

## Pliocene fossils support a New Zealand origin for the smallest extant penguins

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**Abstract.**—A late Pliocene (3.36–3.06 Ma) exposure of the Tangahoe Formation on the North Island of New Zealand preserves close fossil relatives of many extant seabird clades. Here, we report an extinct member of the little penguin (*Eudyptula* Bonaparte, 1856) lineage from the Tangahoe Formation—the smallest extinct crown penguin yet known. *Eudyptula wilsonae* n. sp. is based on the nearly complete skulls of an adult and a fledged but immature individual. Both skulls show more slender proportions than modern little penguins and precede genome-derived estimates for the divergence between *Eudyptula minor minor* Forster, 1781 (endemic to New Zealand) and *Eudyptula m. novaehollandiae* Stephens, 1826 (native to Australia and recently established in New Zealand). This raises the possibility that the fossil taxon represents a lineage directly ancestral to extant little penguins. Our results support a Zealandian origin for little penguins, with subsequent Pleistocene dispersal to Australia and a more recent Holocene range expansion of *Eudyptula m. novaehollandiae* back into New Zealand.

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### Introduction

Aotearoa New Zealand is home to three of the six extant penguin genera, including the little penguins, *Eudyptula* Bonaparte, 1856. Little penguins occur across southern Australia and the New Zealand archipelago. They are remarkable for being among the smallest obligate marine endotherms yet having breeding colonies distributed across the broadest range of mean annual sea-surface temperatures observed in penguins (Stonehouse, 1967; Borboroglu and Boersma, 2013; see also Supplemental data). Their biogeographic origins and morphological evolution are therefore of great interest.

*Eudyptula* currently comprises two lineages: the kororā or New Zealand Little Penguin, *Eudyptula minor minor* Forster, 1781, which is endemic to New Zealand; and the Australian Little Penguin *Eudyptula m. novaehollandiae* Stephens, 1826. The Australian Little Penguin is native to Australia where the majority of its population occurs, but it also breeds in the Otago region of New Zealand, where it likely arrived after humans first settled in the region (Grosser et al., 2015). The status of these two taxa remains unsettled, with some studies considering them separate species (e.g., Grosser et al., 2017; Cole et al., 2022). Their

estimated molecular divergence and relative genetic distance exceed those of other recognized sister species within crown penguins, especially in *Eudyptes* (Cole et al., 2022, fig. S2). However, they are visually indistinguishable morphologically and so it was only recently recognized that some of the little penguins breeding in Otago in fact belong to the Australian lineage (Grosser et al., 2016). Here, we follow the recently published fifth edition to the checklist of New Zealand birds (Ornithological Society of New Zealand Checklist Committee, 2022) in treating the two taxa as subspecies (see also Miskelly et al., 2023).

The fossil record of *Eudyptula* is obscured by sparse data and conflicting fossil identifications. Putative records were summarized by Worthy et al. (2009) and include just two occurrences: a small humerus and ulna from late Oligocene or early Miocene Otekaike Limestone of southern New Zealand (Fordyce, 1991, p. 1247–1249), which was reidentified as a stem penguin by Ando (2007), and ‘a few late Pliocene and Recent specimens, not clearly distinct from living *Eudyptula*,’ which Simpson (1975, p. 21) mentioned in his review of New Zealand penguin fossils without providing specific localities or specimen numbers. We searched several collections to trace this material but found no specimens plausibly assignable to *Eudyptula* that are older than late Pleistocene. We surmise that Simpson’s (1975) reference pertains to material that has since been traced

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to Pleistocene infill deposits, which means that the only substantiated records of *Eudyptula* are late Pleistocene and Holocene subfossils (Worthy, 1998; Worthy and Grant-Mackie, 2003).

Here, we describe two *Eudyptula* fossils recently collected from the Pliocene Tangahoe Formation of New Zealand and, thus, for the first time confidently establish the presence of little penguins in Zealandia during the Neogene.

## Materials and methods

**Skull measurements and specimen age.**—We collected the following measurements from the skulls of *Eudyptula minor minor* (N=68), *Eudyptula m. novaehollandiae* (N=19), and the fossils described here (N=2) (Tables 1, S1): (1) maximum skull length, i.e., the distance between the bill tip and caudal margin of supraoccipital; (2) width of internarial bar, i.e., the maximum distance between the lateral edges of premaxillae in dorsal view; (3) interorbital width, i.e., the minimum distance between the orbits excluding the salt glands; and (4) postorbital width, i.e., the distance between the lateral edges of the postorbital processes. Not all measurements could be collected from all specimens owing to differences in preservation or preparation. Measurements (1) and (4) correspond to greatest length and greatest breadth as reported by Grosser et al. (2017) from the skulls of 84 and 82 individuals, respectively.

