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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

The bears of Scotland

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The brown bear, *Ursus arctos*, has one of the widest geographical distributions of any carnivoran in the world and it also has a rich fossil record. However, in Scotland extensive glaciation and acidic soils have resulted in few fossil or archaeological remains of *Ursus* spp. being discovered. Here, the palaeontological and archaeological records of bears in Scotland are reviewed. The results of recent analytical methods including radiocarbon dating, genetic and stable isotope analyses on many of these specimens are presented and discussed in relation to long-term climatic and ecological changes in Scotland over the last 50 000 years.

Introduction

The brown bear, *Ursus arctos*, is second only to the grey wolf, *Canis lupus*, in having the largest geographical distribution among carnivorans (McLellan *et al*. 2017, Haroldson *et al*. 2020, Swenson *et al*. 2020). Its original range extended from the British Isles throughout Europe, north Africa, the Middle East, northern and central Asia, Japan and North America as far south as Mexico (McLellan *et al*. 2017, Haroldson *et al*. 2020, Swenson *et al*. 2020). Loss and fragmentation of habitat and competition with humans, resulting in conflict and hunting for fur, fat, bones and bile have resulted in extirpation of the brown bear in many areas. Despite this, the species' world population is stable at ca. 200 000 individuals and it is listed as Least Concern in the IUCN Red List of Threatened Species (McLellan *et al*. 2017). Given its extensive distribution it occupies a wide variety of habitats and varying ecological conditions, which have resulted in variable phenotypes across its range and many subspecies have consequently been described (Kitchener 2010, Kitchener *et al*. 2020). Phylogeographical studies have identified several mitochondrial DNA haplotypes, some of which correspond to putative subspecies, while others are sympatric, especially across Asia and North America (Davison *et al*. 2011, Bray *et al*. 2013, de Jong *et al*. 2023). Only recently have two studies been carried out based on whole genomes of nuclear DNA, which have clarified much of the geographical genetic structure of this widespread species (de Jong *et al*. 2023, Tumendemberel *et al*. 2023).

The brown bear is extinct in the British Isles today, although it is unclear when it became extinct, because bears were imported from Europe as dancing bears and for bear baiting long after its demise as an indigenous species (Yalden 1999, Kitchener & Yalden 2008,

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O'Regan 2018). Yalden (1999) listed more than 100 sites in England and Wales, where brown bear remains have been found, and numerous radiocarbon dates for Late Pleistocene and Holocene bears have been collated as part of genetics studies (*see* Edwards *et al*. 2011, 2014). Brown bears likely first entered Britain during the Purfleet Interglacial (MIS 9; Schreve 1997) and were found up until the 12th–13th centuries CE (Yalden 1999), with O'Regan (2018) identifying 85 Holocene localities. Extensive glaciations, especially the Last Glacial Maximum, would have made large areas of (mostly) northern Britain uninhabitable, so that the occurrence of brown bears in Britain was not continuous, but relied on recolonisation from what is now mainland Europe (García-Vázquez *et al*. 2017). Extinction dates for British brown bears are highly variable. It is often claimed that they became extinct in the 10th century CE, or during the first millennium CE, although Yalden (1999) suggested that extinction occurred around 2000 years ago. O'Regan (2018) suggested that the extinction of bears in the British Isles occurred either by the late Neolithic/early Bronze Age, or the early Medieval period, with later bears being imported. In Ireland the chronological range of bears is more restricted, with remains having been found in about 30 localities, ranging in date from pre-LGM (46 200 ± 2500 radiocarbon years BP [uncal.] for a femur (F21148) from Castlepook Cave, Co. Cork (Carden *et al*. 2020) in the Woodgrange Interstadial to about 3000 BP in the Holocene (2956 ± 33 radiocarbon years BP [uncal.] at Poll na mBéar, Co. Leitrim (Edwards *et al*. 2011) (*see* review in Monaghan 2023 for a summary of all dated specimens).

Very few remains of fossil and archaeological bears have been recorded in Scotland (Kitchener 1998), although Scotland might have been expected to have been a stronghold of bears owing to the persistence of extensive woodland in the Highlands until the 18th century, and the low population density of people. However, Late Pleistocene and Holocene remains of large mammals are generally rare in Scotland owing to acidic soils, which are unsuitable for the preservation of bone and a dearth of karst landscapes, in which Late Pleistocene and early Holocene faunal remains are commonly found (Kitchener 1998, Bonsall *et al*. 1999, Kitchener *et al*. 2004). One site, the Creag nan Uamh, has a series of caves in dolomitic limestones in the Assynt area of Sutherland in NW Scotland. These limestone caves are part of the Durness Group and are rich in the fossil remains of bears (mostly identified as *Ursus* sp., *Ursus* cf. *arctos* or *Ursus arctos*) stretching back over at least the last ca. 50 000 years, but elsewhere records are few (Kitchener 1998). Here, we review the fossil and archaeological evidence of bears in Scotland, exploring the history of discoveries and types of contexts in which bear remains have been found. We also summarise the main findings of recent scientific analyses (including genetics, radiocarbon dating and stable isotope analysis), and present new radiocarbon and isotopic data. We explore how these analyses are revealing more about the past lives of Scotland's bears, but also highlighting the need for more comprehensive taxonomic, morphological, genetic and palaeoecological analysis of Scotland's small but potentially significant ursid fossil collections.

A chronology of bear discoveries in Scotland

Below is a list of the bear remains that have been found in palaeontological and archaeological contexts in Scotland, which are listed separately, and broadly follow the chronological order in which they were discovered (for find localities *see* Fig. 1). Palaeontological sites date to both the Late Pleistocene and the Holocene, and these specimens are considered to have been preserved in natural contexts, such as caves, and with no evidence of contemporary human activity. By contrast, the archaeological finds are currently all Holocene and are characterised by coming from sites of known human activity or bearing direct evidence of anthropogenic modification (i.e. cut marks, etc.). This distinction is important given the uncertainty of the date of extinction of the brown bear in Britain, because (and particularly in more recent periods) humans may have imported live European continental bears for entertainment purposes or body parts, such as skins and bones, to be used for a variety of purposes. While we distinguish between these

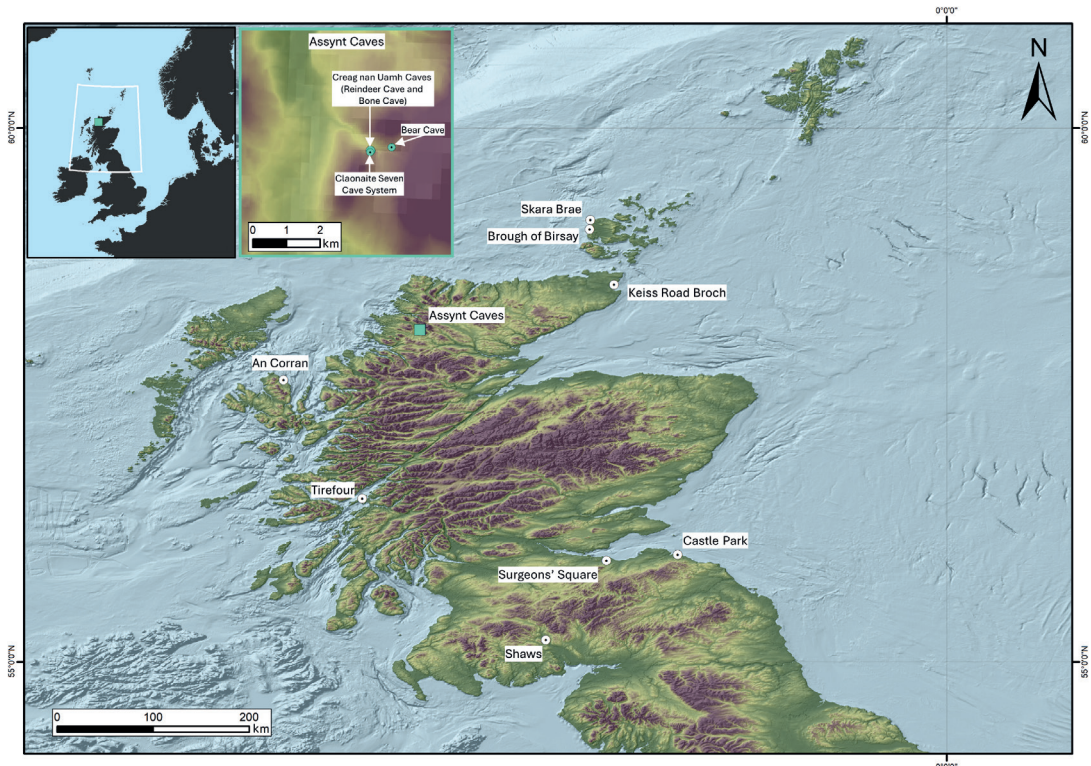

Fig. 1. Localities mentioned in the text for bear, *Ursus* spp., remains. Inset shows cave sites in the Allt nan Uamh Valley, Assynt, Sutherland, NW Scotland. Image: Will Mills, Aberdeen (produced using Ordinance Survey Topo 50 and EMODnet20 for the basemap).

two types of site, it should be noted that the current category for a site (and even a particular find from a site) may change, if, for example, there is new evidence for anthropogenic activity, such as modifications to bones, at a supposed palaeontological site.

