

Research



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Oldest record of monk seals from the North Pacific and biogeographic implications

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True seals (crown Phocidae) originated during the late Oligocene–early Miocene (approx. 27–20 Ma) in the North Atlantic/Mediterranean region, with later (middle Miocene, approx. 16–11 Ma) dispersal events to the South Atlantic and South Pacific. Contrasting with other pinnipeds, the fossil record of phocids from the North Pacific region is scarce and restricted to the Pleistocene. Here we present the oldest fossil record of crown phocids, monachines (monk seals), from the North Pacific region. The specimens were collected from the upper Monterey Formation in Southern California and are dated to 8.5–7.1 Ma, predating the previously oldest known record by at least 7 Ma. This record provides new insights into the early biogeographic history of phocids in the North Pacific and is consistent with a northward dispersal of monk seals (monachines), which has been recognized for other groups of marine mammals. Alternatively, this finding may correspond with a westward dispersal through the Central American Seaway of some ancestor of the Hawaiian monk seal. This record increases the taxonomic richness of the Monterey pinniped assemblage to five taxa, making it a fairly diverse fossil assemblage, but also constitutes the oldest record of sympatry among all three extant pinniped crown clades.

1. Introduction

Modern seals (Phocidae) are a group of pinnipeds that principally inhabit polar and subpolar regions (with the exception of Monk seals in tropical and subtropical latitudes) [1]. From their fossil record, it has been hypothesized that phocids originated in the North Atlantic or Mediterranean region during the late Oligocene–early Miocene with diversification into two subfamilies, Phocinae (or northern seals) and Monachinae (southern seals), during the early–middle Miocene [2–4].

The North Pacific constitutes an enigmatic region for the early evolutionary history of phocids since no fossil remains have been discovered in sediments older than the Pleistocene [5–7]. Phocids are nowadays found in the region, and include the phocine harbour seal (*Phoca vitulina*), and the monachine northern elephant seal (*Mirounga angustirostris*). Their fossil record extends only to the Pleistocene [5–7], comprising a few occurrences from Southern California to Alaska. This scarce evidence in the North Pacific contrasts with the vast fossil record of stem (e.g. enaliarctines and desmatophocids) and other crown pinnipeds (e.g. odobenids and otariids) which are differentially known from the late Oligocene to the Neogene of the North Pacific region [2,3,8–10].

Here we report the oldest record of monachine seals from the North Pacific region, collected from the Monterey Formation in Southern California. This new finding increases the species richness of the pinniped assemblage known from this formation, which includes the desmatophocid *Allodesmus*, the otariid *Pithanotaria starri*, and several odobenids, *Imagotaria* cf. *I. downsi*, and Odobenidae spp. [9] (electronic supplementary material, text S1; table 1), and also provides new clues about the biogeographic hypothesis of phocids during the Miocene.

Institutional abbreviations. LACM, Mammalogy and Vertebrate Paleontology Collections, Natural History Museum of Los Angeles County, Los Angeles, CA, USA; LACM Loc., Vertebrate Paleontology Locality, Natural History Museum of Los Angeles County, Los Angeles, CA, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; UF, Florida Museum of Natural History, Gainesville, FL, USA.

2. Systematic palaeontology

PINNIPEDIA Illiger, 1811

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

MONACHINAE Gray, 1869

Monachinae gen. et sp. indet.

(figure 1a–e; table 2).

(a) Material

LACM 122584, right p4, collected by field party during October–November, 1982; and LACM 52624, left p4 or m1, collected by M. K. Hammer, 27 February 1969.

(b) Locality

LACM Loc. 6902, Laguna Niguel, Orange Co., California, USA, 33°33'51" N, 117°42'53" W. Specimens were collected at this locality between 1969 and 1982; this included a detailed excavation of the bone-bearing horizon [11,14,15]. A list of other fossil vertebrates from this locality and bonebed was published by Barnes *et al.* [11] and the marine mammals are updated herein (electronic supplementary material, text S1; table 1).

