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A new species of penguin (Spheniscidae: *Spheniscus*) and other birds from the late Pliocene of Chile

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Abstract.—We describe a new species of penguin, *Spheniscus chilensis,* from Cuenca del Tiburón, late Pliocene, northern Chile. This species was found in association with a small species of cormorant, *Phalacrocorax* sp., and a caracara, *Milvago* sp., and is the first Pliocene penguin to be described from South America. Other vertebrates at this site include fish, sharks, and cetaceans. An extensive invertebrate fauna, including the late Pliocene muricid gastropod *Herminespina mirabilis,* also is present. The avifauna suggests a low diversity of seabirds existed in northern Chile from the late Pliocene to the present, unlike the much higher diversity found in Patagonia in the late Oligocene/early Miocene.

The coastal region of southern Peru and northern Chile is well known for its massive layers of marine shell beds exposed in cliffs. Geologic studies of these beds have provided considerable information on marine faunas in the Miocene through late Pleistocene of this region. Previous investigations in Chile have concentrated on the age and structure of the invertebrate faunas, and eustatic changes in sea level in correlation with tectonic uplift (Herm 1969, 1970; Tsuchi et al. 1988; Padilla & Elgueta 1992). Deposition of these beds occurred over a period of millions of years in coastal forearc basins, the eastern sections of which were later uplifted during crustal deformations of the continental margin (Dunbar et al. 1990). Extensive and diverse deposits of late Pleistocene marine mollusks also occur throughout this region (Ortleib et al. 1994).

In 1994, we visited an exposure of marine shell beds on the Península de Mejillones and approximately 14 km northwest of the Antofagasta airport and 6 km from the coast (Fig. 1). Here, over 10 m of marine sediments are exposed on eroded slopes of valleys and hills that contain abundant marine mollusks. The upper layers of these exposed sediments also contain numerous sharks' teeth, fish bones, and fragmentary and complete bones of marine mammals and birds. This fossil exposure lies within the upper beds of the Caleta Herradura de Mejillones Formation (23°21.453″S; 70°32.061″W), dating to the late Pliocene (Tsuchi et al. 1988). In addition, the fossils were found in association with the muricid gastropod *Herminespina mirabilis,* which is only known from the late Pliocene of Peru and Chile (DeVries & Vermeij 1997).

The area of concentration of the vertebrate fossils, known locally as Cuenca del Tiburón, is particularly rich in birds. Dozens of disarticulated bones of a single species of penguin (Spheniscidae) and a small cormorant (Phalacrocoracidae) are scattered on the surface, having eroded from exposed layers of shell beds nearby. Fossils of this penguin originally were found by one of us (CGC) at the locality in 1980. We visited the site twice in 1994 and once in 1997 to

