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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 zooarchaeological record (~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, Boessenecker

(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 Hendeby, 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.

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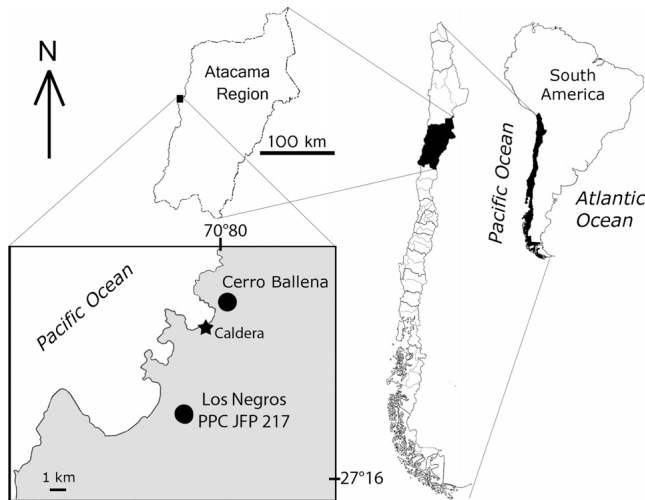


FIGURE 1. Map showing fossiliferous outcrops of the Bahía Inglesa Formation in the Atacama Region. The Estratos de Caldera overlies the Bahía Inglesa Formation at Cerro Ballena.

Geologic Context

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 grandis* (SGO.PV 1104). This stratum has been previously correlated with the Lechero Member of the Bahía Inglesa Formation (Walsh and Suárez, 2006). Microfossil biostratigraphy supports an age of 4.5–2.6 Ma for the Lechero 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 Lechero 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 Lechero Member are more 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 otariid specimens (MPC 15500–15503) were collected from locality PPC CSG 021011-1, 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 concholepas*, *Fisurella crassa*, *Turriella 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 otariid 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 astragalus; **ff**, fibular facet of the astragalus; **if**, infraspinous fossa of the scapula; **m**, lower molar teeth; **maf**, masseteric 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; **rsp**, radial styloid process; **rt**, radial tuberosity; **sap**, secondary angular process; **sf**, sustentacular facet of the astragalus; **ss**, secondary spine of the scapula; **ssp**, scapular spine; **sup**, supraspinous fossa of the scapula; **tf**, tibial facet of the astragalus.

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, Lechero 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 astragal 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 astragal 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