(c) Horizon and formation

Bonebed consisting of coarse, poorly sorted yellow sands of the upper Monterey Formation [11,14,15]. Most of the fossils collected from this unit were concentrated in cobble lenses at the base of the bed [11, fig. 1].

(d) Age

In Southern California the Monterey Formation ranges from the mid Langhian to earliest Messinian (14.9–7.1 Ma) [16–18]. Microfossils (diatoms and silicoflagellates) recovered from LACM Loc. 6901, a diatomaceous unit that is stratigraphically below Loc. 6902 [11], are part of the lower *Thalassiosira antiqua* Subzone a, which ranges from 8.5 to 7.7 Ma [18]. This gives LACM Loc. 6902 an age between 8.5 and 7.1 Ma (late Tortonian–earliest Messinian [19]).

(e) Description and remarks

LACM 122584 and LACM 52624 are a double-rooted, multi-cuspate right p4 and left p4 or m1, respectively (figure 1a–e).

Table 1. Marine mammal assemblage from the upper Monterey Formation at LACM Loc. 6902 (updated from Barnes *et al.* [11]; electronic supplementary material, text S1).

| taxon | specimen number |
|---|--|
| Odontoceti | |
| <i>Atocetus nasalis</i> | LACM 122670, LACM 123872 |
| <i>Piscolithax</i> cf. <i>P. tedfordi</i> | LACM 122673 |
| Mysticeti | |
| Herpetocetinae gen. et sp. indet. | LACM 122682 |
| Balaenopteridae gen. et sp. indet. | LACM 122684 |
| Phocidae | |
| Monachinae gen. et sp. indet. | LACM 52624, LACM 122584 |
| Otariidae | |
| <i>Pithanotaria starri</i> | LACM 115677 |
| Odobenidae | |
| Odobenidae gen. et sp. indet. | LACM 52601, LACM 58548, LACM 73566, LACM 121015 |
| <i>Imagotaria</i> cf. <i>I. downsi</i> | LACM 50971, LACM 57323, LACM 117678 |
| Dugongidae | |
| <i>Dusisiren</i> sp. | LACM 37610, LACM 37611 |

In both, the crown is mesiodistally longer than tall and relatively wide. However, and despite its fragmentary nature, it is possible to infer that LACM 52624 is smaller in size compared with LACM 122584.

The crown of LACM 122584 has relatively smooth enamel (figure 1a–c; table 2) and consists of a main cusp (protoconid) that has a subtriangular outline in lingual or buccal views, and relatively low paraconid and metaconid that are dorsoventrally short and mesiodistally long. The base of the crown has buccal and lingual cingula, with the former being dorsally curved below the main cusp. The protoconid shows minor wear along its mesial edge. The roots are unequal in size; the anterior root is cylindrical and nearly straight, while the posterior root is curved anteroventrally.

LACM 52624 preserves the anterior half of the tooth, including the anterior root and the anterior buccal half of the crown (figure 1d,e and table 2). The latter possesses conspicuous striations in its buccal surface and consists of a principal cusp, the protoconid, and a smaller, conical paraconid that is dorsoventrally shorter, but comparatively taller than that of LACM 122584. A buccal cingulum is present, which is elevated below the main cusp. The anterior root is cylindrical and nearly straight.

The tooth morphology of LACM 122584 and LACM 52624 is unlike that of any coeval pinniped taxon known from the Monterey Formation, which includes the stem phocoid *Allodesmus* sp., the otariid *Pithanotaria starri*, and several species of odobenids [9,11] (electronic supplementary material, text S1; table 1). Postcanine teeth in these other pinniped taxa are characterized by only possessing a single principal cusp and a lingual cingulum (*P. starri* and *Allodesmus* sp.), or a principal cusp with crenulated lingual cingula in coeval basal odobenids (electronic supplementary material, text S1). The new specimens reported here do not resemble any