Palaeontological sites

Shaws, Dumfriesshire — before 1869

Sir William Jardine reported the discovery of the skull and rib of a brown bear when digging for marl from a peat bog about four miles from the property of George Graham, esq. of Shaws (Smith 1869, 1879). The bones were found at the bottom of the peat just above or on the marl. The skull (but not the rib, which was lost before the skull was described by Smith (1879)) is in the collection of National Museums Scotland (specimen NMS.Z.1993.160.9; Fig. 2).

Fig. 2. Brown bear skull found at Shaws, Dumfriesshire before 1869 (NMS.Z.1993.160.9); © National Museums Scotland.

Bone Cave, Creag nan Uamh Caves, Sutherland — 1885

A single (probably upper) canine tooth of a brown bear was found in Bed 5 (limestone fragments) of Bone Cave, Creag nan Uamh Caves, Sutherland, in the northwest of Scotland

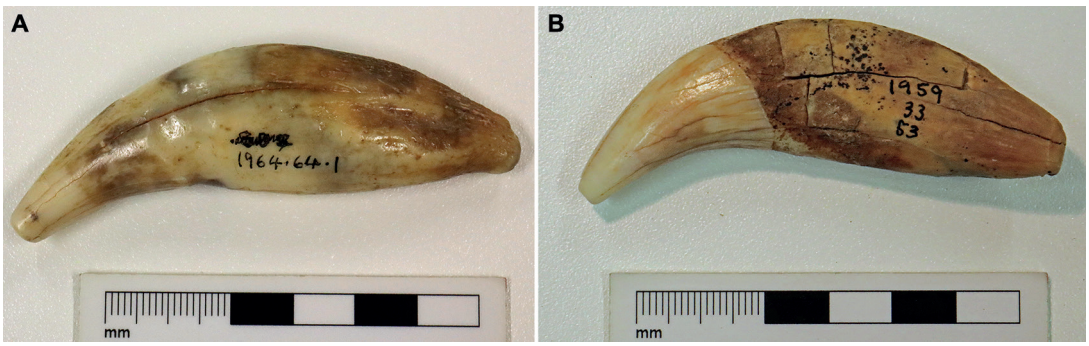

Fig. 3. Canine teeth of brown bears from Scotland. — **A**: Bone Cave, Creag nan Uamh, Assynt, Sutherland (NMS.Z.1964.64.1) (maximum length 82.4 mm). — **B**: Reindeer Cave, Creag nan Uamh, Assynt, Sutherland (NMS.Z.1959.33.53) (maximum length 75.1 mm). ©Andrew Kitchener, National Museums Scotland.

Fig. 4. Cranium of a putative polar bear, *Ursus* cf. *maritimus*, from Reindeer Cave, Creag nan Uamh, Assynt, Sutherland (NMS.Z.1959.33.2777); ©National Museums Scotland.

(58.107989°N, 4.9411924°W; Peach & Horne 1893, 1918, Newton 1918). It is in the collection of National Museums Scotland (specimen NMS.Z.1964.64.1; Fig. 3A). Further bear remains were identified from Bone Cave, following the 1926–1927 excavations by James Cree, John Graham Callender and James Ritchie (*see* below, and Appendix). While the majority of these finds are in the collections of National Museums Scotland, it is possible other remains of bear are in the small collection of the Creag nan Uamh Caves material held by the British Geological Survey, which also originated from the Peach and Horne excavation.

Reindeer Cave, Creag nan Uamh Caves, Sutherland — 1926–1927

A total of around 102 separate remains of bear (*Ursus* spp.) have been identified mostly from Reindeer Cave, but also from Bone Cave, in the 1926 and 1927 excavations at the Creag nan Uamh Caves (*see* Appendix). Amongst these is a (probably lower) canine tooth found on 29th June 1926 (specimen NMS.Z.1959.33.53; Fig. 3B). While the majority of these fossil remains can be assumed to be brown bear (based on initial observations of their size and morphology, and also the palaeogeography of bear species in Europe), detailed study of their morphometrics and genetics would be needed to firmly establish this. Such work would also allow the variable ecomorphology and ecology of Late Pleistocene brown bears in this part of northern Europe to be explored.

During the 1926 and 1927 excavations, Callander *et al*. (1927) reported finding the (supposed) remains of a cave bear, *Ursus spelaeus*, in 18 inches (ca. 46 cm) of deposits in Cave 2A (the Inner Chamber) behind Reindeer Cave. This cranium is in the collections of National Museums Scotland (specimen NMS.Z.1959.33.2777; Fig. 4). From its size and morphology, it is clearly not a cave bear, and was assumed to be a brown bear. However, certain morphological features (a long flat sagittal region, and the occipital crest and large occipital condyles) and radiocarbon dating in the 1990s, which placed it in Assynt during the Late Glacial Maximum (LGM), led to

this being queried and to the designation of the specimen as a possible polar bear, *Ursus maritimus* (Kitchener & Bonsall 1997). However, it should be noted that the more diagnostic teeth and facial region are missing from this specimen, and that the isotopic data associated with this older date almost certainly call that assignment (and the date itself) into question (*see* below).

Bear Cave, Sutherland — 1958–1963

This small cave is on the south side of the Allt nan Uamh (58.109159°N, 4.9294037°W), ca. 500 m east of the Creag nan Uamh caves, and directly opposite the entrance to the large cave system of the Allt nan Uamh Stream Cave, to which it may once have been connected (Young 1988). Bear bones were discovered there by chance in 1958 and the cave was excavated by Dr Arthur Clarke, Keeper of Natural History, Royal Scottish Museum (now National Museums Scotland) in 1960–1963. A summary of Clarke's diary entries and photographs were compiled by Lawson (1999). The brown bear remains comprise an adult female and a juvenile (NMS.Z.2019.74; Fig. 5). The adult remains comprise a left femur, right and left fibulae and astragali, right and left carpals, metacarpals and phalanges, three thoracic and four lumbar vertebrae, and various ribs and teeth. The juvenile remains comprise right and left ulnae, proximal tibia, left pelvis, right ilium, left femur (lacking distal end), left humerus, 6 cervical, 10 thoracic and 8 lumbar vertebrae, and various ribs and teeth. The adult femur was extensively sampled for radiocarbon dating (*see* below; Burleigh *et al*. 1976). The good preservation of the skeletal material suggests these animals died of natural causes during hibernation, but this is a tentative conclusion given their incompleteness.

Claonaite Seven Cave System, Sutherland — since 2002

There have been several finds of brown bear in this extensive cave system, which is adjacent to the Creag nan Uamh Caves. Specimens were retrieved in 2002 and 2008–2009 and are in the collection of National Museums Scotland, but these had been discovered several years before when the cave system was first being explored (Lawson *et al*. 2014). These finds comprise an almost complete skeleton of a brown bear found in the Portobello Promenade (NMS.Z.2014.147.1 and NMS.Z.2002.91 (left mandible); Fig. 6). It is very friable, indicating long-term water damage in the cave system. It is an old male based on its size and tooth wear and probably died during hibernation. There is an isolated left ulna found in the Legless Highway, which is in excellent condition (NMS.Z.2014.147.3; Fig. 7A). There is also a skull (lacking mandible, NMS.Z.2014.147.2; Fig. 7B) and a right humerus (NMS.Z.2014.147.6; Fig. 7C). A scapula was found alongside these remains, but was wedged into a fissure and is currently not retrievable (Lawson *et al*. 2014).

