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Ancient crested penguin constrains timing of recruitment into seabird hotspot

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New Zealand is a globally significant hotspot for seabird diversity, but the sparse fossil record for most seabird lineages has impeded our understanding of how and when this hotspot developed. Here, we describe multiple exceptionally well-preserved specimens of a new species of penguin from tightly dated (3.36-3.06 Ma) Pliocene deposits in New Zealand. Bayesian and parsimony analyses place Eudyptes atatu sp. nov. as the sister species to all extant and recently extinct members of the crested penguin genus Eudyptes. The new species has a markedly more slender upper beak and mandible compared with other *Eudyptes* penguins. Our combined evidence approach reveals that deep bills evolved in both crested and stiff-tailed penguins (Pygoscelis) during the Pliocene. That deep bills arose so late in the greater than 60 million year evolutionary history of penguins suggests that dietary shifts may have occurred as wind-driven Pliocene upwelling radically restructured southern ocean ecosystems. Ancestral area reconstructions using BioGeoBEARS identify New Zealand as the most likely ancestral area for total-group penguins, crown penguins and crested penguins. Our analyses provide a timeframe for recruitment of crown penguins into the New Zealand avifauna, indicating this process began in the late Neogene and was completed via multiple waves of colonizing lineages.

1. Introduction

Estimating the timing and ancestral areas of lineages remains a major frontier for biology and can be especially informative as to how faunas are assembled in geographically isolated regions with high endemism like New Zealand (e.g. [1,2]). The highly productive oceans of the Southwest Pacific today attract seabirds from across the world [3]. The historical absence of terrestrial mammals in New Zealand (with bats being the exception) [4] may have encouraged the formation of seabird colonies in deep time and contributed to the development of the modern-day seabird biodiversity hotspot around New Zealand. Around one-quarter of the approximately 360 extant seabird species known worldwide breed in New Zealand and around 10% of these species are endemic [4]. However, the sparse fossil record for most seabird lineages has made it difficult to constrain when and how this biodiversity hotspot first developed. Penguins are a notable exception and thanks to their dense bone structure have a rich fossil record that allows for more precise estimation of ancestral biogeography [5]. Around 20 fossil species of penguin have been described from New Zealand, with more specimens known and awaiting description, and seven extant species of penguin breed in New Zealand today. Newly discovered fossils help constrain the timing of crown penguins (i.e. all descendants of the most recent common ancestor of all extant penguin species), and recruitment into this globally important region for seabirds.

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2. Systematic palaeontology

Aves Linnaeus, 1758 Sphenisciformes Sharpe, 1891 Spheniscidae Bonaparte, 1831 *Eudyptes* Vieillot, 1816

Type species. *Eudyptes atatu* sp. nov.

Diagnosis. Referred to Eudyptes based on (1) strong sigmoid curvature of jugal bar, (2) presence of shelf of bone bounding the salt gland fossa, (3) greatly deepened temporal fossae, (4) strongly shortened tarsometatarsus (ratio of length to proximal width less than 2.0) and (5) moderately deep sulcus between metatarsals II and III. Characters 1, 2 and 4 also occur within Pygoscelis, which differs from Eudyptes in exhibiting very weakly developed temporal fossae, partial or complete fusion of the ilia to the synsacrum, and a shallow sulcus between metatarsals II and III. Characters 1, 3, 4 and 5 also occur in Megadyptes, which differs from Eudyptes in having a less strongly curved jugal bar and a very deep depression for insertion of the iliotrochanteris muscle near the proximal margin of the trochanteric crest of the femur. Differentiated from all extant and recently extinct species of Eudyptes by (1) upper beak slender in dorsal view (versus rostral tip markedly swollen in extant *Eudyptes*) and (2) mandibular ramus modestly deepened at midpoint (versus strongly deepened in extant Eudyptes). Eudyptes atatu can be differentiated from the poorly known Eudyptes calauina (for which the skull remains unknown) by much smaller size (tarsometatarsus length 29.1 mm in E. atatu versus 41.3 mm in E. calauina holotype) and less robust tarsometatarsus (ratio of length to proximal width 1.9 in E. atatu versus 1.7 in E. calauina).