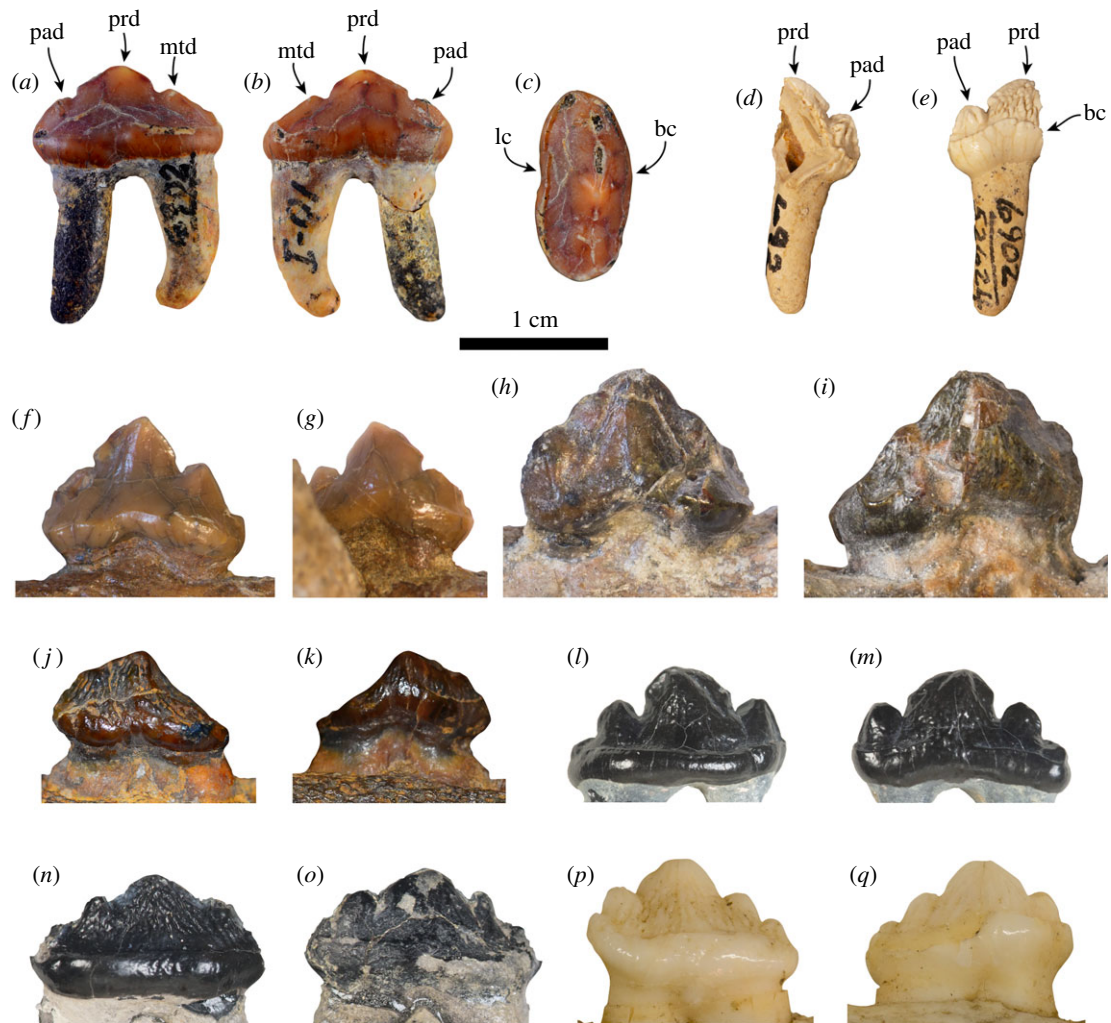


Figure 1. Postcanine teeth of monachines. *Monachinae* gen. et sp. indet. (LACM 122584), right p4 in lingual (a), buccal (b) and occlusal (c) views; *Monachinae* gen. et sp. indet. (LACM 52624), left p4/m1 in lingual (d) and buccal (e) views; *Acrophoca* sp. (MNHN CHL 5), right p4 in lingual (f) and buccal (g) views; *Hadrokirus martini* (MNHN SAS 1627), right p4 in lingual (h) and buccal (i) views; *Properiptychus argentinus* (MACN 3538a), right p4 in lingual (j) and buccal (k) views; Bone Valley *Monachinae* gen. et sp. indet. (UF 45683), left p4/m1 in lingual (l) and buccal (m) views; *Neomonachus tropicalis* (UF 36456), left p4, in lingual (n) and buccal (o) views; *Neomonachus schauinslandi* (LACM 54384), right p4, in lingual (p) and buccal (q) views. Abbreviations: bc, buccal cingulum; lc, lingual cingulum; mtd, metaconid; pad, paraconid; prd, protoconid. (Online version in colour.)

