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ORIGINAL PAPER

Late Holocene occupation of Gentoo Penguins (*Pygoscelis papua*) on Byers Peninsula, Livingston Island, Antarctica

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Abstract We report excavations of an abandoned penguin colony on Byers Peninsula, Livingston Island, Antarctica, in austral summer 2008/2009. Nine abandoned pebble mounds were located on Devils Point, near an active Gentoo Penguin (*Pygoscelis papua*) colony of about 3,000 nests, at an elevation of 40–45 m above sea level. Three of the nine mounds were excavated to recover organic remains for radiocarbon and ancient DNA analyses; two additional mounds were probed to obtain tissue samples for additional dating. All radiocarbon dates were corrected for the marine-carbon reservoir effect using a ΔR of 700 ± 50 years. Calibrated 2-sigma ranges in calendar years before present (B.P.) on 23 samples of egg membrane and bone provided an overall range of 40–1,150 B.P., with most of the dates falling between 225 and 465 B.P. Ancient DNA analysis confirmed that the tissues recovered from these excavations represent Gentoo Penguin. One radiocarbon date from the active Gentoo Penguin colony indicated an age of 285–480 B.P. for the initiation of this current occupation and corresponding in age with most of the abandoned mounds. Although geologic evidence indicates that Byers Peninsula has been ice free for at least 3,000 years, these results indicate that penguin occupation lagged behind deglaciation by over 2,000 years. Small numbers of Chinstrap Penguins (*P. antarctica*) also occupy the same breeding colonies as Gentoo Penguins at Byers Peninsula, but their absence in the ancient sediments suggests that they have only recently colonized this area.

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Introduction

Byers Peninsula, Livingston Island (62°38′S, 61°05′N), is an extensive ice-free area of approximately 60 km^2 located on the west end of the island (Fig. 1). It is one of the largest ice-free areas in the Antarctic Peninsula and is well known for its numerous polar lakes (Björck et al. 1991, 1996; Quesada et al. 2009), complex geology and paleontology, and historic archaeological sites dating to the whaling and sealing era (Pearson et al. 2010). It was first recognized for its diverse fauna and flora and then later for its paleontological and geological resources, producing fossils that provide evidence for a link between Antarctica and other continents in the southern hemisphere. Research began in this region in the 1950s and has continued since that time, most recently by the Spanish Polar Program. For these reasons, Byers Peninsula was originally designated as Specially Protected Area (SPA) No. 10 in 1966, with additions and modifications to this designation in 1975 (when it became a Site of Special Scientific Interest or SSSI 6) and 1991. It currently is recognized as Antarctic SPA 126 (SCAR 2003).

Geologic evidence indicates that Byers Peninsula has been ice free since at least 3,000 years before present (B.P.). Cores from ten lakes were used to develop a deglaciation chronology of the peninsula by Björck et al. (1991, 1996). Bottom sediments indicated that some of these lakes were ice free by 5000 B.P., while others were not ice free until 3500–4000 B.P. Thus, these authors conclude that Byers Peninsula was largely ice free by 3000