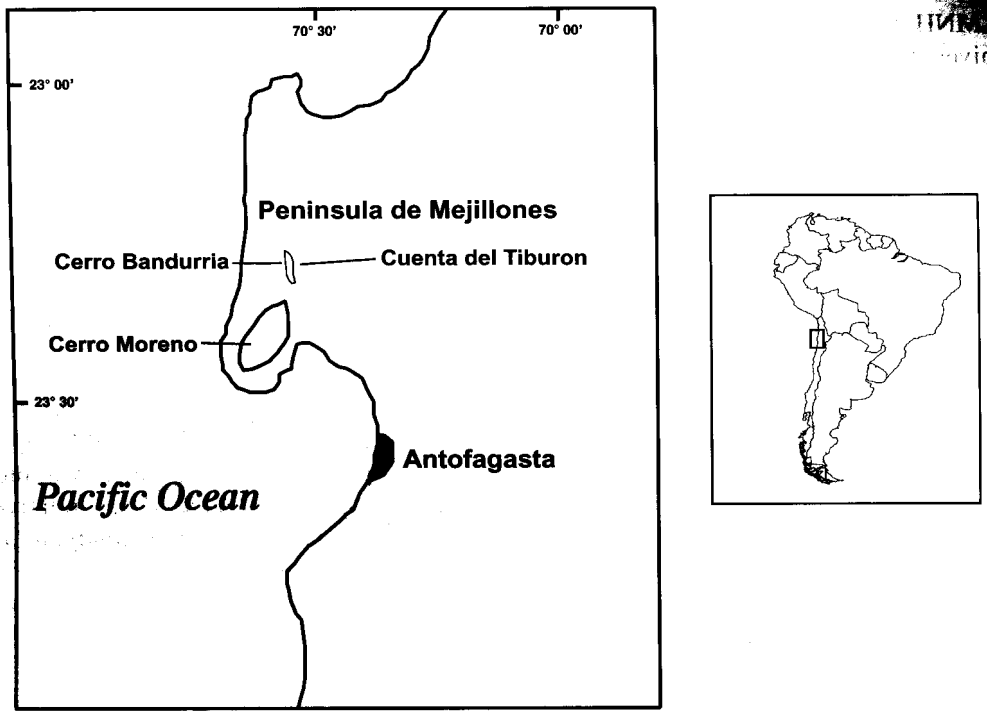

Fig. 1. Map showing the location of Cuenca del Tiburón on the Península de Mejillones, northern Chile.

collect additional material of this and other birds that are presented here.

All the disarticulated penguin material appears to represent a new species of penguin that is referable to *Spheniscus* by the relatively long and slender mandibular shaft, humerus with relatively deep proximal end and large pneumatic fossa that is weakly bipartite, proximal shaft slightly angled internally and not straight, and tarsometatarus relatively short and broad with external proximal foramen equal or larger and placed slightly higher on shaft than internal foramen. The fossil material most closely approaches the living *S. humboldti* and *S. magellanicus* in size and proportions, but differs from all species in this genus by distinct characters of the humerus and other postcranial elements. These comparisons indicate that the fossils represent a new species of penguin that is described herein; fossils of two other taxa of birds associated with the penguin material also are identified.

Materials and Methods

Measurements and comparisons of Recent skeletons of penguins were completed in the collections of the Florida Museum of Natural History (FLMNH), Gainesville, and the American Museum of Natural History (AMNH), New York. Fossil material was examined at the Museo de La Plata (MLP), Argentina, the Universite Claude Bernard Lyon 1, France, and at AMNH. Measurements were taken with Vernier calipers to the nearest 0.1 mm and are self-descriptive. Measurements of the humerus include greatest length (GL), proximal breadth and depth (PB, PD), least breadth and depth of shaft (LBS, LDS), and distal breadth and depth (DB, DD). Terminology follows that of Howard (1929) and Simpson (1946).

Fossil specimens reported here are housed at the Museo Geológico Prof. Humerto Fuenzalida V., Universidad Católica del Norte (UCN), Antofagasta, Chile, or at

FLMNH where they are catalogued with University of Florida (UF) numbers.

Systematic Paleontology

Class Aves
Order Sphenisciformes
Family Spheniscidae

Spheniscus chilensis, new species
Fig. 2

Holotype.—complete left humerus, UCN-1-130697 (Fig. 2A). Collected by Carlos Guerra Correa, 1980. Cast of specimen housed at FLMNH, UF 143300.

Paratypes.—2 left mandibles missing ends, UF 144101, 144153; cervical vertebra, UF 144102; 2 right scapulae, UF 143296–143297; right coracoid, 144154 (Fig. 2B); four right coracoids missing sternal ends, UF 144124–144125, 144155–144156; shaft of right coracoid, UF 144103; two left humeri, UF 144104–144105; 6 left humeri missing proximal ends, UF 144106, 144126, 144157–144159, 144171; 4 right humeri, UF 143295, 144107–144109; 3 right humeri missing proximal ends, UF 144127–144128, 144160; left radius, UF 144129; 6 right radii, UF 143299 (Fig. 2C), 144110, 144130–144133; 3 left ulnae, UF 144134, 144161–144162; right ulna, UF 144163; 3 left carpometacarpi, UF 143298 (Fig. 2C), 144111, 144135; 5 right carpometacarpi, UF 144112, 144136–144138, 144164; wing phalanx, UF 144139; synsacrum, UF 144113; proximal end of synsacrum, UF 144147; left femur with ends damaged, UF 144165; proximal left femur, UF 144114; left femur missing proximal end, UF 144140; 3 distal halves left femora, UF 144115, 144141, 144148; distal end left femur, UF 144166; right femur, UF 144116 (Fig. 2D); two right femora missing proximal ends, UF 144117, 144149; 2 right femora missing distal ends, UF 144118–144119; distal end right femur, UF 144167; shaft of right femur, UF 144142; two distal left tibiotarsi, UF 144150, 144168 (Fig. 2D); proximal end right tibiotarsus, UF 144169; distal shaft of right tibiotarsus, UF 144143; shaft of right tibiotarsus, UF 144170; right fibula, UF 144144; 3 left tarsometatarsi with damaged proximal ends, UF 143293–143294, 144120.