other known pinniped from older, coeval, or younger formations in the North Pacific region [20–24], nor do they resemble any known terrestrial carnivore. Their morphology is instead consistent with that of monachine seals (figure 1), whose postcanines are characterized by having a crown that is longer than tall, buccolingually wide (except *Acrophoca*), with buccal and lingual cingula that are elevated at the level of the main cusp (with some exceptions, e.g. Bone Valley monachine and *Neomonachus tropicalis*; figure 1l–o).

Among monachines, the general morphology of LACM 122584 and LACM 52624 resemble lower postcanine teeth of *Neomonachus* spp., and stem monachines like *Properiptychus argentinus*, *Acrophoca longirostris*, *Hadrokirus martini*, *Piscophoca pacifica*, and some undescribed monachines from the Pisco Formation (i.e. MNHN.F.PPI 269; figure 1; [12,25]). The main similarity is the lack of very prominent and well individualized principal and accessory cusps that occur in modern lobodontines (e.g. leopard seals, *Hydrurga leptonyx*) and some undescribed Pliocene monachines from the Upper Bone Valley Formation (e.g. UF 45683; figure 1). Additionally, the crenulated surface of the enamel of LACM 52624 resembles *Neomonachus* spp., and other fossil monachines like *P. argentinus*, *P. pacifica* and *H. martini*

(figure 1h–q). Differentially, the relatively smooth enamel on the lingual and buccal surfaces of LACM 122584 resembles *A. longirostris* and lobodontines (figure 1f,g).

In size, LACM 122584 is slightly smaller in most dimensions than teeth of *Acrophoca* spp. (table 2), which have buccolingually narrower teeth; and much smaller than *Neomonachus* spp., and *H. martini*, which has teeth larger than any other known Miocene monachine [12,25]; and it is similar in size to teeth of *P. argentinus* [13] (table 2). Overall, LACM 52624 and LACM 122584 show very distinctive morphology (including differences in size and aspect of the surface of the enamel), suggesting that they may belong to different species of monachines; however, the fragmentary nature and lack of additional specimens prevent us from making a more precise taxonomic determination beyond *Monachinae* gen. et sp. indet.

3. Discussion

Understanding and reconstructing the palaeobiogeographic history of marine mammals allow us to track their evolutionary history from a deep time perspective across different ocean

