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First monk seal from the Southern Hemisphere rewrites the evolutionary history of true seals

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Living true seals (phocids) are the most widely dispersed semi-aquatic marine mammals, and comprise geographically separate northern (phocine) and southern (monachine) groups. Both are thought to have evolved in the North Atlantic, with only two monachine lineages—elephant seals and lobodontins—subsequently crossing the equator. The third and most basal monachine tribe, the monk seals, have hitherto been interpreted as exclusively northern and (sub)tropical throughout their entire history. Here, we describe a new species of extinct monk seal from the Pliocene of New Zealand, the first of its kind from the Southern Hemisphere, based on one of the best-preserved and richest samples of seal fossils worldwide. This unanticipated discovery reveals that all three monachine tribes once coexisted south of the equator, and forces a profound revision of their evolutionary history: rather than primarily diversifying in the North Atlantic, monachines largely evolved in the Southern Hemisphere, and from this southern cradle later invaded the north. Our results suggest that true seals crossed the equator over eight times in their history. Overall, they more than double the age of the north–south dichotomy characterizing living true seals and confirms a surprisingly recent major change in southern phocid diversity.

1. Introduction

The reinvasion of the oceans by marine tetrapods ultimately resulted in widespread global distributions from limited ancestral areas, as exemplified by true seals (phocids). Found from pole to pole, the biogeography of living true seals reflects their phylogeny: phocines inhabit Arctic and northern temperate oceans, whereas monachines are found in the (sub)tropics and throughout the Southern Ocean [1]. Despite this marked north–south dichotomy, prevailing biogeographic hypotheses propose that monachines originated and diversified alongside phocines in the North Atlantic [2–7]. Evidence for this scenario comes from a broad geographical overlap in their respective fossil records [1,8–10], as well as the exclusive Northern Hemisphere distribution of monk seals, the earliest diverging of the three extant monachine tribes [6,7,11]. Consequently, true seals are hypothesized to have crossed the thermal equatorial barrier a limited number of times, similar to eared seals [7,12–14].

Yet, current interpretations of true seal evolution have relied on fragmentary fossil specimens, and are challenged by recent taxonomic revisions [8,9,15], as well as the lack of a comprehensive phylogenetic framework [1]. In addition, matters are complicated by a historical research bias towards the Northern Hemisphere and global rarity of informative seal fossils [16], which has led

to a notable collection gap in Antarctica and Australasia [1,17]. This lack of data is critical, considering that monachines today mostly inhabit the Southern Ocean, and have been present in southern waters since at least the late Miocene [18,19]. Therefore, despite decades of research, the evolution of this major group of marine mammals remains vastly underexplored. Here, we describe a new extinct monk seal from the Pliocene of Taranaki (New Zealand), based on one of the best-preserved and richest samples of true seal fossils worldwide. The new species is the first of its kind from the Southern Hemisphere, and has profound implications for phocid evolution and biogeography.

2. Material and methods

Our phylogenetic analysis includes five outgroups, all living phocids, the recently extinct Caribbean monk seal *Neomonachus tropicalis*, and 18 extinct operational taxonomic units, selected on the basis that at least 10% of characters could be coded. Our matrix combines 168 morphological characters (four ordered; electronic supplementary material, dataset S3) with 16 nuclear genes and 12 mitochondrial genes (or, where available, the whole mitochondrial sequence; electronic supplementary material, datasets S2, S3). Molecular data were downloaded from GenBank, and alignment and non-coding regions checked in Aliview [20]. Aligned sequences were imported into PartitionFinder 2 [21], and grouped into partitions according to the best model for each gene.

We employed MrBayes v. 3.2.6 [22] on the CIPRES Science Gateway [23] to run a total evidence fossilized birth–death analysis [24], using node and tip dating (with stratigraphic ranges for tips) to improve accuracy [25,26]. The species sampling strategy parameter (SampleStrat) was set to ‘random’, which allows fossils to be sampled serially along the birth–death tree and thus appear as sampled ancestors [24]. Morphological and molecular partitions were unlinked. The analysis was run for 50 million generations (four runs, four chains) sampling every 5000 generations, with convergence achieved at a standard deviation of split frequencies below 0.01. See electronic supplementary material, dataset S3 for specific settings and data. Concatenated tree outputs were produced using the Perl script ‘burntrees.pl’ [27] and rerun as a maximum clade credibility (MCC) tree with mean node depths using TreeAnnotator v. 2.3.2 [28]. The fossilized birth–death model has the potential to recover some taxa as ancestral to younger sister taxa, as indicated by zero-branch lengths. These taxa are interpreted as ancestors in the context of the posterior tree produced by this model.

