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New Holocene penguin assemblages at South Shetland Islands, Antarctica

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With 2 figures and 1 table

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Abstract: Early Holocene penguin assemblages were exhumed at three localities (Pingfo I, Pingfo II and Pingüi) on the coast of Potter Peninsula, King George Island, South Shetland Islands, Antarctica. The role of taphonomic processes in the preservation of these remains was evaluate in a taphonomic approach, also, the properties of penguin bones were discussed, and available data were compared with those of modern biotic communities and similar deposits from Patagonia and Antarctica. The 606 collected bones were analyzed and assigned mostly to *Pygoscelis* (Adelie Penguin *P. adeliae* and Gentoo Penguin *P. papua*). The high percentage of chick remains at Pingfo I and Pingüi suggests the presence of nearby breeding colonies, whereas Pingfo II represents an assemblage not so close to a breeding area, based on its preservation style.

Key words: subfossil penguins, *Pygoscelis adeliae, Pygoscelis papua*, Holocene, Antarctica.

1. Introduction

Three different subfossil seabird assemblages dominated by penguins (Aves, Spheniscidae) were found in Holocene raised beach deposits on the coast of Potter Peninsula, King George Island (Isla 25 de Mayo, 62°14' S, 58°38' W), South Shetland Islands, Antarctica. Currently, three penguin species breed in this peninsula (see Fig. 1): the Adelie Penguin *Pygoscelis adeliae*, the Gentoo Penguin *P. papua* and the Chinstrap Penguin *P. antarctica*, constituting large colonies near to the beaches (Aguirre 1995; Hahn et al. 1998). Penguin accumulations are peculiar, due to their extremely modified skeleton. Fortunately, the anatomical structure of penguins is very resistant and consists basically of flattened wing bones and a short tarsometatarsus with partially fused metatarsals. Their colonial habits, which result in large bone accumulations, are also advantageous for the preservation of penguin remains. Combined with their particular bone structure, these factors make penguins the best-preserved birds in the fossil record of South America (Acosta Hospitaleche 2004) and Antarctica (Myrcha et al. 2002; Jadwiszczak 2006).

The main objective of this contribution is to analyze the three penguin assemblages and the magnitude of the different taphonomic processes in the conservation and destruction of the remains.

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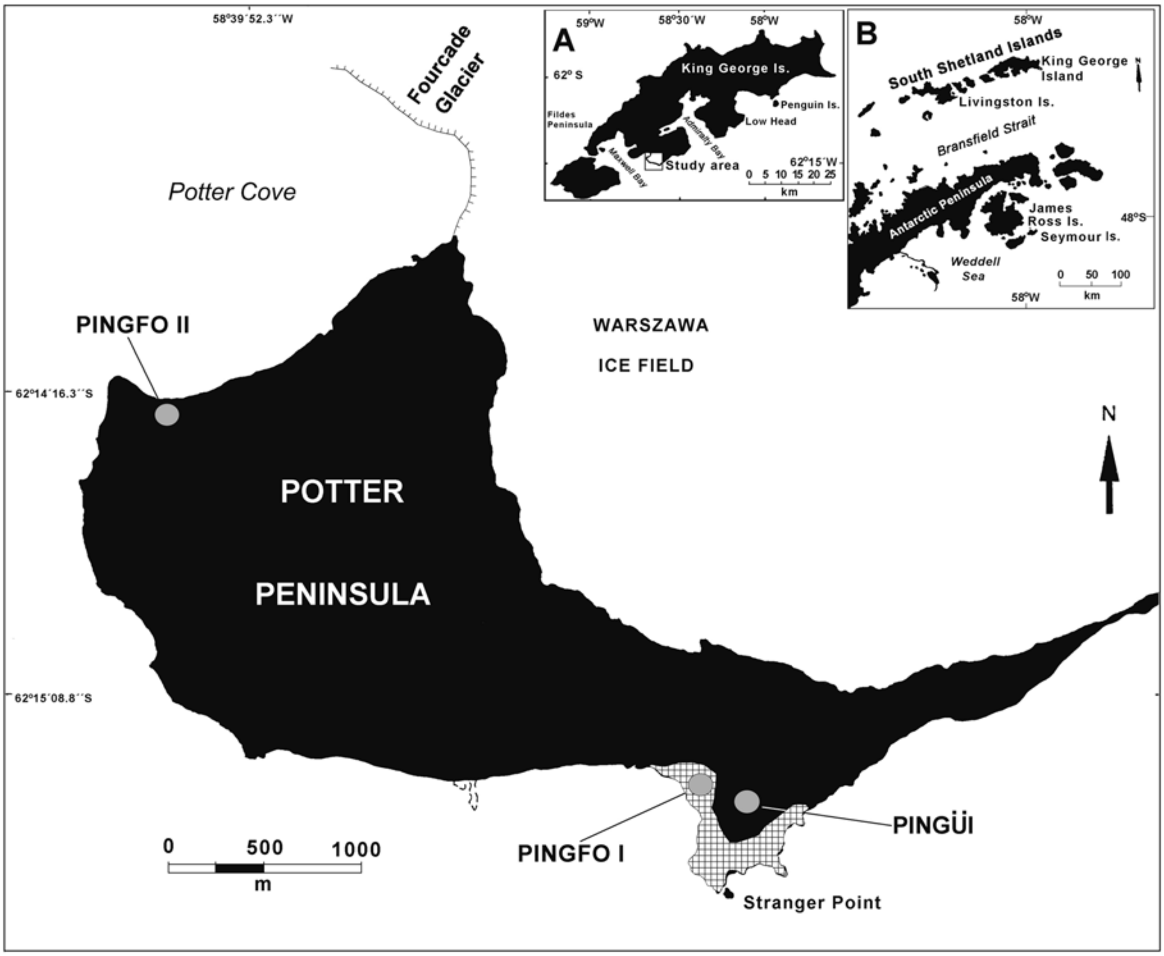