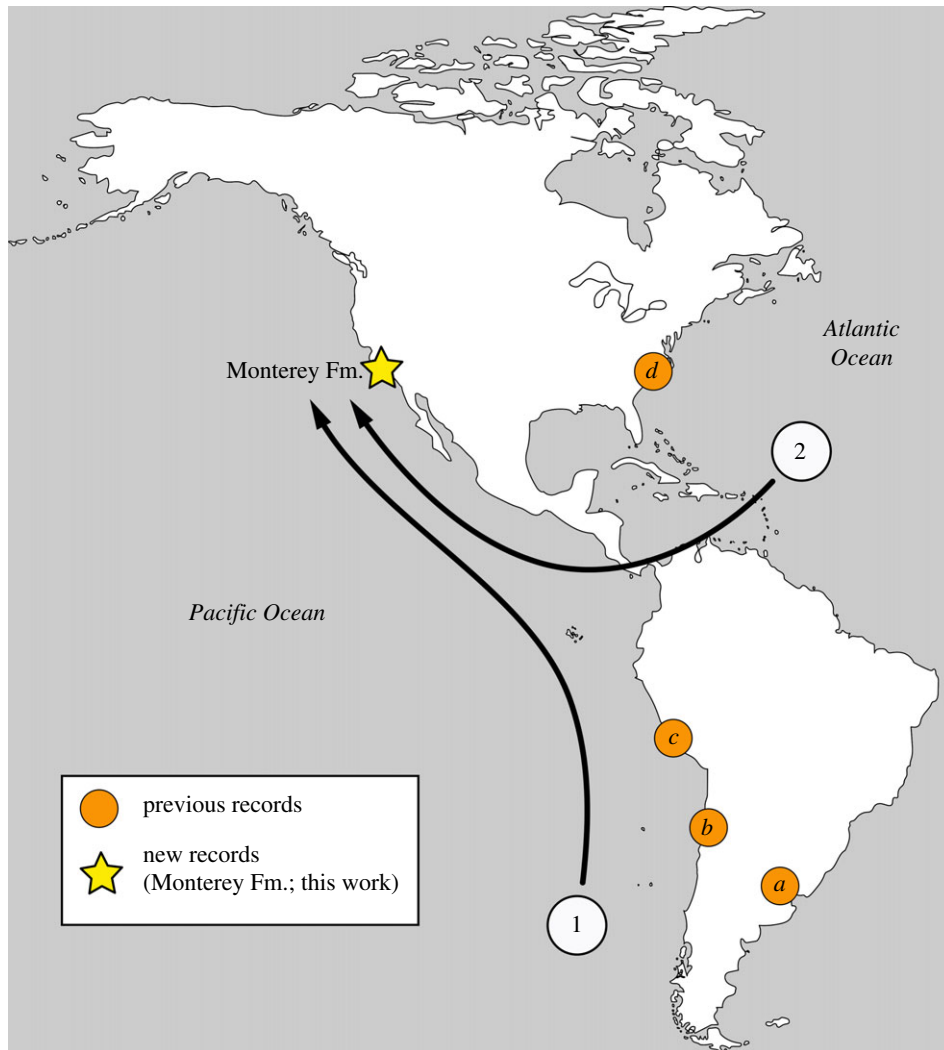


Figure 2. Fossil record of Monachinae seals from the Miocene of the eastern and western coasts of North and South America. Circles represent published occurrences of fossil Monachinae from Miocene levels: (a) Paraná Fm., Argentina [13]; (b) Bahía Inglesa Fm., Chile [29–31], (c) Pisco Fm., Peru [12,25,31], (d) Eastover Fm., Calvert Fm. Choptank Fm., USA [32,33]. Star represents the Monterey Fm. locality (LACM Loc. 6902). Arrows with numbers make reference to the dispersal hypothesis presented in the text: 1, South–north dispersal; 2, east–west dispersal. (Online version in colour.)

Table 2. Comparative measurements (in mm) of monachine p4.

| | length of crown | height of crown | width of crown |
|--|-----------------|-----------------|----------------|
| Monachinae gen. et sp. indet. (LACM 122584) | 12.7 | 6.8 | 6.2 |
| Monachinae gen. et sp. indet. (LACM 52624) | — | 6.1 | — |
| Monachinae gen. et sp. indet. (UF 45683) | 14.5 | 8.1 | 7.0 |
| <i>Acrophoca</i> sp. (MNHN.CHL 5) | 13.4 | 9.3 | 4.4 |
| <i>Acrophoca longirostris</i> (MNHN.F.SAS 644) | 15.5 | 7.5 | 5.2 |
| <i>Acrophoca longirostris</i> (MNHN.F.SAS 648) | 13.8 | 7.3 | 5.0 |
| <i>Hadrokirus martini</i> (MNHN.F.SAS 1627) ^a | 16.0 | 8.7 | 8.8 |
| <i>Properiptychus argentinus</i> (MACN 3538b) ^b | 12.8 | 7.0 | 7.0 |
| <i>Neomonachus schauinslandi</i> (LACM 54438) | 13.7 | 6.5 | 7.9 |
| <i>Neomonachus schauinslandi</i> (LACM 54384) | 13.5 | 7.8 | 8.3 |
| <i>Neomonachus schauinslandi</i> (LACM 52355) | 13.8 | 6.9 | 7.6 |
| <i>Neomonachus schauinslandi</i> (LACM 52392) | 13.0 | 8.3 | 7.7 |
| <i>Neomonachus tropicalis</i> (UF 36456) | 15.5 | 8.2 | 7.7 |

^aMeasurements from Amson & Muizon [12].