Animal age at time of death was inferred from suture closure and supported by museum record data. Individuals were considered adult if the internasal, frontal-nasal, and rostral portion of the interpremaxillary sutures were obliterated, and immature if any of these sutures remained visible. Especially young individuals retain visible sutures in their skull roof. Data from specimens for which all four measurements were available (N=60 for *Eudyptula m. minor*, N=19 for *Eudyptula m. novaehollandiae*, and two fossils) were summarized via principal component analysis using `stats::prcomp` in R ver. 4.1.2 (R Core Team, 2021).

**Phylogenetic analysis.**—We scored the newly-described fossils into a combined morphological and molecular matrix modified from Ksepka et al. (2023). Anatomical terminology is consistent with terminology used in other recent descriptions of fossil penguins (e.g., Ksepka et al., 2023) and originally adapted from Baumel and Witmer (1993). We added one morphological character: (98) lacrimal, descending process: (0) smoothly contacts jugal bar along dorsal edge of latter, (1) ends in a flange formed by laterally deflected and widened ventral extremity. We further modified the scoring for eight taxa for one character: (117) mandible, length of the dorsal edge of the dentary relative to the mandibular ramus length in lateral view. Upon reassessment, we found that *Megadyptes antipodes antipodes* Hombron and Jacquinot, 1841, *Megadyptes a. richdalei* Tennyson and Cole in Cole et al., 2019, *Pygoscelis papua* Forster, 1781, *Spheniscus demersus* Linnaeus, 1758, *S. humboldti* Meyen, 1834, *S. magellanicus* Forster, 1781, and *S. mendiculus* Sundevall, 1871 had been incorrectly scored as state 117:1, dorsal edge of the dentary approximately half the length of the ramus, and changed this scoring to 117:0, dorsal edge of the dentary markedly more than half the length of the ramus. *Madrynornis mirandus*

Acosta Hospitaleche et al., 2007 had previously not been scored for this character, but was scored as 117:0 upon re-examining a cast of the holotype.

The revised matrix comprises 281 morphological characters scored for 70 penguin taxa (20 extant, 3 subfossil, and 47 fossil taxa; see Supplemental data). The morphological dataset originated with the extant penguin matrix of Bertelli and Giannini (2005), which was extended to included fossil taxa by Ksepka et al. (2006) and expanded iteratively over many analyses. Studies that contributed characters include O'Hara (1989), Giannini and Bertelli (2004), Bertelli and Giannini (2005), Ksepka et al. (2006, 2012, 2023), Acosta Hospitaleche et al. (2007), Ando (2007), Clarke et al. (2007, 2010), Ksepka and Clarke (2010), Ksepka and Thomas (2012), Chávez Hoffmeister et al. (2014), Blokland et al. (2019), Thomas et al. (2020), and Giovanardi et al. (2021).

Phylogenetic analyses were performed in PAUP\*4.0a168 (Swofford, 2003) using a heuristic search strategy with 10,000 replicates of random taxon addition (holding 10 trees per replicate), with tree bisection and reconnection branch swapping limited to 10 million rearrangements per replicate. All characters were equally weighted. Multistate codings were considered to represent polymorphism. Zero-length branches were collapsed.

**Repositories and institutional abbreviations.**—The specimens described here are lodged at the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ). Specimens used for comparison were from: Department of Ornithology, American Museum of Natural History, New York, USA (AMNH); Canterbury Museum, Christchurch, New Zealand (CM); Institute of Biology, University of Białystok, Poland (IB/P/B); Museo Egidio Feruglio, Trelew, Argentina (MEF); Museo de La Plata, Argentina (MLP); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museum of San Marcos University, Lima, Peru (MUSM); The Natural History Museum, London, UK (NHMUK); Otago Museum, Dunedin, New Zealand (OM); Geology Museum, University of Otago, Dunedin, New Zealand (OU); Iziko South African Museum, Cape Town (SAM); Sección de Paleontología del Museo Nacional de Historia Natural, Santiago, Chile (SGO-PV); University of California Museum of Paleontology, Berkeley, USA (UCMP); and Western Australian Museum, Perth (WAM). An unnumbered specimen from the teaching collections at Massey University, Auckland, New Zealand, was also studied.

