): 341–347. doi:10.1139/e76-036.
- Coleman, A.P. 1913. Excursion B2 – Toronto and vicinity. In *Excursions in vicinity of Toronto and to Muskoka and Madoc* (Excursion B2, B5, B6, B8 and B10). Ontario Bureau of Mines, Guide Book No. 6, pp. 1–29.
- Coleman, A.P. 1933. The Pleistocene of the Toronto region (including the Toronto Interglacial Formations). Forty First Annual Report of the Ontario Department of Mines 41(7), 69 pp.
- Cournoy, M.E., Chartier, M.D., Dubreuil, M., and Occhietti, S. 2006. Additions to the Champlain Sea faunal assemblage from Saint-Nicolas, Québec, with remarks on its paleoecology. *Canadian Paleontology Conference Proceedings* No. 4, pp. 12–16.
- Cronin, T.M., Manley, P.L., Brachfeld, S., Manley, T.O., Willard, D.A., Guilbault, J.-P., Rayburn, J.A., Thunell, R., and Berke, M. 2008. Impacts of post-glacial lake drainage events and revised chronology of the Champlain Sea episode 13-9 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **262**(2008): 46–60. doi:10.1016/j.palaeo.2008.02.001.
- Drummond, A.J., and Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**: 214. doi:10.1186/1471-2148-7-214. PMID:17996036.
- Drummond, A.J., Rambaut, A., Shapiro, B., and Pylos, O.G. 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, **22**: 1185–1192. doi:10.1093/molbev/msi103. PMID:15703244.
- Elton, C. 1954. Further evidence about the barren-ground grizzly bear in north-east Labrador and Quebec. *Journal of Mammalogy*, **35**: 345–357. doi:10.2307/1375959.
- Faunmap Working Group. 1994. FAUNMAP: a database documenting Late Quaternary distributions of mammal species in the United States. *Illinois State Museum Scientific Papers* **25**(2), pp. 1–690.
- Fischer de Waldheim, G. 1817. *Adversaria zoologica*. Mémoires de la société Impériale des Naturalistes de Moscou, **5**: 368–428.
- Graham, R.W. 1991. Variability in the size of North American Quaternary black bears (*Ursus americanus*) with the description of a fossil black bear from Bill Neff Cave, Virginia. In *Beamers, Bobwhites and Blue Points: Tributes to the Career of Paul W. Parmalee*. Edited by J.R. Purdue, W.E. Klippel, and B.W. Styles. Illinois State Museum Scientific Papers **23**, pp. 210–230.
- Greer, M., Greer, J.K., and Gillingham, J. 1977. Osteoarthritis in selected wild mammals. *Proceedings of the Oklahoma Academy of Sciences*, **57**: 39–43.
- Hanni, C., Laudet, V., Stehelin, D., and Taberlet, P. 1994. Tracking the origins of the cave bear (*Ursus spelaeus*) by mitochondrial-DNA sequencing. *Proceedings of the National Academy of Sciences of the United States of America*, **91**: 12336–12340. doi:10.1073/pnas.91.25.12336. PMID:7991628.
- Harington, C.R. 1977. Pleistocene mammals of the Yukon Territory. Ph.D. thesis, Department of Zoology, University of Alberta, Edmonton, Alberta.
- Harington, C.R. 1978. Quaternary vertebrates of Canada and Alaska and their suggested chronological sequence. *National Museum of Natural Sciences (Canada)*, *Syllogeus* No. 15, pp. 1–105.
- Harington, C.R. 1980a. A preliminary list of faunal remains from two caves (Trou Otis and Spéos de la Fée) in Gaspé, Québec. In *Le karste de plate-forme de Boischâtel et le karste barré de La Rédemption, état des connaissances*. Edited by J. Schroeder. Société Québécoise de Spéléologie, Montréal, pp. 93–105.
- Harington, C.R. 1980b. Faunal exchanges between Siberia and North America: evidence from Quaternary land mammal remains in Siberia, Alaska and Yukon Territory. *Canadian Journal of Anthropology*, **1**(1): 45–49.
- Harington, C.R. 1981. Whales and seals of the Champlain Sea. *Trail and Landscape*, **15**(1): 32–47.
