

A NEW DWARF SEAL FROM THE LATE NEOGENE OF SOUTH AMERICA AND THE EVOLUTION OF PINNIPEDS IN THE SOUTHERN HEMISPHERE

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Abstract: Along the south-western coast of South America, three genera of fossil phocids (true seals) have been formally described from the late Neogene: *Acrophoca* and *Piscophoca* from Chile and Peru, and, more recently, *Hadrokirus* from Peru, which all represent medium- to large-sized phocids. Here, we report the discovery of *Australophoca changorum* gen. et sp. nov., a diminutive phocid from the late Miocene of the Bahía Inglesa Formation (northern Chile) and Pisco Formation (southern Peru), comparable in size with the smallest species of modern phocids. This taxon is based on diagnostic postcranial material, including a humerus that has an elongated deltopectoral crest but lacks an entepicondylar

foramen; a femur with a subtrochanteric fossa, among other characters; in combination with a relatively small body size. All these features together distinguish *A. changorum* from all other reported pinnipeds. This new taxon not only increases the taxonomic and morphological diversity of phocids of the late Neogene of the eastern South Pacific Ocean, but it also provides new insights about the evolutionary history of fossil pinniped assemblages in South America and, broadly, in the southern hemisphere.

Key words: Phocidae, late Miocene, Chile, Peru, South Pacific Ocean.

MODERN pinnipeds are globally distributed, yet their biogeography is not cosmopolitan. For example, living walruses (*Odobenus rosmarus*) are Holarctic, while fur seals and sea lions (Otariidae) and many species of true seals (Phocidae), including elephant seals (*Mirounga* spp.), have disjunct distributions across different latitudes in both hemispheres (see Murray 1866; Davies 1958; Kaschner *et al.* 2011). Recently, combined molecular and morphological approaches have resolved the phylogenetic underpinnings of these patterns (e.g. Fyler *et al.* 2005; Arnason *et al.* 2006, Fulton and Strobeck 2010; Churchill *et al.* 2014a; Scheel *et al.* 2014), which can test potential evolutionary scenarios under which phocids and otariids dispersed across suitable habitats and through oceanic gateways (e.g. Deméré *et al.* 2003; Churchill *et al.* 2014a).

The fossil record has provided a separate source of evidence regarding the evolution of the distribution and composition of pinniped communities through time (e.g. Muizon 1982; Deméré *et al.* 2003). For instance, the surprising discovery of a relict stem pinniped from the

Miocene of Nunavut, Canada, suggests that incipient ecomorphological modes (i.e. otter-like traits) early in pinniped evolution persisted for many millions of years and geographically distant from near relatives (e.g. Oligocene-age pinnipedomorphs of the North Pacific Ocean; Rybczynski *et al.* 2009). Recently, Boessenecker and Churchill (2015) presented findings from California that pushed the origin of otariids to the middle Miocene in the North Pacific Ocean. Discoveries from the Mio-Pliocene of Chile (Valenzuela-Toro *et al.* 2013, 2015) have demonstrated how and when southern hemisphere pinniped communities evolved their modern distributions, although many questions remain about the timing and mechanisms underlying these changes.

In this regard, the western coast of South America has a rich record of fossil pinnipeds (Muizon 1981a; Muizon and Bond 1982; Cozzuol 1996; Cozzuol 2001; Walsh and Naish 2002; Valenzuela-Toro *et al.* 2013, 2015), which provides a basis for clarifying these issues. The fossil record of pinnipeds in South America is dominated by phocids for most

of the Neogene, up until the appearance of otariids in the mid-Pleistocene (Valenzuela-Toro *et al.* 2013). In particular, the fossil-rich marine strata of the Bahía Inglesa Formation, in northern Chile, and the Pisco Formation, in southern Peru, have produced three extinct phocid species that range from middle Miocene to Pliocene levels of these formations: *Acrophoca longirostris*; *Piscophoca pacifica* (Muizon 1981a; Walsh and Naish 2002; Valenzuela-Toro *et al.* 2013; Pynson *et al.* 2014a); and *Hadrokirus martini*, recently described solely from Peru (Amson and Muizon 2014).

Interestingly, the presence of new and undescribed phocids from strata along the western coast of South America has been mentioned in the literature before (e.g. Muizon 1981a; Cozzuol 1996; Walsh and Naish 2002). Most recently, Varas-Malca and Valenzuela-Toro (2011) identified a new morphotype of phocid from the middle Miocene of Pisco Formation, although it is still not described formally. In particular, the presence of a new and small morphotype of phocid from the Pisco Formation has been noted more than once (Muizon and Bellon 1980; Muizon and DeVries 1985; Lambert and Muizon 2013), although a formal and exhaustive description and comparison of this notably diminutive taxon has been elusive. Here, we describe and name this particular diminutive phocid. This taxon is based on new material, consisting of postcranial remains from both the Caldera and Pisco basins of Chile and Peru, respectively. Based on diagnostic features, it belongs to the clade Monachinae, and it is characterized, among other traits, by its diminutive size, comparable with the smallest species of phocids.

This finding augments the taxonomic and morphological diversity of phocids during the late Neogene on the western coast of South America, where at least four species of seals coexisted, ranging from large phocids, such as *Acrophoca*, to the diminutive morphotype represented by our new taxon. This morphological richness is comparable only with the diversity of some fossil pinniped assemblages from the late Neogene from the northern hemisphere and with modern assemblages of the Arctic and Antarctic oceans today. Lastly, we briefly comment about how assemblages of pinnipeds (and other marine vertebrates) have changed over time in the southern hemisphere, likely in conjunction with major tectonic, latitudinal, productivity and sea level changes (Olson 1983; Warheit 1992; Thomas and Ksepka 2013; Chávez Hoffmeister *et al.* 2014; Churchill *et al.* 2014a; Villafaña and Rivadeneira 2014).

MATERIAL AND METHODS

Peruvian material included in this study was collected on 12 February 1988 by the Black Hills Institute, and accessioned in the Department of Paleobiology at the Smithsonian Institution's National Museum of Natural History.

Chilean material was excavated and collected by MES between 2011 and 2013 under permit No 5979 given by the Consejo de Monumentos Nacionales to MES, and deposited at the Museo Nacional de Historia Natural, in Santiago, Chile. Anatomical descriptions follow Berta *et al.* (2015) and Howell (1929).

Institutional Abbreviations. LACM, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MAB, Museum de Groene Poort, Boxtel, North Brabant, the Netherlands; MNHN, Muséum national d'Histoire naturelle, Paris, France; MUSM, Museo de Historia Natural, Universidad Nacional Mayor San Marcos, Lima, Peru; MPC, Museo Paleontológico de Caldera, Caldera, Chile; SGO.PV, Museo Nacional de Historia Natural, Santiago, Chile; USNM, Departments of Paleobiology and Vertebrate Zoology (Division of Mammals), National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

GEOLOGICAL SETTING

Locality and age of the Peruvian material

The holotype and the Peruvian part of the paratype remains were collected from the Aguada de Lomas locality of the Pisco Formation (middle Miocene to early Pliocene age; Muizon and DeVries 1985), in the Sacaco Basin of southern Peru (Fig. 1A). Specifically, USNM 438707 and 438712 were collected at the AGL level of the Pisco Formation at the Aguada de Lomas locality, which is the same locality and stratigraphical horizon where the type material of the aquatic sloth *Thalassocnus antiquus* (MUSM 228) was collected (Muizon *et al.* 2003).

