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## A NEW NEOGENE MARINE AVIAN ASSEMBLAGE FROM NORTH-CENTRAL CHILE

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**ABSTRACT**—Most of South America's diverse avian fossil record is derived from terrestrial deposits. A Late Miocene to Early Pliocene marine avian assemblage is reported here from the Bahía Iglesia Formation of north-central Chile. Sulidae, Phalacrocoracidae, Pelagornithidae, Diomedidae, and Spheniscidae reported here are the earliest occurrences in Chile. The presence of the Chilean spheniscid penguin may prove significant in the taxonomy and radiation of the genus *Spheniscus*.

### INTRODUCTION

Although South America has a diverse and abundant avian fossil record, most of the fossil avifaunas are from terrestrial deposits. Few marine Neogene localities in South America have yielded fossil birds, although there are notable exceptions in Peru (Cheneval, 1993) and Patagonia (e.g., Simpson, 1975; Olson, 1984). Here, we provide a preliminary description of the first marine avian assemblage from the north-central coast of Chile (Fig. 1). This site represents the earliest occurrence in Chile of the Sulidae, Phalacrocoracidae, Pelagornithidae, Diomedidae, and Spheniscidae in Chile. The material was recovered on two field expeditions between 1996 and 1998 from a bonebed approximately 5 km southwest of the small town of Bahía Iglesia. The specimens detailed here are currently in the collections of the University of Portsmouth, England.

**Institutional Abbreviations**—**BMNH**, British Museum of Natural History; **UOP**, University of Portsmouth; **SMNK**, Staatliches Museum für Naturkunde, Karlsruhe.

### GEOLOGY

The study area is structurally complex due to its proximity to active subduction at the Peru-Chile Trench. The Bahía Iglesia Formation was first described by Rojo (1985) and consists of over 42 m of siltstones, fine sands, shelly coquinas, pebble beds, and a phosphorite bonebed (Fig. 2). These sediments rest unconformably on a faulted Paleozoic gabbroic basement, which forms a number of outcrops in the study area. The bonebed (Unit 2, Fig. 2) has a lateral extent of about 8.0 km<sup>2</sup> and is composed of up to four layers of phosphatic arkose, of which the basal layer is the most fossiliferous. All of the material described here came from this layer.

The site has been dated on the basis of shark teeth (Long, 1993), diatoms (Tsuchi et al., 1988), and foraminiferans (Ibaraki, 1995) at between 4.5 and 2.6 Ma. The diatomite sampled by Tsuchi et al. (1988) came from Unit 3 (Fig. 2) in the east of the study area, indicating an Early to Mid-Pliocene age for that unit. The bonebed can be dated to some extent by its shark fauna. The teeth of *Carcharodon carcharias* and *Cosmopolitodus* (= *Isurus*) *hastalis* are used in the Peruvian Neogene as zonal indicators (Muizon and DeVries, 1985); *Cosmopolitodus hastalis* is last observed at the end of the Miocene, while *Carcharodon carcharias* first appears at the beginning of the Pliocene. The teeth of both of these shark species are present in the bonebed, indicating that this unit extends from the Miocene into the Pliocene. However, the dating of Unit 3 indicates that the top of the bonebed (Unit 2) can be no younger than Late

Pliocene. Remains referable to the monachine seal *Acrophoca* sp. are found close to the top of Unit 1 (Fig. 2). This genus is known from Late Miocene to Late Pliocene sediments of the Pisco Formation of Peru (Muizon and DeVries, 1985). Since the bonebed is partially Miocene in age based on the presence of *C. hastalis*, the base of Unit 2 must be Late Miocene.

The final marine terrace deposit at the top of the sequence contains a molluscan assemblage which includes *Mulinia edulis*, *Crepidula dilatata*, *Argopecten purpuratus*, *Trochita trochiformis* and *Oliva peruviana*. This assemblage indicates an Early Pleistocene age for the top of the succession, but as these are extant species they are not useful in constraining a youngest age for this horizon.

### PALEONTOLOGY

The site is highly fossiliferous, with an abundance of both vertebrate and invertebrate body fossils. Invertebrate fossils are concentrated mainly in shelly coquinas (Fig. 2), and consist of gastropods, bivalves, and crustaceans (barnacles and lobsters). Trace fossils (*Skolithos*) are common in the sands above and below the bonebed.

Although most abundant in the bonebed, vertebrate remains are found throughout the sands of the bonebed sequence. The bonebed has yielded at least five avian genera, including *Sula*, *Phalacrocorax*, *Diomedea*, a penguin, and a probable pelagornithid. All of the bird remains in the bonebed are completely disarticulated and most show evidence of transport abrasion and bioerosion. Apart from avian fossils, the bonebed also contains a diverse assemblage of cetaceans, monachine pinnipeds, teleost fish, and selachians totaling over 45 taxa. The anatomical nomenclature used in the text and figures follows that of Van Tets et al., 1988.

### SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

PELECANIFORMES Sharpe, 1891

Family SULIDAE Reichenbach, 1849

Genus *SULA* Brisson, 1760

*SULA* sp.

**Material**—Proximal left ulna (UOP/01/76), proximal right tarsometatarsus (UOP/01/74), posterior right mandible (UOP/01/91).