## Systematic paleontology

Aves Linnaeus, 1758 (sensu Gauthier, 1986)

Sphenisciformes Sharpe, 1891 (sensu Clarke et al., 2003)

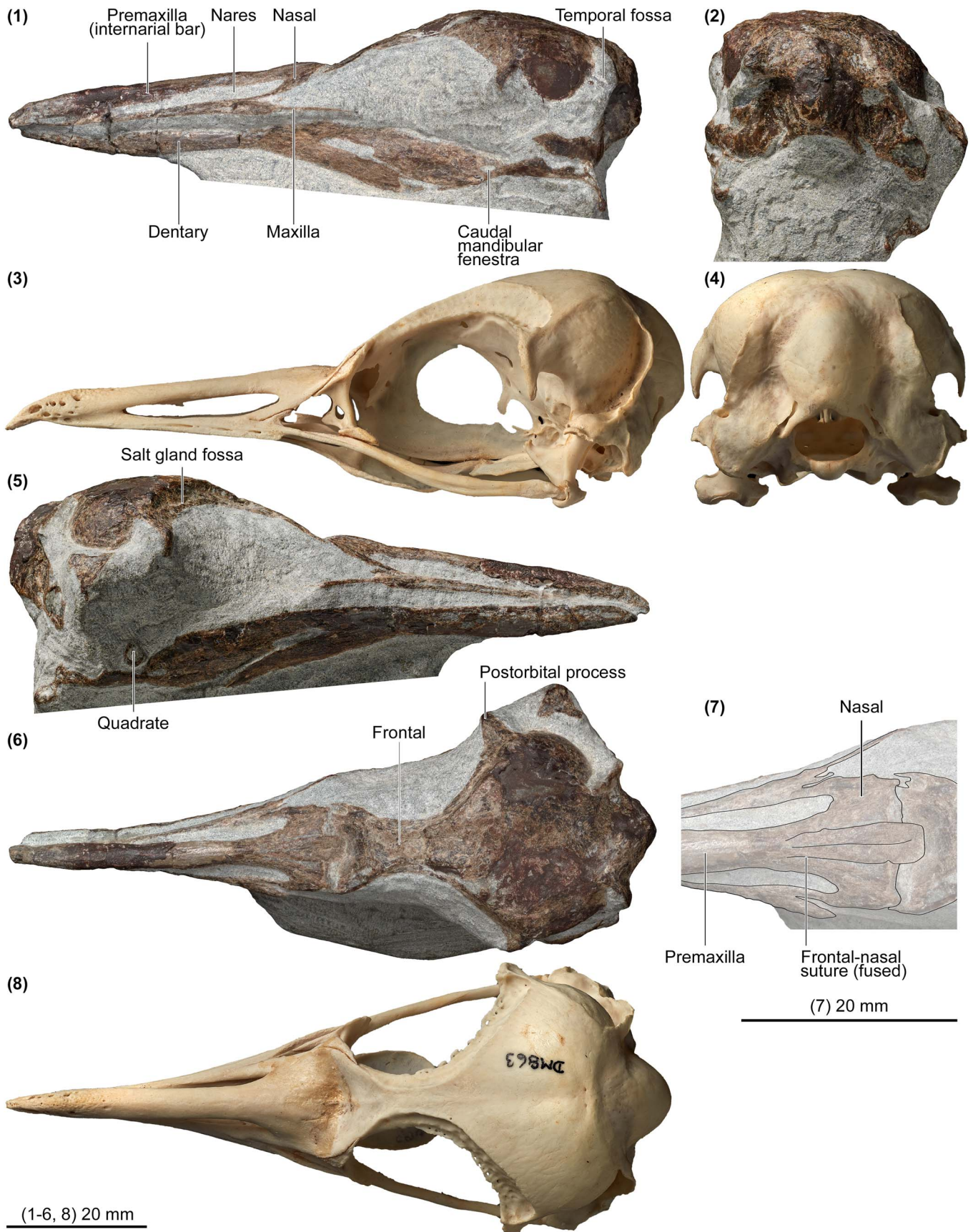
Spheniscidae Bonaparte, 1831

*Eudyptula* Bonaparte, 1856

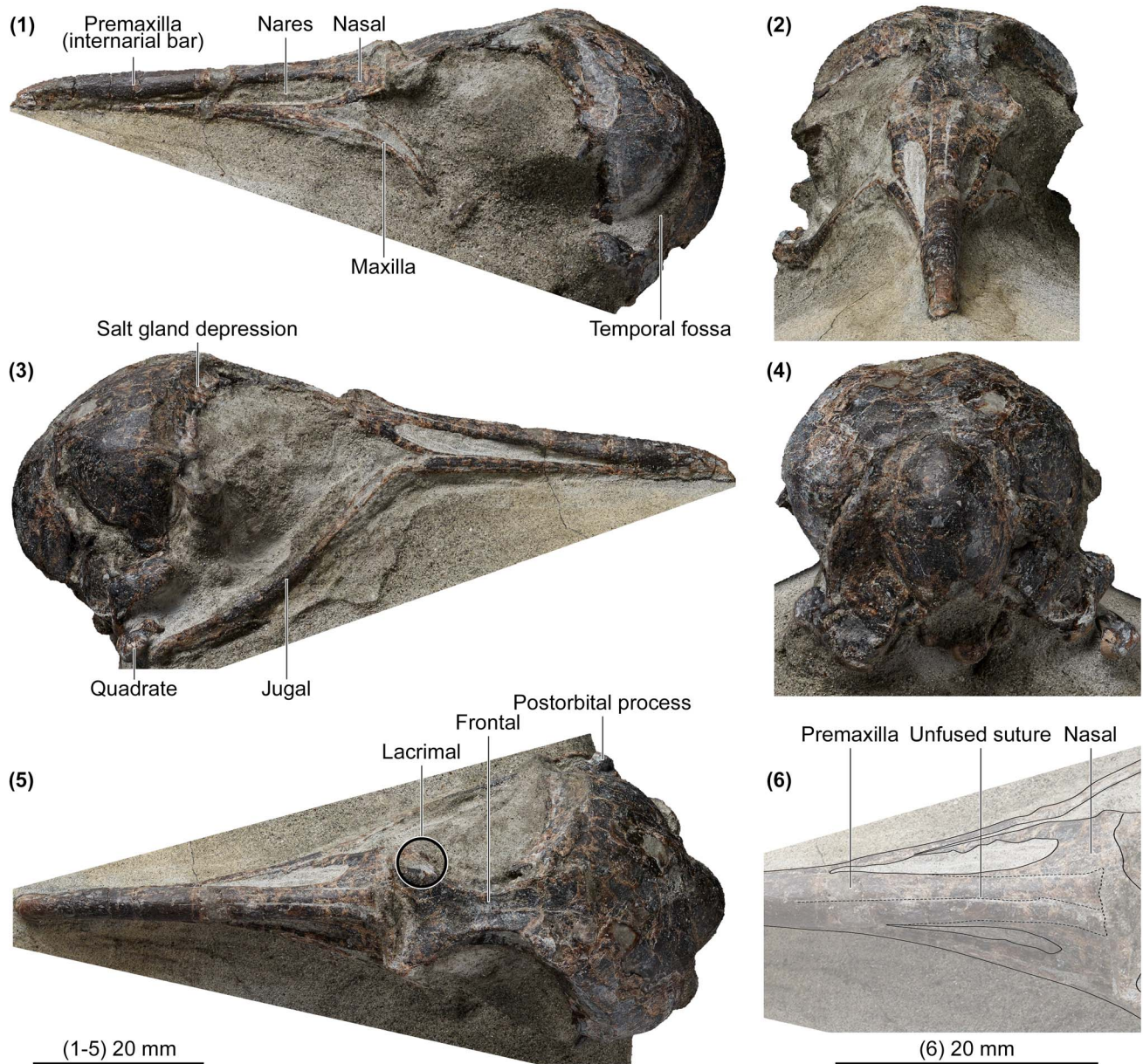
**Type species.**—*Eudyptula minor* Forster, 1781.

*Eudyptula wilsonae* new species

Figures 1–5



**Figure 1.** Skull of *Eudyptula wilsonae* n. sp., specimen NMNZ S.048854, presented alongside a skull from *Eudyptula m. minor* Forster, 1781, specimen NMNZ S.000863, for comparison. Left lateral view: (1) NMNZ S.048854; (3) NMNZ S.000863. Caudal view: (2) NMNZ S.048854; (4) NMNZ S.000863. Right lateral view: (5) NMNZ S.048854. Dorsal view: (6) NMNZ S.048854; (8) NMNZ S.000863. (7) Detail of nasal region of NMNZ S.048854 identifying fused frontal-nasal suture (compare with specimen NMNZ S.048855 in Fig. 1.2).



**Figure 2.** Skull of *Eudyptula wilsonae* n. sp., specimen NMNZ S.048855: (1) left lateral view; (2) cranial view; (3) right lateral view; (4) caudal view; (5) dorsal view. (6) Detail of nasal region of skull identifying unfused sutures between premaxillae and nasals.