Archaeological remains

Keiss Road Broch, Caithness — ca.1890s

A (probable lower) canine tooth of a brown bear was reported by Sir Francis Tress Barry at the Road Broch, Keiss, Caithness, in the late 19th century. This is in the collection of National Museums Scotland (specimen NMS.Z.1997.25; Fig. 8), and probably dates to the mid-first millennium CE (Anderson 1901: 139, Heald & Jackson 2002).

Brough of Birsay, Orkney

The canine tooth of a brown bear, previously misidentified as being from either a walrus, *Odobenus rosmarus*, or a seal, was found supposedly from the 'Lower Norse horizon', dating to the ninth to tenth centuries CE (Morris 2017). However, the style of runic inscriptions on the tooth suggest that it may date later, perhaps to the 11th or 12th centuries CE. However, it is also possible that the tooth could have been imported from Scandinavia or elsewhere. Furthermore, as the specimen has not been directly dated, it is unclear if it is contemporaneous with the inscription or represents use of an older find.

Fig. 5. Brown bear remains found in 1961 in Bear Cave, Creag nan Uamh, Assynt, Sutherland. — **A**: Adult female femur (NMS.Z.2019.74.1), note heavy sampling of bone for an early radiocarbon date when sample sizes were very large. — **B** and **C**: Juvenile left humerus and right pelvis, respectively (NMS.Z.2019.74.2). — **D**: A deciduous canine tooth and two deciduous incisors (NMS.Z.2019.74.2) ©Andrew Kitchener, National Museums Scotland.

Fig. 6. Almost complete skeleton of a male brown bear recovered in 2009 from the Portobello Promenade, Claonaite Seven, Assynt, Sutherland (NMS.Z.2014.147.1); ©Andrew Kitchener, National Museums Scotland.

Surgeons' Square, Edinburgh — 1988

In 1988 an assemblage of 63 bones was recovered by workmen from accumulated deposits inside the Flodden Wall at the Pleasance, Edinburgh (55.949029°N, 3.1828401°W). These were mostly human, but there were five bones from the skeleton of an immature brown bear (Henderson *et al*. 1997). These bear remains probably date from the 18th century and were probably from dissections for the study of comparative anatomy at the Royal College of Surgeons, Surgeons' Hall.

Castle Park, Dunbar — late 1980s/early 1990s

During excavations in the late 1980s and early 1990s the scapula of a brown bear was excavated from Medieval contexts at the Castle Park site in Dunbar and was (given the date) considered to have been a bear imported for baiting or other entertainment. The bear scapula bore cut marks in excess of those that would be required just for skinning, which was interpreted as further carcass processing, possibly to render bear fat, which had a variety of medicinal and cosmetic uses in that period (Smith 2000: 236).

An Corran, Staffin, Skye — early 1990s

In the early 1990s, a second posterior phalanx of a brown bear was found in the Mesolithic shell midden at An Corran, Staffin, Skye (Bartosiewicz 2012). The surface of the bone is badly eroded. Terminal phalanges in isolation are often indicative of skins, in which the phalanges have been left after processing, but it is unclear if this is the case for this specimen.

In addition to the above, a bear metacarpal from the late Scottish Iron Age/early Medieval site of Tirefour on Lismore in the Inner Hebrides has recently been reported (Orton pers. comm. in O'Regan 2018). Another possible bear find originates from the Neolithic site of Skara Brae, Orkney. Listed as '?bear' in the British Museum's catalogue (specimen 138.0101.37), further work to identify the species of this specimen is required (O'Regan 2018).

In this handful of archaeological cases, it remains unclear if remains are from local bears or parts imported from mainland Europe or elsewhere, such as the canine tooth with a Runic inscription from Brough of Birsay and the phalanx from An Corran. Further finds, or the investigation of these few specimens by radiocarbon dating, stable isotope analysis or even genetic analysis, will enhance our understanding of whether these remains have any relevance to indigenous bear populations.

Radiocarbon dating the bears of Scotland

Radiocarbon dates for bears in Scotland are shown in Table 1, alongside collagen stable light isotope data (where available, *see* Discussion

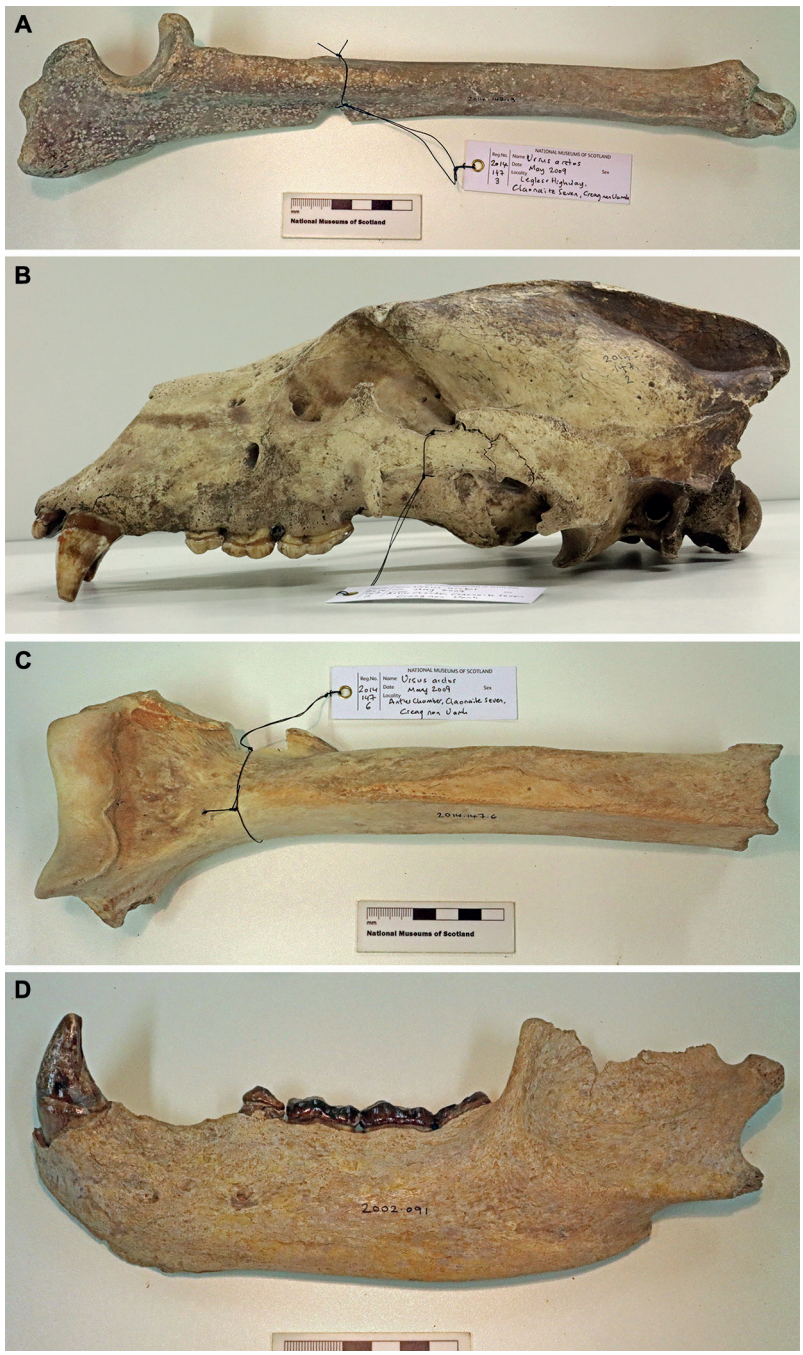

Fig. 7. Brown bear remains recovered in 2002 and 2009 from the Legless Highway, Claonaite Seven, Assynt, Sutherland. — **A**: Left ulna (NMS.Z.2014.147.3) (maximum length 377.9 mm). — **B**: Skull (NMS.Z.2014.147.2). — **C**: Humerus (NMS.Z.2014.147.6) (maximum length 316.5 mm). — **D**: Left mandible (NMS.Z.2002.91) from the almost complete skeleton. ©Andrew Kitchener, National Museums Scotland.

below) including new (this study) and previously published dates. While the dates vary in origin (in terms of year produced and analysing laboratory), they have all been calibrated using the

IntCal20 atmospheric curve. However, please note that due to the likely marine dietary content of a number of the individuals, these calibrated dates may be influenced by the marine reservoir effect. Owing to the long residence time of carbon within some ocean systems, radiocarbon dates of marine species, or species that consume marine or anadromous species (such as salmon), can be offset by up to 400 years (or up to 1200 years in some Arctic regions) (Ascough *et al*. 2005). While corrections for marine dietary contribution can be made based on estimates of marine dietary content (based on carbon isotope data), such estimates are complicated, require input data to calculate dietary contributions, and freshwater inputs (likely in some of the bears, due to possible consumption of river fish) cannot be corrected for. Therefore, no attempts to correct dates based on estimated dietary contributions have been made here, but given the dating of the specimens in Table 1, this is unlikely to have a significant impact on interpretation of radiocarbon dates.