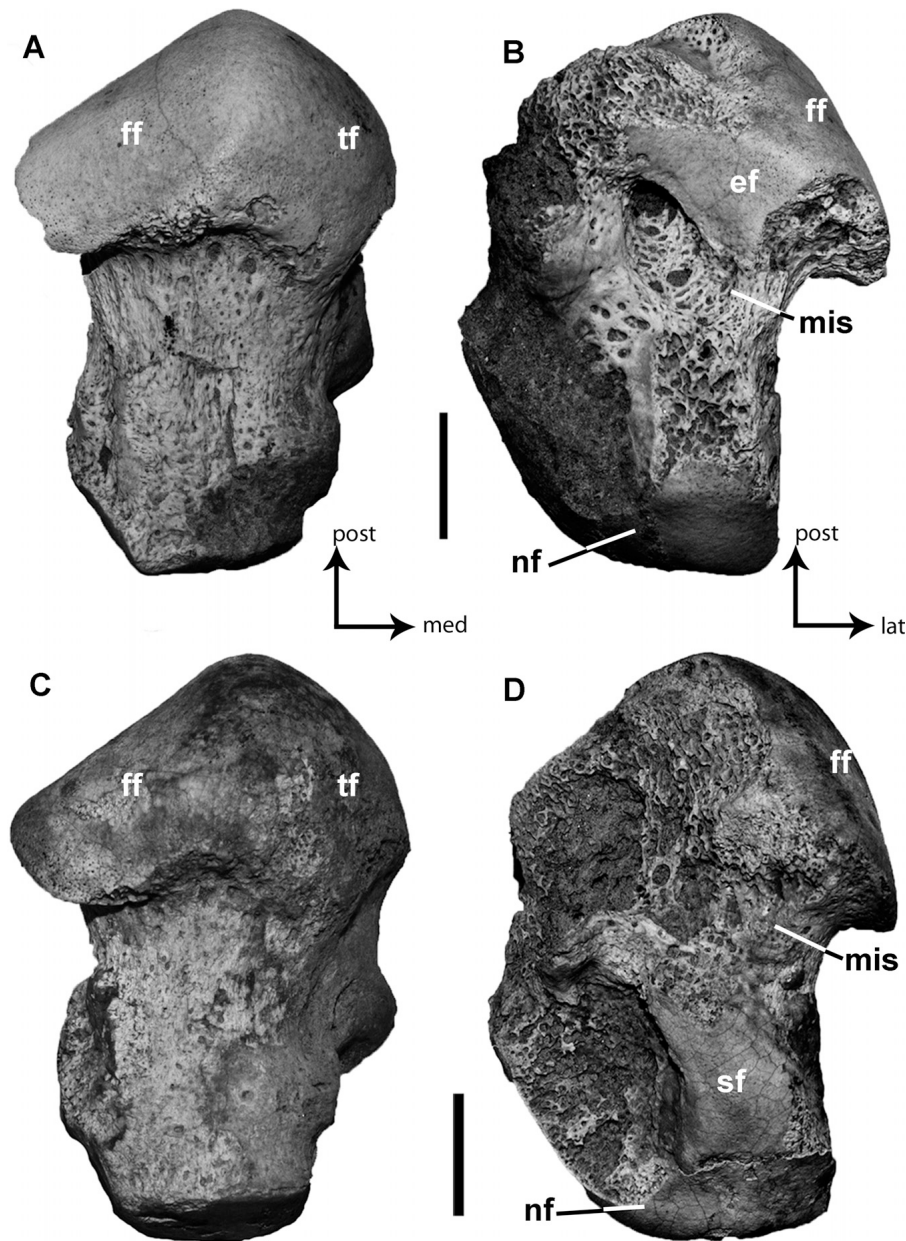


FIGURE 2. Phocid astragali from the Bahía Inglesa Formation. Both astragali are incomplete and missing the calcaneous process. **A–B**, incomplete right astragalus of Phocidae indet. (SGO.PV 21172) in dorsal (**A**) and plantar (**B**) views. **C–D**, incomplete right astragalus of Phocidae indet. (SGO.PV 21173) in dorsal (**C**) and plantar (**D**) views. All scale bars equal 1 cm.

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 anterior-posterior 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 Piérard, 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 suprascapular 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)

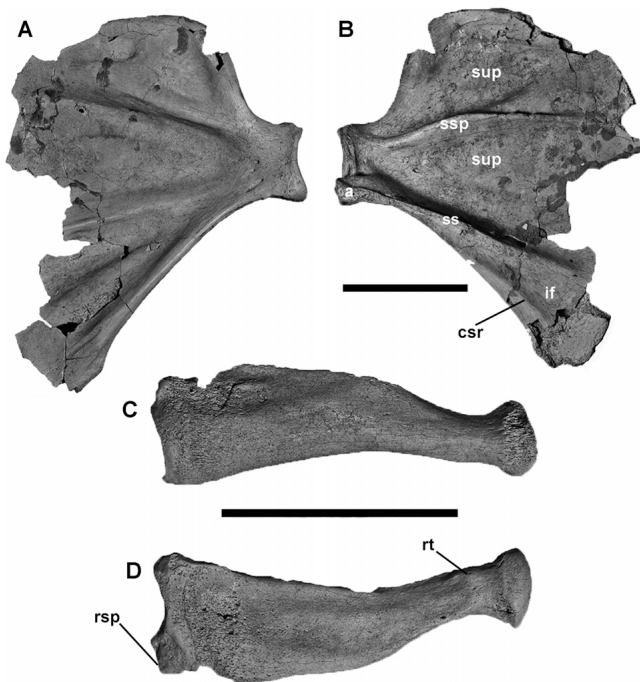


FIGURE 3. Postcranial remains of Otariidae. **A–B**, left scapula of Otariidae indet. (MPC 15502) in medial (**A**) and lateral (**B**) views. **C–D**, left radius of Otariidae indet. (MPC 15503) in lateral (**C**) and medial (**D**) views. Scale bar equals 10 cm.

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 c1, which is partially covered by sediment. The pc1–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 pc1–pc3 alveoli. The coronoid crest extends anteroposteriorly and is more prominent posteriorly. The angular process (sensu Davis, 1964; = pterygoid process in Boesenecker, 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 sinuous 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-

lar condyle is damaged and is located above the level of the alveoli. The coronoid process is high and robust, although in MPC 15500 the dorsal portion is missing. A deep masseteric fossa is located on the lateral surface of coronoid process. The ventral border of the mandibular symphysis reaches posteriorly to the level of the pc4 alveolus. The mandibular foramen is directed downward as in *Arctocephalus* and all sea lions (Berta and Deméré, 1986), and together with the angular process, both are elongated anteroposteriorly.