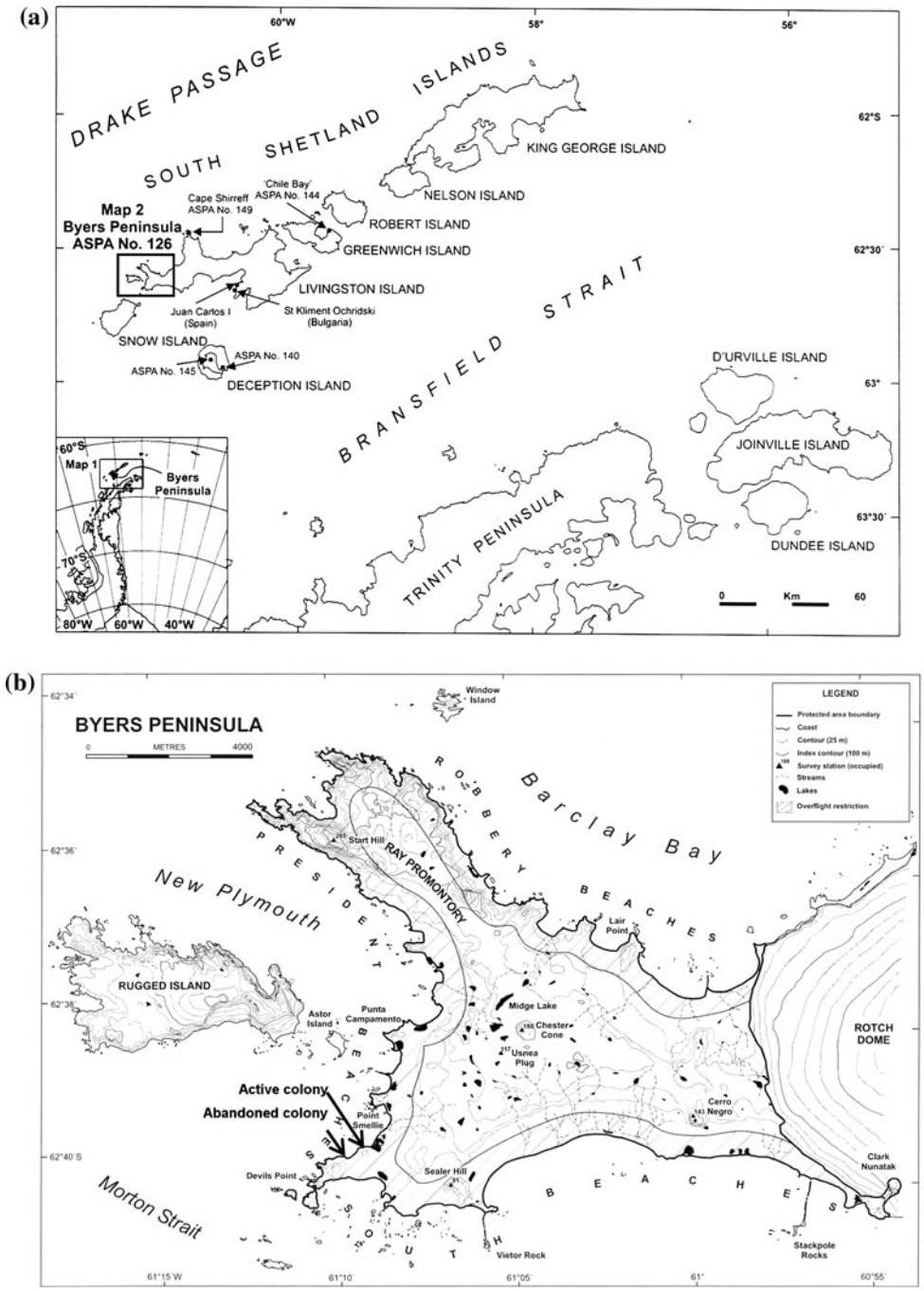

Fig. 1 **a** Location of Byers Peninsula, Livingston Island (in *open square*), and within the Antarctic Peninsula (*inset*, *lower left*). **b** Detailed view of Byers Peninsula showing the location of the active and abandoned Gentoo Penguin colonies at Devils Point. An additional active colony is located at Lair Point on the north side of the peninsula

B.P. though deglaciation is known to have occurred much earlier, by at least 6000 B.P., in other parts of the peninsula (Ingólfsson et al. 2003). The later deglaciation at Byers agrees with other data in the Antarctic Peninsula that indicate a warming trend between 3000 and 4000 B.P. (Ingólfsson et al. 1998, 2003).

The Spanish Polar Program has been operating a base camp at Byers Peninsula since 2000 with a research focus on non-marine aquatic ecosystems. In austral summer 2008/2009, the Spanish program was expanded to include multinational teams of scientists to conduct research at their camp as part of the International Polar Year. To this end, the senior author visited the Spanish camp from 9 to 19 January 2009 to conduct surveys for abandoned penguin colonies and investigate the occupation history of pygoscelid penguins at Byers Peninsula.