The radiocarbon dates range from 'infinite' (i.e., outside the range of radiocarbon dating and therefore could not be calibrated) in an example from Reindeer Cave (OxA-43433, > 46 200 BP, this study), to 2920–2720 cal. BP (95.4%) for the dated individual from Bear Cave (Burleigh *et al*. 1976). These dates, and the other pre- and post-LGM dates from Creag nan Uamh, demonstrate the importance of this region for bears throughout the Late Pleistocene (albeit not during times of extensive glacial cover) and into the Holocene, probably as a hibernation site and a cubbing den site given its numerous limestone caves. Dates in Table 1 include a mixture of recent and older dates, and a variety of sample preparation techniques, including the addition of ultra-filtration and humic acid removal in the case of the most recent dates (as indicated by an asterisk). While these protocols may not be necessary for dates produced on more recent bones and bones with a higher endogenous collagen content, these approaches may be particularly important for older samples and where collagen preservation is low (Higham *et al*. 2006, Talamo *et al*. 2021). In such samples, even small quantities of contaminating carbon (e.g., from humic acids) could influence radiocarbon dates substantially.

Fig. 8. Canine tooth of a brown bear found in the 1890s at the Road Broch, Keiss, Caithness (NMS.Z.1997.25) (maximum length 85.66 mm, antero-posterior crown length 22.71 mm, medio-lateral crown width 14.99 mm); ©Andrew Kitchener, National Museums Scotland.

The bear cranium from Reindeer Cave, which had been identified initially as a cave bear, was (and based largely on its radiocarbon date of 23 230–22 340 cal. BP, 95.4% [calibrated in IntCal20]) described as a possible polar bear by Kitchener and Bonsall (1997). Although some morphological features may support this tentative identification, the rationale was that the date coincided with extensive glaciation across Scotland and that while a brown bear would be unlikely to be able to live in Scotland at that time, a polar bear might be able to. However, the $\delta^{13}C$ value of –21.0‰ was incongruous with the identification. Although it is conceivable that polar bears could subsist on a mostly terrestrial diet, there would have been no such terrestrial resources available in Scotland during this phase of the LGM. Indeed, based on the most recent models of the advance and retreat of the last British–Irish ice sheet, at approximately 23 kyr ago the ice sheet extended across Scotland and was still covering the Outer Hebrides in the west of Scotland (Clark *et al*. 2022). The extent of glaciation, combined with the fully terrestrial $\delta^{13}C$ value, suggest it is this older radiocarbon date that is in itself questionable. Indeed, contamination by humics in the burial environment, combined with a low remaining amount of endogenous collagen, would serve to both lower the $\delta^{13}C$ (towards fully terrestrial values) and to bring the date forward in time through the addition of 99 more recent contaminating organics.

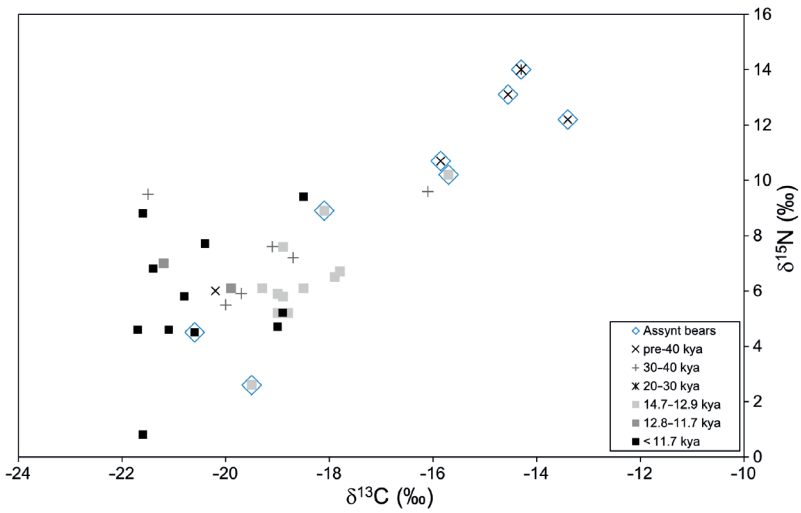

Fig. 9. Stable carbon and nitrogen isotope data for bears from Late Pleistocene and Holocene Scotland, England and Ireland. Data originate from this study and from H. Taekema *et al.* (unpubl. data) for Scotland, and from Edwards *et al.* 2011 and 2014 for England and Ireland. Data are divided into six time periods based (broadly) on climatic phases, including the pre-LGM (20–30 kya, 30–40 kya and 40+ kya) and the post-LGM (including the Allerød, Younger Dryas, and Holocene).

The colour of the fossil, which is stained to an almost black colour, might support this hypothesis. The dark coloration may also be from a consolidant applied historically in the museum, which may also be the contaminating agent (as many glues are animal-based). In light of recent developments in radiocarbon dating, including ultra-filtration, the removal of contaminating humic acids and of organic compounds used in conservation, re-evaluation of this specimen is now recommended.

Another date that requires some scrutiny with regards to its chronological relationship to recent models of glacial advance and retreat is SUERC-25560 for the almost complete skeleton from Portobello Promenade in the Claonite Seven System (NMS.Z.2014.147.1), which dates to approximately 28 000–27 000 cal. BP (IntCal20) (Lawson *et al*. 2014). At this time glaciation is thought to have extended across Scotland, with Lewis and Cape Wrath (Durness region) being ice-marginal areas in northern and northwestern Scotland (Clark *et al*. 2022). Of note, this individual has a δ^{13}C of –14.3‰ and a δ^{15}N of 14‰, which is the most elevated δ^{15}N value in any of the bears discussed in this study. This indicates a diet rich in marine protein, which could be consistent with life on an ice-margin, although this would be inconsistent with contemporary brown bear feeding ecology. Similarly elevated isotopic values are seen in a number of specimens now analysed from the Assynt bone caves (Table 1 and Fig. 9), which are now explored below.

The dietary ecology of bears in Scotland

Stable isotopes are a powerful means of exploring the dietary palaeoecology of extinct and ancestral species, and are particularly useful in exploring trophic levels and extent of carnivory (δ^{15}N), as well as the proportional contribution of marine foods to the diet (δ^{13}C). For example, these methods have even been applied to modern animals as a means of tracking the seasonal contributions of salmon to the diets of grizzly bears (Ben-David *et al*. 2004) and to explore diachronic change in recent polar bear feeding ecology with climatic change (Routledge *et al*. 2023, Westbury *et al*. 2023). A small number of studies have taken a targeted look at Late Pleistocene bear diets through the stable isotope analysis of extracted

Table 1. Radiocarbon dates of bears from Scotland. All dates were calibrated using the IntCal20 Terrestrial Curve. However, based on δ13C data, individuals SUERC-26400, OxA-43750, SUERC-25560, OxA-43432, SUERC-26399 and OxA-43433 all had a significant marine component to their diet (up to 100%). Therefore, calibrated dates may be several hundred years too 'old', due to the marine reservoir effect. Stable carbon and nitrogen isotope data as well as C:N ratios are presented alongside dates. Asterisk (*) denotes dates generated from collagen that had been subjected to humic acid removal and ultrafiltration at ORAU, with associated stable isotope data generated (in duplicate) at SUERC from the same extracts (this study).