- Harington, C.R. 1989. Pleistocene vertebrate localities in the Yukon. In *Late Cenozoic History of the Interior Basins of Alaska and the Yukon*. Edited by L.D. Carter, T.D. Hamilton, and J.P. Galloway. U.S. Geological Survey Circular **5026**, pp. 93–98.
- Harington, C.R. 1997. Pleistocene vertebrates of Sixtymile, Yukon Territory: a preliminary discussion. In *Terrestrial Paleoenvironmental Studies in Beringia, Alaska*. Edited by M.E. Edwards, A.V. Sher, and R.D. Guthrie. University Quaternary Center, University of Alaska, Fairbanks, pp. 83–90.
- Harington, C.R. (Editor). 2003. *Annotated bibliography of Quaternary vertebrates of northern North America – with radiocarbon dates*. University of Toronto Press, Toronto. 539 pp.
- Harington, C.R., and Occhietti, S. 1988. Inventaire systématique et paléocologie des mammifères marins de la Mer de Champlain (fin du Wisconsinien) et des voies d'accès. *Géographie physique et Quaternaire*, **42**: 45–64. doi:10.7202/032708ar.
- Harington, C.R., Lebel, S., Paiement, M., and deVernal, A. 2006. Félix: a Late Pleistocene white whale from Champlain Sea deposits at Saint-Félix-de-Valois, Québec. *Géographie physique et Quaternaire*, **60**(2): 183–198. doi:10.7202/016828ar.
- Heaton, T.H. 1995. Colonization of southeast Alaska by *Ursus arctos* prior to the peak of the Wisconsin glaciation. *Journal of Vertebrate Paleontology*, *Abstracts of Papers 15* (Supplement to No. 3), p. 34A.
- Heaton, T.H., and Grady, F. 1992. Preliminary report on the fossil bears of El Capitan Cave, Prince of Wales Island, Alaska. *Current Research in the Pleistocene*, **9**: 92–99.
- Heaton, T.H., and Grady, F. 1993. Fossil grizzly bears (*Ursus arctos*) from Prince of Wales Island, Alaska, offer new insights into animal dispersal, interspecific competition and age of deglaciation. *Current Research in the Pleistocene*, **10**: 98–100.
- Heaton, T.H., and Grady, F. 1997. The preliminary Late Wisconsin mammalian biochronology of Prince of Wales Island, southeastern Alaska. *Abstracts of Papers. Fifty-seventh Annual Meeting, Society of Vertebrate Paleontology, Journal of Vertebrate Paleontology* (Supplement to No. 3), p. 52A.
- Heaton, T.H., Talbot, S.I., and Shields, G.F. 1996. An ice age refugium for large mammals in the Alexander Archipelago, southeastern Alaska. *Quaternary Research*, **46**: 186–192. doi:10.1006/qres.1996.0058.
- Karrow, P.F., McAndrews, J.H., Miller, B.B., Morgan, A.V., Seymour, K.L., and White, O.L. 2001. Illinoian to Late Wisconsinan stratigraphy at Woodbridge, Ontario. *Canadian Journal of Earth Sciences*, **38**(6): 921–942. doi:10.1139/e00-108.
- Kurtén, B. 1968. *Pleistocene mammals of Europe*. Weidenfeld and Nicholson, London, 317 pp.
- Kurtén, B., and Anderson, E. 1980. *Pleistocene mammals of North America*. Columbia University Press, New York, 442 pp.
- Laurioli, B., Deschamps, E., Carrier, L., Grimm, W., Morlan, R., and Talon, B. 2003. Cave infill and associated biotic remains as indicators of Holocene environ-



- ment in Gatineau Park (Quebec, Canada). *Canadian Journal of Earth Sciences*, **40**(6): 789–803. doi:10.1139/e03-015.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis. Laurentii Salvii, Stockholm* 1. 532 pp.
- Loring, S., and Spiess, A. 2007. Further documentation supporting the former existence of grizzly bears (*Ursus arctos*) in northern Quebec-Labrador. *Arctic*, **60**(1): 7–16. doi:10.14430/arctic260.