Materials and methods

Survey and excavations

In January 2009, the senior author surveyed on foot numerous beaches and terraces on the south side of the peninsula, from Cerro Negro to Devils Point, the west side from Devils Point to Punta Campamento, and the north side of the peninsula from Lair Point to approximately 3 km to the east (Fig. 1b). Only two areas were found with active penguin colonies. The largest is a Gentoo Penguin colony on the north side of Devils Point comprised of approximately 3,000 nests divided two subcolonies with one on the beach and the other on a marine terrace above the beach at an elevation of 40–45 m above present sea level. A small number of Chinstrap Penguin nests (~50) were noted in the middle of the lower beach colony of Gentoo Penguins (Andres Barbosa, personal communication). A second active penguin colony of approximately 1,200 Gentoo and 20 Chinstrap Penguin nests was located at Lair Point on the north side of the peninsula.

Extensive surveys of beaches and terraces produced only one area where an abandoned penguin colony was located. This colony is comprised of a series of nine pebble mounds positioned along the north edge of the marine terrace and west of the upper Gentoo Penguin subcolony at Devils Point. These mounds vary in size from 3 to 5 m in diameter and are covered with grass, lichens, and moss indicating abandonment in the past (Fig. 2). Three of these mounds were sampled by placing a 1 × 1 or 1 × 0.5 m pit at the top of the mound and excavating in 5-cm levels to the bottom of the ornithogenic sediments as recognized by a distinct change in soil color and texture. Surface vegetation was carefully removed and saved for replacement at the end of the excavation when the pits were backfilled. All sediments were screened through 0.64- and 0.32-cm^2-mesh screens to recover all organic remains. Sediments in the top screen were sorted in the field to recover any organic material (bone, feather, eggshell). All sediments in the lower screen were saved for additional screen washing in the laboratory. A subsample (1–2 l) of the finer sediments that passed through these two screens also was saved for screen washing in the laboratory. At the end of excavations, all sites were backfilled with rocks and any remaining sediments and the surface vegetation replaced.

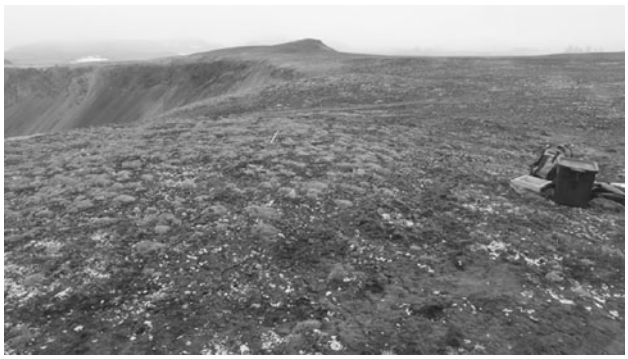

Fig. 2 View, looking east, of abandoned mounds with mound 2 in foreground, before excavation. The next two mounds beyond mound 2 are where probe samples 1 and 2 were collected, respectively. Mound 1 is located approximately 35 m behind the photographer. The active Gentoo Penguin colony is in the far left background on the same level of marine terrace as the mounds

In addition to these excavations, small test holes or probes were excavated in two other mounds to extract additional organic remains for radiocarbon dating. Probe 1 was placed in the first mound east of mound 2 with organic remains (eggshell membrane) recovered from two levels at 0–10 and 10–20 cm in depth. Probe 2 was placed in the largest mound in the colony, the sixth from the east end. Eggshell membrane, feather, and bone fragments were recovered in this probe at depths of 16, 20, and 40–50 cm. A small section of an eroded exposure on the side of one of the active mounds in the upper subcolony, near the abandoned mounds, was fully exposed with a shovel and sampled.

