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Pinniped turnover in the South Pacific Ocean: new evidence from the Plio-Pleistocene of the Atacama Desert, Chile

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Pinniped turnover in the South Pacific Ocean: New evidence from the Plio-Pleistocene of the Atacama Desert, Chile

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ABSTRACT—Modern pinnipeds distributed along the coasts of continental South America consist almost entirely of otariids (sea lions and fur seals). In contrast, phocids (true seals) are present only on the southernmost extreme of Chile. This recent biogeographic pattern is consistent with the zoological record (c. 8–2 ka), but it is incompatible with the pinniped fossil record during the Neogene. From the middle Miocene to the Pliocene, true seals exclusively dominated pinniped assemblages, and they were only replaced by the fur seals and sea lions sometime after the early Pliocene. Here, we describe pinniped material collected from two new localities in the Atacama Desert, northern Chile, that clarifies this marine mammal faunal turnover. Specifically, these finds provide records of the first occurrence of Otariidae (late Pleistocene) and the last occurrence of Phocidae (early Pliocene) in Chile, which in turn constrain the timing of this turnover to between the early Pliocene and late Pleistocene. The stratigraphic context of these findings provides new insights into hypotheses that explain this faunal turnover in South America, and we briefly discuss them in the context of turnover events involving other marine vertebrates throughout the Southern Hemisphere.

INTRODUCTION

Modern members of the carnivoran clade Pinnipedia are included in three families: Phocidae (true seals), Otariidae (fur seals and sea lions), and Odobenidae (walruses), which together constitute one of the most widely distributed groups of marine mammals (Deméré et al., 2003). Their global, historical biogeography and dispersal patterns have attracted considerable attention (e.g., Davies, 1958; Repenning et al., 1979; Arnason et al., 2006; Koretsky and Barnes, 2006), although few publications (e.g., Deméré et al., 2003; Fulton and Strobeck, 2010) have developed testable hypotheses for observed patterns, invoking changes in global ocean circulation as putative evolutionary drivers during the late Paleogene and Neogene. Equally interesting, though sometimes neglected, are the faunal turnovers or evolutionary changes within regional assemblages over geologic time. In this approach, the fossil record provides important data about the taxonomic composition of assemblages, which can be compared with extant distributions, evoking questions about the pace and degree of evolutionary change and extinction (Jernvall and Fortelius, 2004; Badgely et al., 2008; Raia et al., 2012). Previously, evidence for wholesale faunal turnovers in pinnipeds had been noted by Olson (1983) along South African coasts during the Neogene, where the once abundant monachine seals (Homiphoca capensis) have gone extinct and been completely replaced by the extant otariid Arctocephalus pusillus. In the same way, Boesseneker (2011) offered turnover hypotheses to explain the evolution of otariids in the eastern North Pacific Ocean during the Neogene, where the basal otariid genus Callorhinus maintained its northern distribution after the extinction of stem walruses in the Pliocene, concomitant with the arrival of other otariid and phocid species in the area.

In South America, phocids were present from the middle Miocene until the early Pliocene in Peru and Argentina (Muizon and Hendey, 1980; Muizon, 1981; Muizon and Bond, 1982; Cozzuol, 1996, 2001; Varas-Malca and Valenzuela-Toro, 2011). In Chile, the published record of pinnipeds prior to the present study is restricted to late Miocene phocid records from upper units of the Bahía Inglesa Formation (Walsh and Naish, 2002; Valenzuela et al., 2009). On the other hand, the oldest fossil records of otariids in South America are from the late Pliocene–early Pleistocene of Peru (Muizon, 1978; Muizon and Domning, 1985), and the Pleistocene Chuí Formation of Brazil (Drehmer and Ribeiro, 1998). The relatively poor pinniped fossil record in South America during the late Neogene–Pleistocene has limited our understanding of faunal turnover in this part of the world.