For the biogeographic analysis, outgroup taxa were pruned from trees in Mesquite v. 3.51 [29] and zero-length branches were set to 0.1 Myr in RStudio v. 1.2.1335 (R v. 3.6.0) using the package ‘ape’ [30]. Analysis was performed in RStudio using the packages ‘BioGeoBEARS’, ‘rexpokit’, ‘cladoRcpp’ and ‘phytools’ [31,32]. See electronic supplementary material, datasets S4–S11 for specific settings. The best model was selected based on likelihood ratio tests and AICc (Akaike information criterion) model weights. The selected model was simplified for figure 3; full models and ancestral area probabilities are provided as electronic supplementary material.

3. Systematic palaeontology

Carnivora Bowdich, 1821.
Pinnipedia Illiger, 1811.
Phocidae Gray, 1821.
Monachinae Gray, 1869.

Monachini Gray, 1869.

Eomonachus belegaerensis. gen. et sp. nov.

(a) Etymology

From the ancient greek ‘*ēō*’ (eos) meaning ‘dawn’ and *Monachus*, the generic name originally applied to all extant monk seals. The species name, ‘*belegaerensis*’ references the fictional ‘Great Sea’ Belegaer to the west of J. R. R. Tolkien’s Middle-Earth [33], paying homage to both the Tasman Sea which the new species inhabited, and the role of New Zealand in bringing Middle-Earth to the big screen.

(b) Holotype

Museum of New Zealand Te Papa Tongarewa (NMNZ; Wellington, NZ) specimen S.047422, comprising a partial dorsoventrally distorted skull missing the anterior portion of the premaxilla, the jugals and the teeth (figure 1a–c; electronic supplementary material, figures S1, S2).

(c) Paratypes

Paratypes are housed at NMNZ and Canterbury Museum (CM), Christchurch, New Zealand. NMNZ S.046692, partial cranium preserving the interorbital region and posterior zygomatic arches (figures 1d–f, 2g); CM 2017.62.7, partial cranium preserving the interorbital region, right posterior zygomatic arch, a natural brain endocast and the basicranium (figure 1g); CM 2020.74.1, rostrum with canines, P2s and P3s *in situ* (figures 1h–i, 2e); NMNZ S.047433, partial palate and nasal region; CM 2016.33.9, abraded cranium missing most of the dorsal surface; NMNZ S.047276 dorsoventrally crushed cranium (electronic supplementary material, figures S3–S7).

(d) Type locality and horizon

The holotype and paratypes were collected from sandy mudstone concretions northwest of Waihi Stream on Ohawe and Waihi Beaches, Taranaki, New Zealand. Concretions originate from the Tangahoe Mudstone Formation [34], a mid-Pliocene shallow marine sequence dated to 3.0–3.4 Ma [35].

(e) Diagnosis

Medium-sized monachine characterized by the carotid foramen being visible in ventral view, the mastoid being obscured in dorsal view, subparallel major axes of the glenoid fossa and the presence of four incisors. Differs from all other monachines in having a shortened ectotympanic tubercle (less than half the width of the postglenoid process) that is reflected dorsally to frame the external auditory meatus, a small fovea on the anteroventrolateral surface of the mastoid, a carotid foramen that is medially framed by the basioccipital (also present in *Mirounga*), and circular postcanines (in occlusal view) with a broad semicircular shelf making up half the crown with a small cusplet distolabial to the main cusp. Further differs from all monachines except *Monachini* in having a petrosal lobe extending between the mastoid and the tympanic bulla, and postcanines with a dominant main cusp, a broad lingual shelf, and no prominent accessory cusps; from Lobodontini and Miroungini in lacking a posterior extension of the tympanic posteromedial to the carotid foramen, and in having the M1 alveoli aligned with the infraorbital foramen; from Lobodontini in lacking a