Fig. 1. Studied localities at Potter Peninsula, King George Island (Isla 25 de Mayo), South Shetland Islands, Antarctica. Grid area showing current penguin colonies of Adelie, Gentoo and Chinstrap penguins. Grey dots indicate the three localities.

2. Material and methods

The study area is located at Potter Peninsula, where three localities informally named "Pingfo I", "Pingfo II" and "Pingüi" (Fig. 1) were investigated by researchers of the Instituto Antártico Argentino. "Pingfo I" locality (62°15'26.483"S, 58°37'08.530"W) is located within the "Potter Peninsula" Antarctic Specially Protected Area (ASPA 132) that includes the south-eastern coastal area of this peninsula (Fig. 1). This site was declared ASPA because it is an active breeding colony for several seabirds, including Adelie Penguin (*Pygoscelis adeliae*, number of pairs: NP = 14554), Gentoo Penguin (*P. papua*, NP = 2325) and Chinstrap Penguin (*P. antarctica*, NP = 265), Southern Giant Petrel (*Macronectes giganteus*, NP = 75), South Polar Skua (*Catharacta maccormicki*, NP = 44), Brown Skua (*C. antarctica*, NP = 35), Black-backed Gull (*Larus dominicanus*, NP = 44), Antarctic Tern (*Sterna vittata*, NP = 250), Sheathbill (*Chionis alba*, NP = 14), as well as for Southern Elephant Seals (*Mirounga leonina*); the area is also a haulout place for Fur Seals (*Arctocephalus gazella*), and Weddell Seals (*Leptonichotes weddelli*) (AGUIRRE 1995; HAHN et al. 1998).

In this area, a 2.6 m thick fossiliferous sedimentary succession is exposed in the upper part of a 17.3 m high precipitous cliff that forms the western limit of a NE-dipping terrace. Two sedimentary facies were identified in the succession which unconformably covers Lower Tertiary volcanic rocks, consisting of basaltic-andesite lavas and pyroclastic rocks (DEL

Valle et al. 2002; Montalti et al. 2004). Bones from Pingfo I were dated to 5750 ± 40 yr BP and 5840 ± 40 yr BP (del Valle et al. 2002). The second locality, named "Pingfo II" (62°13'20.73"S, 58°40'21.00"W), is in the northern coast of Potter Peninsula (Fig. 1), and contains raised marine beach deposits elevated 2.17-2.77 m above sea level (a.s.l.). Bones from Pingfo II yielded 7780 ± 60 yr BP and 7600 ± 80 yr BP (del Valle et al. 2007). Finally, the last location, 'Pingüi' (62º15'00'S, 58º36'48'W), is placed at the slope of a hill some 500 m northward from Pingfo I (Fig. 1). It consists of abandoned penguin colonies located from 20 to 50 m.a.s.l., where bones yielded c. 2000 yr BP as a mean age, with a high dispersion probably due to mixture of different bones during their gradual slide down the hill. Nevertheless, this dating confirms early proposals on the downward movement of many rookeries since about 2500 years ago (Tatur et al. 1997).

The materials analyzed from Pingfo I were found *in situ* during the Southern Hemisphere summers of 1998 and 2001, when the site was surveyed and GPS positioned, whereas the remains from Pingfo II and Pingüi were obtained during the 2002/2003 summer season. Penguin bones from the study sites were sent to the Weizmann Institute of Science, Rehovot (Israel) for radiocarbon dating. Carbon samples were obtained from the inner part of bones to ensure accurate dating.