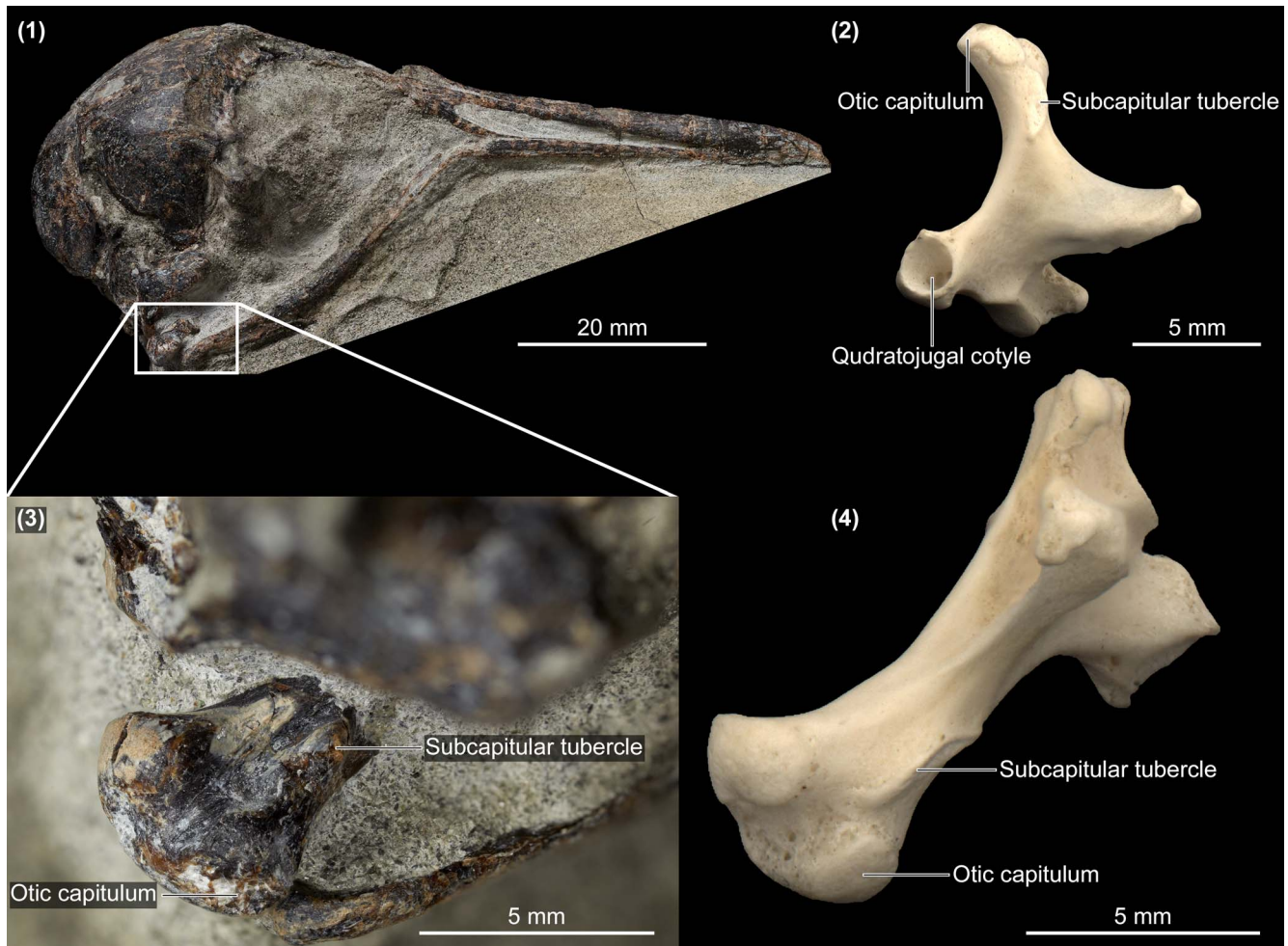
**Holotype.**—NMNZ S.048854: cranium and upper beak, mandible, and right quadrate of an adult individual (Figs. 1, 5; Table 1).

**Paratype.**—NMNZ S.048855: cranium and upper beak, right lacrimal, and right quadrate of immature individual (Figs. 2–5; Table 1).

**Diagnosis.**—Differs from extant *Eudyptula minor* in having more slender skull proportions, including proportionally narrower transverse distances between the caudal margins of the nares, the lateral edges of the salt-gland fossae, and the dorsal rim of the temporal fossae (Figs. 4, 5).