The AGL level is one of the five stratigraphic levels previously identified in the Neogene marine strata of the Sacaco Basin, which have been defined based on its vertebrate faunal assemblages and the presence of fossil vertebrates with chronostratigraphic value (Muizon and DeVries 1985; Dunbar *et al.* 1990). The levels have been named according to the locality of their original description: the ELJ level at the El Jahuay locality; the AGL level at the Aguada de Lomas locality; the MTM level at the Montemar locality; the SAS level at the Sud-Sacaco locality; and the SAO at Sacaco locality (Muizon and DeVries 1985; Marocco and Muizon 1988; Lambert and Muizon 2013).

Previous K–Ar dating for the ELJ level (the lowermost section of the Pisco Formation; Muizon and Bellon 1986) gave an age of 9.5 myr, which contrasts with the mean 7.46 myr obtained by Sr dating of mollusc samples (Ehret *et al.* 2012). From AGL level, two tuffs have been K–Ar dated at Aguada de Lomas, yielding ages of 8 and 8.8 myr (Muizon and DeVries 1985; Muizon and Bellon 1986). The MTM level has been dated to 7.3–7.0 Ma, based on the co-occurrence of *Carcharodon hubbelli* and

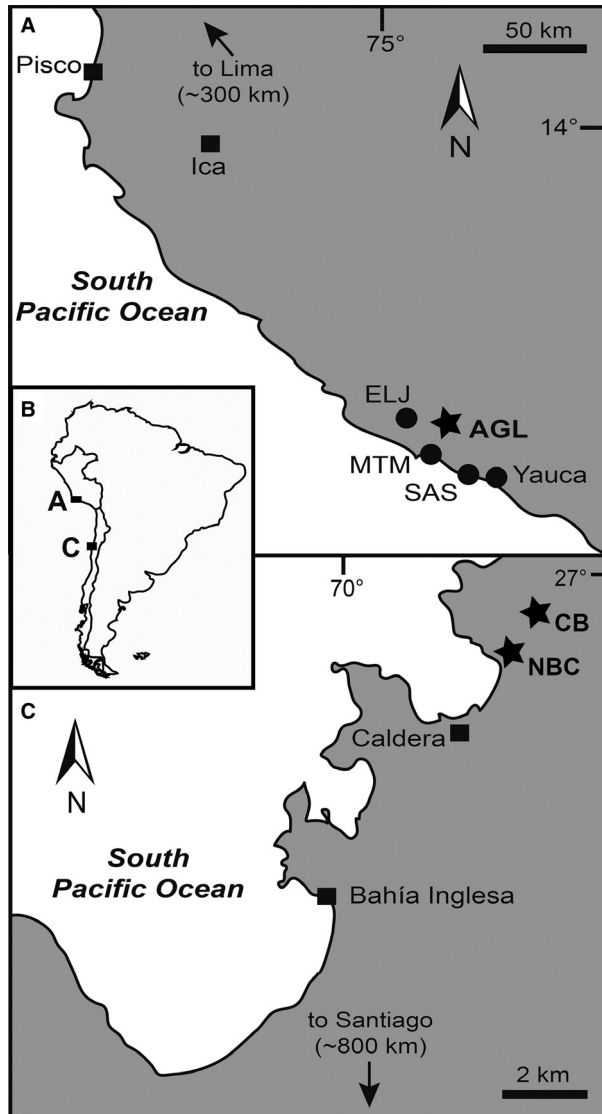


FIG. 1. Map showing the provenance of material assigned to *A. changorum*. A, the holotype USNM 438707 and the paratype USNM 438712 from Aguada de Lomas Locality, Pisco Formation, Peru. C, the paratype material from Cerro Ballena Locality (SGO.PV 21569) and Norte Bahía Caldera Locality (SGO.PV 22105, 22106), from Bahía Inglesa Formation, Chile. Black circles represent fossiliferous outcrops, black squares represent towns, and black stars represent the fossiliferous localities where *A. changorum* remains were discovered.

invertebrate biostratigraphy (Muizon and DeVries 1985; Ehret *et al.* 2012), being congruent with the mean 7.30 myr age obtained by Sr dating by Ehret *et al.* (2012). U–Pb and Sr isotopic data at the SAS level has yielded dates of 6.59 Ma and 7.1 Ma, respectively (Ehret *et al.* 2012), which is approximately 1.0–2.0 myr older than the previously reported age (Muizon and DeVries 1985). Finally, Sr dating of mollusc samples from SAS level yielded a mean date of 5.89 Ma (Ehret *et al.* 2012), which

is older than the previous K–Ar date obtained by Muizon and Bellon (1980). Thus, Ehret *et al.* (2012) obtained an earlier depositional age for all levels of Pisco Formation, confirming an overall late Miocene age for the sequence (see Lambert and Muizon (2013) for further details).

Thus, based on K–Ar dating of two tuff levels at the AGL level, previous workers suggested an age between 8.8 and 8.0 Ma (Tortonian) for the lower section of rocks at Aguada de Lomas (Muizon and Bellon 1980; Muizon and DeVries 1985). Additionally, the sequence of these tuff layers and the presence rounded boulder conglomerates, similar to the ELJ level, the lowermost section of the Pisco Formation in the Sacaco area, point to similar depositional processes and a possible contemporaneity of the AGL and ELJ levels (Muizon and DeVries 1985). The vertebrate-bearing horizon of the AGL level consists of a cross-bedded sandstone, well-sorted sandstones with *Skololithos* burrows, and well-preserved, but disarticulated, vertebrate remains (Muizon and DeVries 1985; Ehret *et al.* 2012). Initially, the sedimentary environment of the lower section of Pisco Formation was described as a protected marine embayment (Muizon and DeVries 1985). Later, Marocco and Muizon (1988) described the depositional environment of the AGL level as an agitated beach (described in the original Spanish text as ‘playa agitada’), which was characterized by having an erosive base followed, in the upper part, by a sequence of sandstones with better preservation of sedimentary structures, exhibiting mostly disarticulated skeletons but generally grouped in the same area (Marocco and Muizon 1988).

Both USNM 438707 and 438712 represent separate individuals of comparable sizes and they consist of complementary anatomical elements (e.g. humerus, radius, ulna, femur, tibia, tarsal bones) that additionally share similar texture, colour and preservation. Thus, based on these taphonomic features, the depositional environment of the AGL level, and the fact that the field data are identical, we propose a common stratigraphical origin for the all specimens (~30 osteological parts, mostly unidentifiable fragments) included with USNM 438707 and 438712. We follow Cohen *et al.* (2013) in recognizing the Gelasian age as the base of the Pleistocene.

Locality and age of the Chilean material

Paratype material at SGO.PV was collected at two different localities of the Bahía Inglesa Formation (Rojo 1985, middle Miocene – late Pliocene, based on the work of Achurra 2004; Achurra *et al.* 2009) in the Atacama Region of northern Chile (Fig. 1C). The humerus (SGO.PV 21569) was found at the Cerro Ballena locality, which is located approximately 5 km north of the town of Caldera, along the Pan-American Highway (Pyenson *et al.* 2014a).