The sampling method was similar at Pingfo I and Pingfo II localities, where excavations were performed by digging short tunnels of 1 m^2 surface in each investigated layer, and organic remains (bones, feathers, seaweeds) were collected. Tunnels were homogeneously distributed in every bed and sediments were systematically sampled. Due to the recent deposition of bones at Pingüi, no deep excavations were needed, but only the lichen carpet was temporarily removed to establish 1 m^2 sample grids at each of four stations. Organic remains (e.g. invertebrates, bones, seaweeds) from surface beds and sediments were systematically sampled. At the end of the task, the holes were filled with the remaining sediments and the lichen carpet was restored. We used the stratigraphic classification of marine beaches and glacial events proposed by del Valle et al. (2002, tab. 4).

Penguin bones were compared with reference material from Departamento de Biología at Instituto Antártico Argentino, and División Paleontología Vertebrados, Museo de La Plata (Argentina). All the paleontological materials listed in Appendix 1 were examined and taxonomically determined to species level when possible and are housed at the Instituto Antártico Argentino (IAA). Osteological features used for *Pygoscelis* species identification agree with Acosta Hospitaleche et al. (2006).

Preservation styles as proposed by Martill (1985) were also identified. These styles classify bones and other fossils according to their wholeness, distinguishing articulated skeletons (1), disarticulated skeletons (2), isolated bones and teeth (3), worn bones and teeth (4), and coprocoenosic accumulations (5). These states of preservation are potentially indicative of degree of transportation and other taphonomic processes. In this context, the categorization of Behrensmeyer (1991), which considered penguins as microvertebrates, was taken into account to predict the consequences of the transportation. Taphonomic comments were performed through comparisons with modern biotic communities (Cruz 2006a, b) and correlation with known similar deposits from Patagonia and Antarctica (Emslie 1995).

3. Results

All the penguin recognized belong to modern species living currently in the area (see Table 1). Independent analyses of bone composition from each locality were performed for a better comprehension of the different fossil assemblages.

Pingfo I locality. – From the approximately 500 bones collected, 474 were assigned to Adelie Penguin (*Pygoscelis adeliae*) and Gentoo Penguin (*P. papua*). The remaining elements corresponded to Brown Skua (*Catharacta antarctica*) and Southern Elephant Seal (*Mirounga* sp). Penguin bones comprised 8 skulls, 254 appendicular elements, 12 sterna, 131 appendicular girdle elements, 13 synsacra, 50 vertebrae (Table 1) and five rachises of tail feathers (Fig. 2a). From the total sample, about 77% of the bones correspond to chicks. When analyzing preservation styles, penguin bones were classified into the three first categories established by Martill (1985). The first one includes partially articulated skeletons with mostly intact bone-to-bone contacts, where ligaments are still recognized. A complete and articulated penguin wing (Fig. 2b) was found with some of the ligaments preserved. In addition, a synsacrum and a pelvic girdle still joined to each other and fused to some caudal vertebrae were identified. The second preservation style comprises dismembered skeletons with several dissociated bones. A limited degree of scattering within beach