- Matheus, P.E. 1995. Diet and co-ecology of Pleistocene short-faced and brown bears in Eastern Beringia. *Quaternary Research*, **44**: 447–453. doi:10.1006/qres.1995.1090.
- Matheus, P., Burns, J., Weinstock, J., and Hofreiter, M. 2004. Pleistocene brown bears in the mid-continent of North America. *Science*, **306**: 1150. doi:10.1126/science.1101495. PMID:15539594.
- McAllister, D.E., Harington, C.R., Cumbaa, S.L., and Renaud, C.B. 1988. Paleoenvironmental and biogeographic analyses of fossil fishes in peri-Champlain Sea deposits in Eastern Canada. In *The Late Quaternary Development of the Champlain Sea Basin*. Edited by N.R. Gadd. Geological Association of Canada Special Paper 35, pp. 241–258.
- Naughton, D. 2012. *The Natural History of Canadian Mammals*. Canadian Museum of Nature and University of Toronto Press, Toronto, 784 pp.
- Occhiotti, S., Chartier, M., Hillaire-Marcel, C., Cournoyer, M., Cumbaa, S.L., and Harington, C.R. 2001. Paléoenvironnements de la Mer de Champlain dans la région de Québec, entre 11 300 et 9 750 BP: le site Saint-Nicolas. *Géographie physique et Quaternaire*, **55**: 23–46. doi:10.7202/005660ar.
- Paetkau, D., and Strobeck, C. 1996. Mitochondrial DNA and the phylogeography of Newfoundland black bears. *Canadian Journal of Zoology*, **74**: 192–196. doi:10.1139/z96-023.
- Peterson, R.L. 1965a. A well-preserved grizzly bear skull recovered from a late glacial deposit near Lake Simcoe, Ontario. *Nature*, **208**(5016): 1233–1234. doi:10.1038/2081233a0.
- Peterson, R.L. 1965b. The Lake Simcoe grizzly. *Meeting Place, Journal of the Royal Ontario Museum*, **1**(4): 82–87.
- Pigott, P. 1999. Tracking a phantom grizzly. *Equinox*, **102**: 64–74.
- Posada, D., and Crandall, K.A. 1998. Model Test: testing the model of DNA substitution. *Bioinformatics*, **14**: 817–819. doi:10.1093/bioinformatics/14.9.817. PMID:9918953.
- Rambaut, A. 2002. Se-al2.0 all Available online at <http://tree.bio.ed.ac.uk/software/tracer/>.
- Rambaut, A., and Drummond, A.J. 2007. TGracer v.1.4. Available online at <http://tree.bio.ed.ac.uk/software/tracer/>.
- Rohland, N., and Hofreiter, M. 2007. Ancient DNA extraction from bones and teeth. *Nature Protocols*, **2**: 1756–1762. doi:10.1038/nprot.2007.247. PMID:17641642.
- Spiess, A., and Cox, S. 1976. Discovery of the skull of a grizzly bear in Labrador. *Arctic*, **29**(4): 194–200. doi:10.14430/arctic2804.
- Steffen, M.L., Hebda, R.J., McLaren, D.S., and Fedje, D.W. 2008. P2 Cave paleontological recovery and archaeological potential. Abstract of poster paper presented at the Northwest Anthropological Conference (April 23-26, 2008), Victoria, B.C., Preliminary Schedule, p. 24.
- Stovall, J.W., and Johnston, C.S. 1935. Two fossil grizzly bears from the Pleistocene of Oklahoma. *Journal of Geology*, **43**(2): 208–214.
- Tovell, W.M., and Deane, R.E. 1966. Grizzly bear skull: Site of a find near Lake Simcoe. *Science*, **154**: 158. doi:10.1126/science.154.3745.158-a. PMID:5922863.
- Valdiosera, C.E., Garcia, N., Anderung, C., Dalen, L., Cregut-Bonnoure, E., Kahlke, R.-D., Stiller, M., Brandstrom, M., Thomas, M.G., Arsuaga, J.L., Gotherstrom, A., and Barnes, I. 2007. Staying out in the cold: glacial refugia and mitochondrial DNA phylogeography in ancient European brown bears. *Molecular Ecology*, **16**: 5140–5148. doi:10.1111/j.1365-294X.2007.03590.x. PMID:18031475.