Marine rocks at Cerro Ballena include both the Bahía Inglesa Formation and the overlying Pleistocene-aged Estratos de Caldera (Godoy *et al.* 2003). Notably, the Bahía Inglesa Formation strata at Cerro Ballena contain four bone-bearing horizons that have produced over 40 complete and partial skeletons of rorqual whales (Balaenopteridae indet.), sperm whales (Physeteroidea indet.), other toothed whales (Delphinoidea indet.), a walrus-like dolphin (*Odobenocetops* sp.) aquatic sloths (*Thalassocnus natans*), bony fishes (Istiophoridae indet., Xiphiidae indet.), sharks (*Carcharodon hastalis*) and true seals (*Acrophoca* sp. and the new taxon described herein; Pyenson *et al.* 2014a). At the second bone-bearing horizon (BL2), two pinniped taxa were recovered in close proximity as two sets of associated remains: SGO.PV 21569, which belong to the new taxon, and remains assigned to the genus *Acrophoca* (SGO.PV 21563-21568, MPC 692). Although Cerro Ballena is stratigraphically separate from other fossil-bearing horizons of the Bahía Inglesa Formation (Carreño 2012), Pyenson *et al.* (2014a) argued for a late Miocene age (or late Tortonian to early Messinian stage) of this unit at Cerro Ballena, based on the co-occurrence of marine vertebrates with chronostratigraphic significance: *Thalassocnus natans* and *Carcharodon hastalis*. Both species occur in the ELJ and MTM levels (~9 Ma and ~6 Ma; Muizon and DeVries 1985; Ehret *et al.* 2012; Lambert and Muizon 2013) from the Sacaco Basin, Pisco Formation, Peru.

The tarsal bones (SGO.PV 22105-22106) were collected from the locality called Norte Bahía de Caldera, which is located ~4 km north of the town of Caldera and ~2 km west of Cerro Ballena. Norte Bahía de Caldera is the same locality that produced remains referred to the aquatic sloth, *Thalassocnus* (Canto *et al.* 2008), including the most complete skeleton of this genus in Chile (Suárez *et al.* 2011; Velez-Juarbe *et al.* 2012). The levels of Norte Bahía de Caldera were previously correlated with the Lechero Member of the Bahía Inglesa Formation (according to Walsh and Suarez 2006) by Canto *et al.* (2008). The age of Lechero Member (=Unit 3 of Walsh and Hume 2001) has been dated to 4.5–2.6 Ma based on microfossil biostratigraphy evidence (Tsuchi *et al.* 1988; Ibaraki 1995). However, a late Miocene age for this member has been proposed based on molluscan biostratigraphy (Guzmán *et al.* 2000). Similarly, Marquardt *et al.* (2000) and Godoy *et al.* (2003) supported a late Miocene age for the lower part of the Lechero Member based on the presence of an ash level approximately 7 m above the top of the underlying Bonebed Member of the Bahía Inglesa Formation, with a K–Ar date of 7.6 ± 1.3 Ma. Specifically, the *Thalassocnus* remains from Norte Bahía de Caldera were referred to *T. natans* (Pyenson *et al.* 2014a), which has been described from MTM level (upper Miocene according to Muizon and DeVries 1985) of the Pisco Formation (Muizon and McDonald 1995; Muizon *et al.* 2003). Thus, we accept a

late Miocene age (approximately 7.6 Ma) for material from the Norte Bahía de Caldera locality.

SYSTEMATIC PALAEOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: <http://zoobank.org/References/C6E5BC04-1F2D-4068-89C4-50DDBB6F546B>

CARNIVORA Bowdich, 1821

PINNIPEDIA Illiger, 1811

PHOCIDAE Gray, 1821 (*sensu* Berta and Wyss 1994)

MONACHINAE Gray, 1869

Australophoca gen. nov.

LSID. urn:lsid:zoobank.org:act:968D7BCA-93D9-4AA6-AD31-629CC8D97BA1

Type species. *Australophoca changorum* sp. nov.

Diagnosis. As for the type species.

Australophoca changorum sp. nov.

LSID. urn:lsid:zoobank.org:act:EA3B867A-E137-46B1-B3D8-0275A18E6D4F

Derivation of name. From the Latin *austral*, referring to the southern hemisphere origin of this taxon; and from Changos, a group of native South Americans that inhabited the coastal region from the Atacama of Chile to southern Peru and made extensive use of marine resources, while having generally a short stature.

Holotype. USNM 438707. Postcranial remains belonging to at least one individual, represented by an incomplete right ulna, right radius, right and left humeri, and other unidentified remains, collected at the AGL level of the Aguada de Lomas locality in the Pisco Formation of Peru.

Paratypes. USNM 438712, SGO.PV 21569, SGO.PV 22105 and SGO.PV 22106. We refer four isolated specimens to the paratype series: one from the Pisco Formation (Peru) and three from the Bahía Inglesa Formation (Chile). USNM 438712, a right femur, right astragalus, calcaneum and cuboid, from the AGL level of the Aguada de Lomas locality in the Pisco Formation of Peru; SGO.PV 21569, a complete left humerus from Cerro Ballena, Atacama Region, Chile; SGO.PV 22105, a left astragalus; and SGO.PV 22106, a right astragalus, calcaneum and cuboid, both from Norte Bahía de Caldera, Atacama Region, Chile.

Diagnosis. *Australophoca* is a pinniped based on the presence of a short and robust humerus with a prominent

deltopectoral crest and a greater and lesser tuberosities enlarged, combined with a short, wide and dorsoventrally flattened femur (Berta and Wyss 1994). It is unequivocally a phocid based in the presence of a hypertrophied astragalar process (= caudal process of the astragalus) and a greatly reduced calcaneal tuberosity, which are considered synapomorphies of Phocidae (Berta and Wyss 1994). Also, the femur of *Australophoca* lacks a lesser trochanter, as occurs in all phocids. Additionally, *Australophoca* differs from all other fossil and living phocids by having the combination of: a small inferred adult size, despite exhibiting indicators of physical maturity (i.e. fused epiphysis, low porosity and deep muscle insertions); the possession of a humerus with an elongated deltopectoral crest that is smoothly attenuated in its caudal end, and the absence of an entepicondylar foramen, which is shared by monachine seals (except for the extinct *Homiphoca capensis*, which exhibits an entepicondylar foramen) a femur with a conspicuous subtrochanteric fossa, similar to *Piscophoca*, *Homiphoca*, and in *Leptony-*

chotes (see Pierard 1971); a greater trochanter slightly higher than its head; and, lastly, an astragalus and a calcaneum with an elongated sustentacular and ectal facet, similar to *Piscophoca*. The radius, ulna and innominate are fragmentary, but we assign them to *Australophoca* based on their relatively small size and by association with more diagnostic material with which they were collected.

Description and comparison

Humerus. The holotype consists of an incomplete right and left humerus, possibly referred to the same individual (USNM 438707, Fig. 2A–F). The right specimen preserves the proximodistal shaft of the humerus including the head. The lateral portion of the deltopectoral crest and the anterior portion of the trochlear surface are not preserved. The left specimen consists of the caudal third of the body of the humerus, including the trochlear area. The paratype (SGO.PV 21569, Fig. 3A–E) is a left complete humerus, relatively small in size with a total length