**Occurrence.**—Late Pliocene (Piacenzian) Tangahoe Formation, exposed in the southern Taranaki region of the North Island of New Zealand (Naish et al., 2005). Local Waipipian stage, with exposure constrained to 3.36–3.06 Myr based on oxygen isotope stage and magnetic polarity data (Naish et al., 2005; Raine et al., 2015). Specimens were surface collected as boulders from the base of a nearby exposure of the Tangahoe Formation and do not have an exact location lodged in the Fossil Record Electronic Database (<https://fred.org.nz/>), but see Q21/f0002 for a nearby location).

**Description.**—The holotype (adult) skull falls within the size range of adult modern little penguins, whereas the paratype



**Figure 3.** Skull of *Eudyptula wilsonae* n. sp., specimen NMNZ S.048855, with emphasis on right quadrate, compared to right quadrate from extant *Eudyptula minor minor* Forster, 1781. (1) Right lateral view of NMNZ S.048855 with emphasis on quadrate; image taken before acid preparation to expose right quadrate. (2) Right lateral view of right quadrate from an immature *Eudyptula m. minor* (unnumbered specimen from Massey University teaching collection). (3) Otic process of right quadrate from NMNZ S.048855 in oblique dorsolateral view; image taken after acid preparation. (4) Right quadrate from immature *Eudyptula m. minor* in similar orientation to quadrate in (3) (unnumbered specimen from Massey University teaching collection).

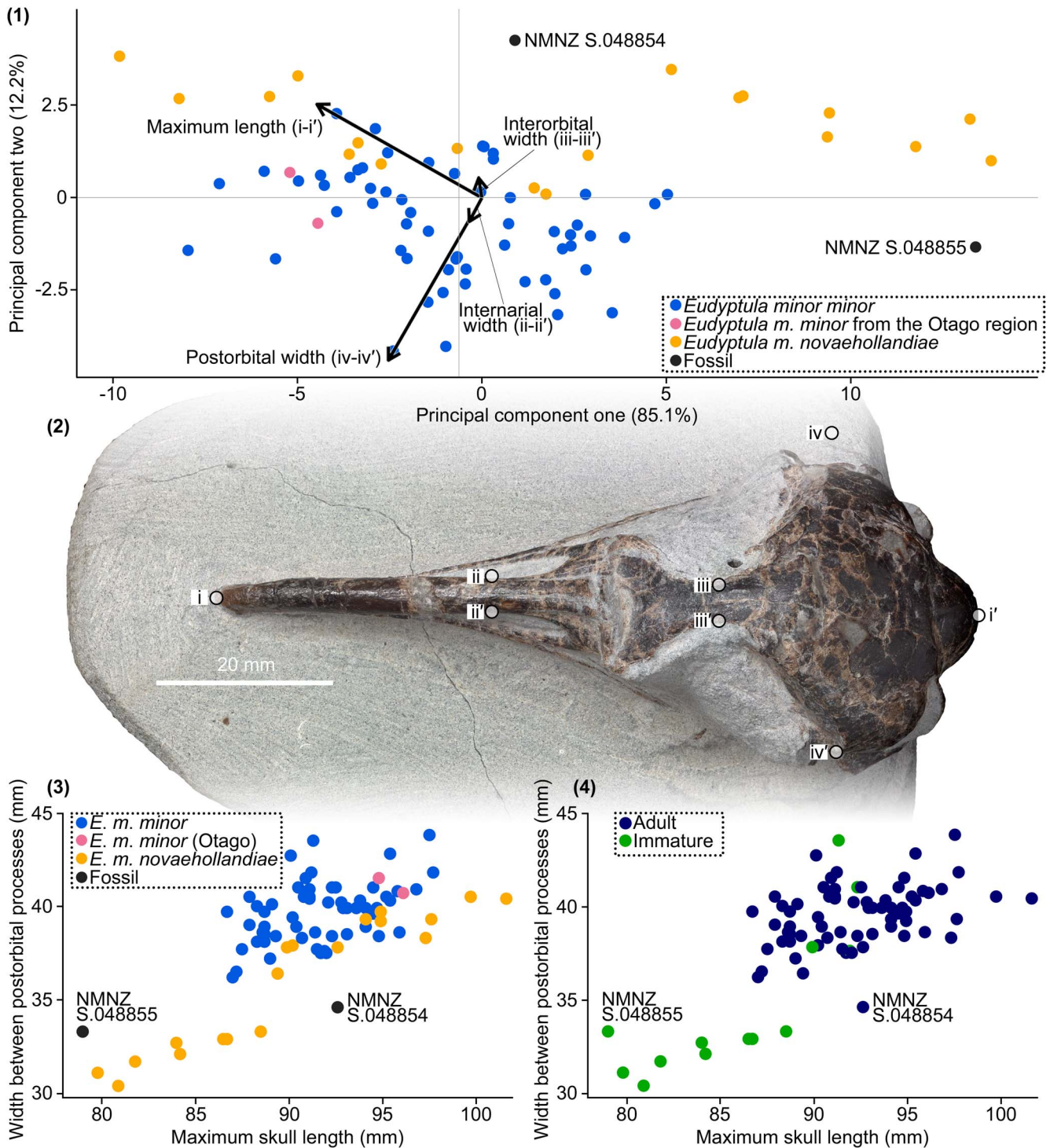
(immature) specimen is smaller than any of the individuals examined here or by Grosser et al. (2017) (Tables 1, S1). The parietal region of the holotype has been slightly compressed dorsoventrally as shown by the apex of the nuchal crest nearly aligning with the dorsalmost regions of the temporal fossae, and the temporal crests and lateral margins of the postorbital processes have been eroded in both skulls. There is, however, no sign of transverse compression, indicating that the slenderness of the skull is a genuine feature.