Radiocarbon and ancient DNA analyses

All material for radiocarbon dating was submitted to the University of California, Irvine, Keck Radiocarbon AMS Facility (UCIAMS) for accelerator mass spectrometry (AMS) dating. Each sample was assigned a UCIAMS number. Resulting dates (in radiocarbon years B.P.) were corrected for the marine-carbon reservoir effect using CALIB 5.0.1 with a $\Delta R = 700 \pm 50$ years (see Emslie 2001) and the MARINE04 database (Hughen et al. 2004, Stuiver et al. 2005). Calibrated 2σ range(s) that yield a 95% confidence interval for each date are given in calendar years B.P. All penguin dates discussed in the text refer to these calibrated ages.

Strict ancient DNA procedures were followed to prevent contamination. All DNA extractions took place in a sterile ancient DNA laboratory lacking any previous contact with avian material. Entrance and exit to this laboratory was controlled and minimized, counters were cleaned with bleach and equipment treated with UV light, and controls were run alongside each extraction step. Pre-PCR procedures were performed in a designated hood to prevent contamination, while PCR was executed on a different floor and post-PCR procedures were performed in a separate building. Prior to DNA extraction, eggshell membrane or feather material was rinsed twice with 500 µl of 1× PBS for 15 min each. Upon discarding the solution, samples were cut into small pieces and placed in a tube with 275 µl of extraction buffer (0.5 M EDTA, 10% SDS and 40 µl of

10 μg/ml Proteinase K). Samples were incubated and agitated at 55°C for 48 h.

DNA was extracted following the Qiaquick PCR clean-up protocol. Three sets of primer pairs were designed to assist in genetic species diagnosis. From the DNA extracts, informative 150–175 base pair fragments were amplified from the mitochondrial genes cytochrome oxidase I (BC) and cytochrome b (cytb) using the following primer pairs (5′–3′): GACCAAATYTACAACGTAATCG (BC154-F) and GGTAGYAGTCAGAAGCTTATG (BC320-R); GAA ACACAGGCATCATCCTC (cytb340-F) and CAGGCY CATTCTACGAGGGTTTG (cytb490-R); as well as CCA GAAAACTTYACCCCAGC (cytb757-F) and GATTAGG AATAGGAYTAGTACGG (cytb915-R). Amplified samples were cleaned following the EXO-SAP-IT protocol and submitted to Macrogen, Inc., (Seoul, Korea) for sequencing. DNA sequences were cleaned using Sequencher (version 4.8) and diagnosed to species using the BLAST engine in GenBank (version 2.2.22).

Results

Three abandoned mounds were excavated and designated mounds 1, 2, and 3. Mound 1 is at the west end of the abandoned colony, farthest from the active colony, and appeared to be the oldest based on the greater amount of vegetation (grass and moss) on its surface. However, the excavation of a 1 × 1 m pit revealed that this mound was very shallow as only one 5-cm level was excavated before reaching the bottom of ornithogenic sediments. Eggshell membrane and feather fragments were recovered, but no bone. Mound 2 was located to the east of mound 1 and had an inactive Giant Petrel (*Macronectes giganteus*) nest on its north edge and on the edge of the marine terrace. Here, a 1 × 0.5 m pit was established and excavated in four levels to the bottom of the ornithogenic sediments. Eggshell membrane and feather fragments were recovered from all levels, with small pieces of bone also found in levels 1 and 3. Mound 3 is the second mound from the east end and the largest of all the abandoned mounds. A 1 × 0.5 m pit was placed on the top center of this mound and excavated to level 8 before reaching the bottom of the ornithogenic sediments (Fig. 3). The organic remains from each level were dominated by eggshell membrane and feather fragments, with some bone fragments in level 1 and a broken penguin femur in level 7.

The exposure in the active colony revealed two layers of occupation to a depth of 22 cm below surface. The first or more recent occupation layer consists of 1–2 cm of black guano and organic debris with lighter brown ornithogenic sediments below to a depth of 13 cm below surface. A layer of reddish sand below this, to a depth of 18 cm below surface, is not ornithogenic and may represent a break in the penguin occupation of the site. From 18 to 22 cm, there is another layer of light brown to gray ornithogenic sediments before more reddish sands were encountered that are over 20 cm in depth with no further occupation levels below. Two sediment samples were collected from the top and lower ornithogenic layers. The active colony at Lair Point also was probed in several areas but was found to be very shallow (only 1–2 cm of guano with no soil development), and no samples were collected at this location.