Type locality and horizon.—Cuenca del Tiburón Fossil Locality, Península de Mejillones, Chile, late Pliocene (upper beds, Caleta Herradura de Mejillones Formation, Tsuchi et al. 1988). This is the only locality in which the fossil species occurs.

Diagnosis.—Humerus with deep fossa at proximal anconal surface below head (fossa is shallow in *Spheniscus humboldti, S. demersus,* and *S. mendiculus,* shallow to moderately deep in *S. magellanicus*), relatively smaller and narrower entepicondylar process (broad and rounded in all living *Spheniscus*), relatively slender shaft similar to *S. magellanicus* and *S. demerus* (more robust in *S. humboldti*; Table 1), and distal end with or without pneumatic fossa in distal view (no fossa present in all living *Spheniscus*). Tibiotarsus with relatively larger distal foramina and broader distal external shaft than in all living *Spheniscus.* Tarsometatarsus with shallow anterior grooves below proximal foramina (grooves deep in all Recent *Spheniscus*). The ulna, radius, carpometacarpus and femur of the fossil species show minor differences with the living species.

Etymology.—Named after Chile, the country in which the fossil site is located.

Description.—The fossil material most closely approaches the living *S. humboldti* and *S. magellanicus* in size and proportions, but differs from all species in this genus by distinct characters of the humerus and tarsometatarsus. The fossil species is slightly smaller than *Spheniscus humboldti* and similar in size to *S. magellanicus* (Table 1). Only one other fossil species is known, *S. predemersus* from the early Pliocene of South Africa (Simpson 1971). The humerus of that species, however, is much longer (length, 84.7 mm) and more slender in the shaft (medial breadth, 8.6 mm) than *S. chilensis* (Table 1, plus see measurements in