Institutional Abbreviations: CM, Canterbury Museum, Christchurch, New Zealand; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand. *Eudyptes atatu* sp. nov. Thomas, Tennyson, Scofield and Ksepka.

Holotype. NMNZ S.046318—cranium, mandible, seven vertebrae, sternum, left coracoid, right coracoid, right humerus, right scapula, right ulna, right radius (figure 1, see electronic supplementary material, S1 for measurements).

Referred material. CM 2017-62-8-1 cranium; CM 2016.33.4.1 synsacrum and pelvis; CM 2016.33.4.2 femur; CM 2016.33.4.3 tibiotarsus; CM 2016.33.5 sternum, scapula, coracoid, humerus, ulna (proximal end), radius (proximal end); CM 2016.33.6.1 cranium; 2016.33.6.2 mandible fragment; CM 2016.33.7 cranium; 2016.33.8 cranium; NMNZ S.046315 cranium; NMNZ S.046317 cranium; NMNZ S.046319 synsacrum and pelvis, femur, tibiotarsus, tarsometatarsus; NMNZ S.046320 rib fragment, scapula, humerus, femur. See electronic supplementary material, S1, figures S1–S8.

Etymology. From Te reo Māori, ata tū ('dawn'), referencing the stem position within *Eudyptes* and the earliest recorded appearance of *Eudyptes* in New Zealand.

Type locality and horizon. Late Pliocene (Piacenzian) Tangahoe Formation in the southern Taranaki region of the North Island of New Zealand [6]. Local Waipipian stage, constrained to 3.36–3.06 Ma based on oxygen isotope stage and magnetic polarity data (see [6,7]). Holotype and referred specimens were surface collected and do not have an exact Fossil Record Database record, but see Q21/f0002 for nearby location.

3. Description

Eudyptes atatu was closest in size to the modern erect-crested penguin Eudyptes sclateri [8] (see electronic supplementary material, S1). Size variation within the referred specimens of E. atatu likely reflects sexual dimorphism, which is pronounced in extant Eudyptes compared with other modern penguins (e.g. [9]). The skull of *E. atatu* is more gracile than that of any extant Eudyptes species, with a more slender, gently hooked beak lacking the strong swelling of the beak tip rostral to the nares characteristic of extant crested penguins (figure 1). As in extant Eudyptes and Megadyptes, the temporal fossae are deep and widely separated. The salt gland fossae are bordered laterally by broad shelves of bone and excavate the interorbital part of the skull roof so to create a narrow midline bridge. The jugal bar is strongly sigmoid with an inflection point near the maxilla-jugal junction. Sutures remain clearly visible between the premaxilla, maxilla and nasal.

The most striking difference between *E. atatu* and extant *Eudyptes* is the shape of the mandible. Whereas the mandible of modern *Eudyptes* species shows a pronounced deepening towards the midpoint, in *E. atatu* the mandible retains a more slender shape (figure 1). In other regards, the mandible is similar to extant *Eudyptes* in showing a gentle sigmoid curvature, a short symphysis and elongate dentary (accounting for more than half of overall mandible length). At the rostral tip, the dense neurovascular foramina coalesce to form a channel, a feature that is variably developed but commonly present in extant *Eudyptes* and *Pygoscelis*, as opposed to other penguins, in which these foramina usually remain discrete.

The humerus of *E. atatu* preserves several traits characteristic of crown penguins (e.g. supracoracoideus and latissimus dorsi muscle scars separated by a small gap; figure 1) [10], being especially similar to the humeri of *Eudyptes* (including *E. calauina*), *Megadyptes* and *Pygoscelis* (see electronic supplementary material, S1). The tricipital fossa does not have the projecting and straight proximal margin found only in *Spheniscus* and some individuals of *Pygoscelis antarctica* among extant penguins and has a weakly projecting preaxial angle similar to *E. calauina, Eudyptes chrysolophus, Eudyptula minor* and *Madrynornis mirandus* [8].