Figure 1. New species of monk seal, *Eomonachus belegaerensis* from the Pliocene of Taranaki, New Zealand. Holotype NMNZ S.047422 in (a) dorsal, (b) ventral and (c) right lateral views. Paratype NMNZ S.046692 in (d) right lateral, (e) dorsal and (f) ventral views. Paratype CM 2017.62.7 in (g) dorsal view. Paratype CM 2020.74.1 in (h) left lateral and (i) ventral views. All fossils except CM 2017.62.7 were whitened with ammonium chloride. Darkened regions indicate mudstone, dashed lines indicate broken surfaces. Anatomical abbreviations: boc, basioccipital; bsph, basisphenoid; c, canine; eam, external auditory meatus; fro, frontal; gf, glenoid fossa; ioof, infraorbital foramen; jug, jugal; m, mastoid; max, maxilla; nas, nasal; oc, occipital; pal, palatine; par, parietal; P, premolar; M, molar; pmax, premaxilla; poc, paroccipital process; psph, presphenoid; ptry, pterygoid; tb, tympanic bulla. (Online version in colour.)

mastoid lip; from crown Miroungini in lacking a vaulted basi-cranium, and in having double-rooted P2–M1, separate auricular and external cochlear foramina, and a posteroventrally oriented mastoid; from crown Monachini in having the posterolateral mastoid obscured by the supramastoid ridge in dorsal view, and M1 alveoli that are almost as large as those for P2–P4; from *Monachus* in lacking a dorso-ventrally thickened petrosal lobe; from *Neomonachus* in lacking an anteroposteriorly thick ectotympanic tubercle, and in having an inflated entotympanic that does not taper medially; and from *N. tropicalis* in lacking an opening on the posterodorsal surface of the bulla immediately lateral to the carotid foramen.

4. Results and discussion

(a) Fossil record of true seals

Owing to their poor fossil record, extinct true seals are often based on isolated postcranial material [16], and frequently restricted to just a single specimen. In this light, both the quality (skulls instead of postcrania) and abundance of the type series of *Eomonachus* are unprecedented [16] and substantially improves the historically poor fossil record of Australasia

[36–41]. Specimens from Taranaki are often remarkably complete, thanks to being protected inside concretions. The latter aid three-dimensional preservation and increase resistance to erosion, and as such deserve attention as potential sources of exceptional fossil assemblages [42]. The position of Australasian seals in our phylogeny highlights the importance of the region in global marine tetrapod evolution, as also evident in the local diversity of whales, dolphins and seabirds [43–45]. Overall, *Eomonachus* demonstrates the potential of New Zealand and other underexplored parts of the Southern Hemisphere (e.g. Antarctica) to elucidate fundamental gaps in the evolutionary history of seals.

(b) True seal phylogeny

To determine the evolutionary relationships of our new fossil, we performed the most comprehensive total evidence analysis of true seal phylogeny to date (figure 3; electronic supplementary material). Our results recover both *Eomonachus* and an ancestral form from the latest Miocene of Beaumaris (Victoria, Australia) [36] as monk seals, and as such deeply nested within crown monachines.

True seals originated around 27.9 Ma, earlier than in most previous studies [7,47]. This was followed by the divergence

Figure 2. *Eomonachus belegaerensis* compared with extant monk seals. Left lateral view of (a) *Monachus monachus* NHMUK 1863.4.1.1, (b) *Neomonachus schauinslandi* NHMUK 1958.11.26.1, and line reconstruction of *Eomonachus belegaerensis*. Postcanines of (d) *Monachus monachus* NHMUK 1894.7.27.2 and (e) *Eomonachus belegaerensis* CM 2020.74.1 in ventral view. Right ear regions of (f) *Monachus monachus* NHMUK 1894.7.27.1 and (g) *Eomonachus belegaerensis* NMNZ S.046692 in ventral view. Fossils were whitened with ammonium chloride. NHMUK: National History Museum London. Anatomical abbreviations: cf, carotid foramen; eam, external auditory meatus; et, ectotympanic tubercle; gf, glenoid fossa; jf, jugular foramen; lc, lingual cingulum; m, mastoid; P, premolar; M, molar; pl, petrosal lobe; poc, paroccipital process; ps, postcanine shelf; tb, tympanic bulla; tf, tympanohyal fossa. (Online version in colour.)