### Description

**Tarsometatarsus (Fig. 3A, B)**—The shaft is anteroposteriorly compressed with a somewhat wider proximal end diag-

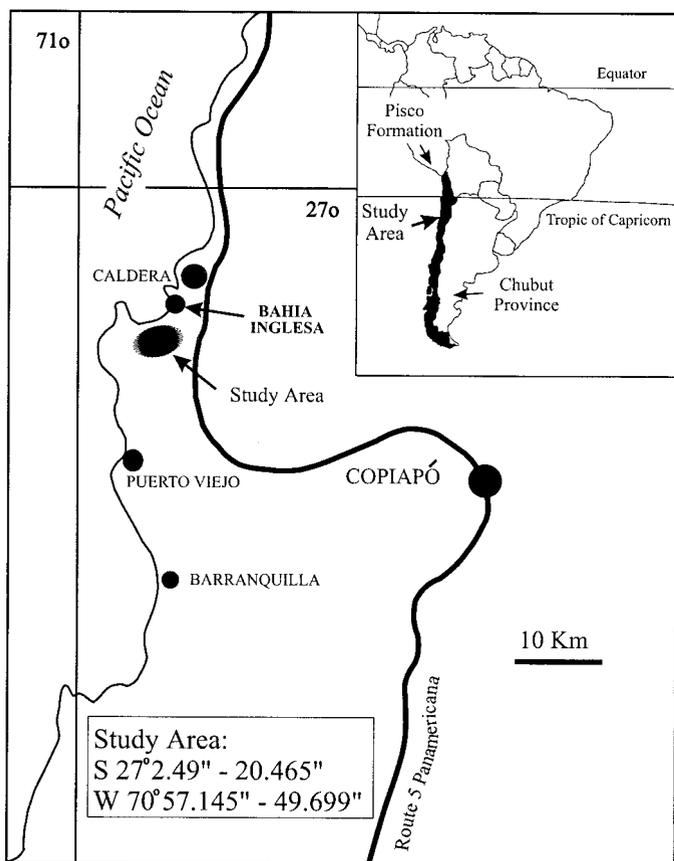


FIGURE 1. Location of study area. Approximate area of phosphorite development is shown by shaded oval.

nostic of *Sula* (Van Tets et al., 1988). The hypotarsus is damaged and contains a fairly small enclosed medial canal, which is situated centrally in the medial calcaneal ridge. Both the outer and middle calcaneal ridges are fused and lack a tendinal canal. This condition is diagnostic for *Sula* (excluding *S. abbotti*, Van Tets et al., 1988). The arrangement and relative size of these features of the hypotarsus are very similar to *S. leucogaster*. Two large foramina are present on the proximal medial surface, a distinctive feature of the Sulidae.

**Ulna (Fig. 3C–E)**—The proximal radial depression of this specimen is a moderately-deep equilateral triangle with two foramina. The presence of these foramina is diagnostic for *Sula* (Van Tets et al., 1988), and this feature is identical to that seen in *S. variegata*.

**Mandible (Fig. 3F, G)**—The medial cotyla is deep and lunate due to the position of the intercotylar crest. The fossa for the aditus canal is small, deep and situated in the dorsal half of the medial surface where it is bounded dorsally by the thickening of the coronoid process. The coronoid process is strong and well defined, as is the tubercle for the post-orbital ligament. The arrangement and position of these features is similar to *Sula variegata*.

**Discussion**

The Sulidae has an extensive and diverse fossil record (Olson, 1985) with Neogene sulids recorded from the Miocene and Pliocene Pacific areas of Japan, Mexico and California (Warheit, 1992). They also are known in the Atlantic Miocene, Maryland (Wetmore, 1938) and the Pliocene of Florida (Emslie