MPC 15501 is a right dentary, with a gracile and straight aspect in lateral view. In addition, c1 is small and unerupted, which combined with the high bone porosity, suggests the specimen is from a juvenile. The symphysis area is partially broken. In general, the ventral border of the dentary is almost straight and smooth. The angular process is oriented dorsal-posteriorly. The secondary angular process is small, unlike the angular process of MPC 15500, which is directed posteriorly. The condylar process is small, with a horizontal surface that is slightly deviated laterally. The coronoid process is broken at its dorsal end, and it is not very prominent but bears a shallow masseteric fossa in lateral view. The horizontal ramus is laterally directed at its front end. At the anterior edge of the lateral surface, five mental foramina of various sizes are present. The mandibular foramen is anteroposteriorly elongated and is directed downward. Considering the great individual variation seen within extant species and the poor fossil record of South American fossil otariids, MPC 15500 and MPC 15501 are attributed to cf. *Otaria flavescens* (= *O. byronia* fide Berta and Churchill, 2012).

DISCUSSION

Today, South American otariids (*Otaria* and *Arctocephalus* = *Arctophoca*, according to Berta and Churchill, 2012) are widely distributed along all South American coastlines: from Ecuador to Chile's Cape Horn in the Pacific Ocean, and from southern Brazil to southern Argentina in the Atlantic Ocean (Sepúlveda et al., 2011). In contrast, phocids in the Southern Hemisphere are currently limited to rookeries located on the Antarctic and sub-Antarctic islands (Shirihai and Jarret, 2009), although they occasionally extend to the southernmost region of South America (see Jefferson et al., 1993). The occurrence data reported here, along with the known fossil record of pinnipeds in South America (Fig. 5), shows a different configuration for otariid and phocid biogeographic distributions during the Neogene. The entire middle Miocene to early Pliocene pinniped record in the southeastern Pacific Ocean is represented by the phocids *Piscophoca* and *Acrophoca*, both from the late Miocene of the Bahía Inglesa Formation and the Pisco Formation in Peru (Muizon, 1981; Walsh and Naish, 2002; Valenzuela et al., 2009), along with other undescribed phocids from the latter unit (see Muizon and DeVries, 1985). In contrast to the North Pacific Basin, neither otariids nor odobenids have been reported from this interval in South America.

The oldest known record of otariids from South America is from the late Pliocene–early Pleistocene levels of the Pisco Formation of Peru, represented by *Hydrarctos lomasiensis* (Muizon, 1978), a primitive otariid (Berta and Deméré, 1986; Berta, 2009). On the Atlantic coast, there have been some reports of otariids from the Pleistocene of Argentina, but their taxonomic assignment is dubious (Cozzuol, 1996). In the upper Pleistocene marine rocks of Brazil, both *Arctocephalus* sp. (Oliveira and Drehmer, 1997) and *Otaria flavescens* (= *O. byronia* fide Berta and Churchill, 2012; Drehmer and Ribeiro, 1998; Rodrigues et al., 2004) have been reported, with the latter as the oldest unequivocal record of *Otaria* in South America. To date, the Chilean fossil record of Otariidae is fragmentary and sparse and the stratigraphic provenance could not be accurately established in most cases (Valenzuela-Toro et al., 2010b).