Figure 3. Total evidence phylogeny (maximum clade credibility tree) of Phocidae, with DIVALIKE + J ancestral range estimation. Black lines indicate outgroup relationships, coloured lines indicate the (simplified) biogeographic estimation and dots on branches represent ancestors (as resolved by the FBD model). Numbers at nodes and on ancestors represent posterior probabilities above 0.5. Daggers represent extinct species. Middle Miocene Climatic optimum range from Song *et al.* [46]. Biogeographic node labels are only shown where the reconstructed range differs from the previous (basal) node. Ancestral area estimations with a probability of less than 50% are indicated with an asterisk (*). Posterior tree output and the full biogeographic model (including ancestral area support values) are provided as electronic supplementary material. (Online version in colour.)

Figure 4. Previous and new biogeographic hypotheses for global crown monachine origins and dispersal. (a) Previous hypothesis from Fulton & Strobeck [7], (b) current hypothesis, as informed by our new fossils and total evidence phylogeny. Extant ranges for phocines and each of the monachine tribes are mapped. Squares represent the divergences of crown Monachinae and Phocinae, respectively, while circles indicate estimated areas of origin of each monachine tribe. Dashed lines indicate alternative monk seal dispersal routes from Australasia to the North Atlantic. (Online version in colour.)

of *Noriphocia*, which thus appears to be a stem phocid, rather than a monachine [8]. Other stem taxa include *Devinophoca*, in line with most previous analyses [48,49]; and *Kawas* from the Miocene of Argentina, previously thought to be the only known phocine from the Southern Hemisphere [8–10]. Its reidentification here as a stem phocid is significant, as it substantially reduces the geographical overlap between phocines and monachines in the fossil record.

Monachines are monophyletic and comprise five distinct lineages: a basal clade comprising *Homiphoca*, *Acrophoca*, *Piscophoca* and *Hadrokirus*; a second lineage comprising only the Lee Creek monachine and its (poorly supported) ancestor *Australophoca*; and crown monachines, including monk seals (Monachini), elephant seals (Miroungini) and lobodontins. Whereas previous analyses interpreted *Homiphoca*, *Acrophoca*, *Piscophoca* and *Hadrokirus* as either stem lobodontins [9,50,51] or a succession of stem monachines [8,15,49], our results cluster them into a novel, albeit poorly supported, extinct clade. With pinniped phylogeny remaining in flux, we refrain from formally naming this group. Nevertheless, it is tempting

to speculate that monachines once included a fourth tribe, which coexisted with the others in the Southern Hemisphere.

Neomonachus schauinslandi is the earliest diverging monk seal, followed by *Eomonachus*, *N. tropicalis* and *Monachus*, with *Pliophoca etrusca* ancestral to the latter two (figure 3). The paraphyly of *Neomonachus* mirrors disagreements between previous studies [15,52,53] and probably reflects the limited amount of molecular information for the extinct Caribbean monk seal, *N. tropicalis* (just a single gene, *cytb* [53], compared with 28 genes for all other extant pinnipeds in our dataset). Despite the strong morphological arguments in favour of *Neomonachus* [53], additional molecular work is required to confirm the status of this genus.

(c) First monk seal from the Southern Hemisphere

Until now, monk seals had only been known from the Northern Hemisphere [1], with pre-Pleistocene fossils being restricted to the Mediterranean [15]. This pattern led to the assumption that they were an exclusively northern clade, and had

dispersed to the Pacific via the Central American Seaway [15,53]. *Eomonachus* and its ancestor from Beaumaris now reveal a much broader geographical range, and necessitate a history of monk seal dispersal across the equator. Together, they represent the oldest evidence of monk seals in the world. Like their living relatives, both *Eomonachus* and the seal from Beaumaris appear to have inhabited warm waters, with local sea surface temperatures during the late Neogene rivalling those of the modern Mediterranean [54,55]. Monk seals appear to be sensitive to temperature fluctuations [56], and as such may have become locally extinct when temperatures cooled at the end of the Pliocene [57,58].

(d) Equatorial crossings in true seal evolution

The best-supported biogeographic model (DIVALIKE + J) implies that stem phocids and monachines crossed the equator eight times over the past 15 Ma (figure 3). This figure is far higher than previously assumed [2–7], and yet may still be an underestimate given the recent description of North Pacific monachine remains resembling fossils from Peru [59]. Even today, southern elephant seals have been noted north of the equator [60]. The apparent ease with which phocids cross the tropics is remarkable [12], and notably contrasts with the single dispersal event that gave rise to southern fur seals and sea lions (otariids) [13,14]. Perhaps their mobility was facilitated by a broad environmental tolerance, as reflected today in the contrast between the tropical monk seals and the polar phocines and lobodontins [1]. By contrast, otariids appear to be tied to cool, highly productive waters, which probably limited opportunities for equatorial dispersal [13]. This suggests that true seals, despite being semi-aquatic, have dispersal capabilities and environmental tolerances approaching those of cetaceans. Overall, this has enabled true seals to conquer more of the world's oceans than any other semi-aquatic tetrapod, such as walruses, eared seals, penguins, auks and living sea turtles.