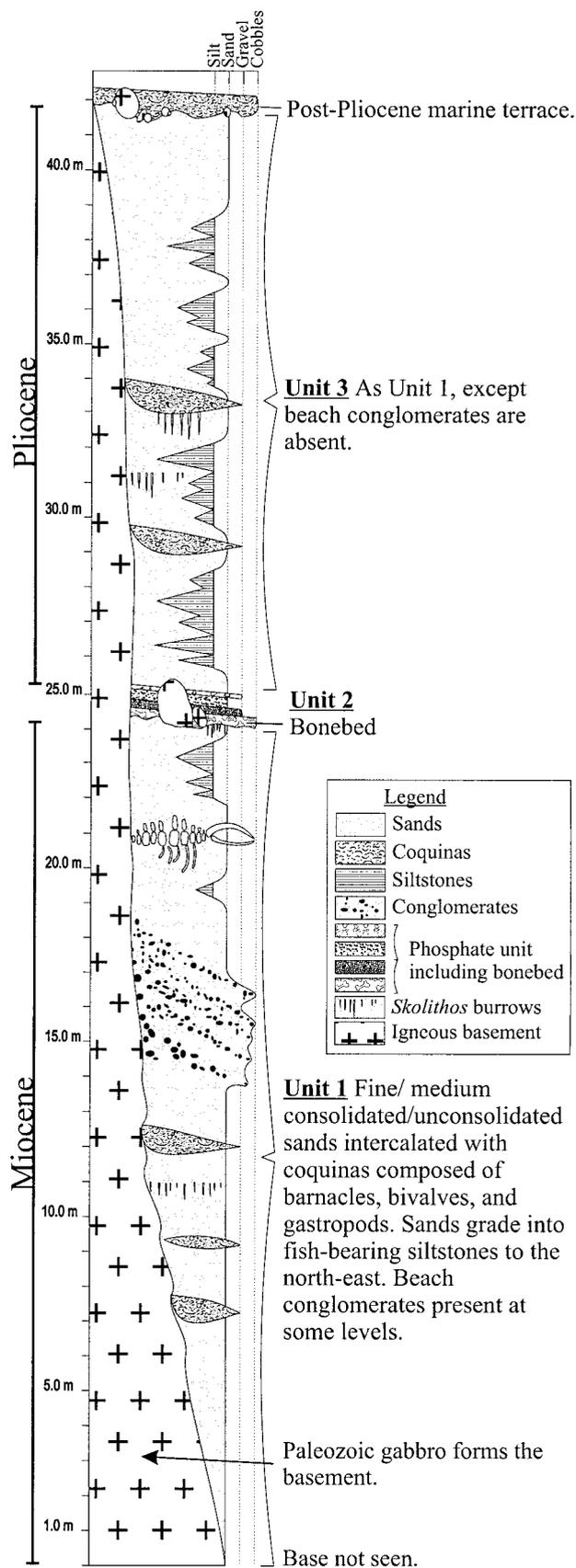


FIGURE 2. Composite log of the Bahía Inglesa bonebed sequence.

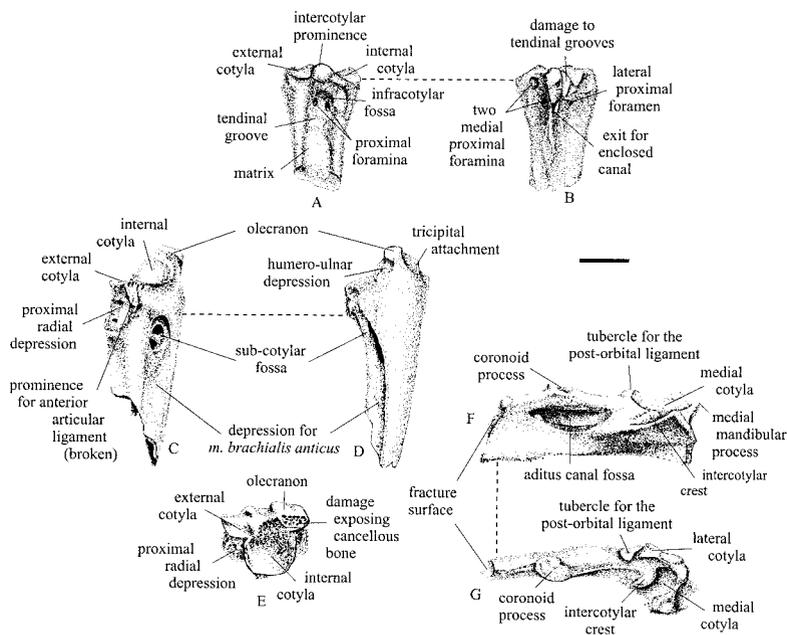


FIGURE 3. *Sula* sp. tarsometatarsus (UOP/01/74) in **A**, anterior and **B**, posterior aspects; left ulna (UOP/01/76) in **C**, medial, **D**, medio-anconal, and **E**, proximal aspects; and right mandible (UOP/01/91) in **F**, medial, and **G**, dorsal aspects. Scale bar equals 10 mm.

and Morgan, 1994). Sulid remains also are abundant in the Miocene and Pliocene sediments of the Pisco Formation, Peru, where up to three species of sulid are suspected (Cheneval, 1993). Considering the comparative proximity of the two sites on the western coast of South America, the Chilean sulid specimens might be referable to one or more of the Peruvian taxa. Unfortunately, the Peruvian sulids have not been described. As that material is more abundant and complete than ours, a description based on the Pisco avifauna is more appropriate.

Family PHALACROCORACIDAE Bonaparte, 1854  
 Genus *PHALACROCORAX* Brisson, 1760  
*PHALACROCORAX* sp.

**Material**—Distal right humerus (UOP/01/01).

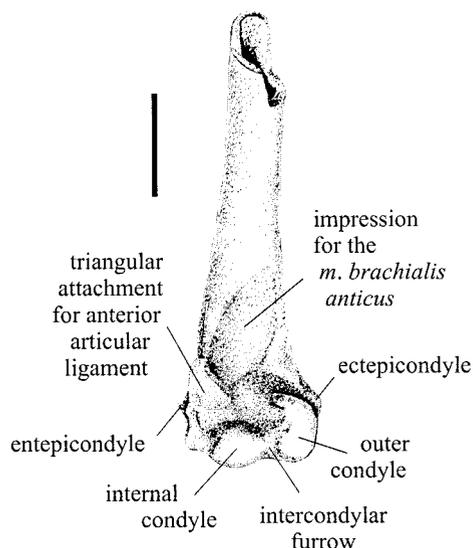


FIGURE 4. *Phalacrocorax* sp. distal left humerus (UOP/01/01) in palmar aspect. Scale bar equals 10 mm.

**Description**

**Humerus (Fig. 4)**—This specimen is well preserved. The impression for *m. brachialis anticus* is well defined and trap-ezoidal in outline. The attachment for the anterior articular ligament is flat and triangular in shape, unlike the raised oval seen in *Anhinga*. Although slightly smaller, this element is most similar to *P. bougainvillii*, especially in the shape of the anterior articular ligament attachment.