Fig. 3 Stratigraphic profile of mound 3 showing the depth of the ornithogenic sediments at this site. A clear break in soil texture is visible at the bottom of the pit where natural terrace sediments are exposed

These excavations and subsequent screen washing of sediments in the laboratory recovered hundreds of tissue samples, primarily eggshell membrane and feather fragments. Very little bone was encountered in the sites, with only a few small fragments recovered. Thus, bone could not be used to identify the species of penguin that formerly occupied this site. Eggshell membrane and feathers, however, were abundant and well preserved and therefore used for most radiocarbon and ancient DNA analyses.

A total of 26 samples of eggshell membrane, feather, and bone were submitted for radiocarbon analysis, of which 23 produced dates (Table 1). These samples included six from levels 2–5 of mound 2, 16 from levels 1–8 of mound 3, and three from the top and lower layers (0–10 and 10–20 cm depth) of probe 1. One sample also was submitted from the lower gray ornithogenic layer in the active colony. Four of the radiocarbon samples from

Table 1 Radiocarbon dates (in years B.P.) on penguin (*Pygoscelis* sp.) tissue from three pebble mounds at an abandoned colony and one from an active Gentoo Penguin colony on Byers Peninsula, Livingston Island, Antarctica

UCIAMS No.	Site/Provenience	Material	Radiocarbon age	Calibrated range
59978	M2 Level 2, 5–10 cm	Egg membrane	1225 ± 20	260–40
59993	M2 Level 3, 10–15 cm	Feather	1285 ± 15	330–50
59979	M2 Level 4, 15–20 cm	Egg membrane	1320 ± 20	415–115
59994	M2 Level 4, 15–20 cm	Feather	1420 ± 15	465–270
59995	M2 Level 5, 20–25 cm	Feather	2175 ± 15	1155–915
59996	M2 Level 5, 20–25 cm	Feather	1690 ± 20	655–500
59997	M3 Level 1, 0–5 cm	Feather	1290 ± 15	360–60
59980	*M3 Level 2, 5–10 cm	Egg membrane	1235 ± 15	270–45
68272	M3 Level 2, 5–10 cm	Egg membrane	1260 ± 15	295–50
9981	M3 Level 3, 10–15 cm	Egg membrane	1260 ± 15	295–50
59982	M3 Level 4, 15–20 cm	Egg membrane	1290 ± 20	360–60
68273	M3 Level 4, 15–20 cm	Egg membrane	1365 ± 15	160–150
				215–190
				450–220
59998	*M3 Level 5, 20–25 cm	Feather	1280 ± 20	325–50
59985	M3 Level 6, 25–30 cm	Bone	1410 ± 20	465–265
59999	M3 Level 7, 30–35 cm	Feather	1370 ± 15	160–150
				210–200
				455–225
59986	*M3 Level 7, 30–35 cm	Bone	1370 ± 15	160–150
				210–200
				455–225
59987	*M3 Level 8, 35–40 cm	Bone	1450 ± 15	480–290
60000	M3 Level 8, 30–35 cm	Feather	1565 ± 20	605–390
60001	M3 Level 8, 30–35 cm	Feather	1545 ± 20	345–335
				550–350
60003	Probe 1, 0–10 cm	Feather	1170 ± 15	230–0
59988	Probe 1, 0–10 cm	Bone	1150 ± 20	230–160
60002	Probe 1, 10–20 cm	Feather	1295 ± 20	375–65
75932	Upper subcolony, lower gray layer	Feather	1445 ± 20	480–285

Laboratory number is assigned by the University of California, Irvine, Keck Radiocarbon AMS Facility (UCIAMS). Site number and stratigraphic position for each date are provided with depth of each level below modern ground surface; M refers to mound. Conventional radiocarbon age is given in radiocarbon years B.P., and calibrated 2σ range(s) are in calendar years B.P. Multiple ranges are provided for corrected dates that intersected two or more regions on the calibration curve. An asterisk (*) indicates those samples that were split in half for ancient DNA analysis