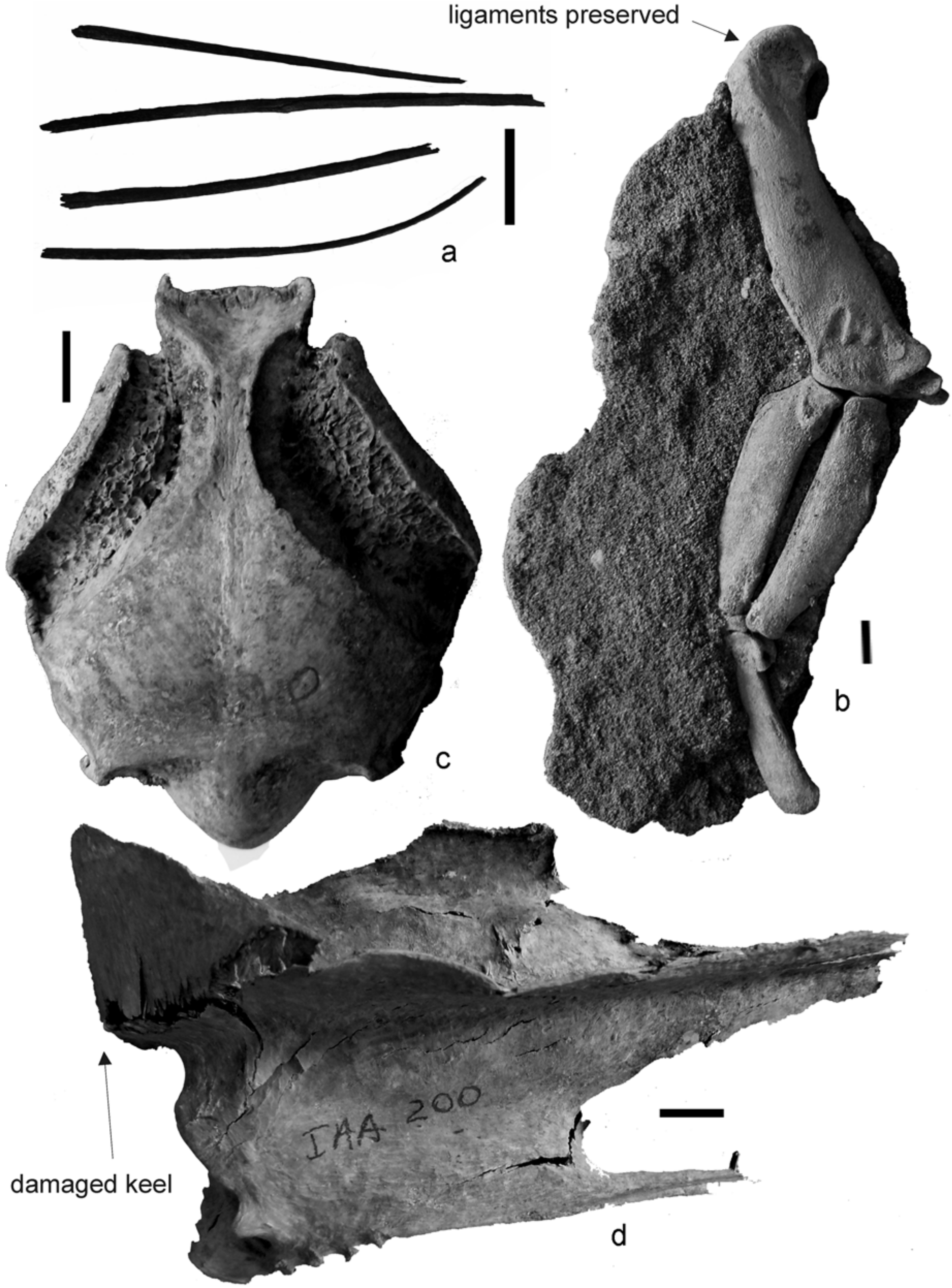

Fig. 2. (Legend see p. 353)

sediments is generally the result of scavenging, predation or disturbance patterns (*i.e.* storm waves). A few bones were found close to each other but not in actual physical contact. For example, a tibiotarsus and its corresponding fibula which were found very close to each other in the same sandy level, suggesting that they belonged to the same specimen. Finally, the third preservation style is represented by isolated bones resulting from skeleton disarticulation by wave action or other dispersal mechanisms, such as scavengers or predators. Most of the isolated osseous elements were assigned to this last category, including abundant well-preserved skulls (Fig. 2c) and several sterna with the badly damaged keels (Fig. 2d).

Pingfo II locality. – The 43 bones from Pingfo II (Table 1) were assigned to *Pygoscelis* sp, except two remains corresponding to a marine mammal, which were assigned to Southern Elephant Seal (del Valle et al. 2007). All the remains belong to Martill's (1985) third category, corresponding to isolated and reworked bones, without any articulated or associated elements.

Pingüi locality. – This assemblage is composed exclusively by penguins, mainly *Pygoscelis adeliae*, and includes mostly chicks (38.5 %) and some adult specimens. From a total of 65 elements (Table 1), we identified 53 complete appendicular bones and several fragments, all corresponding to the third preservation style. The only complete penguin tail feather, still bearing barbs, was found here; this is not too remarkable since this was the younger association studied.

4. Discussion

Three different topics will be discussed: bone structure, preservation styles, and skeletal element representation.

Fig. 2. Early Holocene-Recent subfossil materials assigned to *Pygoscelis* sp, found at Pingfo I locality. **a** – Penguin tail feathers, IAA 204. **b** – A partially articulated right wing keeping the bone-to-bone contacts in posterior view, IAA 203. **c** – An isolated skull of Gentoo penguin *Pygoscelis papua* in dorsal view, IAA 198. **d** – A sternum assigned to *Pygoscelis* sp. with the damaged keel, showing predatory signs in ventral view, IAA 200.

Table 1. Number of identified specimens (NISP) from each penguin assemblages. All specimens were identified as *Pygoscelis*, and when possible is given the species assignment. Numbers in columns indicate (adults; chicks).