**Discussion**

*Phalacrocorax* in the east Pacific is known from the Mid-Miocene and Late Pliocene of California (Warheit, 1992), and from the Late Pliocene of Florida (Emslie and Morgan, 1994; Emslie, 1995a). As the earliest record of the genus in South America is from the Mid-Miocene Pisco Formation, Peru (Muiszon and DeVries, 1985; Cheneval, 1993), it is not surprising that *Phalacrocorax* was present in Chile by the Early Pliocene. It is again possible that this taxon is conspecific with the Pisco cormorant, but the latter material is presently undescribed.

ODONTOPTERYGIA Spulski, 1910  
 Family PELAGORNITHIDAE Fürbringer, 1888  
 Indeterminate pelagornithid

**Material**—Left carpal digit (UOP/01/81), two right tarsometatarsi (UOP/01/79, UOP/01/80). One tarsometatarsus (UOP/01/79) is missing the central portion of the diaphysis. The other (UOP/01/80) is still in a block of matrix and is missing the anterior surface of the diaphysis including most of the distal cotylae.

**Description**

**Tarsometatarsus (Fig. 5A–E)**—These bones are very large (UOP/01/80 is 105 mm in length) and thin walled. The diaphysis is square in section, becoming anterior dorsally compressed and more rounded toward the distal end. The extensor groove is deep and extends three quarters of the way to the distal cotylae. Proximally, the extensor groove holds a deep fossa in

which the proximal foramina are partially hidden by matrix. In proximal aspect, the outer cotyla rises higher than the inner, and the intercotylar depression is a flattened. The hypotarsus is triangular in posterior view and nearly identical to BMNH A4962, a “procellariiform” formerly identified as *Odontopteryx* from the London clay of England (Harrison and Walker, 1976). In UOP/01/79, the lateral tendinal canal is damaged, but was almost certainly open to form a groove. The middle canal is enclosed but small and the medial canal forms a distinct groove as in BMNH A4962. The hypotarsus becomes more prominent laterally. The medial calcaneal ridge is damaged, but does not appear to have risen higher than the intercotylar prominence. The distal end (UOP/01/79) is similar to *Diomedea*, where the trochlea for digit II is flared and turned proximally and posteriorly. All trochleae are deeply grooved and trochleae II and IV are shorter than trochlea III, such that the distal end is rounded in dorsal aspect.

**Digit (Fig. 6)**—The specimen has slight damage on both proximal and distal extremities and is set in a block of matrix. The bone is large for a wing digit (length = 79 mm) and, as on all of the specimens, the bone wall is extremely thin (less than a millimeter in places). Such large yet thin bones are characteristic of the pelagornithids (Olson, 1985).

## Discussion

Due to lack of comparative material, the digit and tarsometatarsi do not allow identification to genus. However, the bones are similar to pelagornithid specimens in the collections of the U.S. National Museum, Smithsonian Institution. At present, pelagornithid taxonomy is unresolved and many specimens appear to have been named and referred to this group purely on the basis of size and bone wall thinness. These are unsound characteristics on which to base a taxonomic diagnosis. Until a thorough review has been published, we prefer not to name these specimens as a new taxon.

Pelagornithids must have had a near cosmopolitan distribution during the Neogene, and are recorded from the Early Miocene of British Columbia and Oregon (Olson, 1985), Middle Miocene of Japan (Warheit, 1992), France, Maryland and Virginia (Olson, 1985), Late Miocene of California (Warheit, 1992), Miocene and Pliocene of New Zealand (Scarlett, 1972; McKee, 1985), and Miocene or Early Pliocene of Carolina (Olson, 1985). Remains referred to *Pelagornis* (Cheneval, 1993) have been recovered from the Miocene and Pliocene sediments of the Peruvian Pisco Formation (Muizon and DeVries, 1985). The Chilean material falls within the size range of *Pelagornis*, but as none of the specimens described here are known for this genus, direct comparison is presently not possible.

PROCELLARIIFORMES Fürbringer, 1888

DIOMEDEIDAE Gray, 1840

Genus *DIOMEDEA* Linnaeus, 1758

*DIOMEDEA* sp.

**Material**—Proximal right humerus (UOP/01/78), synsacrum (UOP/01/75) missing small portions of lateral margins and anterior and posterior surfaces.

## Description

**Humerus (Fig. 7A, B)**—This specimen is missing much of the distal portion of the palmar surface; most of the anconal surface is covered by matrix. The deltoid crest is well developed and is thicker and more prominent than in *Macronectes*, becoming thicker distally on the anconal surface. The bicapital crest extends one and a half times the length of the deltoid crest and terminates in a well-developed tuberosity as in *D. chrysoloma* and *D. melanophrys*.