Species/register no.	Locality	Material	Lab ID	Radiocarbon age (BP)	Cal BP range		δ^{13}C	δ^{15}N	C:N	Source
					68.3%	95.4%				
Ursus sp. NMS.Z.1959.33.1074	Reindeer Cave (Outer), Assynt	Bone (?ulna)	OxA-43433	> 46200	not available	not available	–14.55	13.1	3.2	This study*
Ursus arctos NMS.Z.2014.147.3	Legless Highway, Claonaite, Assynt	Bone (ulna)	SUERC- 26399	45000 ± 1000	48310–46170	50040–45460	–15.9	10.7	3.3	Date: Lawson *et al.* 2014; Isotopes: H. Taekema *et al.* unpubl. data
Ursus sp. NMS.Z.1959.33.1601	Reindeer Cave (Outer), Assynt	Bone (diaphysis fragment)	OxA-43432	42400 ± 1800	47020–43380	50830–42640	–13.4	12.2	3.2	This study*
Ursus arctos NMS.Z.2014.147.1	Portobello Promenade, Claonaite, Assynt	Bone (rib)	SUERC-25560	23560 ± 110	27830–276600	27890–27440	–14.3	14	3.5	Date: Lawson *et al.* 2014; Isotopes: H. Taekema *et al.* unpubl. data
Ursus cf. *maritimus* NMS.Z.1959.33.2777	Inner Chamber, Reindeer Cave, Assynt	Bone (cranium)	AA-18504	18855 ± 215	22960–22530	23230–22340	–21			Kitchener and Bonsall 1997
Ursus sp. NMS.Z.1959.33.2383	Tunnel between Bone Cave and Reindeer Cave, Assynt	Bone (metatarsal)	OxA-43751	12300 ± 40	14310–14110	14810–14080	–19.5	2.6	3.2	This study*
Ursus sp. NMS.Z.1959.33.2119	Reindeer Cave (Outer), Assynt	Tooth root (M1)	OxA-43750	12085 ± 40	14060–13860	14070–13800	–18.1	8.9	3.3	This study*
Ursus arctos NMS.Z.2014.147.6	Antler Chamber, Claonaite	Bone (humerus)	SUERC-26400	11625 ± 40	13580–13450	13590–13350	–15.7	10.2	3.3	Date: Lawson*et al.* 2014; Isotopes: H. Taekema *et al.* unpubl. data

continued

Table 1. Continued.

Species/register no.	Locality	Material	Lab ID	Radiocarbon age (BP)	Cal BP range 68.3%	Cal BP range 95.4%	δ^{13}C	δ^{15}N	C:N	Source
Ursus arctos NMS.Z.1993.160.9	Shaws, Dumfriesshire	Bone (skull)	AA-18503	7590 ± 95	8520–8220	68590–8180	–21.2			Kitchener & Bonsall 1997
Ursus arctos NMS.Z.2019.74.1	Bear Cave, Assynt	Bone (femur)	BM-724	2673 ± 54	2850–2740	2920–2720	–20.6	4.5	3.4	Date: Burleigh *et al.* 1976; Isotopes: H. Taekema *et al.* unpubl. data
Ursus arctos NMS.Z.2019.74.2	Bear Cave, Assynt	Bone (rib)	not available	not available			–21.9	4.4	3.4	H. Taekema *et al.* unpubl. data

bone collagen (often alongside genetic analysis), including European cave bears (Hilderbrand *et al*. 1996, Richards *et al*. 2008, Bocherens 2019) and brown bears in Ireland and England (Edwards *et al*. 2011, 2014), NW Iberia (García-Vázquez *et al*. 2018), NE Siberia (Rey-Iglesia *et al*. 2019) and Beringia (Barnes *et al*. 2002).

Stable isotope data (carbon and nitrogen) for the Scottish bears discussed in this study are given in Table 1. Isotopic values show great variation, ranging from –21.9‰ to –13.4‰ for carbon and from 2.6‰ to 14.0‰ for nitrogen. As shown in Fig. 9, many of the Assynt bears (particularly those dating to before the Late Glacial Maximum) have elevated δ^{13}C and δ^{15}N values, indicating a high contribution of marine protein to the diet. Indeed, values for five of the nine specimens with isotope data from Assynt (including NMS.Z.2014.147.1 mentioned above from Claonite Seven, but also including NMS.Z.1959.33.1074, NMS.Z.2014.147.3, NMS.Z.1959.33.1601, and NMS.Z.2014.147.6) far exceed values determined in the bone collagen of grizzly bears from coastal Alaska and the Columbia River drainage, which have a significant dietary contribution of salmon (up to 90%) (Hilderbrand *et al*. 1996). This suggests that the origin of this marine signal could not be achieved with a diet consisting solely of (anadromous) Atlantic salmon, *Salmo salar*, but likely included seabirds/seabird eggs, estuarine resources, such as shellfish, marine fishes or even marine mammals, including stranded cetaceans. Owing to the likely diversity of diet, and the issue of equifinality in isotope values of tissues, it may also be possible that the diet also included a minor component of terrestrial plants, or mammals, such as reindeer, *Rangifer tarandus*, alongside these marine resources. Seasonal intertidal foraging on clams, crabs and other species has been observed in coastal populations of brown bear in Alaska (Smith & Partridge 2004), along with the scavenging of carcasses of beached cetaceans and seals (Lewis & Lafferty 2014). However, marine-dominated or exclusively marine-feeding behaviours are not found in populations of brown bears today. Instead, such a dietary composition would mirror that of coastal polar bears in Svalbard, Norway, which are known to have a diverse diet including marine algae, seabirds and their eggs,

seals, terrestrial plants and reindeer (Iversen *et al*. 2013).

In contrast, the diet of the majority of the post-LGM bears in Assynt, and bears analysed throughout the rest of Britain and Ireland (data from Edwards *et al*. 2011, 2014), demonstrate a predominantly terrestrial diet, albeit with some minor contribution of marine-anadromous or freshwater protein. However, post-LGM and Holocene bear dietary ecology in Britain and Ireland is diverse, with some very low nitrogen isotope ratios, indicative of herbivorous diets, and higher values demonstrating omnivory or moderate carnivory. These data serve to highlight the flexible dietary ecology of brown bears throughout the Late Pleistocene and early Holocene. The pre-LGM isotope data from Assynt may indeed highlight a hitherto undocumented dietary niche of brown bears living in high-latitude, coastal environments as a maritime-feeding species. However, the distinct grouping of data in Fig. 9, may also highlight the need to further explore species determinations in the case of some Late Pleistocene bears from Britain. Multiple hybridisations of brown bears and polar bears are thought to have occurred over the past 100 000 years, and the modern polar bear matriline is shared with brown bears that lived near Ireland prior to or during the Last Ice Age (Edwards *et al*. 2011, 2014). This suggests that polar bears and brown bears must have had overlapping ranges at different points in northwestern Europe during the Late Pleistocene, perhaps occupying similar niches, owing to a lack of terrestrial feeding opportunities. It also raises the issue of the potential of finding Late Pleistocene polar bears in the fossil record in Great Britain or Ireland, and highlights problems with identifying fragmentary fossil specimens based on morphology alone.

The genetics of bears in Scotland

Considerable research has been done on the phylogeography of extant brown bears using mitochondrial DNA and it is only recently that whole genome sequencing studies have been carried out on nuclear DNA (e.g., de Jong *et al*. 2023, Tumendemberel *et al*. 2023). These mtDNA studies show that today Europe is occupied by mitochondrial haplotype 1 (mostly 1a in the west and 1b in the east), whereas the brown bears of much of northern Eurasia have haplotype 3a (Barnes *et al*. 2002, Valdiosera *et al*. 2007, de Jong *et al*. 2023). To date, four Scottish bear specimens have been sampled for their mitochondrial DNA. A phalanx from the adult female brown bear from Bear Cave dated to ~2900 to 2700 cal. BP is haplotype 1a, which now occurs in the Iberian Peninsula (Barnes *et al*. 2002, Valdiosera *et al*. 2007). The juvenile brown bear from Bear Cave also has mtDNA haplotype 1a (Bray *et al*. 2013). Attempts were made to extract DNA from three specimens from the Claonaite Seven, but none was recoverable of sufficient quality from the almost complete skeleton from Portobello Promenade (NMS.Z.2014.147.1). However, mtDNA was recovered from the other two specimens. The humerus (NMS.Z.2014.147.6) is haplotype 1a as expected, but the oldest specimen, the ulna (NMS.Z.2014.147.3), has haplotype 3a (J. Austin pers. comm.), which is now found across northern Eurasia from Finland to Japan and even Alaska (Davison *et al*. 2011). Attempts have also been made to extract DNA from the putative polar bear from Reindeer Cave (NMS.Z.1959.33.2777), but that was also unsuccessful (C. Edwards pers. comm.).