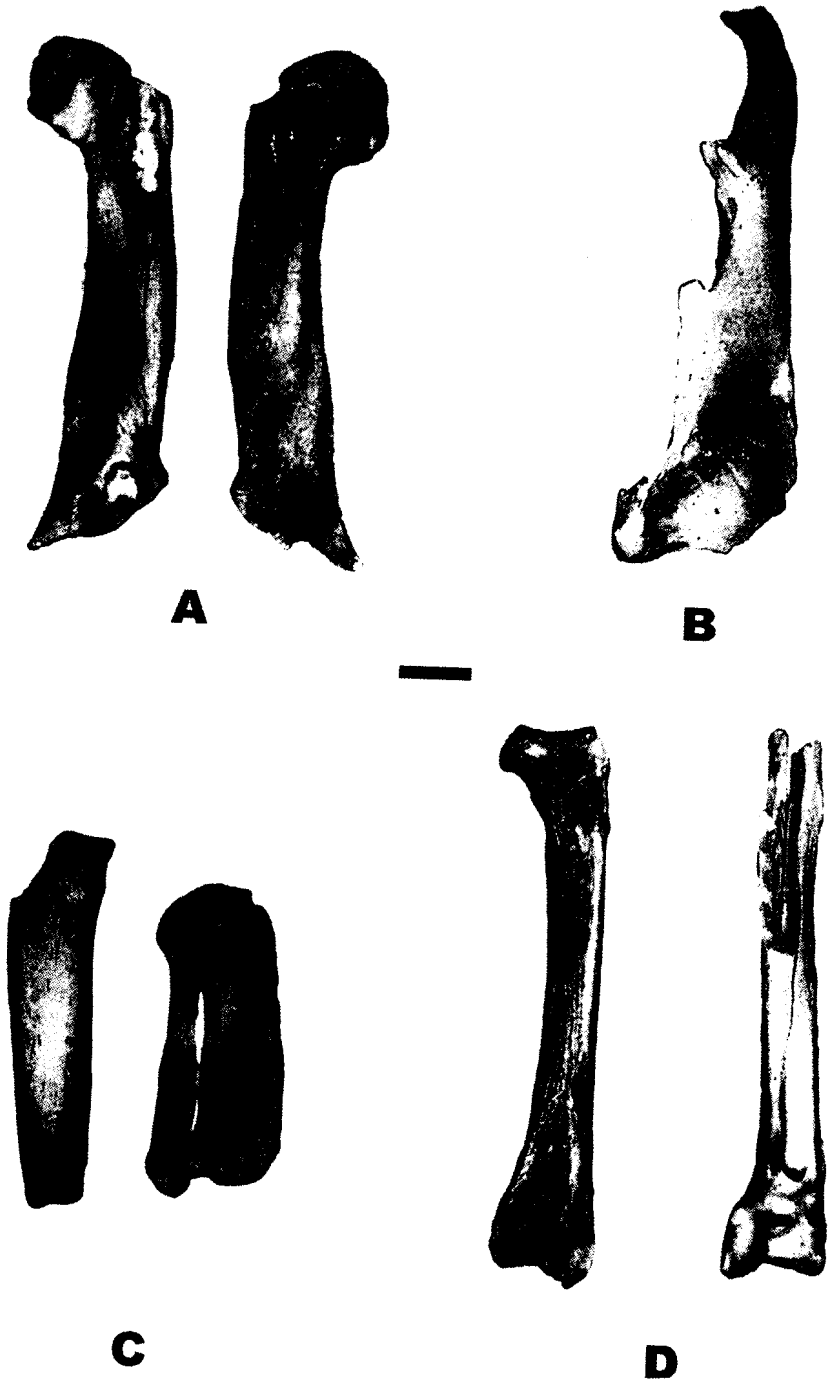

Fig. 2. Fossil specimens of *Spheniscus chilensis* from Cuenca del Tiburón: (A) holotype left humerus, UCN-1-130697, in palmar (left) and anconal (right) view; (B) dorsal view of right coracoid, UF 144154; (C) anconal view of right radius (left), UF 144110, and internal view of left carpometacarpus (right), UF 144111; (D) posterior view of right femur, UF 144116 (left), and anterior view of distal left tibiotarsus, UF 144168. Scale bar = 1 cm.

Table 1.—Measurements (mm) of humeri of Recent *Spheniscus* in comparison to *S. chilensis*. For each entry, the top row is mean ± standard deviation and bottom row is range. See text for key to measurement acronyms.

Species	GL	PB	PD	LBS	LDS	DB	DD
S. humboldti	75.3 ± 1.5	22.8 ± 0.9	15.9 ± 0.8	13.1 ± 0.5	5.8 ± 0.3	21.3 ± 1.1	8.0 ± 0.4
(N = 8)	73.3–78.1	21.8–24.2	14.5–16.8	12.6–14.1	5.5–6.4	20.2–23.3	7.5–8.7
S. magellanicus	69.1 ± 5.7	20.1 ± 1.2	14.5 ± 0.8	11.6 ± 0.6	5.0 ± 0.4	19.9 ± 0.7	7.2 ± 0.4
(N = 4)	62.8–75.0	18.9–21.1	13.8–15.6	11.0–12.5	4.5–5.5	19.2–20.8	6.8–7.8
S. demerus	70.7 ± 4.7	21.4 ± 2.6	14.7 ± 2.6	12.3 ± 2.1	5.2 ± 1.3	20.0 ± 1.9	7.2 ± 0.6
(N = 2)	67.3–74.0	19.5–23.2	12.9–16.5	10.8–13.7	4.2–6.1	18.6–21.3	6.8–7.6
S. mendiculus	57.0 ± 1.6	16.7 ± 0.1	11.2 ± 0.2	9.6 ± 0.5	4.1 ± 0.2	16.0 ± 1.3	6.2 ± 0.1
(N = 3)	56.0–58.8	16.6–16.8	11.1–11.4	9.2–10.1	3.9–4.3	14.8–17.3	6.1–6.3
S. chilensis							
UCN-1-130697	72.2	20.3	15.5	12.5	5.6	19.0	7.4
UF 144109	68.2	20.7	14.2	11.9	5.2	20.3	7.4
UF 144107	69.2	18.1	13.1	10.1	4.8	16.7	6.3
UF 144105	71.6	20.3	—	12.5	6.4	19.4	7.5
UF 144104	—	22.3	14.6	12.5	6.4	—	—
UF 144157	—	—	—	11.5	5.1	17.7	6.7
UF 144158	—	—	—	12.3	5.7	20.0	8.1