The tip of the premaxilla is weakly hooked in both skulls, as in extant *Eudyptula*. The tip is deeply pitted with neurovascular foramina and bears a shallow groove that is continuous with the anteroventral margin of the nares. The internarial bar is slender and slightly swollen near its midpoint in the adult skull (but not in the immature skull); in lateral view, its dorsal edge curves smoothly to the tip of the beak. In the adult skull, the premaxilla-nasal suture is largely obliterated and only visible caudally as in adults of extant *Eudyptula* and *Spheniscus* Brisson, 1760. In other extant penguins, this suture remains visible along its entire length. In the immature skull, both the premaxilla-nasal and the interpremaxillary sutures remain visible, the premaxillae

are elevated dorsally above the nasals and frontal (further indicating an open premaxilla-nasal suture), and the left and right premaxillae are visibly separated along the caudal section of internarial bar.

The salt gland fossae are relatively wide, rugose, and oriented dorsolaterally. They are strongly excavated and each terminates in a sharp edge without a raised lateral margin as in extant *Eudyptula* (but not in *Eudyptes* Vieillot, 1816, *Megadyptes* Milne-Edwards, 1880, and *Pygoscelis* Wagler, 1832). The postorbital processes are directed ventrally and taper to a narrow point. The temporal fossae are deep, as in most extant penguins (shallower in *Pygoscelis* and *Aptenodytes* Miller, 1778); and widely separated, as in all crown penguins except *Spheniscus*. The jugal lacks a prominent dorsal process (present in *Eudyptes*) and is only slightly curved in lateral view, as in extant *Eudyptula*, *Spheniscus*, and *Madrynornis*. A small portion of the right lacrimal is preserved in the immature skull. As in most extant penguins, the dorsal portion of the lacrimal is exposed in dorsal view (hidden in *Spheniscus*).