Element	NISP		
	Pingfo I	Pingfo II	Pingüi
Skull	*P. papua* (2;1)		
	Pygoscelis sp. (5;0)	*Pygoscelis* sp. (1;0)	-
Jaw	*Pygoscelis* sp. (3;0)	-	-
Humerus	*P. adeliae* (12;0)		
	Pygoscelis sp. (7;38)	*Pygoscelis* sp. (5;0)	*Pygoscelis* sp. (18;2)
Radius	*Pygoscelis* sp. (1;0)	-	*Pygoscelis* sp. (7;1)
Ulna	*Pygoscelis* sp. (3;29)	*Pygoscelis* sp. (2;0)	*Pygoscelis* sp. (0;2)
Carpometacarpus	*Pygoscelis* sp. (6;7)	*Pygoscelis* sp. (2;0)	-
Femur	*P. adeliae* (1;11)		
	P. papua (1;12)	*Pygoscelis* sp. (2;0)	*Pygoscelis* sp. (2;15)
	Pygoscelis sp. (13;32)		
Tibiotarsus	*P. adeliae* (1;0)		
	P. papua (1;0)	*Pygoscelis* sp. (8;0)	*Pygoscelis* (1,0)
	Pygoscelis sp. (4;41)		
Fibula	*Pygoscelis* sp. (3;2)	*Pygoscelis* sp. (1;0)	*Pygoscelis* (1;0)
Tarsometatarsus	*P. adeliae* (0,2)		
	Pygoscelis sp. (2;0)	-	*Pygoscelis* sp. (1;0)
Phalanx	*Pygoscelis* sp. (5;4)	*Pygoscelis* sp. (5;0)	*Pygoscelis* sp. (3;0)
Scapula	*Pygoscelis* sp. (5;19)	*Pygoscelis* sp. (2;0)	*Pygoscelis* sp. (2;0)
Coracoid	*Pygoscelis* sp. (4;43)	*Pygoscelis* sp. (5;0)	*Pygoscelis* sp. (2;6)
Clavicle	*Pygoscelis* sp. (6;9)	*Pygoscelis* sp. (1;0)	-
Pelvic girdle	*Pygoscelis* sp. (3;42)	*Pygoscelis* sp. (1;0)	*Pygoscelis* sp. (2;0)
Vertebra	*Pygoscelis* sp. (11;39)	*Pygoscelis* sp. (5;0)	-
Sternum	*Pygoscelis* sp. (7;5)	*Pygoscelis* sp. (2;0)	-
Rib	*Pygoscelis* sp. (1;18)	*Pygoscelis* sp. (1;0)	-
Synsacrum	*Pygoscelis* sp. (2;11)	-	-
Total	(109;365)	(43;0)	(40;25)

Bone structure and preservation styles. – Most birds have thin and pneumatic bones, but penguin skeletons are heavy and compact in structure. This allows large bone accumulations to be preserved in the record, as it happened in the three localities under study. Additionally, penguins are medium-sized birds; this is an important factor, since the size of the remains is essential for preservation studies (larger elements have higher probability of being preserved) (Behrensmeyer & Dechant-Boaz 1980).

However, the remains of penguins (as those of any marine vertebrate) are hardly ever preserved as whole skeletons; usually they occur as dispersal bones (*sensu* Martill 1985). The preservation of whole skeletons is only favored by special conditions, such as anoxic environments combined with absence of predators, which are extremely rare in the avian fossil record. Nevertheless, we found several cases of articulated elements in our samples, which can be explained by rapid burial of the skeletons. In fact, after death, penguin carcasses may be subjected to various degrees of dispersal. Of the five preservation styles (see Martill 1985), we have recorded styles 1, 2 and 3 among our samples. The identification of these styles together with the skeletal part representation suggests the transportation degree that bones have suffered and consequently the proximity to the breeding colony. These data and the sedimentological information taken from del Valle et al. (2002), permitted to propose hypothesis about location of the breeding colonies of Pygoscelis.

Skeletal elements representation. – Appendicular bones are more resistant and consequently more frequent in the record (Myrcha & Tatur 1991; Emslie 1995; Tatur et al. 1997; Muñoz & Savanti 1998; Emslie & Woehler 2005). For example, the effect of trampling by inhabitants of the colony is commonly observed on sterna and ribs, whereas other bones such as the skulls are susceptible to fragmentation resulting in small parts that end up being buried (Cruz 2003, 2007). Thus, the representation of the skeletal parts helps to establish the type of operating processes that produced this pattern.

In modern assemblages of flying birds, wing elements are more commonly preserved than those of the legs and axial skeleton, while skulls and jaws are scarcely found (see Muñoz & Savanti 1998). Concurrently, previous studies of marine birds show that humeri, tibiotarsi, femora, coracoids and furculae are the most common elements (Cruz 2005, 2007). Thus, the larger, more durable and well preserved wing and leg elements appear frequently in both active colonies (Cruz 2005, 2007) and abandoned rookeries (see Emslie 1995). This differential preservation and destruction of parts results from several processes that act jointly: the action of predators, trampling by members of the colony and weathering effects.