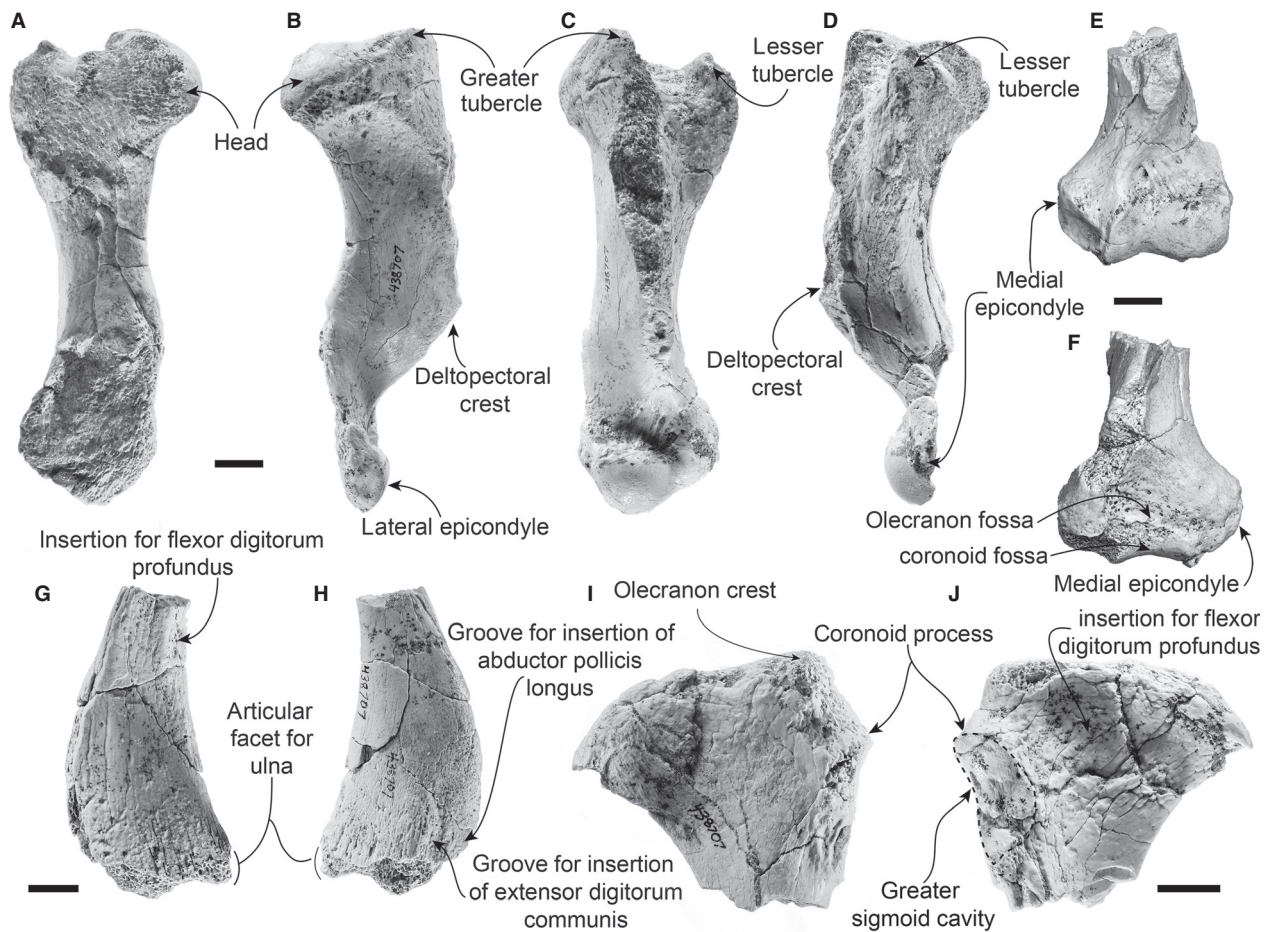


FIG. 2. Holotype material of *A. changorum* (USNM 438707). A–D, right humerus in: A, dorsal; B, lateral; C, anterior; and D, medial view. E–F, left humerus in: E, anterior; and F, dorsal view. G–H, right radius in: G, lateral; and H, medial view. I–J, right ulna in: I, lateral; and J, medial view. All scale bars represent 1 cm.

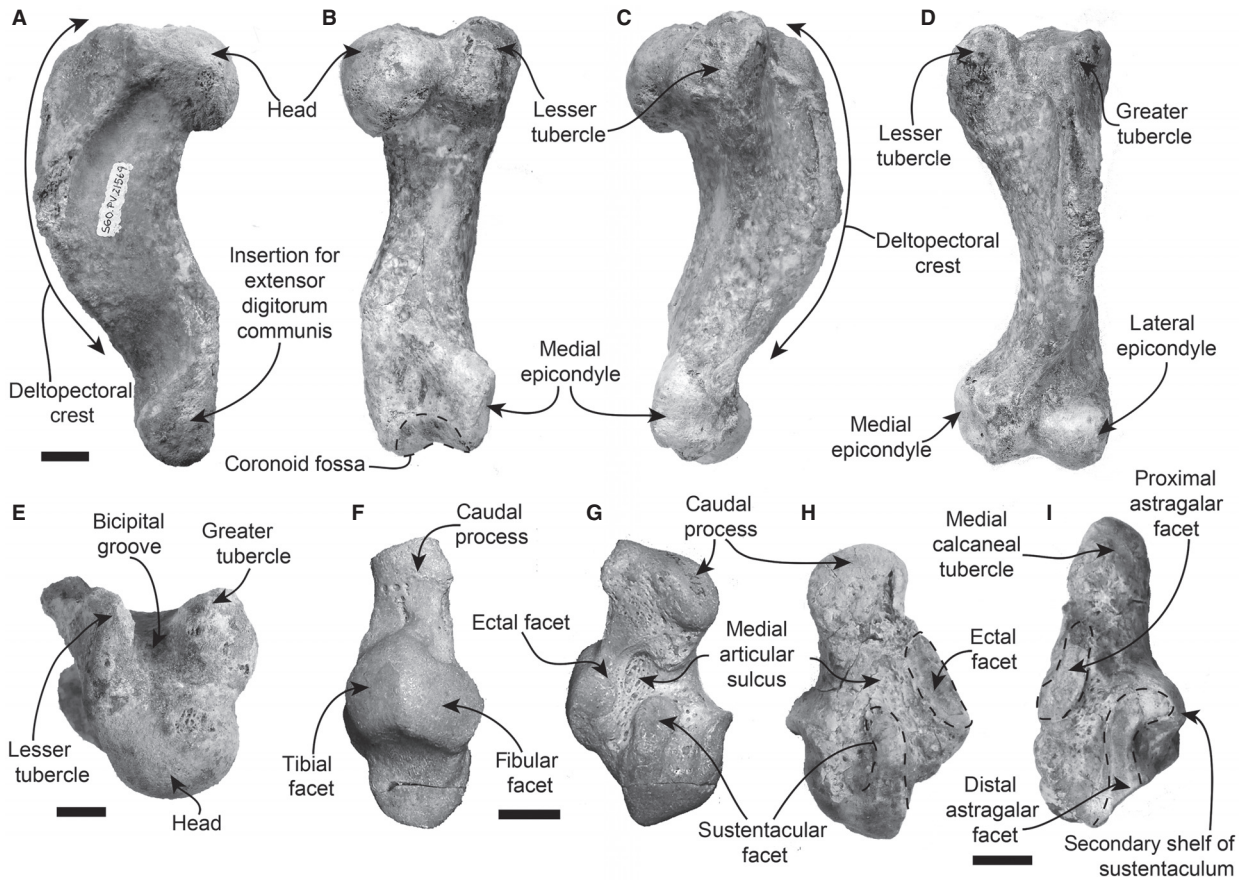


FIG. 3. Paratype material of *A. changorum*. A–E, SGO.PV 21569, left humerus in: A, lateral; B, dorsal; C, medial; D, anterior; and E, proximal view. F–G, SGO.PV 22105, left astragalus in: F, dorsal; and G, ventral view. H–I, SGO.PV 22106; H, right astragalus in ventral view; I, right calcaneum in medial view. All scale bars represent 1 cm.