The tarsometatarsus has long been considered a key element in fossil penguin systematics [11]. Eudyptes atatu exhibits a strongly shortened and block-like tarsometatarsus (figure 1) [12]. Proportions are similar to extant Eudyptes and Pygoscelis, and the fossil differs from the latter genus in having a medial hypotarsal crest projecting further in plantar direction than the lateral hypotarsal crest. The lateral hypotarsal crest is furthermore short and triangular in plantar view. The medial and lateral dorsal longitudinal sulci are moderately deep, subequal in length, and become shallow at the distal end near the intertrochlear incisures, a conformation shared by Eudyptes, Megadyptes and the fossil taxon Pygoscelis grandis. The medial proximal vascular foramen opens on the medial edge of the medial crest in E. atatu as in all extant penguins except Pygoscelis; the alternative or additional opening distal to the medial crest as observed in Aptenodytes, Pygoscelis and Nucleornis is absent. Metatarsal trochleae III and IV are aligned in the same plane in distal view as in most crown penguins except Spheniscus, in which trochleae IV is dorsally displaced. See electronic supplementary material, S1 for measurements,

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Figure 1. *Eudyptes atatu* sp. nov. showing key diagnostic features. Holotype specimen NMNZ 5.046318 showing (*a*) right lateral view of skull and block with (*c*) mandible and (*d*) postcranial elements. (*b*) Right lateral view of Snares crested penguin *Eudyptes robustus* NMNZ 0R.023746 for comparison. Referred material of *E. atatu* including (*e*) 5.046315 dorsal view of skull, (*f*) CM 2017-62-8-1 left lateral view of skull, (*g*) NMNZ 5.046320 right humerus caudal view, and (*h*) dorsal and (*i*) plantar views of NMNZ 5.046319 right tarsometatarsus. Ano, apertura nasale ossea (naris). Clh, crista lateralis hypotarsi (lateral hypotarsal crest); Co, coracoid; Cmh, crista medialis hypotarsi (medial hypotarsal crest); F*, frontal with wide shelf bordering the salt gland fossa; Fte*, fossa temporalis (temporal fossa) that is relatively deep; Fvpl, foramen vasculare proximale lateralis (medial proximal vascular foramen); Fvpm, foramen vasculare proximale mediale (medial proximal vascular foramen); Hu, humerus; Ic, incisura capitus (capital incisure); Imp, impressio musculus pectoralis (pectoral muscle impression); Mr, ramus mandibula (mandibular ramus); Oj*, os jugale (jugal bar) showing distinct curvature; Op, os palatinum (palatine); Ma, articular end of mandible; Mr*, mandibular ramus that is relatively narrow at midpoint; Ra, radius; Sc, scapula; Sldl, sulcus longitudinalis dorsalis lateralis (medial dorsal longitudinal sulcus) which is moderately deep; St, sternum; Tmtc, tuberositas musculus tibialis cranialis (tuberosity for cranial tibial muscle); Tv, tuberculum ventral (ventral tubercle); Ve, vertebra. Asterisks denote diagnostic characters. Photographs (a)–(e), (g)–(i) from Jean-Claude Stahl at Museum of New Zealand Te Papa Tongarewa, photograph (*f*) from R. Paul Scofield at Canterbury Museum. (Online version in colour.)

additional details of the osteology and comparisons with other fossil taxa.

4. Phylogenetic analysis

We scored *E. atatu* into a modified version of a recent morphological matrix [13], to which we added 30 new morphological characters and eight recently described

fossil penguins: *Sequiwaimanu rosieae*, *Pygoscelis calderensis*, *Eudyptes warhami*, *E. calauina*, *Megadyptes antipodes richdalei* and *Megadyptes antipodes waitaha*. The updated matrix contains 274 morphological characters and 66 penguin taxa as well as complete mitochondrial genomes [14] for all extant and recently extinct taxa.