Evidence from bones of Pingfo I indicates a possible occurrence of predation or scavenging. Predation by birds is mainly inferred from fractures and perforations in the keel (see Cruz 1999), and does not cause major transport or relocation of the skeleton. This type of predation was identified in penguin bones from Pingfo I, where several sterna with badly damaged keels were recovered. It would be not surprising that these damages were caused by skuas, which are also present in this sample and predate and scavenge on penguins today.

The presence of articulated skeletons and disarticulated but associated elements (see results above), besides the isolated remains found at the Pingfo I locality suggests that a penguin breeding colony probably existed close to the site of burial. Additionally, the composition of skeletal parts is very similar to the one found in deposits from extant penguin colonies, where seabird remains constitute large accumulations. In comparison with the data reported by Emslie (1995) and Cruz (2005, 2007), the Pingfo I locality displays a skeletal content characteristic of a deposit from an abandoned penguin colony. Another interesting point is that 77 % of parts correspond to chicks, another indication of the existence of a breeding colony formed by *Pygoscelis adeliae* and *P. papua* in the area. Up to the present, no other articulated mid-Holocene fossil penguin bones like these, have been reported from the South Shetland Islands.

It is noteworthy that all the remains collected at Pingfo II belong to the third category of preservation styles. This suggests that the bones from this locality would have undergone more intense transportation than those of Pingfo I and Pingüi. The distance between Pingfo II and the nearest active (or perhaps abandoned) penguin breeding colony implies displacement of the bones before burial (Myrcha & Tatur 1991; Tatur et al. 1997). Additionally, the absence of chick remains in the samples indicates that breeding colonies were not very close to Pingfo II, where only adult remains were identified. On the other hand, the sedimentological features and associated invertebrate fauna (del Valle et al. 2002) suggest that Pingfo II sediments were deposited mostly in a high-energy marine beach, probably related to a deltaic environment.

Finally, all the remains from Pingüi were also assigned to the third category, which comprises isolated elements. This suggests that penguin bones were transported after death, resulting in disarticulation of skeletons that left only isolated bones. The total absence of any evidence of predators in this fossil assemblage suggests a non-biological transport agent. Nevertheless, the high percentage of penguin chick bones indicates their provenance from a nearby colony. Also, the differential representation of skeletal parts from this locality seems to be similar to the proportion found in modern colonies (Emslie 1995; Cruz 2003), in which limb bones are the most commonly preserved remains.

5. Conclusions

Differences in the representation of skeletal elements among the three localities studied imply the action of different taphonomic factors, such as transportation or predation activity. The present analyses of the fossil penguin assemblages collected at the Potter Peninsula lead to the following conclusions: (1) the preservation styles documented at each locality vary, representing different depositional environments, (2) the penguin bone assemblages from Pingfo I and Pingüi were probably accumulated directly in a marine beach environment without important transport, whereas the bones of the Pingfo II assemblage might be originated in a site above the coast, and transported before burial, (3) the Pingüi assemblage probably represents a colony, or at least was very near to one, while the Pingfo I assemblage doubtlessly represents a penguin breeding colony. On the contrary, the Pingfo II assemblage represents a site located far from a colony area during Early Holocene times.

Pingfo I would represent a beach where adult and chick bodies from a nearby *P. adeliae* and *P. papua* breeding colony were deposited during mid-Holocene times. It is also possible that the colony was settled in the excavated area. The proximity of a breeding colony and the absence of evidence of transportation are supported by the ages composition of the penguin assemblage and the finding of several cranial elements and sterna. These elements are the weakest of the penguin skeleton and are easily fractured with minimum transport.

On the other hand, the sedimentological features and associated invertebrate fauna at Pingfo II (John & Sugden, 1971; del Valle et al. 2007) suggest that it would represent a marine sedimentary beach related to a high energy deltaic environment, where adult penguin bodies were individually accumulated at a considerable distance from active breeding colonies. This interpretation agrees with the low amount of delicate bones and the total absence of chicks.

Pingüi would not be a marine beach at the time of the deposition of penguin bones. The site was located at a relatively high altitude above sea level. According to our results, this locality could correspond to a recently abandoned penguin colony, where the trampling of its members would have destroyed the carcasses, breaking the weakest elements. However, proximity to a colony could be inferred from the presence of chicks.

Beyond the differences among the three localities, the Potter Peninsula has been a suitable region for the settlement of *Pygoscelis* colonies for at least the last 8000 years. This implies the presence of accessible beaches topographically protected from high-energy waves, as well as availability of food. The notorious lack of *Pygoscelis antarctica* in the samples could obey to taphonomic issues, due to the low number of couples in the current breeding colonies of Potter Peninsula, or maybe to its total absence in the area at the time the bones were deposited.