(with the condyles in one plane) of 94.9 mm (which represents 63.3% and 61.3% of the length of the humerus of *Acrophoca longirostris* and *Piscophoca pacifica* respectively, see Fig. 4 and Table 1), which is similar in size to *Phoca* spp. Overall, the head is rounded in shape and slightly laterally directed in both specimens. The bicipital groove is relatively wide and shallow. The neck of the humerus is short and the greater tubercle (= tuberosity of Howell 1929) is slightly higher than the head and is wide and semi-rounded in its proximal end. The insertion of the supraspinatus and infraspinatus muscles is transversely broad. The lesser tubercle is higher (~1 mm) than the head and rounded in shape in its proximal end. The deltopectoral crest (=deltoid crest of Howell 1929 and Wyss 1988) is elongate and reaches approximately two-thirds of the total length of the shaft, with a gradual attenuation in its caudal end, which is a characteristic of monachines seals (Berta and Wyss 1994). The insertion of the deltoideus muscle is proximodistally elongated, exhibiting a flat and wide surface in its proximal extreme. In contrast, the distal end is narrower, slightly damaged, and its surface has a porous texture (especially in the paratype). The insertion of the brachialis muscle is relatively deep (especially in its lateral margin), elongate and narrow in its proximal and distal end, which provides a crescent shape for this insertion.

The entepicondylar foramen (= supracondylar foramen of King 1966) is absent, as it is in most monachine seals (King 1966; Wyss 1988), with the exception of the fossil *Homiphoca capensis*; in contrast, all other fossil and living Phocinae exhibit an entepicondylar foramen. The supinator ridge is poorly developed in comparison with phocines and it is reduced in comparison with *Acrophoca*. The insertion area for the extensor digitorum communis muscle is reduced too. The lateral and epicondyle has a rounded aspect. The olecranon and coronoid fossa are semi-triangular and similarly shallow.

Radius. The diaphysis of a right radius is preserved (USNM 438707, Fig. 2G–H), and this material exhibits a marked antero-posteriorly flattening and more expanded distal half, which is characteristic of the radius in all pinnipeds (Berta and Wyss 1994). The proximal section is oval in cross section. The lateral margin of the radius is proximodistally damaged. However, the general shape of this margin indicates the presence of a pronator teres process, which occurs mostly in fossil phocids (Berta and Wyss 1994). Additionally, in lateral view of the caudal section, the radius exhibits a deep insertion area for the abductor pollicis longus muscle, although it is less developed in *Australophoca* than in *Acrophoca* and *Piscophoca*. The insertion for the extensor

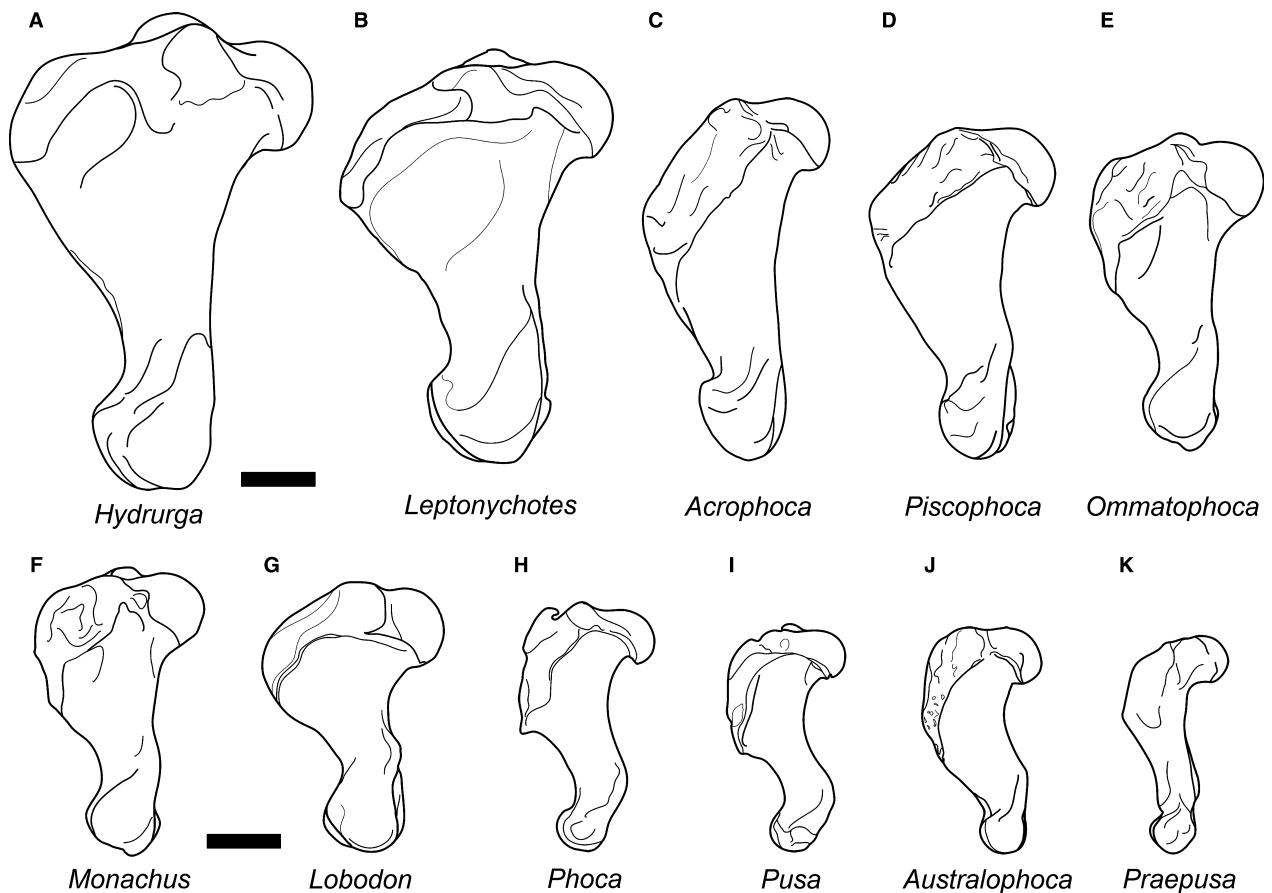


FIG. 4. Comparative outline of the paratype humerus of *A. changorum* (J, SGO.PV 21569) with *Hydrurga leptonyx* (A, USNM 275208), *Leptonychotes weddellii* (B, USNM 550359), *Acrophoca longirostris* (C, MNHN SAS 563), *Piscophoca pacifica* (D, MNHN SAS 564), *Ommatophoca rossii* (E, USNM 275206), *Monachus schauinslandi* (F, USNM 395999), *Lobodon carcinophagus* (G, USNM 269722), *Phoca vitulina* (H, USNM 250712), *Pusa hispida* (I, LACM 54781), *Praepusa boeska* (K, MAB 4686). Outlines A, C–E, G–H and K are inverted with respect to the original material. Both scale bars represent 3 cm.

digitorum communis tendon exhibits a porous and slightly deep surface, as observed in *Pliophoca*. The surface for the insertion of the brachioradialis muscle is partially broken, but it appears that it was broad and distally oriented. In medial view, the surface of insertion of the flexor digitorum profundus muscle is wide and shallow.

Ulna. The incomplete right ulna (USNM 438707, Fig. 2I–J) preserves the olecranon and coronoid processes. The olecranon process is partially damaged in its proximal section. The olecranon crest is eroded. The anconeal fossa is relatively deep, similar to *Pliophoca*, but lesser than in *Piscophoca*. In lateral view, the insertion of the abductor pollicis longus muscle is shallow. In medial view, the ulna exhibits a wide and deep insertion for the flexor digitorum profundus muscle. The greater sigmoid cavity is broad, while the lesser sigmoid cavity is smaller and deep.