We conducted a Bayesian analysis of the combined morphological and molecular datasets in RevBayes [15] using a



Figure 2. Phylogeny, biogeography and mandible depth variation across crown penguins. The maximum sampled-ancestor clade credibility tree is modified so that taxa recovered as potential ancestors are given a short terminal branch to accommodate downstream analyses. Ancestral area reconstructions show results from dispersal-extinction-cladogenesis with jump parameter as calculated in the BioGeoBEARS package in R 3.5.0 [19,20]. Tip and node colours correspond to areas in inset map (extant taxon biogeography from [21]). Closed symbols on nodes indicate an ancestral area with greater than 50% proportional likelihood when compared with other possible areas. Open symbols show when the greatest proportional likelihood for an ancestral area at that node is less than 50%. Multiple colours at the same node indicate an estimated presence in multiple regions. Mandibles scaled to the same size. Arrows on *Eudyptes atatu* mandible show length and depth measurement guide for calculating mandible depth ratio. Mandible images from three-dimensional scans of specimens from: American Museum of Natural History, New York, USA; Canterbury Museum, Christchurch, New Zealand; Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand. Full list of mandible specimens in electronic supplementary material, S1. Mandible images not available for *Eudyptes chrysocome* and *Spheniscus mendiculus*. (Online version in colour.)

specimen-level fossilized birth-death process prior on the tree topology and divergence times [16,17], with exponential hyperpriors on the diversification parameters. The backbone relationships of extant taxa were constrained to match those in [18]. See electronic supplementary material for RevBayes scripts used to conduct this analysis. These analyses follow the protocol found in the RevBayes tutorial: https://revbayes.github.io/tutorials/fbd/fbd_specimen.html.

In the maximum sampled-ancestor clade credibility (MSACC) tree *E. atatu* was recovered as the sister taxon to all extant *Eudyptes* species (figure 2). Owing to the highly incomplete nature of *E. calauina*, we consider both the originally proposed placement within *Eudyptes* [9] and the placement recovered here as a direct ancestor of

Megadyptes to be tenuous at best. All sampled fossil species of *Aptenodytes*, *Pygoscelis* and *Spheniscus* are recovered as stem members of their respective genera, with the poorly known *Nucleornis* recovered along the stem lineage of *Pygoscelis*. We note that the placement of *E. warhami* is unstable. Although the MSACC tree places this recently extinct species within the rockhopper subclade, many trees in the overall sample instead place it as sister to *E. sclateri* as originally reported based on mtDNA alone [14]. We attribute this uncertainty to the large amount of missing morphological data for *E. warhami* introducing added instability in our sampled-ancestor analyses.

We also conducted a parsimony analysis in PAUP*4.0a build 166 [11], using the heuristic search option and 10 000

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replicates of random taxon addition, with multistate codings treated as uncertainty and branches of minimum length zero collapsed. This resulted in 189762 most parsimonious trees of 8712 steps (see electronic supplementary material, S1). The strict consensus of these trees was almost entirely collapsed owing to three 'wildcard' taxa: E. calauina, Spheniscus chilensis and P. calderensis. A second analysis with these taxa excluded resulted in 5614 most parsimonious trees of 8711 steps. Four notable differences occur in the parsimony results compared with the Bayesian results: (i) Madrynornis is recovered as the sister taxon to the Spheniscus + Eudyptula + Inguza clade rather than the Eudyptes + Megadyptes clade, (ii) Nucleornis is recovered as a stem representative of the Aptenodytes lineage rather than as a stem representative of the Pygoscelis lineage, (iii) Marplesornis is recovered as the sister taxon to crown penguins rather than sister to the Spheniscus + Eudyptula + Inguza clade, and (iv) E. warhami is recovered as sister to E. sclateri.