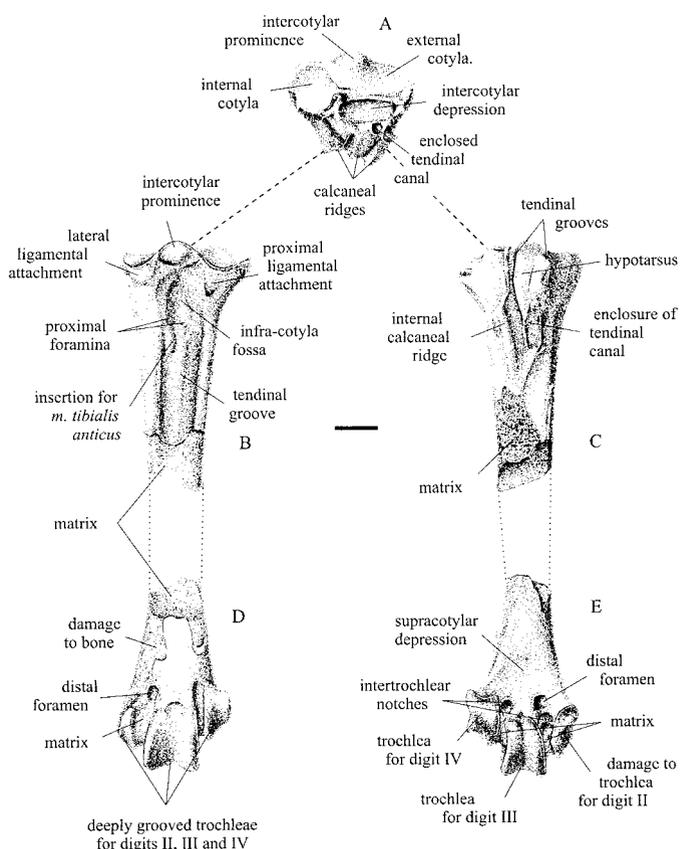


FIGURE 5. Pelagornithid right tarsometatarsus (UOP/01/79) in **A**, proximal aspect; **B** and **D**, anterior aspect; **C** and **E**, posterior aspect. Scale bar equals 10 mm.

**Synsacrum (Fig. 7C)**—Much of the cortical bone is missing on the dorsal surface, and the bone wall is thinner here than on the ventral surface. The ventral surface is flattened with a slight concavity extending along its length. The acetabulae are slightly damaged, but are fully fused to the synsacral body.

## Discussion

This material is smaller than the equivalent elements in *Diomedea cauta* and *D. exulans*, the two largest extant species of albatross in the area. The synsacrum is comparable in size and shape to that of *D. melanophrys*, but the vertebral transverse processes in that species are more dorsoventrally flattened than in UOP/01/75. The synsacrum is most similar to *D. bulleri* (Buller's Albatross) in both size and morphology, but the humerus is insufficiently complete to allow identification beyond generic level.

Fossils of *Diomedea* are known in the Pacific from the Mid-Miocene to Late Pliocene of California (Warheit, 1992), Mid-Miocene of Oregon (Olson, 1985) and the Late Miocene of Australia (Wilkinson, 1969). The Diomedidae has also been reported from the Atlantic Late Miocene of Argentina (Olson, 1984). Albatrosses currently are common on the coast of Chile, but occur more frequently over the open sea. Except for nesting, this would seem to limit their potential for fossilization in a coastal environment.

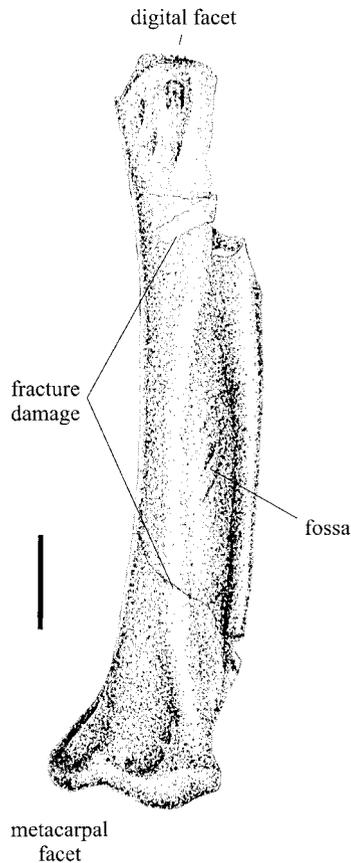


FIGURE 6. Pelagornithid major carpal digit (UOP/01/81) in lateral aspect. Scale bar equals 10 mm.

SPHENISCIFORMES Sharpe, 1891  
 Family SPHENISCIDAE Bonaparte, 1831  
 cf. *SPHENISCUS* Moehring, 1758

**Material**—Incomplete skull (UOP/01/93), rostrum (UOP/01/89), seven left humeri (UOP/01/35–UOP/01/37, UOP/01/39–UOP/01/41, UOP/01/84), six right humeri (UOP/01/34, UOP/01/38, UOP/01/42–UOP/01/45), two humeri of indeterminate side (UOP/01/46, UOP/01/47), right ulna (UOP/01/72), four left carpometacarpi (UOP/01/64–UOP/01/67), right carpometacarpus (UOP/01/68) five left coracoidea (UOP/01/48, UOP/01/50, UOP/01/52, UOP/01/55, UOP/01/57), eight right coracoidea (UOP/01/49–UOP/01/51, UOP/01/53, UOP/01/54, UOP/01/56, UOP/01/58, UOP/01/92), 8<sup>th</sup> thoracic vertebra (UOP/01/02), caudal vertebra (UOP/01/05), three cervical vertebrae (UOP/01/03 (9<sup>th</sup>), UOP/01/04 (11<sup>th</sup>), UOP/01/83), five synsacra (UOP/01/59–UOP/01/63), seven left femora (UOP/01/21–UOP/01/24, UOP/01/28–UOP/01/30), nine right femora (UOP/01/19, UOP/01/20, UOP/01/25–UOP/01/27, UOP/01/31–UOP/01/33, UOP/01/85), eight left tibiotarsi (UOP/01/07–UOP/01/09, UOP/01/14–UOP/01/18), six right tibiotarsi (UOP/01/06, UOP/01/10–UOP/01/13, UOP/01/82), left fibula (UOP/01/90), left tarsometatarsus (UOP/01/71), two right tarsometatarsi (UOP/01/69, UOP/01/70), and left pelvis (UOP/01/73).