These data could suggest that some genetically different bears occupied Scotland prior to the LGM, which originated in northern Eurasia. However, studies of mtDNA haplotypes of Late Pleistocene and Holocene brown bears from Europe suggest that different haplotypes were not restricted to refugia in peninsulae in the south, as previously thought (e.g., Taberlet and Bouvet 1994). Instead, there was considerable mixing of different haplotypes pre-LGM, during the LGM and during the Holocene (Valdiosera *et al*. 2007). García-Vázquez *et al*. (2019) analysed mtDNA haplotypes of fossil brown bears in Europe in comparison with published data. This study showed that clades 1b and 2 occurred in the British Isles before the LGM, only clade 1a and 2 survived after the LGM, with the last clade 2 specimen dated to the early Holocene (9700 years cal. BP). There is also evidence of genetic turnover before the LGM in Europe (Ersmark *et al*. 2019). The current phylogeographi-

cal structure among contemporary brown bears has probably arisen as a result of high female philopatry (reflecting maternal inheritance of mtDNA) and a severe reduction of population sizes during the Holocene, owing to loss of habitat and hunting/persecution by humans (Valdiosera *et al*. 2007).

Given the relatively small number of Scottish bears represented in the European dataset, further genetic analysis of Scotland's Pleistocene and Holocene bear remains is warranted. Such studies could be pivotal to validating species determinations challenged by isotopic data (with regards to maritime specialisation) and thus for extending our knowledge of brown bear ecology. Conversely, such studies could, in theory, be employed to confirm the presence of polar bears (or indeed polar bear-brown bear hybrids) in NW Europe by direct analysis of the fossils. Furthermore, genetic testing may be useful in the question of the origin of some later archaeological bear specimens. For example, in determining whether they relate to post-LGM populations isolated in Britain after the North Sea breach during the early Holocene, or whether they do indeed represent 'imports' from other areas.

Conclusion

The history of discovery of the remains of bears, *Ursus* spp., in Scotland has resulted in mostly poor information about the contexts in which they were found and the *ad hoc* way they were recovered. Even with planned excavations, such as those of Peach and Horne in 1885 and Cree, Callander and Ritchie in the 1920s, much contextual information was lost, or not recorded, and interpretations of cave deposits were not consistent (Lawson 1982). However, the advent of modern analytical techniques, such as radiocarbon dating, stable isotope analysis, and genetics has allowed us to reveal new information and many new insights into the few palaeontological and archaeological remains that have been found.

In drawing together these multiple lines of enquiry from both recent and historical research efforts, here we have demonstrated that the Creag nan Uamh and Claonoaite Seven caves in Assynt, NW Scotland were an important area for brown bears for at least 50 000 years (albeit non-continuously, i.e. during the Last Glacial Maximum), probably because of access to caves for hibernation and rearing of cubs. However, this may also reflect a bias because of the ideal preservation conditions afforded by the caves of dolomitic limestones in the area (Lawson 1993), but other areas in Scotland may also have been important for foraging because brown bears are adept at digging their own hibernation burrows when required (Shiratsuru *et al*. 2020).

Despite the paucity of finds, radiocarbon dating has confirmed a long fossil history of the brown bear in Scotland from the Late Pleistocene until at least the Bronze Age and this mirrors the dating of remains from the rest of Britain (Yalden 1999, O'Regan 2018). Stable isotope analysis has shown that the diets of bears in the past have ranged from extremely marine-based to almost completely vegetarian, reflecting the changing environment of the Last Glaciation and the availability of habitats and food resources. Intriguingly, our review has opened up the possibility that Late Pleistocene brown bears in Scotland had a unique maritime ecology, which has not been recorded previously amongst extant or fossil bears. However, we are aware that many fossils are only identified firmly to genus, that polar bear may have been present, and that introgression with polar bears may have affected local populations and their foraging preferences. Limited genetic data suggest either a greater diversity of mtDNA haplotypes in the Late Pleistocene or a replacement following deglaciation, and that populations of bears pre- and post-LGM were possibly distinct, and thus may have also had distinct ecological or ecomorphic traits.

In light of the isotope data explored here, further investigations of Late Pleistocene bear palaeoecology in Scotland, coupled with detailed taxonomic assessments, are warranted. The maritime dietary niche highlighted by the pre-LGM (and some post-LGM) specimens may provide tantalising evidence of behaviour not seen in contemporary brown bears. However, given the potential for the occurrence of polar bears during this period, future radiocarbon dating and isotope investigations should ideally be paired with ancient DNA analyses (or advanced geometric

morphometric analysis) for species determinations. Future isotope studies should include other species (such as reindeer, wolf, *Canis lupus*, lynx, *Lynx lynx*, etc. but also marine species such as seals and fishes) to better understand Late Pleistocene and early Holocene isotopic food webs of the region. Finally, investigations could also include $\delta^{34}S$ (sulphur) isotopes, or $^{87}Sr/^{86}Sr$ (strontium), which can be used to explore the mobility of Late Pleistocene fauna (e.g., Britton *et al*. 2023). We recommend that thorough morphological investigation, along with 3D scanning, to create a permanent record of the specimens, should ideally precede any further destructive sampling.

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Appendix. A list of the finds from the Creag nan Uamh Caves, Sutherland collected by Cree, Callander and Ritchie 1926–1927 that have been identified as *Ursus* sp. and *Ursus* cf. *maritimus*. Identifications were made by Nicola Murray (Edinburgh) who compiled this list.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.53	Reindeer Cave (Outer)	Teeth of bear. 29th June 1926. Reindeer cave. From brown cave earth (top layer).	Mandibular tooth	Permanent canine	*Ursus* sp.	R	Root closed	Cave earth
1959.33.54	Reindeer Cave (Inner)	Reindeer Cave (Inner cave). From top layer between lip of chimney and south east wall. 31st July & 2nd August 1926.	Vertebra	Fragment of cervical vertebra	*Ursus* sp.		Fused	Top layer
1959.33.79	Reindeer Cave (Outer)	Reindeer Cave. Gravel deposit in chimney about 6'6" below mouth. Canine and molars of bear. 8th July 1926.	Mandibular tooth	m2	*Ursus* sp.			3rd layer (gravel), shaft, depth of 6'6"
1959.33.80	Reindeer Cave (Outer)	Reindeer Cave. Gravel deposit in chimney about 6'6" below mouth. Canine and molars of bear. 8th July 1926.	Mandibular tooth	m1	*Ursus* sp.	L	Roots are closed	3rd layer (gravel), shaft, depth of 6'6"
1959.33.81	Reindeer Cave (Outer)	Reindeer Cave. Gravel deposit in chimney about 6'6" below mouth. Canine and molars of bear. 8th July 1926.	Mandibular tooth	m1	*Ursus* sp.	R	Roots are broken	3rd layer (gravel), shaft, depth of 6'6"
1959.33.82	Reindeer Cave (Outer)	Reindeer Cave. Gravel deposit in chimney about 6'6" below mouth. Canine and molars of bear. 8th July 1926.	Mandibular tooth	m2	*Ursus* sp.	L		3rd layer (gravel), shaft, depth of 6'6"
1959.33.83	Reindeer Cave (Outer)	Reindeer Cave. Gravel deposit in chimney about 6'6" below mouth. Canine and molars of bear. 8th July 1926.	Mandibular tooth	m2	*Ursus* sp.	L		3rd layer (gravel), shaft, depth of 6'6"

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.84	Reindeer Cave (Outer)	Reindeer Cave. Gravel deposit in chimney about 6'6" below mouth. Canine and molars of bear. 8th July 1926.	Mandibular tooth	m1	*Ursus* sp.	R		3rd layer (gravel), shaft, depth of 6'6"
1959.33.94	Bone Cave	1927. From Bone Cave	Tooth	Fragment of molar	*Ursus* sp.			
1959.33.303	Reindeer Cave (Outer)	No paper label. Bag reads "Reindeer Cave, near mouth of cave between layers."	Maxillary tooth	Incisor with broken crown	*Ursus* sp.	R		
1959.33.304	Reindeer Cave (Outer)	No paper label. Bag reads "Reindeer Cave, near mouth of cave between layers."	Tooth	Fragment of canine crown	*Ursus* sp.			
1959.33.305	Reindeer Cave (Outer)	No paper label. Bag reads "Reindeer Cave, near mouth of cave between layers."	Tooth	Canine crown	*Ursus* sp.			
1959.33.306	Reindeer Cave (Outer)	No paper label. Bag reads "Reindeer Cave, near mouth of cave between layers."	Tooth	m1	*Ursus* sp.		No roots	
1959.33.479	Bone Cave	No paper label. Bag reads "Bone Cave. No. 2 layer (not including peat). 17th June 1927. 18" down."	Mandibular tooth	m2	*Ursus* sp.	R	Worn	2nd layer
1959.33.507	Inchnadamph ?	No label	Metacarpal II	Complete	*Ursus* sp.	R	Proximal end fused	
1959.33.508	Inchnadamph ?	No label	Metatarsal IV	Complete	*Ursus* sp.	R	Proximal end fused	
1959.33.510	Inchnadamph ?	No label	Mandibular tooth	m1	*Ursus* sp.	R		
1959.33.513	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top 18" of deposit close to wall, west side. July 20 and 21, 1927.	Maxillary tooth	Canine	*Ursus* sp.	R		Top 18"
1959.33.514	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top 18" of deposit close to wall, west side. July 20 and 21, 1927.	Maxillary tooth	Canine	*Ursus* sp.	L		Top 18"