New pinniped material from the coast of northern Chile, reported herein, includes phocid and otariid remains from a new Pliocene locality of the Bahía Inglesa Formation, and a new Pleistocene locality called Cerro Ballena, both in the Caldera Basin. These finds constitute the youngest and the oldest unequivocal records of Phocidae and Otariidae, respectively, in Chile, and provide new information regarding the timing of pinniped faunal turnover that occurred in the eastern South Pacific Ocean.
The phocid specimens (SGO.PV 21172–21173) were the only phocid specimens recovered from locality PPC JFP 217, near Caldera, Atacama Region, Chile (Fig. 1). This locality is part of a broad exposure called Los Negros, within the Bahía Inglesa Formation (Rojo, 1985; middle Miocene–late Pliocene, based on the work of Achurra, 2004; Achurra et al., 2009). Phocids are from the same level that has produced a tarsometatarsus referred to the penguin *Pygoscelis grandid* (SGO.PV 1104). This stratum has been previously correlated with the Lecher Member of the Bahía Inglesa Formation (Walsh and Suárez, 2006). Microfossil biostratigraphy supports an age of 4.5–2.6 Ma for the Lecher Member (Tsuchi et al., 1988; Ibaraki, 1995). However, Marquardt et al. (2000) and Godoy et al. (2003) assigned a late Miocene age for the lower part of the Lecher Member based on an ash bed situated approximately 7 m above the top of the Bonebed Member of the Bahía Inglesa Formation that yielded a K-Ar date of 7.6 ± 1.3 Ma. Although this ash could be reworked (Achurra, 2004), all of the known fauna from the Lecher Member are in line with the marine vertebrate occurrences from Los Negros. The presence of the shark *Carcharodon carcharias* suggests a Pliocene age for this locality, as this taxon has for Neogene localities in Peru (Muizon and DeVries, 1985). Unfortunately, the oldest record of this species also occurs in the late Miocene of Chile (Suárez and Marquardt, 2003; Walsh and Martill, 2006), which means that this taxon cannot be used to distinguish Miocene and Pliocene strata in Chile. A Pliocene age for the Los Negros locality is supported by the occurrence of another shark, *Prionace glauca*, which Suárez and Marquardt (2003) recognized as a better Pliocene age marker than *Carcharodon* for Neogene, Chilean localities. In fact, the global fossil record of *P. glauca* indicates an age range no older than Zanclean (lower Pliocene) (see Landini, 1977; Cappetta, 1987; Suárez and Marquardt, 2003). The preponderance of available faunal evidence leads us to propose a Zanclean age for locality PPC JFP 217 and phocids SGO.PV 21172 and SGO.PV 21173.

The otarid specimens (MPC 15500–15503) were collected from locality PPC CSG 021011, approximately 5 km north of Caldera, along the Pan-American Highway (Fig. 1). MPC 15500–15503 were recovered from the basal part of a transgressive-regressive marine terrace sequence, corresponding to the Pleistocene marine deposit called Estratos de Caldera (Godoy et al., 2003). The Estratos de Caldera unconformably overlies the Bahía Inglesa Formation at the Cerro Ballena locality, and associated molluscan species with chronostratigraphic ranges known throughout the Pleistocene (*Concholepas concaveolas, Fisurrella crassa, Turritella cingulata, Chorus giganteus*, and *Protothaca thaca*; Guzmán et al., 2000) confirm this age assignment. More recent studies on the marine isotope stage (MIS) of the specific marine terrace where the otarid fossils were found indicate a geochronologic age of 105 ± 5 ka (MIS 5 of Marquardt et al., 2004; Quezada et al., 2007), and thus assign this sequence a late Pleistocene age. We follow Gibbard et al. (2010) in recognizing the Gelasian as the base of the Pleistocene.

**Institutional Abbreviations**—MPC, Museo Paleontológico de Caldera, Caldera, Chile; SGO.PV, Museo Nacional de Historia Natural, Santiago, Chile.

**Anatomical Abbreviations**—a, acromion; anp, angular process; c, lower canine; cc, coronoid crest of the scapula; cp, coronoid process of the scapula; csr, caudal scapular ridge; ef, ectal facet of the astragalis; ff, fibular facet of the astragalis; if, infraspinous fossa of the scapula; lf, lower molar teeth; mf, maseteric fossa; mc, mandibular condyle; mef, mental foramina; mf, mandibular foramen; mis, medial interarticular sulcus; nf, navicular facet; pc, lower postcanine teeth, with number corresponding to alveolar position(s); pec, partially erupted canine; r, radial styloid process; rt, radial tuberosity; sap, secondary angular process; sf, sustentacular facet of the astragalis; ss, secondary spine of the scapula; sp, scapular spine; sup, supraspinous fossa of the scapula; tf, tibial facet of the astragalis.

**SYSTEMATIC PALEONTOLOGY**

**PINNIPEDIA** Illiger, 1811 (sensu Bryant, 1996)

**PHOCIDAE** Gray, 1821 (sensu Berta and Wyss, 1994) Gen. et sp. indet.

**Referred Specimens**—SGO.PV 21172 and SGO.PV 21173, two mostly complete right astragali (Fig. 2); collected from locality PPC JFP 217, Lecher Member of the Bahía Inglesa Formation.