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Appendix – List of material housed at the Instituto Antártico Argentino (IAA) studied in the present contribution

Pygoscelis papua:
Adults: skull (IAA 198, IAA 205), femur (IAA 370), tibiotarsus (IAA IAA 448).
Chicks: skull (IAA 206), femur (IAA 371, IAA 372, IAA 373, IAA 374, IAA 375, IAA 376, IAA 377, IAA 378, IAA 379, IAA 380, IAA 381, IAA 382).

Pygoscelis adeliae:
Adults: humerus (IAA 216, IAA 217, IAA218, IAA 219, IAA 220, IAA 221, IAA 222, IAA 223, IAA 224, IAA 225, IAA 226, IAA 227), femur (IAA 358), tibiotarsus (IAA 447).
Chicks: femur (IAA 359, IAA 360, IAA 361, IAA 362, IAA 363, IAA 364, IAA 365, IAA 366, IAA 367, IAA 368, IAA 369), tarsometatarsus (IAA 510, IAA 511).

Pygoscelis sp.:
Adults: skull (IAA 207, IAA 208, IAA 209, IAA 210, IAA 211, IAA 212), jaw (IAA 213, IAA 214, IAA 215), humerus (IAA 228, IAA 229, IAA 230, IAA 231, IAA 232, IAA 233, IAA 234, IAA 273, IAA 274, IAA 275, IAA 276, IAA 277, IAA 278, IAA 279, IAA 280, IAA 281, IAA 282, IAA 283, IAA 284, IAA 285, IAA 286, IAA 287, IAA 288, IAA 289, IAA 290, IAA 291, IAA 292, IAA 293, IAA 294, IAA 295), radius (IAA 298, IAA 300, IAA 301, IAA 302, IAA 303, IAA 304, IAA 305, IAA 306), ulna (IAA 307, IAA 308, IAA 309), ulna (IAA 339, IAA 340) carpometacarpus (IAA 343, IAA 344, IAA 345, IAA 346, IAA 347, IAA 348, IAA 356, IAA 357), articulated wing (IAA 203), femur (IAA 383, IAA 384, IAA 385, IAA 386, IAA 402, IAA 403, IAA 404, IAA 405, IAA 406, IAA 407, IAA 408, IAA 409, IAA 410, IAA 411, IAA 412, IAA 413, IAA 414), tibiotarsus (IAA 449, IAA 450, IAA 451, IAA 452, IAA 453, IAA 454, IAA 455, IAA 456, IAA 457, IAA 458, IAA 459, IAA 460, IAA 461), fibula (IAA 503, IAA 504, IAA 505, IAA 508, IAA 509), tarsometatarsus (IAA 512, IAA 513, IAA 514), phalanx (IAA 515, IAA 516, IAA 517, IAA 518, IAA 519, IAA 524, IAA 525, IAA 526, IAA 527, IAA 528, IAA 529, IAA 530, IAA 531), scapula (IAA 532, IAA 533, IAA 534, IAA 535, IAA 536, IAA 556, IAA 557, IAA 558, IAA 559), coracoid (IAA 560, IAA 561, IAA 562, IAA 563, IAA 607. IAA 608, IAA 609, IAA 610, IAA 611, IAA 612, IAA 613), clavicle (IAA 620, IAA 621, IAA 622, IAA 623, IAA 624, IAA 625, IAA 635), pelvic girdle (IAA 636, IAA 637, IAA 638, IAA 681, IAA 682, IAA 683), vertebra (IAA 684, IAA 685, IAA 686, IAA 687, IAA 688, IAA 689, IAA 690, IAA 691, IAA 692, IAA 693, IAA 694, IAA 734, IAA 735, IAA 736, IAA 737, IAA 738), sternum (IAA 739, IAA 740, IAA 741, IAA 742, IAA 743, IAA 744, IAA 745, IAA 751, IAA 752), rib (IAA 753, IAA 772), synsacrum (IAA 773, IAA 774), penguin tail feathers (IAA 204).