^bMeasurements from Muizon & Bond [13].

basins by identifying the timing of diversification, diversity patterns, local extinctions, and faunal turnovers (e.g. [26–28]). Phocids nowadays found along the eastern coast of the North Pacific include the phocine *Phoca vitulina*, and the monachine *Mirounga angustirostris*, and in the central North Pacific the monachine *Neomonachus schauinslandi* (Hawaiian monk seals). But their fossil record is limited [5–7], obscuring our interpretations about early dispersals of phocids in the region. In this regard, discoveries like the one described here contribute significantly to the understanding of patterns of phocid biodiversity over time and space.

The Monterey Formation monachines represent the earliest evidence of phocids on the North Pacific region and earliest example of sympatry among all three extant pinniped crown clades (i.e. Phocidae, Odobenidae and Otariidae). We propose three potential scenarios that are not mutually exclusive to explain these findings (figure 2). The strong morphological similarities between the Monterey monachines and some monachine species from the south Eastern Pacific hint at a close relationship between these taxa, suggesting a south–north dispersal. This would be consistent with some late Miocene occurrences of marine mammals, which are present in levels of the Pisco Formation (Peru) that are either older or contemporaneous with the Almejas and upper Monterey formations in Baja California and California, respectively (electronic supplementary material, table S1).

Alternatively, the Monterey specimens could also represent some monachine taxa that arrived from the Caribbean region through the Central American Seaway, a finding consistent with the hypothesis of the origin and dispersal for *Neomonachus* [2]. Under this scenario, the record reported here would suggest that a westward dispersal through the Central American Seaway of some ancestor of monk seals would occur sometime before 8.5 Ma, an estimate older than divergence times estimated between *N. schauinslandi*, and the recently extinct *N. tropicalis* [34,35]. Unfortunately, the fossil record of Caribbean monk seals is sparse and includes few occurrences from Pleistocene levels of the Caribbean Sea and the Gulf of Mexico [35], which are consistent with the historical distribution of this species in the region. Unfortunately, there are no other shared taxa among similar-age deposits in the north Western Atlantic and north Eastern Pacific that may

support this hypothesis. Further, another possible scenario is that these fossils represent vagrant individuals since extralimital records of extant phocids are not rare, including across hemispheres (e.g. [36,37]). But given the presence of shared cetacean genera (electronic supplementary material, table S1), and the potentially high fidelity of time-averaged units [38], we are inclined towards the first scenario proposed here. Nevertheless, new fossil findings are needed to clarify the mechanisms associated to a potential dispersal of ancient monk seals into the Pacific Ocean during the Neogene.

Finally, this record increases the overall taxonomic richness of the known pinniped assemblage for the Monterey Formation, which includes the desmatophocid *Allodesmus*, the stem otariid *P. starri* and the odobenids *Imagotaria* cf. *I. downsi* and Odobenidae spp. [9] (electronic supplementary material, text S1; table 1). Furthermore, the pinniped assemblage in the upper Monterey Formation locality studied here constitutes the earliest co-occurrence of crown pinnipeds (phocids, otariids and odobenids). The fossils described here extend the fossil record of seals in the region by at least 7 million years, leaving a number of questions regarding the habitat and niche segregation between these taxa that should be addressed in the future.

Ethics. No ethical assessments were required to conduct this research. No fieldwork was conducted by the authors for this project.

Data accessibility. Additional data are in the electronic supplementary material.

Authors' contributions. J.V.-J. designed the research, and photographed and measured the specimens. J.V.-J. and A.M.V.-T. described the specimens, analysed the data and wrote the paper. All authors approved the final version of this manuscript, and agree to be held accountable for the content therein.

Competing interests. We have no competing interests.

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