### Description

The post-cranial remains compare well with *Spheniscus* and are most similar to those of *Spheniscus humboldti*, the dominant species presently living in the area. However, by using reconstructed lengths of the humeri ( $n = 13$ , mean = 92 mm, SD =

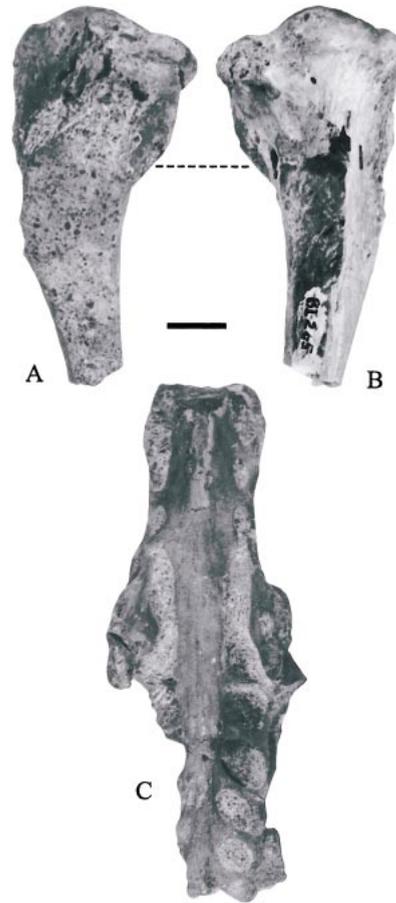


FIGURE 7. *Diomedea* sp. right humerus (UOP/01/78) in **A**, palmar and **B**, anconal aspects; **C**, synsacrum (UOP/01/75) in ventral aspect. Scale bar equals 10 mm.

9.3 mm) we note that these penguins were apparently 25% larger than *S. humboldti*. Most of the skeletal elements of this penguin are represented, although our skull specimen is presently under preparation. Caution should be exercised when using post-crania in a diagnosis of spheniscid species, and it is thus not the intention of this paper to describe the specimens as a new taxon.

### Discussion

Fossil penguins are well known in South America (Fordyce and Jones, 1990). The only fossil record of *Spheniscus* comes from the Late Pliocene of South Africa (Simpson, 1971; but see Olson, 1983). Two species of fossil spheniscid are reported from the coeval sediments of the Pisco Formation, Peru (Muirson and DeVries, 1985; Cheneval, 1993), although neither has been described despite the recovery of abundant articulated and well-preserved remains. Comparison of our post-crania with specimens of the larger of these two species housed at SMNK indicates that the Chilean and larger Pisco specimens are probably referable to the same species. Comparison of skull characters is needed to test this hypothesis, but this cannot be achieved until preparation of the Chilean material is complete.

Extant species of *Spheniscus* are moderately sexually dimorphic (Livezey, 1989), but there is no evidence of sexual dimorphism in the Chilean specimens. Juveniles are well represented close to penguin rookeries (Emslie, 1995b), but do not appear to be represented in the bonebed. This would seem to