Innominate. The known material of the innominate for *Australophoca* consists of a portion preserving the acetabulum of a right innominate (Fig. 5A), which is rounded in shape; its medial surface is eroded and covered by sediment, which could not

be removed. The specimen preserves ~1 cm of the proximal portion of the pubis and ischium.

Femur. In USNM 438707 (Fig. 5B–C), the capitulum is rounded and is partially damaged in its lateral margin. The neck is short, rounded in cross section, giving a relatively robust aspect to the proximal section, as occurs in *Homiphoca*, *Piscophoca*, *Acrophoca* and *Monachus*. The preserved portion of the shelf is slender and narrower than in *Acrophoca*. The greater trochanter is anteroposteriorly wide and rugose in its anterior margin, and it is slightly taller (~1 mm) than the head, as in *Acrophoca*. USNM 438707 exhibits a deep and conspicuous trochanteric fossa medially directed, as occurs in some monachines as *Piscophoca*, *Homiphoca* and *Leptonychotes* and all phocines. In dorsal view, the insertion of the gluteal muscles is rugose and wide. Similarly, in ventral view, the insertion of the pectineus muscle is rugose and wide.

Tarsal bones. The paratype series is also represented by a right astragalus, calcaneum and cuboid (USNM 438712, Fig. 5D–F) all of which are badly preserved. Another specimen that we refer to the paratype includes a complete left astragalus, calcaneum

TABLE 1. Measurements of the most complete elements of the holotype and paratype (based on Ericson and Stora (1999)).

	USNM 438707 (right)	USNM 438707 (left)	USNM 438712	SGO.PV 21569	SGO.PV 22105	SGO.PV 22106
Humerus						
Total (greatest) length	?	?	–	98.5	–	–
Total (greatest) length with the condyles in one plane	?	?	–	94.9	–	–
Total (greatest) length from head	?	?	–	94.4	–	–
Depth of the proximal end	?	?	–	44.2	–	–
Greatest diameter of caput	?	?	–	25.0	–	–
Greatest breadth of distal end	?	35.0	–	34.7	–	–
Greatest breadth of trochlea	?	28	–	?	–	–
Greatest diagonal height of the lateral condyle	?	?	–	17.5	–	–
Femur						
Greatest breadth of the proximal end	38.0	–	–	–	–	–
Greatest diagonal breadth of the major trochanter	24.0	–	–	–	–	–
Astragalus						
Total length	–	–	–	–	47.2	51.7
Total length from the most proximal point of the trochlea to the most distal point of the astragalus	–	–	–	–	32.9	36.6
Greatest breadth of the trochlea	–	–	–	–	?	26
Greatest height	–	–	–	–	29.8	31.3
Calcaneum						
Greatest length: greatest diagonal length	–	–	44.0	–	–	53.4
Greatest height	–	–	24.0	–	–	25.3

? Measurement not preserved.

All measurements in millimetre.

and cuboid of one individual (SGO.PV 22106, Fig. 3H–I) and an isolated left astragalus (SGO.PV 22105, Fig. 3F–G). In ventral view, the holotype astragalus is mostly covered by sediment with the exception of a section of the navicular facet area. The paratype astragali both exhibit a sustentacular facet (= lower articulation of King 1966) that is elongated and slightly widened in the proximal end, similar to *Piscophoca*, *Monachus* and Phocinae, but differing from the condition seen in *Acrophoca* and modern monachines, which have a relatively short and wide sustentacular facet. The ectal facet (defined as the upper articulation by King (1966) and the calcaneoastragal facet by Polly (2008)) is proximomedially elongated and exhibits a constriction in its medial section, giving it a figure-of-eight shape, which is especially pronounced in SGO.PV 22105. Both the sustentacular and ectal facets are separated by a wide and deep sulcus (= medial interarticular sulcus of Walsh and Naish 2002) transversely directed, which is anterior to the caudal process (= calcaneal process of Polly 2008). The astragal canal is rounded.

The calcaneum exhibits an elongated and curved distal astragal facet (= anteromedial articular surface of Robinette and Stains 1970), giving a sickle-shaped profile, differing from all phocines, as well as monachines such as *Pliophoca* and *Monachus*. The secondary shelf of sustentaculum is prominent and rounded. The proximal astragal facet (or posterior articular surface in Robinette and Stains 1970) is elongated and laterally oriented, which differs from modern monachines such as *Leptonychotes*, *Hydrurga*, *Ommatophoca* and *Mirounga*. The calcaneal tubercle is hypertrophied (as it is in the astragali) and its proximal end is narrow and pointed. The peroneal tubercle is pronounced and

the sulcus for the peroneus longus muscle is narrow and short. The trochlear sulcus is proximodistally elongated. The cuboid facet is square in shape and slightly deep. Finally, the cuboid exhibits a deep groove in the lateral margin, and the articulation facet with the calcaneum is square in outline.

DISCUSSION

Phylogenetic affinities of Australophoca

Australophoca exhibits a hypertrophied caudal process in the astragalus and a calcaneum with a greatly reduced calcaneal tuberosity, which are traits that are considered synapomorphies of Phocidae. Additionally, the femur of the paratype specimen (USNM 438707) exhibits a conspicuous subtrochanteric fossa in the femur, which is shared by all living phocines. However, this trait is also present in some fossil monachines such as *Homiphoca* and *Piscophoca*, suggesting some variability in the acquisition of this character state. On the other hand, *Australophoca* differs from all fossil and modern phocines in possessing a humerus with an elongated deltopectoral crest, reaching three-quarters of the length of the shaft, while lacking an entepicondylar foramen. The elongate deltopectoral crest is shared by monachine phocids (Wyss 1988; Berta and Wyss 1994; Cozzuol 2001); meanwhile, the absence of an entepi-