Table 2 Samples of eggshell membrane and feather shafts that were positively diagnosed as Gentoo Penguin by ancient DNA

Site (Tissue)	Level	Gene used
Probe 1 (feather shaft)	Level 1, 0–10 cm	Cytochrome oxidase I
M2 (egg membrane)	Level 4, 15–20 cm	Cytochrome oxidase I
M3 (egg membrane)	*Level 2, 5–10 cm	Cytochrome b
M3 (egg membrane)	*Level 5, 20–25 cm	Cytochrome oxidase I
M3 (egg membrane)	Level 6, 25–30 cm	Cytochrome oxidase I
M3 (egg membrane)	*Level 7, 30–35 cm	Cytochrome b
M3 (egg membrane, $n = 3$)	*Level 8, 35–40 cm	Cytochrome b

All samples are based on one tissue extraction except as noted. An asterisk (*) indicates samples that were split in half for radiocarbon analysis, but only one (M3 Level 2) produced a date

mound 3 were large enough to split in half and use for ancient DNA extraction as well, but only one produced sufficient material for a date (Table 2). Most of the dates from the abandoned mounds indicate a relatively recent occupation of this colony by breeding penguins. These dates indicate occupation of Byers Peninsula by breeding penguins perhaps as early as 1100 B.P., but the occupation seems to have been well established by 400–500 B.P.

Occupation since that time appears to have been continuous to the present, though the size of the population did not change substantially.

A total of 31 DNA extractions were completed on 19 feather and egg membrane samples, of which 12 were subjected to two separate extractions. Ten extractions did not yield a successful amplification, but ancient DNA was successfully extracted from nine feather and eggshell membranes from five abandoned mounds; the samples also came from various stratigraphic levels (Table 2). Nine samples (47% amplification success) provided good sequences with generally >1 successful amplification per source, for a total of 24 DNA sequences. Amplification in the control tubes was never observed. Six samples (12 sequences, two per sample) were sequenced for the cytochrome oxidase I fragment. From this marker, two samples yielded human contamination, one sample was positively identified as Gentoo Penguin, and three PCR products contained a mixture of both human and Gentoo Penguin DNA. The remaining samples were used to sequence the cytochrome b fragments. Of these, five samples (ten sequences) were positively identified as Gentoo Penguin based on the cytochrome B gene. Overall, although some contamination was present, none of the samples yielded sequences that were identifiable as Adélie (*Pygoscelis adeliae*) or Chinstrap Penguins.

Discussion

Most research on abandoned penguin colonies has focused on the Adélie Penguin as it is the most abundant species in Antarctica with the most extensive fossil record (Emslie et al. 2007). This species also is found exclusively in Antarctica and thus is an excellent indicator of changes in climate and the marine environment in this region (Ainley 2002). Gentoo Penguins are less well known for their occupation history and are more sub-Antarctic in distribution with the most southern extent of its range in the Antarctic Peninsula (Williams 1995). In recent decades, this species has increased in numbers and extended its range to the south, now breeding as far south as Palmer Station, Anvers Island (Smith et al. 1999, McClintock et al. 2008). Previous investigations into abandoned penguin colonies at Palmer Station revealed an occupation record extending to 600–700 B.P., but only for Adélie Penguins (Emslie et al. 1998). Gentoo Penguins first occupied Palmer Station in 1994, apparently for the first time in at least the past 700 years, indicating that the southward expansion by this species is a recent event.

Only two other abandoned Gentoo Penguin colonies have been investigated prior to now, Copa Sites 1 and 3 in Admiralty Bay, King George Island, Antarctic Peninsula (Emslie et al. 2003). These sites also were relatively young when first occupied, with Site 1 slightly older at less than 600 B.P. and Site 3 at less than 500 B.P. The site at Byers Peninsula is now the oldest known Gentoo Penguin colony in Antarctica, but still relatively young at less than 1100 B.P. These young occupation ages reflect a general trend for all three pygoscelid penguins in the northern Antarctic Peninsula. To date, no older abandoned colonies have been found in this region, though more ancient sedimentary deposits containing penguin remains have been reported.