(e) A southern cradle for monachine evolution

The DIVALIKE + J biogeographic model suggests that phocids originated in the Paratethys–Mediterranean, with phocines and monachines later diverging in the North Atlantic. While phocines continued to disperse entirely within the Northern Hemisphere (especially the Arctic), monachines quickly moved southwards across the equator (figure 3). It currently remains unclear whether this dispersal occurred through the Central American Seaway or via the South Atlantic (figure 4b), as perhaps indicated by the fragmentary remains of *Properiptychus* from the late Miocene of Argentina [18,19].

Contrasting with previous biogeographic hypotheses [2–7,11,61] (figure 4a), much of subsequent monachine evolution appears to have unfolded in the Southern Hemisphere. Stem monachines, monk seals, elephant seals and lobodontins all originated here, even though some of them later reinvaded the north (figures 3 and 4b). Rather than in the North Atlantic [7] (figure 4a), elephant seals and lobodontins diverged in the Southern Ocean, suggesting that monachines reached the Antarctic as early as 9.2 Ma. Elephant seals then diversified in Australasia, and crossed into the Northern Hemisphere during the Pleistocene, as previously proposed [41].

Monk seals emerged in Australasia around 10.8 Ma, but then seemingly diversified in the North Pacific. From here,

they reinvaded Australasia, before spreading to the North Atlantic around 7.1 Ma, and finally to the Mediterranean around 3 Ma. This scenario corroborates a relatively long history of monachines in the Pacific [59], and questions earlier suggestions that monk seals dispersed westwards from the Atlantic via the Central American Seaway [53,59]. Instead, they either migrated in the opposite direction, or entered the Atlantic by dispersing around the southern tip of South America (figure 4b). Note, however, that this interpretation partly rests on the basal position of *N. schauinslandi* in our phylogeny. Future changes to this assumption might simplify the biogeographic scenario proposed here, especially if *Neomonachus* were found to be monophyletic [53] and extant monk seals formed a clade to the exclusion of *Eomonachus*.

Overall, our biogeographic scenario identifies the north–south split characterizing living phocids as a surprisingly ancient pattern stretching back to around 15 Ma. Both our divergence times and geographical estimates suggest that all three monachine tribes coexisted in the Southern Hemisphere for several million years, even though their fossil records remain relatively sparse and so far only partially overlap [37,41,62]. The disappearance of southern monk seals and stem monachines marks a major turnover in pinniped and, indeed, global marine megafauna diversity [58], during which southern phocids were broadly replaced by fur seals and sea lions [40,62,63]. The fact that the role of monk seals in these profound changes had so far gone unnoticed testifies to the still underexplored nature of the austral fossil record, and its potential to elucidate—and at times rewrite—marine mammal evolution.

Data accessibility. Files and data used in the phylogenetic and biogeographic analyses are available at Figshare repository (doi: 10.6084/m9.figshare.12762836; 10.6084/m9.figshare.12762845; 10.6084/m9.figshare.12762905; 10.6084/m9.figshare.12762827; 10.6084/m9.figshare.12762851; 10.6084/m9.figshare.12762893; 10.6084/m9.figshare.12762869; 10.6084/m9.figshare.12763028; 10.6084/m9.figshare.12762830; 10.6084/m9.figshare.12762914; 10.6084/m9.figshare.12762917; 10.6084/m9.figshare.12762929; 10.6084/m9.figshare.12763055; 10.6084/m9.figshare.12762887; 10.6084/m9.figshare.12762923). Additional data are available in the electronic supplementary material file. The LSID (life science identifier) for *Eomonachus* is urn:lsid:zoobank.org:act:42C918B7-EF30-45CC-AF28-5E161415787A, and for *Eomonachus belegaerensis* is urn:lsid:zoobank.org:act:1BAFB80D-07B9-486C-99C0-5822563505B7.

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Competing interests. We declare we have no competing interests.

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