Simpson 1971, table 1). A large undescribed species of penguin close to *Spheniscus* is known from the late Miocene/Pliocene Pisco Formation, Peru (Cheneval 1993). Bones of this species were examined at the Universite Claude Bernard Lyon 1, France, and differ by their greater size, humerus with more strongly bipartite pneumatic fossa (see Simpson 1946 for description of this character) and deeper medial fossa, and broad and rounded entepicondylar processes. Another fossil penguin from the late Miocene to middle Pliocene Bahía Inglesa Formation in north-central Chile was referred to cf. *Spheniscus* sp. and described as very similar to *S. humboldti,* but at least 25% larger (Walsh & Hume 2001) and could not be referable to *S. chilensis.*

Other fossil penguins that have been described from South America are restricted to the late Oligocene/early Miocene of Patagonia where nine species and four genera are known from this region (Simpson 1946, 1972; Tonni 1980). Species in the genera *Arthrodytes* and *Paraptenodytes* are relatively large penguins with the largest (*A. grandis*) near the size of the modern Emperor Penguin (*Aptenodytes forsteri*). In these genera, the humerus has a relatively straight shaft and, in *Paraptenodytes,* the tarsometatarsus is relatively long and slender. A partial associated skeleton of *P. antarcticus* (AMNH 3338) and several isolated bones of *P. robustus* were examined at AMNH and found to differ from *Spheniscus chilensis* in the characters above and by their greater size and robustness.

Two proximal humeri (AMNH 3341 and 3346) of *Chubutodyptes biloculata* differ from *Spheniscus chilensis* by their larger, more robust size, presence of a strongly bipartite pneumatic fossa, and relatively longer and deeper bicipital furrow. Numerous specimens of *Palaeospheniscus patagonicus* and *P. wimani* at AMNH and MLP approach the size of *S. chilensis,* but are more robust and have a distinctly bipartite pneumatic fossa on the humerus. The tarsometatarsus of this genus also is relatively long and slender with the medial proximal foramen greatly reduced or absent.

Order Pelecaniformes
Family Phalacrocoracidae
Genus *Phalacrocorax* Brisson, 1760

Referred material.—right coracoid missing ends, UF 144122; distal left humerus, UF 144151; proximal half left ulna, UF 144123; proximal end right ulna, UF 144152; left carpometacarpus with ends damaged, UF 144146; right carpometacarpus, UF 144145.

Measurements.—Ulnae, UF 144123 and 144152: PB, 9.3 and 9.4 mm; PD, 8.1 and 8.5 mm, respectively. Carpometacarpus, UF 144145: GL, 50.1 mm; PB and PD, 5.3 and 10.6 mm; LBS and LDS, 3.7 and 2.8 mm. UF 144146: GL, 48.3 mm; LBS and LDS, 3.5 and 2.8 mm.

Discussion.—This material is from a small species of cormorant, near the size of the living *Phalacrocorax brasilianus.* It is possible that it represents an undescribed species, but the material is too fragmentary for systematic analysis with other fossil and living species. Another small cormorant is known from the late Miocene/Pliocene Pisco Formation, Peru (Cheneval 1993). An ulna and carpometacarpus (both catalogued as AGL PPI 139) of this species were examined at the Universite Claude Bernard Lyon 1, France, and found to be slightly larger and more robust than the Cuenca del Tiburón material. In addition, the proximal ulna (PB and PD, 10.0 and 9.3 mm) has a relatively broader impression of brachialis anticus and the carpometacarpus (GL, 51.8; PB, 5.7 mm; LBS and LDS, 5.5 and 5.3 mm) has a proximal end with a relatively deeper intercondylar fossa in anterior view compared to the Cuenca del Tiburón material. A distal humerus from a larger cormorant, near the size of *P. bougainvilli,* also is known from the Bahía Inglesa Formation in north-central Chile (Walsh & Hume 2001). It was not examined here, but

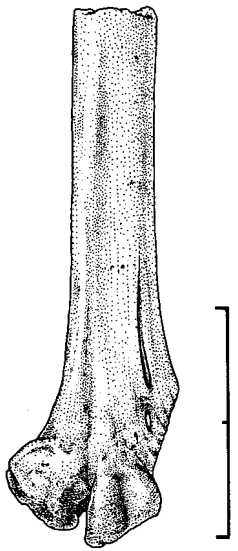

Fig. 3. Distal left tarsometatarsus, UF 144121, of *Milvago* sp. Scale bar = 1 cm.

is considered too large to represent the fossil species at Cuenca del Tiburón.