**Description**

**Astragali**—The astragali have elongated sustentacular and ectal facets, broadly separated by a wide interarticular sulcus immediately anterior to the caudal process, which is considered diagnostic for Phocidae (Wyss, 1988). This condition differs from that of otariids, which are characterized by long sustentacular facets that span the entire length of the astragalar neck, allowing for sustentacular and ectal facets to almost meet in this region (Wyss, 1988). The shape of the hypertrophied calcaneal process (= caudal process of Walsh and Naish, 2002) is the hind limb character that is used most often to differentiate among pinnipeds (Berta and Wyss, 1994; Wyss, 1988). The calcaneal process is very elongate in phocids, odobenids have a slight posterior extension of the calcaneal process, whereas in otariids, this process is absent (Wyss, 1988; Berta and Ray, 1990; Deméré, 1994). The calcaneal processes of the astragali reported here are mostly broken, although the incomplete base of the astragalus (which is better preserved in SGO.PV 21173; Fig. 2C–D) indicates the presence of this process. The navicular facet is preserved in both specimens and the proportions of the sustentacular facet, which is wider than the navicular facet, resembles the astragalar features of the phocid *Callophoca*. The overall rounded shape of the tibial and fibular facets, the extension of the plantar interarticular sulcus, and the shape of the sustentacular facet are similar to phocids such as *Piscophoca* (already described from other levels of the Bahía Inglesa Formation; Walsh and Naish, 2002). However, the incompleteness of SGO.PV 21172 and SGO.PV 21173 prevents us from...
making a more precise taxonomic determination beyond Phocidae.

OTARIIDAE Gray, 1825 (sensu Berta and Wyss, 1994) Gen. et sp. indet.

Referred Specimens—MPC 15503, a left radius, and MPC 15502, a left scapula (Fig. 3); collected from locality MPC CSG 021011-1.

Description

Radius—MPC 15503 is a complete left radius with marked anterio-posteriorly flattening and an expanded distal half, which is characteristic of Pinnipedia (Berta and Wyss, 1994). The styloid process is reduced, which is different from odobenids in which it is elongated (Deméré and Berta, 2005). The general shape of MPC 15503 is similar to extant otariid radii (i.e., the radius is narrow and rounded in cross-section at the radial neck, as well as broad, flat, and thin, dorsoventrally, at its distal end). In medial view, there is a prominent medial ridge (= bicipital rugosity in Pérard, 1971; bicipital tubercle in English, 1977) on the articular surface of the radius and the ventral limit of the articular circumference of the radius is raised, which according to Pérez-García (2003) is more prominent in Otaria than in Arctocephalus. However, because the radii of otariids lack additional diagnostic traits, it was not possible to give a more precise identification.

Scapula—MPC 15502 is an almost complete left scapula of an adult. The scapular spine is strongly extended along the lateral surface of the scapula. MPC 15502 has a robust secondary scapular spine (= scapular ridge of English, 1977) that extends along the entire length of the scapula, and subdivides the large supraspinous fossa. The secondary scapular spine is only found in Otariidae (Howell, 1930; Berta and Wyss, 1994). This structure has a small inflection in its most proximal half, which is Otaria-like in having a small curvature. This feature is different from Arctocephalus, which has a strong curvature (Pérez-García, 2003).
and similar to *Eumetopias*, which has a small curvature. The caudal scapular ridge borders the infraspinous fossa and nearly reaches the vertebral border.

**OTARIA** Perón, 1816
cf. **OTARIA FLAVESCENS** Shaw, 1800

**Referred Specimens**—MPC 15500, a left dentary, and MPC 15501, a right dentary (Fig. 4); collected from locality MPC CSG 021011-1.

**Description**

**Dentary**—MPC 15500 is a left dentary that is larger and more robust than MPC 15501. MPC 15500 only preserves the lateral part of cl, which is partially covered by sediment. The p1–m1 alveoli are also preserved. In dorsal view, the horizontal ramus is slightly bowed laterally at its anterior and posterior extremities. In lateral view, the mental foramina vary in size and are located below the p1–p3 alveoli. The coronoid crest extends anteroposteriorly and is more prominent posteriorly. The angular process (sensu Davis, 1964; = pterygoid process in Boesneck, 2011) is dorsomedially directed. The angular process is robust and located near the base of the ascending ramus, which is characteristic of otariids (Berta and Wyss, 1994). The marginal process (sensu Davis, 1964; = secondary angular process in Sanfelice and Ferigolo, 2008) is strongly projected dorsally, and its posterior border has a triangular shape. A well-developed marginal process is also present in Odobenidae (Deméré, 1994); nevertheless, it is useful to discriminate among otariids because in *Arctocephalus* it is barely patent, whereas in *Otaria* it is well developed (Sanfelice and Ferigolo, 2008). Therefore, the presence of a well-developed marginal process and the presence of a sinus ventral margin of the horizontal ramus allows us to identify this specimen as *Otaria*. The condylar process is incomplete (i.e., the medial portion absent), but its lateral portion is large, thick, and maintains a predominantly horizontal orientation. The mandibu-
The new phocid material from the lower Pliocene Los Negros locality of the Bahía Inglesa Formation represents the Lower Stratigraphic Datum (LSD; Walsh, 1998) of this family in the Caldera Basin. Additionally, the cranial and postcranial remains of indeterminate Otariidae and cf. *Otaria flavescens* (= *O. byronia* fide Berta and Churchill, 2012) from the late Pleistocene Estratos de Caldera are the oldest unequivocal records of this family in Chile. Together, these aggregate occurrences from Chile provide new stratigraphic data on the timing of pinniped faunal turnover in South America. Specifically, these data restrict the timing of the phocid to otariid transition to being between the late Pliocene to the middle Pleistocene.