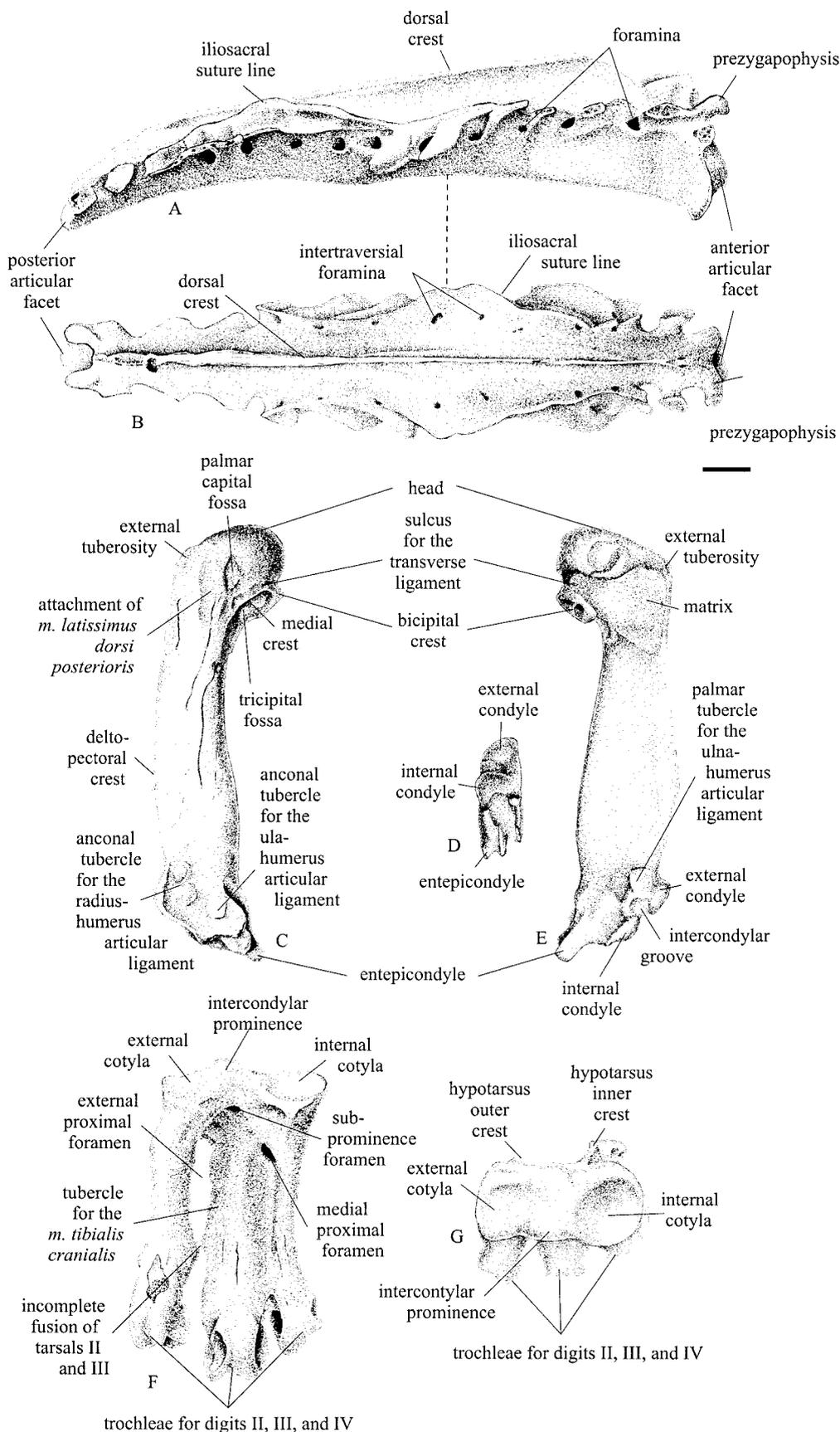


FIGURE 8. Spheniscid material. Synsacrum (UOP/01/59) in **A**, right lateral and **B**, dorsal aspects; left humerus (UOP/01/41) in **C**, anconal, **D**, distal, and **E**, palmar aspects; right tarsometatarsus (UOP/01/70) in **F**, anterior, and **G**, proximal aspect. Scale bar equals 10 mm.

exclude the possibility that the penguin remains were derived from a terrestrial breeding colony. However, the absence of juveniles is probably a taphonomic artifact, as individuals too young to swim are presumably unlikely to be buried in a marine environment.

#### PALEOECOLOGY

The faulted gabbro basement apparently formed emergent outcrops throughout much of the depositional period of the sequence. Comminuted remains of barnacles and cementing bivalves become more common proximal to the largest basement outcrop, where an accretionary wedge onlaps the basement beneath the bonebed. Cementing *Ostrea* sp. also are observed in situ, suggesting strong wave action on a rocky feature that may have been at least partially emergent during bonebed formation. The gabbro outcrops probably formed a shallow, partially enclosed bay similar to that in the same area today. It is therefore likely that the gabbro was an island habitat for seabirds; a reconstruction further supported by the abundance of penguin bones. There presently are many analogous rocky islands in the area used by seals and various sea birds for refuge and breeding.

The fully marine composition of the avifauna suggests a distal setting relative to the paleoshoreline, and the selachian fauna is characterized by sublittoral species (e.g., Karasawa, 1989), indicating a water depth of less than 200 m. *Skolithos* facies is common in the sands above and below the bonebed. Burrow preservation of such opportunistic organisms is really a taphofacies (Bromley and Asgaard, 1991) indicating the presence of shifting sand environments subject to rapid deposition and erosion. Normally this is common in the shallower littoral zone (0–10 m), but *Skolithos* may be present in much deeper waters (Bromley, 1996). Today, water deeper than 200 m is encountered in the area no more than 5 km from shore. Given that the tectonic setting throughout the depositional period of the bonebed would have been as it is today, the shore was probably less than 5 km from the site of deposition.

As in the area today, predation of the birds probably would have been by selachians and pinnipeds. Direct evidence for shark predation is provided by UOP/01/92, a spheniscid right coracoid that shows the bite marks of a shark with a cutting type of dentition similar to that of *Carcharhinus* (Fig. 9). These cuts were made by a shark with small teeth, probably biting obliquely across the width of the penguin toward the head region. The cut marks follow the curve of the bone, perhaps indicating that the shark was in motion as it made the bite. Although this suggests active predation, scavenging of a carcass is not precluded.

#### CONCLUSIONS

The Bahia Inglesa bonebed represents an important and abundant source of marine avian fossils. Furthermore, as the assemblage is the first of its kind in Chile, the specimens recovered provide important information regarding the paleobiogeography of seabird families during the late Tertiary. The presence of the spheniscid may prove significant in the taxonomy and radiation of the genus *Spheniscus*, but the relationship of the Chilean penguin is at present unclear. The Chilean penguin specimens are similar to those from the Pisco Formation of Peru, and the two may prove to be synonymous. Formal descriptions of both taxa are still required for this to be resolved. Although bulk sampling is not possible due to the nature of the matrix, it is likely that further collection from the site will yield additional taxa.