5. Ancestral area estimation

Ancestral areas were estimated with BioGeoBEARS [18]. We used the MSACC tree for these analyses because branch lengths are required by BioGeoBEARS. We compared six models: dispersal-extinction-cladogenesis (DEC) [22], dispersal vicariance analysis (DIVA, similar to [23]) and Bayesian analysis of biogeography (BAYAREA, after [24]), and a second implementation of each of these three models with an additional parameter that allows lineages to 'jump' to areas not previously occupied (+j, founder event speciation), using weighted Akaike information criterion (wAIC) values [25]. Bayesian stochastic mapping was performed on all six models (100 maps). The dispersal-extinctioncladogenesis model with the jump parameter (DEC + j) was the best supported of the six models (wAIC = 0.453) and we focus on those results here (see figure 2 for crown penguin biogeography), though see electronic supplementary material, S2 for results with alternative models. Our results suggest that founder event speciation was common across the biogeographic history of penguins. Although +j models implemented in BioGeoBEARS have attracted criticism [26], we note that the prevalence of founder event speciation is logically consistent with the geographic distribution of modern congenerics (e.g. Eudyptula and Spheniscus) and abundant records of penguins appearing as vagrants thousands of kilometres outside their normal ranges [27].

In our primary results, New Zealand is recovered as the most likely ancestral area for the most recent common ancestor (MRCA) of all penguins (58% proportional likelihood, see electronic supplementary material, S2) and all crown-clade penguins (56% proportional likelihood). New Zealand (either exclusively or with other areas) is identified as the most likely ancestral area for all penguins in all 100 of the Bayesian stochastic maps performed on the DEC + jmodel, and as the most likely ancestral area for crown-clade penguins in 87% of Bayesian stochastic maps (see electronic supplementary material, S2). Both New Zealand and South America were estimated to have been ancestral areas for the Eudyptes MRCA (i.e. a wide ancestral area encompassing both regions; 25% proportional likelihood). New Zealand was identified as an ancestral area for the Eudyptes MRCA in 83% of Bayesian stochastic maps, and New Zealand and

South America either as a pair or with other regions were identified as ancestral areas in 53% of the maps. New Zealand alone was estimated as the most likely ancestral area for the MRCA of the three extant species of *Eudyptes* endemic to New Zealand today (erect-crested *E. sclateri*, Snares-crested *E. robustus* and tawaki *Eudyptes pachyrhynchus*; 99% proportional likelihood, 100% of stochastic maps).

Eudyptes calauina, from the Pliocene of Chile, is the only previously reported fossil representative of Eudyptes, but is known only from extremely sparse material. We consider the weakly supported position of E. calauina in the MSACC tree doubtful at best, and this could potentially cause spurious results for ancestral area estimation. Thus, we ran a supplementary BioGeoBEARS analysis after pruning E. calauina to explore the potential confounding impact of this uncertainty. Bayesian stochastic mapping was performed on all six models (100 maps). The BAYAREA model with jump parameter was the best supported of the six models for the pruned tree (wAIC = 0.545; see electronic supplementary material, S2). New Zealand was estimated to be the most likely ancestral area (either exclusively or with other areas) for the most recent common ancestor of all penguins (97% proportional likelihood; 100% of stochastic maps), all crownclade penguins (61% proportional likelihood, 96% of stochastic maps) and the Eudyptes MRCA (98% proportional likelihood, 89% of stochastic maps) and the most likely ancestral area for Eudyptes endemic to New Zealand today (100% proportional likelihood; 100% of stochastic maps).