Chicks: humerus (IAA 235, IAA 236, IAA 237, IAA 238, IAA239, IAA 240, IAA 241, IAA 242, IAA 243, IAA 244, IAA 245, IAA 246, IAA 247, IAA 248, IAA 249, IAA 250, IAA 251, IAA 252, IAA 253, IAA 254, IAA 255, IAA 256, IAA 257, IAA 258, IAA 259, IAA 260, IAA 261, IAA 262, IAA 263, IAA 264, IAA 265, IAA 266, IAA 267, IAA 268, IAA 269, IAA 270, IAA 271, IAA 272, IAA 296, IAA 297), radius (IAA 299), ulna (IAA 310, IAA 311, IAA 312, IAA 313, IAA 314, IAA 315, IAA 316, IAA 317, IAA 318, IAA 319, IAA 320, IAA 321, IAA 322, IAA 323, IAA 324, IAA 325, IAA 326, IAA 327, IAA 328, IAA 329, IAA 330, IAA 331, IAA 332, IAA 333, IAA 334, IAA 335, IAA 336, IAA 337, IAA 338), ulna (IAA 341, IAA 342), carpometacarpus (IAA 349, IAA 350, IAA 351, IAA 352, IAA 353, IAA 354, IAA 355), femur (IAA 387, IAA 388, IAA 389, IAA 390, IAA 391, IAA 392, IAA 393, IAA 394, IAA 395, IAA 396, IAA 397, IAA 398, IAA 399, IAA 400, IAA 401, IAA 415, IAA 416, IAA 417, IAA 418, IAA 419, IAA 420, IAA 421, IAA 422, IAA 423, IAA 424, IAA 425, IAA 426, IAA 427, IAA 428, IAA 429, IAA 430, IAA 431, IAA 432, IAA 433, IAA 434, IAA 435, IAA 436, IAA 437, IAA 438, IAA 439, IAA 440, IAA 441, IAA 442, IAA 443, IAA 444, IAA 445, IAA 446), tibiotarsus (IAA 462, IAA 463, IAA 464, IAA 465, IAA 466, IAA 467, IAA 468, IAA 469, IAA 470, IAA 471, IAA 472, IAA 473, IAA 474, IAA 475, IAA 476, IAA 477, IAA 478, IAA 479, IAA 480, IAA 481, IAA 482, IAA 483, IAA 484, IAA 485, IAA 486, IAA 487, IAA 488, IAA 489, IAA 490, IAA 491, IAA 492, IAA 493, IAA 494, IAA 495, IAA 496, IAA 497, IAA 498, IAA 499, IAA 500, IAA 501, IAA 502), fibula (IAA 506, IAA 507), phalanx (IAA 520, IAA 521, IAA 522, IAA 523), scapula (IAA 537, IAA 538, IAA 539, IAA 540, IAA 541, IAA 542, IAA 543, IAA 544, IAA 545, IAA 546, IAA 547, IAA 548, IAA 549, IAA 550, IAA 551, IAA 552, IAA 553, IAA 554, IAA 555), coracoid (IAA 564, IAA 565, IAA 566, IAA 567, IAA 568, IAA 569, IAA 570, IAA 571, IAA 572, IAA 573, IAA 574, IAA 575, IAA 576, IAA 577, IAA 578, IAA 579, IAA 580, IAA 581, IAA 582, IAA 583, IAA 584, IAA 585, IAA 586, IAA 587, IAA 588, IAA 589, IAA 590, IAA 591, IAA 592, IAA 593, IAA 594, IAA 595, IAA 596, IAA 597, IAA 598, IAA 599, IAA 600, IAA 601, IAA 602, IAA 603, IAA 604, IAA 605, IAA 606, IAA 614, IAA 615, IAA 616, IAA 617, IAA 618, IAA 619), clavicle (IAA 626, IAA 627, IAA 628, IAA 629, IAA 630, IAA 631, IAA 632, IAA 633, IAA 634), pelvic girdle (IAA 639, IAA 640, IAA 641, IAA 642, IAA 643, IAA 644, IAA 645, IAA 646, IAA 647, IAA 648, IAA 649, IAA 650, IAA 651, IAA 652, IAA 653, IAA 654, IAA 655, IAA 656, IAA 657, IAA 658, IAA 659, IAA 660, IAA 661, IAA 662, IAA 663, IAA 664, IAA 665, IAA 666, IAA 667, IAA 668, IAA 669, IAA 670, IAA 671, IAA 672, IAA 673, IAA 674, IAA 675, IAA 676, IAA 677, IAA 678, IAA 679, IAA 680), vertebra (IAA 695, IAA 696, IAA 697, IAA 698, IAA 699, IAA 700, IAA 701, IAA 702, IAA 703, IAA 704, IAA 705, IAA 706, IAA 707, IAA 708, IAA 709, IAA 710, IAA 711, IAA 712, IAA 713, IAA 714, IAA 715, IAA 716, IAA 717, IAA 718, IAA 719, IAA 720, IAA 721, IAA 722, IAA 723, IAA 724, IAA 725, IAA 726, IAA 727, IAA 728, IAA 729, IAA 730, IAA 731, IAA 732, IAA 733), sternum (IAA 746, IAA 747, IAA 748, IAA 749, IAA 750), rib (IAA 754, IAA 755, IAA 756, IAA 757, IAA 758, IAA 759, IAA 760, IAA 761, IAA 762, IAA 763, IAA 764, IAA 765, IAA 766, IAA 767, IAA 768, IAA 769, IAA 770, IAA 771), synsacrum (IAA 775, IAA 776, IAA 777, IAA 778, IAA 779, IAA 780, IAA 781, IAA 782, IAA 783, IAA 784, IAA 785).