Order Accipitriformes
Family Falconidae
Genus *Milvago* Spix, 1824
Fig. 3

Referred material.—Distal left tarsometatarsus missing external trochlea, UF 144121.

Description.—The specimen is referable to Falconidae by the presence of two openings of the distal anterior foramen and by the morphology of the distal trochlea. It differs from *Falco* in lacking a long posterior ridge extending distally from the hypotarsus to nearly ¾ the length of the shaft and is most similar to *Milvago* and *Polyborus* in this feature. *Polyborus* and *M. chimachima* have only a single opening for the distal anterior foramen. The specimen is most similar to *M. chimango* in this feature and in size, but the fossil differs in having more robust trochleae similar to *M. chimachima.* UF 144121 also is similar to *M. chimachima* is having only a single opening of the anterior distal foramen. It may represent an undescribed species of *Milvago,* but additional specimens are needed.

Discussion.—Three fossil species have been described in this genus: *Milvago readei,* from the late Pleistocene of Florida (Brodkorb 1959; Campbell 1980) which has been synonymized with the living *M. chimachima* by Emslie (1998), and *M. alexandri* and *M. brodkorbi* from the late Pleistocene of Haiti (Olson 1976) and Peru (Campbell 1980), respectively. These last two species were not examined here, but *M. brodkorbi* is much larger than *M. chimachima* (Campbell 1980) and probably does not represent the fossil species from Cuenca del Tiburón.

Discussion

Only one other marine Pliocene fossil locality is known in Chile, also on the northern Coast. Walsh & Hume (2001) reported a marine avifauna within the Bahía Inglesa Formation, near Copiapó dating to the late Miocene to middle Pliocene based on associated shark teeth, diatoms, and foraminiferans. This deposit contained the earliest records of a cormorant (*Phalacrocorax* sp.) and penguin (cf. *Spheniscus* sp.) in Chile, as well as several other species of seabirds, sharks, fish, reptiles, and marine mammals. Cuenca del Tiburón is now the second marine deposit that also contains fossil sharks, fish, marine mammals, and birds. The vertebrate fauna other than birds remains largely unstudied. The sharks represented at this site include *Carcharodon carcharias, Carcharias* sp., and *Carcharhinus* sp., plus mouth plates from unidentified Myliobatidae. In addition, there are at least two large species of bony fish (Osteichthyes), two small species of dolphin (Odontoceti), one small baleen whale (Balaenopteridae), and one sea lion (Otariidae) (G. Morgan, pers. comm.).

Based on this fauna, as well as invertebrate taxa, the Cuenca del Tiburón deposit represents a nearshore marine community, including both sandy subtidal (from the

presence of *Perna, Glycymeris,* and *Chorus*) and rocky intertidal zones (from the presence of *Trochita* and several barnacle genera). Most of the shells appear to have been transported a short distance before deposition occurred, based on leaching and abrasion plus the lack of paired valves (R. Portell, pers. comm.). The penguin remains also exhibit moderate wear and abrasion indicating that they are in a secondary site of deposition.

The fossil record of penguins has been reviewed by Simpson (1946) and Fordyce and Jones (1990). *Spheniscus chilensis* is the first fossil penguin to be described from Chile and from the Pliocene of South America. One other fossil species within this genus was described by Simpson (1971) from the early Pliocene of South Africa. Olson (1983), however, reviewed this and three other taxa named by Simpson from this locality and concluded that they all belong to either one extinct genus or represent a primitive form of *Spheniscus.* In South America, at least nine fossil species have been described from the rich late Oligocene/early Miocene Patagonia Formation of Argentina (see reviews by Simpson 1946 and Tonni 1980), and one from the early Miocene of the Pisco Formation in southern Peru (Cheneval 1993).

The material from Cuenca del Tiburón suggests that a low diversity of penguins occurred on the west coast of South America, similar to today and unlike the earlier fossil record in Argentina and South Africa. This relative low diversity of penguins and other seabirds appears to have persisted along the Chile and Peruvian coasts for millions of years. In Patagonia, penguin diversity has declined considerably since the early Miocene as only one species (*S. magellanicus*) breeds in that region today, while only two species are found along the Chilean and Peruvian coasts (*S. magellanicus* and *S. humboldti*). Future investigations of fossil deposits in northern Chile are needed to further understand the paleoceanographic conditions that prevailed during the Pliocene.

Acknowledgments

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