The zooarchaeological record of South America, like that of North America (e.g., Rick and Erlandson, 2008), includes abundant otariid remains, which are associated with the northernmost Chilean, pre-Hispanic populations, dated ∼8 ka before present (Ovalle, 2011). Standen et al. (2004) documented otariid use and consumption ∼4.8 ka before present, and otariids were a strong component of the diet of the pre-Hispanic people of the south-central Chile (∼36°S; Quiroz and Sánchez, 2004). Until now, no phocid remains have been found associated with the zooarchaeological record of Chile.

The fossil and zooarchaeological records of both pinniped clades in Chile present two main (although not mutually exclusive) hypotheses to explain the phocid to otariid transition. In the first turnover hypothesis, early Pliocene phocids became regionally or globally extinct as a result of oceanographic changes or the elimination of their breeding habitat (see below). By the Pleistocene, the coasts were completely repopulated with otariids, which maintained a dominance of rocky shore habitats to the present day (Sielfeld, 1999). In the second turnover hypothesis, phocids and otariids co-occurred in the late Neogene, with a total richness of species greater than that observed today, until changing environments or habitats led to the persistence of otariids and the extirpation of phocids. According to this hypothesis, the absence of otariids in Pliocene rocks and the absence of phocids in Pleistocene rocks could be attributed to a poor fossil record. However, at least four phocid taxa have collectively been identified from the Neogene of Chile and Peru: *Piscophoca*, *Acrophoca*, and two new morphotypes: one from the late Miocene of the Bahía Inglesa Formation (Valenzuela-Toro et al., 2010a) and the other from the middle Miocene of the Pisco Formation (Varas-Malca and Valenzuela-Toro, 2011). The regional pinniped replacement seen along Chilean coasts is part of a broader Plio-Pleistocene pattern among marine vertebrates in the Southern Hemisphere, with faunal turnovers also occurring in South Africa (Olson, 1983), and possibly in Australia and New Zealand as well, although the fossil record of pinnipeds for this interval from Oceania is almost entirely represented by Pleistocene occurrences of extant lineages (King, 1983). In South Africa, the abundantly represented early Pliocene *Homiphoca capensis* was replaced by extant *Arctocephalus pusillus*, which is the dominant pinniped, by abundance, on the coast today, although putative otariid material from Koeberg hints at the coexistence of phocids and otariids in the early Pliocene as well (Avery and Klein, 2011). Olson (1983) observed a similar faunal
turnover in seabird communities off South Africa, which he associated with an intensifying Pleistocene shift in the oceanic currents of the Benguela Current System to colder conditions. Along the western coast of South America, Cione et al. (2007) also invoked similar mechanisms to explain the disjunct distribution patterns of pinnipeds in the Southern Hemisphere, it is clear that more collecting in productive, stratigraphically constrained sequences will yield better information to test the two hypotheses outlined above. Regardless, our new data from the Atacama Desert of Chile constrain the faunal turnover there to the time interval between the late Pliocene to the middle Pleistocene.

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**LITERATURE CITED**


Berta, A., and T. A. Deméré. 1986. Callorhinus gilmorei n. sp., (Carnivora: Otarididae) from the San Diego Formation (Blancan) and its regional assemblages from well-sampled sequences in the eastern North Pacific Ocean. For the strongly disjunct distribution patterns of pinnipeds in the Southern Hemisphere, it is clear that more collecting in productive, stratigraphically constrained sequences will yield better information to test the two hypotheses outlined above. Regardless, our new data from the Atacama Desert of Chile constrain the faunal turnover there to the time interval between the late Pliocene to the middle Pleistocene.

**FIGURE 5.** Map showing the occurrences of fossil pinnipeds in South America.
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