Older penguin deposits have been reported from raised beaches, terraces, and lake deposits at King George Island, indicating that pygoscelid penguins have been in this region as early as the mid-Holocene (Tatur 1989, Sun et al. 2000; del Valle et al. 2002; Wang et al. 2007). Tatur (1989) reported buried deposits of penguin bones on Penguin Ridge, Thomas Point. His Trench X, 45 m above sea level, produced two buried layers (levels 3–5) over 1 m deep with penguin bones identified as Adélie and Chinstrap Penguin mixed with gravel, sand, and silts. While the bones were too mineralized for radiocarbon dating, a peat deposit above these layers at 40–50 cm depth provided an age of 4950 ± 50 B.P. at the base of the peat (Birkenmajer et al. 1985). Thermoluminescence dating of sands covering the bones supports this age (A. Tatur, personal communication). If correct, this would represent one of the earliest dates of pygoscelid occupation in the northern Antarctic Peninsula. Also on King George Island, del Valle et al. (2002) report buried layers of penguin and other bird remains in raised beach deposits at Potter Peninsula. Most of the bones were identified as Adélie Penguin, with some Gentoo Penguin as well. Radiocarbon dates placed these remains in the mid-Holocene, or 4450–4540 B.P. On Ardley Island, Maxwell Bay, Sun et al. (2000, 2004) and Wang et al. (2007) report lake and sediment cores with penguin guano (based on geochemical composition) dating to 3000 B.P. Fluctuations in bio-elements in these cores revealed that penguin populations (based on guano impact on the sediments) fluctuated through time, with the lowest populations levels from 1800 to 2300 B.P. and highest at 1400–1800 B.P. Finally, Zale (1994) also studied biochemical composition of penguin-impacted lake sediments near an active Adélie Penguin colony at Lake Boeckella, Hope Bay, to hypothesize that this area has been occupied by breeding penguins since 5550 B.P.

Ancient penguin DNA was first successfully sequenced from Adélie Penguin bones in Antarctica by Lambert et al. (2002) to investigate rates of mitochondrial evolution in this species over the past 6,000 years. Emslie et al. (2003) used ancient DNA methodology to positively identify pygoscelid species that occupied abandoned colonies in Admiralty Bay, King George Island, using bone fragments recovered from excavations at five of these sites. This

research was followed by that of Shepherd et al. (2005) who used ancient microsatellite DNA, also from Adélie Penguin bones, to determine microevolutionary change in Antarctica at one location over 6,000 years. Subramanian et al. (2009) used mitochondrial genomes to investigate microevolutionary rates in Adélie Penguins from bones dating as old as 44,000 years.

Our results add new information to the occupation history of Gentoo Penguins in the Antarctic Peninsula. These data so far indicate that this species did not expand into the peninsula from northern sub-Antarctic regions until the late Holocene, or within the past 1,100 years, even though suitable habitat existed in locations such as Byers Peninsula by 3000 B.P. This record also indicates an over 2000-year lag after deglaciation of Byers Peninsula before penguins moved into this region. Geochemical analysis of soils at Barton Peninsula, King George Island, indicates rapid expansion of the Gentoo Penguin colony there over the past 60 years (Zhu et al. 2005). Expansion by Gentoo Penguins as far south as Palmer Station, Anvers Island, occurred only within the past 20 years, perhaps in response to warming trends that are especially impacting the Antarctic Peninsula (McClintock et al. 2008). Data from geological deposits demonstrate that Adélie and Chinstrap Penguins were present in the Antarctic Peninsula by the mid-Holocene. Thus, it appears that Gentoo Penguins were relatively late in colonizing the Antarctic Peninsula from sub-Antarctic regions. This hypothesis can be tested with additional sampling of fossil and sub-fossil penguin deposits in the Antarctic Peninsula.

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