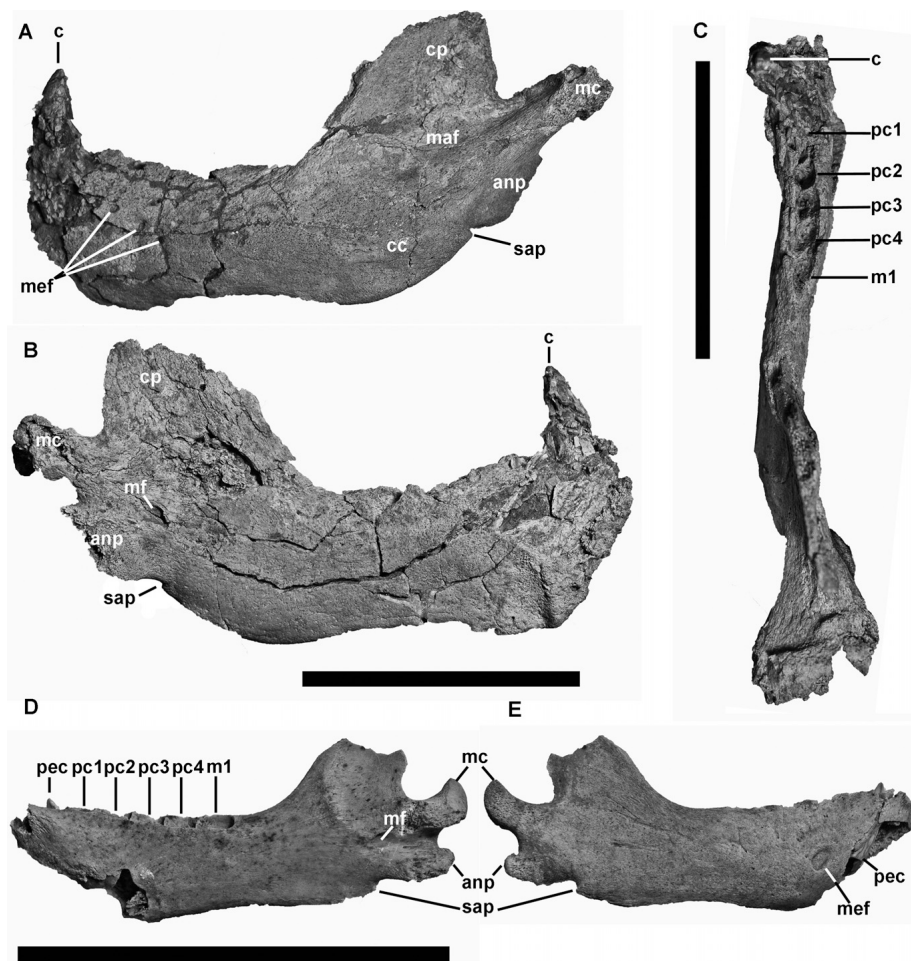


FIGURE 4. Mandibular remains of cf. *Otaria flavescens* (= *O. byronia* fide Berta and Churchill, 2012). **A–C**, left dentary of (MPC 15500) in lateral (**A**), medial (**B**), and dorsal (**C**) views. **D–E**, right dentary of (MPC 15501) in medial (**D**) and lateral (**E**) views. Scale bar equals 10 cm.

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

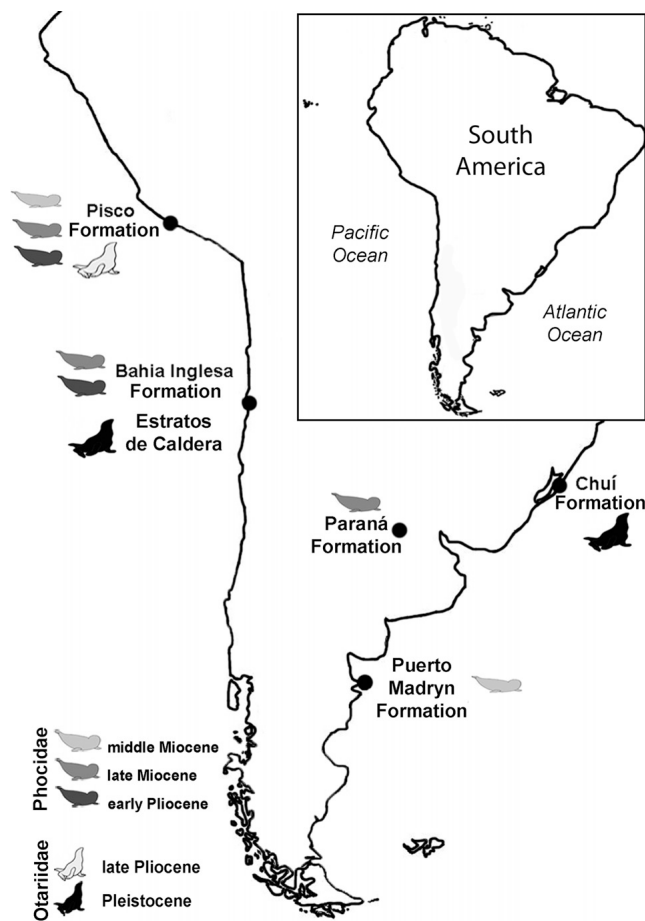


FIGURE 5. Map showing the occurrences of fossil pinnipeds in South America.

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 of *Carcharias taurus*, whose regional extinction coincided with a reduction of shallow continental shelf environments during Plio-Pleistocene cooling.

We propose that the local extirpation of phocids in Chile was linked to large-scale marine transgressions that occurred during the late Pliocene. Marine transgressions would have decreased phocid haul-out and rookery habitats such as sandy beaches, and increased deeper coastal environments with rocky islands (formed by basement rock of Jurassic age; Marquardt et al., 2004). Such transgressions would have occurred during the increased tectonic subsidence along the Chilean coastline during the late Neogene, especially in the Caldera Basin (Achurra, 2004), and nearby in Coquimbo Bay (LeRoux et al., 2005). Alternatively, phocid haul-out habitats might have also been lost during Pleistocene glacial-interglacial eustatic sea-level changes, although the evolution of the Caldera Basin seems primarily driven by tectonic changes rather than sea-level alone (Le Roux et al., 2005; Encinas et al., 2008). Understanding patterns of faunal turnover (Badgley and Gingerich, 1988) generally requires larger data sets than is typically available for fossil marine mammals, although Barnes (1977), Deméré (1994), and Deméré et al. (2003) have outlined possible approaches using compos-

ite 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.

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