6. Mandible depth

As the first stem species of crested penguin, *E. atatu* reveals that a slender bill similar to that of extant Megadyptes was ancestral for the 'yellow penguin' clade (Megadyptes + Eudyptes) and that a deeper bill arose independently in crown Eudyptes and Pygoscelis. Here, we tested whether variation in bill depth across crown penguins represented meaningful phylogenetic signal (i.e. trait evolution not that expected under Brownian motion; [28-31]), and hence whether bill depth may have been subject to an evolutionary driver (e.g. potential changes in prey availability; [32]). Mandible depth was calculated as dorsoventral distance across mandibular ramus midpoint divided by mandible length (figure 2; see electronic supplementary material, S1). Pagel's λ and Blomberg's K were calculated in R 3.5.0 [19] using 'phylosig' from phytools 0.6-60 [31], using the MSACC phylogeny from this study pruned to include only extant species. We found strong evidence that mandible depth has phylogenetically meaningful variation within crown penguins (Pagel's $\lambda = 0.905$, p < 0.001; Blomberg's K = 0.92, p < 0.001). Continuous trait mapping of bill depth across crown penguins using 'contMap' from phytools further supports a Pliocene transition from slender to deep bills in an ancestor to crown Eudyptes (see electronic supplementary material, S1).

7. Discussion

The newly discovered and well-preserved fossil *E. atatu* sp. nov. reveals that crested penguins (*Eudyptes*) had been recruited into the Zealandian avifauna by the late Pliocene. *Eudyptes* is the most species-rich genus among living penguins, and today the New Zealand region is home to four

breeding species of *Eudyptes*, including three extant endemics [21]. The recently recognized E. warhami also lived in the New Zealand region but became extinct in the thirteenth century [14]. The crown Eudyptes that contribute to the New Zealand biodiversity hotspot today are potentially the descendants of a lineage that has lived in Zealandia for several million years. The presence of crested penguins (Eudyptes) and yellow-eyed penguins (Megadyptes) in the New Zealand region since the late Neogene is here supported by historical biogeographic analyses, implying ghost lineages for *Eudyptes* and *Megadyptes* extending back at least 3 million years. Thus, the biogeographic history of Eudyptes in New Zealand is primarily one of local radiation after founder events. This contrasts starkly with the biogeographic history of penguins in southern Africa, which was marked by repeated colonization events rather than endemic radiation [33].

Eudyptes atatu reveals that the deep bill of crested penguins evolved comparatively recently, most likely in the past 2-5 million years. The apomorphic deep bill in crown radiation of *Eudyptes* affords accommodation for a larger, bristle-covered tongue, which is considered an adaptation for securing small prey items [34] and may also serve to increase overall gular volume (R. E. Fordyce 2019, personal communication). The shift to deeper bills in Eudyptes is coeval with the shift in body size for several groups of baleen whales hypothesized to be linked to foraging, perhaps implying a common underlying mechanism [35]. Beginning in the Pliocene, intensified, wind-driven upwelling radically reformed oceanic food webs [32], triggering a boom in krill biomass that led to the explosive diversification of cetaceans [35]. We hypothesize that crested penguins were also affected by this food web restructuring, though with much more subtle manifestation in their morphology than in the case of cetaceans.

In sum, *E. atatu* provides an important new window into the evolution and palaeobiology of crown penguins and reinforces the importance of Zealandia for seabird evolution. The rapidly improving fossil record of both early stem penguins (e.g. [36]) and Pliocene–Holocene stem penguins [18] suggests that Zealandia was an incubator of penguin diversity in which the first penguins, the first crown penguins, and likely the first crested penguins evolved and later dispersed throughout the Southern Hemisphere.

Ethics. This article does not present research with ethical considerations. Data accessibility. Scripts and data associated with RevBayes analysis and parsimony analysis are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.kprr4xh1x [37]. The Life Science Identifier for *Eudyptes atatu* is urn:lsid:zoobank. org:pub:6AD6F64A-3180-4732-886B-2FD0F297E9DA.

Author contributions. D.B.T. and D.T.K. collected the morphological data. D.T.K., T.A.H. and W.P. conducted the phylogenetic analyses. D.B.T. conducted the other analyses. A.J.D.T, D.B.T and R.P.S. conceived of the study. D.B.T., D.T.K., A.J.D.T. and R.P.S. wrote and edited the manuscript.

Competing interests. We declare we have no competing interests.

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