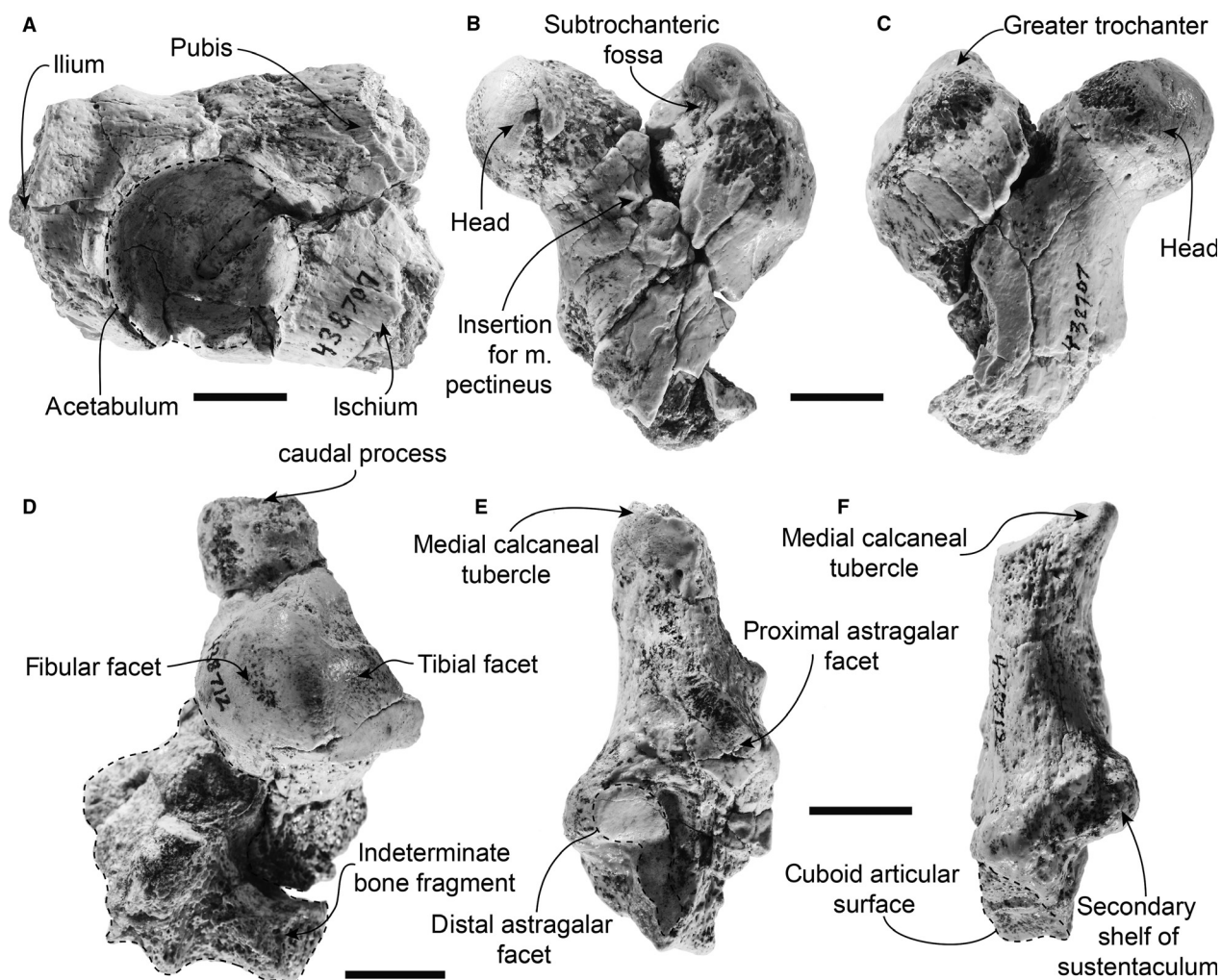


FIG. 5. Paratype material of *A. changorum*. A, USNM 438712, right innominate in dorsal view. B–C, USNM 438712, right femur in: B, ventral; and C, dorsal view. D–F, USNM 438712; D, right astragalus in ventral view; E–F, left calcaneum in: E, medial; and F, lateral view. All scale bars represent 1 cm.

condylar foramen occurs in all modern monachines, and also most fossil monachines (one exception is *Homiphoca*). Thus, the combined presence of an elongated deltopectoral crest and the absence of an entepicondylar foramen in the humerus are traits only found in monachine seals, which supports our assignment of *Australophoca* to this subfamily. Morphological differences exhibited by *Australophoca*, including its diminutive size with respect to the already described phocid species in the southern hemisphere, support this new systematic identity. A phylogenetic analysis is not included herein pending the description of more complete specimens from Peru.

The body size of Australophoca

Unfortunately, the absence of any cranial remains of *Australophoca changorum* prevents us from performing

multivariate regressions for the estimation of the body size proposed by Churchill *et al.* (2014b), and the study of unpublished material at MUSM may provide a data source for such estimates. Nonetheless, Howell (1929, p. 27) indicated that, in *Phoca*, the humerus represents 14% of the body length. Thus, based only in the total length of the humerus, we can calculate a total body length of ~68 cm for *A. changorum*, which is smaller than all known fossil and extant monachine and is in the range of the body length of some of the smallest species of modern phocines, such as Baikal seal (*Pusa sibirica*), Caspian seal (*P. caspica*) and Ringed seal (*P. hispida*), in which adults all barely exceed 1.5 m in body length (Bonner 1989; Shirihai and Jarret 2006). The holotype specimen of *Praepusa boeska*, a fossil phocine from the Mio-Pliocene of the Antwerp Basin in Belgium, is represented by an isolated right humerus that is even smaller than *Australophoca* (Koretsky *et al.* 2015), with a total length (with the condyles in one plane)

of the humerus (= absolute length in Koretsky *et al.* 2015) of 81.1 mm in *P. boeska* versus 94.9 mm in *Australophoca* (see Fig. 4 and Table 1).

Phocid diversity in the South Pacific Ocean during the Neogene and evolution of pinniped communities in the southern hemisphere

Considering the known pinniped genera from western South America (*Acrophoca*, *Piscophoca* and *Hadrokirus*), the occurrence of the diminutive *Australophoca* expands the taxonomic and size diversity of the late Miocene pinniped assemblage, which previously had only medium- to large-sized seals (~2.3–2.5 m according to Churchill *et al.* 2014b). Assuming our current sampling of the late Miocene pinniped assemblages from western South America is not biased or missing additional taxa, the diversity of fossil phocids is comparable to the richest pinniped communities at polar latitudes today (Kaschner *et al.* 2011).

Notably, the range of phocid body sizes in the aggregate late Miocene assemblage from Chile and Peru is greater than either in the Bering and Chukchi seas or in Antarctic Convergence today, although the overall size range for the living pinniped communities is greater, as is the taxonomic richness in both regions, which includes otariids in both hemispheres and *Odobenus* in the northern hemisphere (Fig. 6A, C–D).

The western South American fossil assemblage can also be compared with the relatively well-sampled and reported assemblage from the late Miocene to Pliocene of western North America, composed mostly of fossil taxa from California. We included taxa from several co-eval units from the same general region in Figure 6. During this time frame, the pinniped assemblage from this region included large-sized odobenids, such as *Pontolis*, *Gomphotaria*, and otariids such as *Thalassoleon*, as well as medium to small odobenids, such as *Dusignathus* and *Valenictus*, and otariids such as *Pithanotaria* and *Callorhinus* (see Fig. 6B; Repenning and Tedford 1977;