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.515	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top 18" of deposit close to wall, west side. July 20 and 21, 1927.	Mandibular tooth	Canine	*Ursus* sp.	L		Top 18"
1959.33.516	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top 18" of deposit close to wall, west side. July 20 and 21, 1927.	Maxillary tooth	Incisor	*Ursus* sp.	R		Top 18"
1959.33.517	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top 18" of deposit close to wall, west side. July 20 and 21, 1927.	Maxillary tooth	Incisor	*Ursus* sp.	L		Top 18"
1959.33.519	Reindeer Cave (Outer)	Reindeer Cave. From 3rd layer (gravel) near bottom of cave. Found 3rd July 1926.	Mandibular tooth	m2	*Ursus* sp.	L		3rd layer (gravel)
1959.33.520	Reindeer Cave (Outer)	Reindeer Cave. From 3rd layer (gravel) near bottom of cave. Found 3rd July 1926.	Maxillary tooth	m1	*Ursus* sp.	R		3rd layer (gravel)
1959.33.600	Bone Cave	Two labels "Bone Cave. Canine from inside cave" & "Bone Cave (3'0" down) No. 3 layer (not including peat of which we found no remains) 15 June 1927."	Mandibular tooth	Canine, in 4 pieces (glued)	*Ursus* sp.	L		3rd layer
1959.33.601	Bone Cave	Jaw from terrace outside cave	Palate and two molar teeth		*Ursus* sp.	L		Outside cave
1959.33.605	Reindeer Cave (Inner)	From Inner Reindeer Cave. August 1927	Atlas	Almost complete, in two pieces	*Ursus* sp.			
1959.33.616	Reindeer Cave (Inner)	Found in top layer 12" about 4'0" from lip of chimney, close to east and west wall of cave. 6 August 1926.	Mandibular tooth	Canine, crown and root cracked	*Ursus* sp.	R		Top layer
1959.33.617	Reindeer Cave (Inner)	Found in top layer 12" about 4'0" from lip of chimney, close to east and west wall of cave. 6 August 1926.	Tooth	Canine, 10+ pieces	*Ursus* sp.			Top layer

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.619	Reindeer Cave (Inner)	From top layer at foot of chimney and about 6'0" towards the west from east wall. 30 July 1926.	Cranium	Maxilla with tooth row from c-m2, p4 present	*Ursus* sp.	L		Top layer
1959.33.620	Reindeer Cave?	Two labels "Inner Cave in top 12". July 1926" & "Reindeer Cave. Portions of bones (fossil) found in gravel and brownish sand in 'chimney' at back of cave 4'0" to 5'0" below mouth. 4 July 1926."	Mandible	Fragment with p3–p4	*Ursus* sp.	L		
1959.33.646	Reindeer Cave (Inner)	Reindeer Cave. Lower Cavern. From top layer about 6'0" from foot of chimney. 8'0" above floor. 21st July 1926.	Maxillary tooth	Incisor	*Ursus* sp.	R		Top layer
1959.33.668	Reindeer Cave (Inner)	Inner lower Reindeer Cave. Left hand side far in (east) on surface.	Ulna	Proximal end, articulation damaged	*Ursus* sp.	R		
1959.33.671	Inchnadamph ?	No label	Cranium	Two matching pieces of maxilla and zygomatic arch. No teeth but several root holes.	*Ursus* sp.	R	Teeth in crypt	
1959.33.722	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top layer between lip of chimney and south east wall of cave. 31st July and 2nd August 1926.	Cranium	Fragment	*Ursus* sp.			Top layer
1959.33.742	Bone Cave	From small terrace outside Bone Cave approximately 12'0" from cave entrance. Depth about 15". 7 and 8 June 1927.	Mandibular tooth	Premolar	*Ursus* sp.			Terrace
1959.33.767	Reindeer Cave (Inner)	Bone Cave. July 1927.	Rib	Rib fragment	*Ursus* sp.			

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.769	Bone Cave	1927. Bone Cave. From 2nd layer "gravel above clay".	Mandibular tooth	m1	*Ursus* sp.	R	Very heavily worn	2nd layer (gravel above clay)
1959.33.773	Bone Cave	Bone Cave	Maxillary tooth	m2	*Ursus* sp.	L		
1959.33.807	Inchnadamph ?	Box labelled "Bones found in cave. Dr Horne. Royal Soc. Edin." Paper label reads "may be wanted for figure".	Maxillary tooth	Canine	*Ursus* sp.	R	Roots closed	
1959.33.814	Reindeer Cave (Inner)	Bone labelled "Young bear. Uncut permanent dentition. Inner Cave".	Mandible	Complete, no teeth present, m1 and m2 in crypt.	*Ursus* sp.	R	m1 and m2 in crypt	
1959.33.846	Reindeer Cave (Inner)	No paper label. Bag reads "Reindeer Cave (Inner Cavern). From top layer about 8'0" back from lip of chimney. 3rd and 4th August 1926."	Ulna	Complete	*Ursus* sp.	L	Proximal end unfused	
1959.33.1061	Reindeer Cave (Outer)	Reindeer cave. From shaft at back of cave 5'0" to 6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1064	Reindeer Cave (Outer)	Reindeer cave. From shaft at back of cave 5'0" to 6'6" below the mouth. 8th July 1926.	Mandible	Fragment	*Ursus* sp.	L		3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1065	Reindeer Cave (Outer)	Reindeer cave. From shaft at back of cave 5'0" to 6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1067	Reindeer Cave (Outer)	Reindeer cave. From shaft at back of cave 5'0" to 6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1068	Reindeer Cave (Outer)	Reindeer cave. From shaft at back of cave 5'0" to 6'6" below the mouth. 8th July 1926.	Cranium	Maxilla, with tooth row C-P4	*Ursus* sp.	R		3rd layer (gravel), shaft, depth of 5'0" to 6'6"

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.1069	Reindeer Cave (Outer)	Reindeer cave. From shaft at back of cave 5'0" to 6'6" below the mouth. 8th July 1926.	Vertebra	Dorsal fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1070	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragments	25 fragments	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1071	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Radial carpal bone	Almost complete	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1072	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1073	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Radius	Proximal end	*Ursus* sp.	R	Proximal end fused	3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1074	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1076	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Metapodial	Distal end, fits with specimen 1084	*Ursus* sp.		Distal end unfused	3rd layer (gravel), shaft, depth of 5'0" to 6'6"

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.1077	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1078	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Scapula	Distal end	*Ursus* sp.	L		3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1079	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragment	One bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1080	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Middle phalanx	Complete	*Ursus* sp.		Proximal end fused	3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1081	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Cranium	Fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1082	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Rib	Fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1083	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragment	1 bone fragment	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.1084	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Metatarsal III	Proximal end, fits with specimen 1076	*Ursus* sp.	L		3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1085	Reindeer Cave (Outer)	Reindeer Cave. 82 burrs from sand mixed with some gravel found in chimney 5'0"–6'6" below the mouth. 8th July 1926.	Fragments	25 bone fragments	*Ursus* sp.			3rd layer (gravel), shaft, depth of 5'0" to 6'6"
1959.33.1146	Reindeer Cave (Outer)	Bones found on surface within Cave 2 adjoining Bone Cave by Jas. Cree. Summer 1925.	Tooth	Incisor	*Ursus* sp.	R		
1959.33.1293	Foxes' Den	Cave No. 4. Foxes Den. Bone found about 2'4" below surface in undisturbed layer of whitish-grey clay, containing many splinters of limestone. Cave earth 8" thick on top. 1'6" outside mouth of cave. 1927.	Rib	Almost complete	*Ursus* sp.	R		Clay
1959.33.1330	Reindeer Cave (Inner)	1927. August. From Inner Reindeer Cave.	Cranium	Maxilla with m1 in crypt	*Ursus* sp.	R	m1 in crypt	
1959.33.1370	Reindeer Cave (Outer)	Reindeer Cave. From 3rd layer (gravel). 28th June 1926.	Astragalus	Complete	*Ursus* sp.	L		3rd layer (gravel)
1959.33.1371	Reindeer Cave (Inner)	E. Fragment of bear jaw, found in top layer of glacial silt almost filling Inner Cave, 6 ft. distant from chimney access. July 1927.	Cranium	Fragment of maxilla	*Ursus* sp.			Top layer
1959.33.1385	Inchnadamph ?	No label	Metatarsal III	Complete	*Ursus* sp.	R	Distal end fused	
1959.33.1398	Inchnadamph ?	No label	Fragments	Five bone fragments	*Ursus* sp.			