FIGURE 9. Shark predation/scavenging marks on a spheniscid right coracoid (UOP/01/92). Diagonal cut marks cover most of the ventral surface, and the larger cuts extend from lateral to medial margins. Note the lifted bone slivers that indicate that the bite was angled distally. Scale bar equals 10 mm.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- Bromley, R. G. 1996. Trace fossils: Biology, Taphonomy and Applications, 2nd ed. Chapman and Hall, London, pp. 361.  
 ———, and U. Asgaard. 1991. Ichnofacies: a mixture of taphofacies and biofacies. *Lethaia* 24:153–163.  
 Cheneval, J. 1993. L'Avifaune Mio-Pliocène de la Formation Pisco (Pérou) Étude préliminaire. Documents des Laboratoires de Géologie Lyon 125:85–95.

- Emslie, S. D. 1995a. A catastrophic death assemblage of a new species of cormorant and other seabirds from the Late Pliocene of Florida. *Journal of Vertebrate Paleontology* 15:313–330.
- . 1995b. Age and taphonomy of abandoned penguin rookeries in the Antarctic Peninsula region. *Polar Record* 31:409–418.
- , and G. S. Morgan. 1994. A catastrophic death assemblage and paleoclimatic implications of Pliocene seabirds of Florida. *Science* 264:684–685.
- Fordyce, R. E., and C. M. Jones. 1990. Penguin history and new fossil material from New Zealand; pp. 419–446 in L. S. Davis and J. T. Darby (eds.), *Penguin Biology*. Academic Press.
- Harrison, J. O., and C. A. Walker. 1976. A review of the bony-toothed birds (Odontopterygiformes): with descriptions of some new species. *Tertiary Research Special Paper* 2.
- Ibaraki, M. 1995. Neogene chronostratigraphy of biosiliceous sediments on the Pacific coast of South America based on planktonic foraminifera. *Reports of the Faculty of Science, Shizuoka University* 29:63–71.
- Karasawa, H. 1989. Late Cenozoic elasmobranchs from the Hokuriku district, central Japan. *Science Reports of Kanazawa University* 34: 1–57.
- Livezey, B. C. 1989. Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). *Journal of the Zoological Society of London* 219:269–307.
- Long, D. J. 1993. Late Miocene and Early Pliocene fish assemblages from the north central coast of Chile. *Tertiary Research* 14:117–126.
- McKee, J. W. A. 1985. A pseudodontorn (Pelecaniformes: Pelagornithidae) from the middle Pliocene of Hawera, Taranaki, New Zealand. *New Zealand Journal of Zoology* 12:181–184.
- Muizon, C. de, and T. J. DeVries. 1985. Geology and Paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74:547–563.
- Olson, S. L. 1983. Fossil seabirds and changing marine environments in the Late Tertiary of South Africa. *South African Journal of Science* 79:399–402.
- . 1984. Evidence of a large albatross in the Miocene of Argentina (Aves: Diomedidae). *Proceedings of the Biological Society of Washington* 97:741–743.
- . 1985. The fossil record of birds; pp. 79–252 in D. S. Farner, J. R. King, and C. Parkes (eds.), *Avian Biology* 8. Academic Press, New York.
- Rojo, M. A. 1985. Un aporte al conocimiento del Terciario marino: Formacion Bahía Inglesa. *Actas Congreso Geológico Chileno* 4: 1.514–1.533.
- Scarlett, R. J. 1972. Bone from a presumed odontopterygian bird from the Miocene of New Zealand. *New Zealand Journal of Geology and Geophysics* 15:269–274.
- Simpson, G. G. 1971. Fossil penguin from the late Cenozoic of South Africa. *Science* 171:1144–1145.
- . 1975. Fossil Penguins; pp. 19–44 in B. Stonehouse (ed.), *The Biology of Penguins*. MacMillan Press.
- Tsuchi, R., T. Shuto, T. Takayama, A. Fujiyoshi, I. Koizumi, M. Ibaraki, and P. R. Martinez. 1988. Fundamental data on Cenozoic biostratigraphy of Chile; pp. 1–108 in R. Tsuchi (ed.), *Reports of Andean studies, Shizuoka University-Trans-Pacific correlation of Cenozoic Geohistory* 2. Kofune Printing, Shizuoka.
- Van Tets, G. F., C. W. Meredith, P. J. Fullagar, and P. M. Davidson. 1988. Osteological differences between *Sula* and *Morus*, and a description of an extinct new species of *Sula* from Lord Howe and Norfolk Islands, Tasman Sea. *Notornis* 35:35–57.
- Warheit, K. I. 1992. Overview of the fossil seabirds from the Tertiary of the North Pacific: plate tectonics, paleoceanography, and faunal change. *Paleobiology* 18:401–424.
- Wetmore, A. 1938. A Miocene booby and other records from the Calvert Formation of Maryland. *Proceedings of the United States National Museum* 85:21–25.
- Wilkinson, H. E. 1969. Description of an upper Miocene albatross from Beaumaris, Victoria, Australia, and a review of fossil Diomedidae. *Memoirs of the National Museum of Victoria* 29:41–51.

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