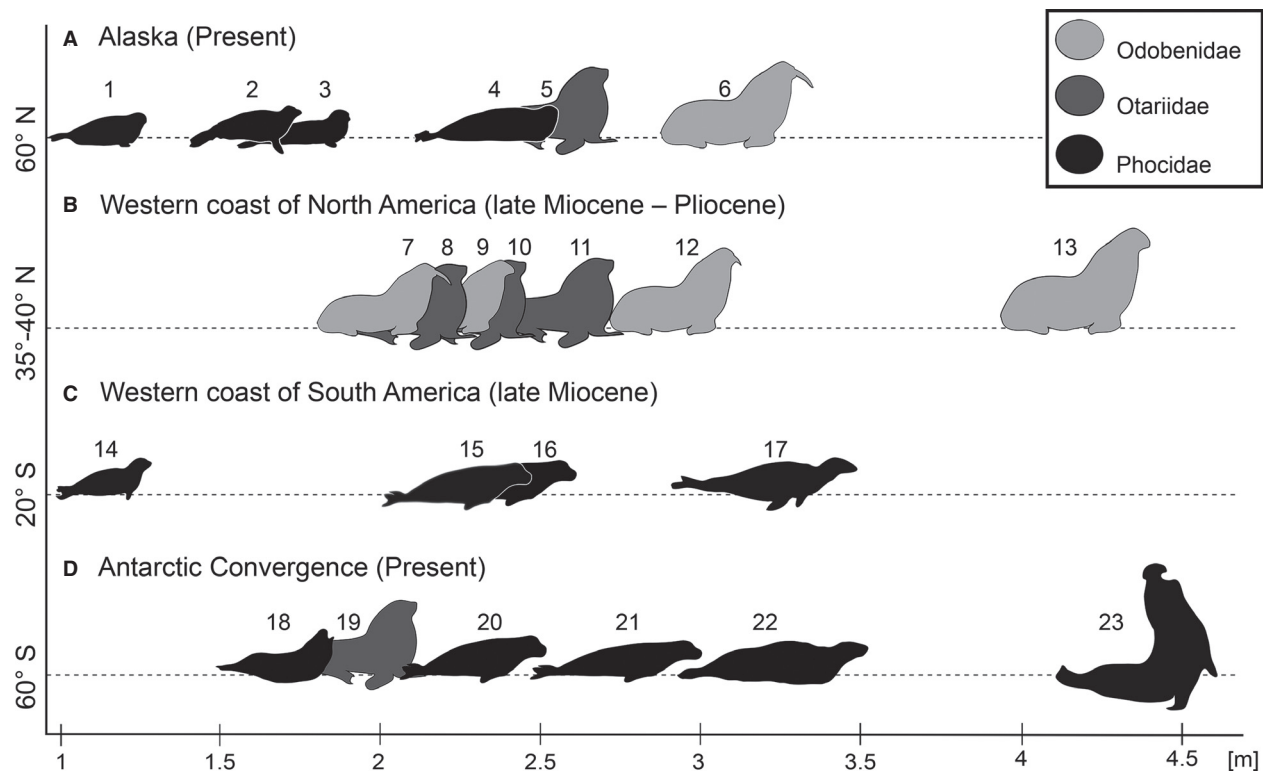


FIG. 6. Silhouettes comparing the differences in taxonomic composition and body size of representative modern and fossil communities of pinnipeds from: A, Alaska; B, western coast of North America during the late Miocene – Pliocene; C, western coast of South America during the late Miocene; and D, Antarctic Convergence. 1, *Pusa hispida*; 2, *Histriophoca fasciata*; 3, *Phoca vitulina*; 4, *Erignathus barbatus*; 5, *Eumetopias jubatus*; 6, *Odobenus rosmarus*; 7, *Valenictus chulavistensis*; 8, *Callorhinus gilmorei*; 9, *Dusignathus santacruzensis*; 10, *Pithanotaria starri*; 11, *Thalassoleon mexicanus*; 12, *Gomphotaria pugnax*; 13, *Pontolis magnus*; 14, *Australophoca changorum*; 15, *Hadrokirus martini*; 16, *Piscophoca pacifica*; 17, *Acrophoca longirostris*; 18, *Ommatophoca rossii*; 19, *Arctophoca gazella*; 20, *Lobodon carcinophagus*; 21, *Leptonychotes weddellii*; 22, *Hydrurga leptonyx*; 23, *Mirounga leonina*. Body lengths are based on Churchill *et al.* (2015) and Shirihai and Jarret (2006). Silhouettes are based on illustrations from Reeves *et al.* (1992) and Shirihai and Jarret (2006).

Barnes and Raschke 1991; Deméré 1994; Deméré *et al.* 2003; Deméré and Berta 2005; Boessenecker 2011). Interestingly, the overall breadth of size ranges in the western North American pinniped assemblage is roughly similar to that from modern communities, although the maxima and minima differ. The taxonomic richness of western South America is certainly lower than any of the other living communities, and lower than the fossil assemblage from California, although the latter is devoid of crown phocids.

The fossil record of pinnipeds in the southern hemisphere is mostly represented by Neogene occurrences of phocids in Africa, Oceania and South America. In southern Africa, one fossil species has been recognized: *Homiphoca capensis* from the upper Miocene – Lower Pliocene of South Africa (Hendey and Repenning 1972; Muizon and Hendey 1980; Avery and Klein 2011; Govender *et al.* 2012). From Oceania, isolated remains of an indeterminate phocid have been described from the Pliocene of Australia (Fitzgerald 2005), as well as two new specimens of an unidentified monachinae from the middle Miocene – Pliocene of Australia and New Zealand (Fitzgerald *et al.* 2013). With *Australophoca*, six different extinct seal taxa are now known from the Mio-Pliocene of South America: *Kawas benegasorum* and *Properitycus argentinus* from the middle Miocene of Argentina (Muizon and Bond 1982; Cozzuol 2001); *Acrophoca longirostris* and *Piscophoca pacifica* from the late Miocene – early Pliocene of Peru and Chile (Muizon 1981a; Walsh and Naish 2002; Pyenson *et al.* 2014a); and *Hadrokirus martini* from Peru (Amson and Muizon 2014). Thus, pinniped assemblages during the late Miocene on the south-western coast of South America were composed of, at least, four different species of true seals, which contrasts with the current absence of phocids in the area today (see Valenzuela-Toro *et al.* 2013). Furthermore, the Pleistocene fossil record of phocids is sparse, consisting of the isolated occurrence of modern genera *Mirounga* from Chile (Valenzuela-Toro *et al.* 2015) and *Ommatophoca* from the Pleistocene of New Zealand (King 1973).

The fossil record of otariids in the southern hemisphere is even sparser still, consisting solely of *Hydrarctos lomasiensis*, from the late Pliocene – Pleistocene of Peru (Muizon 1978), at the moment, the oldest fossil record of this family in the southern hemisphere. Other otariid records from the Pleistocene consist of modern genera as *Otaria* cf. *O. flavescens* from Brazil and Chile (Drehmer and Ribeiro 1998; Rodrigues *et al.* 2004; Valenzuela-Toro *et al.* 2013), and *Arctocephalus* (*Arctophoca* according to Berta and Churchill 2011) from Brazil and South Africa (Oliveira and Drehmer 1997; Avery and Klein 2011). Additionally, from the Pleistocene of New Zealand, a skull of the extinct otariid, *Neophoca palatina*, has been reported (King 1983). Thus, based on fossil evidence from

the Pleistocene, it is clear that during this time, pinniped communities exhibited mostly a modern configuration.

These data from the southern hemisphere are broadly consistent with the diversification of otariids into the southern hemisphere during the Pliocene that Churchill *et al.* (2014a) proposed and related to changes in the surface sea temperature and primary productivity. These latter proxies are known determinants for marine mammal richness in large-scale analyses of modern diversity (Kaschner *et al.* 2011), and it is likely that changes in these oceanographic variables, which track changes in upwelling and productivity, have shaped the evolution of marine vertebrate communities since the late Miocene in the Humboldt Current System (e.g. Villafañá and Rivadeneira 2014). Better geochronological constraints, in addition to broader geographical sampling in other sedimentary basins in Chile (Gutierrez *et al.* 2013; Chávez Hoffmeister *et al.* 2014), will improve the constraints on the timing of these faunal turnovers (*sensu* Valenzuela-Toro *et al.* 2013), especially relative to broader oceanographic changes in the southern hemisphere, such as the onset of the El Niño Southern Oscillation (Galeotti *et al.* 2010), or the closure of the Panamanian Seaway (O’Dea *et al.* 2012; Jackson and O’Dea 2013).

This evolutionary turnover in the late Cenozoic austral pinniped fauna can also be directly compared to contemporaneous records of large marine vertebrates from other marine upwelling systems elsewhere in the world, which may reveal common evolutionary trends or patterns in the structure of marine communities through geological time. Thus, other marine vertebrates, such as seabirds, sharks and cetaceans, exhibit a similar pattern with a restructuring in their diversity and distribution during the Pliocene–Pleistocene transition (see Olson 1983; Warheit 1992; Whitmore 1994; Fordyce *et al.* 2002; Cione *et al.* 2007; Marx and Uhen 2010; Boessenecker 2013; Thomas and Ksepka 2013; Villafañá and Rivadeneira 2014), pointing to the strong potential of abiotic drivers in the evolution of these groups (Pyenson *et al.* 2014b). Future analyses taking into account both the richness and abundances of large marine vertebrate assemblages will be critical for better understanding the palaeoecological role of marine mammals in ocean food webs (Kelley and Pyenson 2015).

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