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.1400	Inchnadamph ?	No label	Metatarsal IV	Proximal end, pair of specimen 1401	*Ursus* sp.	L		
1959.33.1401	Inchnadamph ?	No label	Metatarsal IV	Distal end, pair of specimen 1400	*Ursus* sp.	L	Distal end fused	
1959.33.1403	Inchnadamph ?	No label	Metapodial	Distal end and diaphysis	*Ursus* sp.		Distal end fused	
1959.33.1405	Inchnadamph ?	No label	Metapodial	Distal end	*Ursus* sp.		Distal end fused	
1959.33.1407	Inchnadamph ?	No label	Rib	1 rib fragment	*Ursus* sp.			
1959.33.1449	Reindeer Cave (Outer)	Reindeer Cave. Portions of antlers and bones. From 3rd layer (gravel). 3rd July 1926.	Mandible	Fragment, with no teeth	*Ursus* sp.	L	Tooth crypt indicates eruption	3rd layer (gravel)
1959.33.1477	Reindeer Cave (Outer)	Reindeer Cave. From “shaft” at back of cave. 4’0” to 5’0” below the mouth. 7th July 1926.	Metapodial	Distal end	*Ursus* sp.		Distal end fused	3rd layer (gravel), shaft, depth of 4’0” to 5’0”
1959.33.1481	Reindeer Cave (Outer)	Reindeer Cave. Portions of antler and some bones from gravel on east side opposite natural pillar 18th & 19th August 1926.	Metacarpal IV	Almost complete	*Ursus* sp.	L	Distal end unfused	3rd layer (gravel)
1959.33.1486	Reindeer Cave (Outer)	Reindeer Cave. Portions of antler and some bones from gravel on east side opposite natural pillar 18th & 19th August 1926.	Vertebra	Fragment	*Ursus* sp.			3rd layer (gravel)
1959.33.1582	Reindeer Cave (Outer)	Reindeer Cave. From 3rd layer (gravel). All found on 28th June 1926.	Metatarsal I	Complete	*Ursus* sp.	L	Distal end fused	3rd layer (gravel)
1959.33.1599	Reindeer Cave (Outer)	Reindeer Cave. From shaft at back of cave 4’0” to 5’0” below the moth. 7th July 1926.	Ulna	Fragment of diaphysis with articulation	*Ursus* sp.	R		3rd layer (gravel), shaft, depth of 4’0” to 5’0”
1959.33.1600	Reindeer Cave (Outer)	Reindeer Cave. From shaft at back of cave 4’0” to 5’0” below the moth. 7th July 1926.	Femur	Fragment of diaphysis	*Ursus* sp.	R		3rd layer (gravel), shaft, depth of 4’0” to 5’0”

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.1601	Reindeer Cave (Outer)	Reindeer Cave. From shaft at back of cave 4'0" to 5'0" below the moth. 7th July 1926.	Fragment	Fragment of diaphysis	*Ursus* sp.			3rd layer (gravel), shaft, depth of 4'0" to 5'0"
1959.33.1602	Reindeer Cave (Outer)	Reindeer Cave. From shaft at back of cave 4'0" to 5'0" below the moth. 7th July 1926.	Fragment	Fragment of diaphysis	*Ursus* sp.			3rd layer (gravel), shaft, depth of 4'0" to 5'0"
1959.33.2118	Reindeer Cave (Outer)	Reindeer Cave. From 2nd? layer (red cave earth). 2 reindeer teeth. 1 bear incisor?. 1 human. 1 limpet. 3 pcs charcoal. 2nd July 1926.	Mandibular tooth	Incisor	*Ursus* sp.	L	Very worn	
1959.33.2119	Reindeer Cave (Outer)	Reindeer Cave. From 2nd? layer (red cave earth). 2 reindeer teeth. 1 bear incisor?. 1 human. 1 limpet. 3 pcs charcoal. 2nd July 1926.	Mandibular tooth	m1	*Ursus* sp.	L	Very worn	
1959.33.2120	Reindeer Cave (Outer)	Reindeer Cave. From 2nd? layer (red cave earth). 2 reindeer teeth. 1 bear incisor?. 1 human. 1 limpet. 3 pcs charcoal. 2nd July 1926.	Mandibular tooth	m1	*Ursus* sp.	L	Roots open	
1959.33.2122	Bone Cave	Bone Cave (east side). 1919–1934. July 1927.	Carpal bone III	Complete	*Ursus* sp.	R		
1959.33.2283	Tunnel between Bone Cave and Reindeer Cave	1927. From Bone Cave above tunnel running east from chimney.	Rib	Fragment	*Ursus* sp.			
1959.33.2370	Bone Cave	1927. From Bone Cave.	Metapodial	Complete, proximal end damaged	*Ursus* sp.		Distal end fused	
1959.33.2383	Tunnel between Bone Cave and Reindeer Cave	1927. July. From cave earth in tunnel between Bone Cave and Reindeer Cave (south side).	Metatarsal V	Proximal end	*Ursus* sp.	R		Cave earth in tunnel
1959.33.2489	Reindeer Cave (Outer)	Reindeer Cave. June, July, August 1926.	Cranium	Occipital condyle	*Ursus* sp.	R		

continued

Appendix. Continued.

Specimen NMS.Z.	Site	Label	Element	Part	Species	Side	Age data	Context
1959.33.2490	Reindeer Cave (Outer)	Reindeer Cave. June, July, August 1926.	Cranium	12 skull fragments	*Ursus* sp.			
1959.33.2584	Reindeer Cave (Outer)	Reindeer Cave. June, July, August 1926.	Cranium	Fragment	*Ursus* sp.			
1959.33.2585	Reindeer Cave (Outer)	Reindeer Cave. June, July, August 1926.	Cranium	Fragment	*Ursus* sp.			
1959.33.2619	Reindeer Cave (Outer)	Reindeer Cave. From 3rd layer (gravel) in depression on east side of cave. Entrance to communicating passage with Bone Cave. 12 burrs and portions of antlers. 11th August 1926.	Rib	Almost complete	*Ursus* sp.			3rd layer (gravel)
1959.33.2626	Reindeer Cave (Inner)	Reindeer Cave (Inner Cavern). 2 burrs and bones from top layer (12 inches) east of lip of chimney. 6th August 1926.	Vertebra	Fragment of thoracic vertebra	*Ursus* sp.			Top layer
1959.33.2689	Reindeer Cave (Outer)	Reindeer Cave. June, July, August 1926.	Tooth	Fragment of canine, in two pieces	*Ursus* sp.			
1959.33.2731	Reindeer Cave (Inner)	Reindeer Cave (Inner). From top layer about 30'0" from lip of chimney. 26th July 1926.	Crania	57 cranial fragments	*Ursus* sp.			
1959.33.2748	Reindeer Cave (Outer)	Teeth of bear. 29th June 1926. Reindeer cave. From brown cave earth (top layer).	Tooth	Canine, hollow crown	*Ursus* sp.		Hollow crown, no root	Cave earth
1959.33.2749	Reindeer Cave (Outer)	Teeth of bear. 29th June 1926. Reindeer cave. From brown cave earth (top layer).	Tooth	Canine, hollow crown	*Ursus* sp.		Hollow crown, no root	Cave earth
1959.33.2777	Reindeer Cave (Inner)	Reindeer Cave. Cave 2A.	Cranium	Incomplete	*Ursus* cf. *maritimus*			18" of deposit