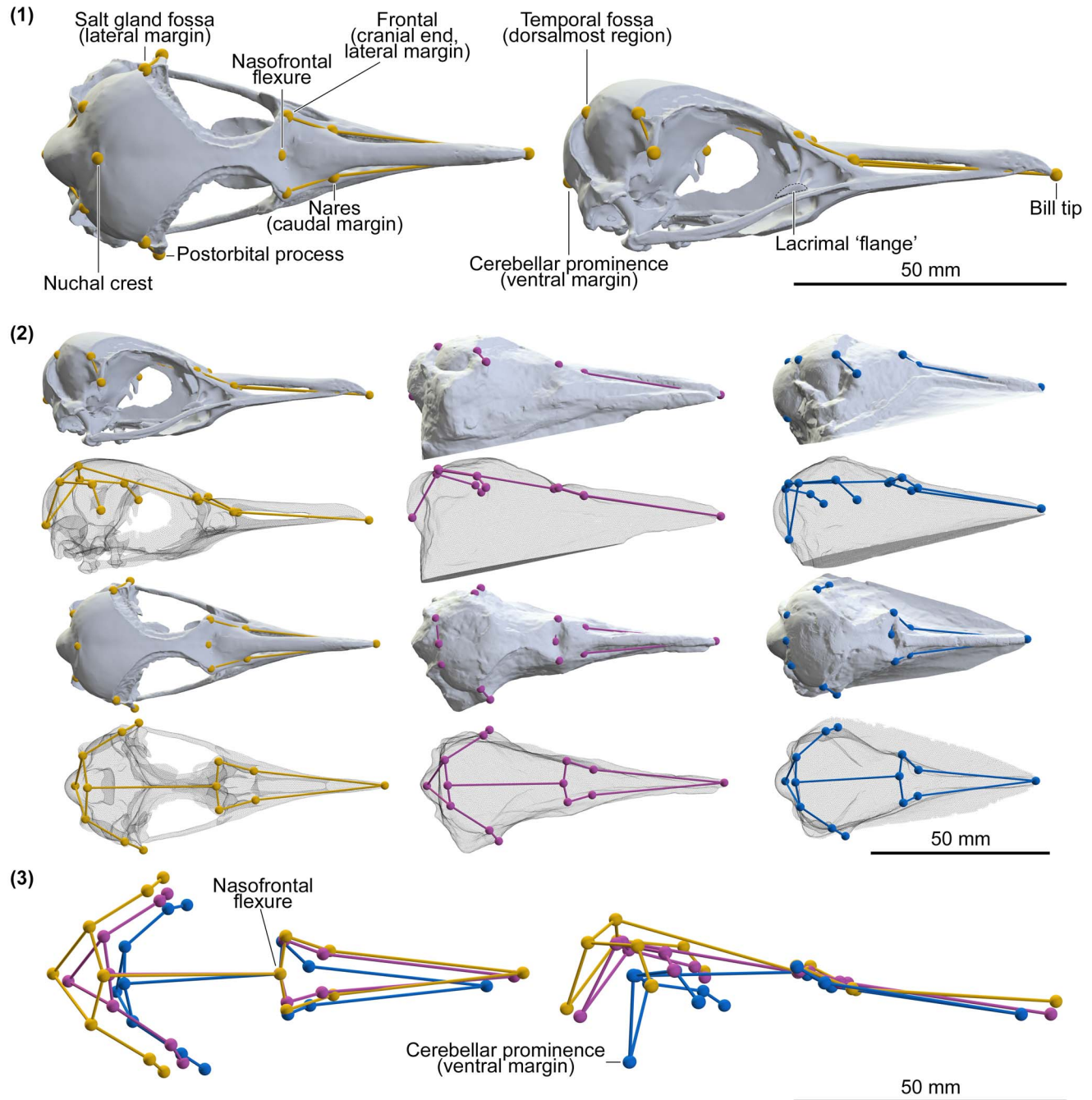
The adult mandible has a short bony symphysis and slender proportions resembling those of extant *Eudyptula*. The dentary



**Figure 4.** Analysis of measurements from modern and fossil *Eudyptula* skulls. (1) Principal component biplot from analysis performed on four measurements; biplot shows scores and loadings for principal component one (PC1) and PC2. (2) Four measurements used for analyses and shown on *Eudyptula wilsonae* n. sp. paratype, specimen NMNZ S.048855. i-i' = distance between bill tip and caudalmost surface of the supraoccipital (i.e., maximum length); ii-ii' = maximum distance between lateral edges of premaxillae in dorsal view (i.e., internarial width); iii-iii' = minimum distance between the left and right frontals between the orbits in dorsal view without including the salt gland depressions (i.e., interorbital width); iv-iv' = distance between lateral edges of postorbital processes (i.e., postorbital width). (3) Maximum length of skull shown against distance between lateral edges of postorbital processes. (4) Maximum length of skull shown against distance between lateral edges of postorbital processes; specimen age inferred from suture closure.

makes up markedly more than half the total length of the ramus. The mandible is dorsoventrally narrow across the first third of the ramus and then modestly deepens near the midpoint, but it

lacks the strong expansion characterizing *Eudyptes* and some species of *Pygoscelis*. The apparent presence of a large rostral fenestra is likely an artifact of matrix filling in the area between



**Figure 5.** Skulls of extant *Eudyptula* and *Eudyptula wilsonae* n. sp., comparisons using placement of homologous points. (1) Dorsal and right lateral views of *Eudyptula m. minor* skulls with features identified. (2) Solid and wireframe views of modern and fossil skulls in dorsal and right lateral views. (3) Homologous points from all three skulls overlain in dorsal and right lateral views, aligned on point demarking the nasofrontal flexure. yellow = *Eudyptula m. minor* Forster, 1781 (adult, NMNZ S.000863); purple = *Eudyptula wilsonae* n. sp. (adult, NMNZ S.048854); blue = *Eudyptula wilsonae* n. sp. (immature, NMNZ S.048855).

the angular, surangular, and dentary. There is a small, ovoid caudal mandibular fenestra. The retroarticular process is moderately elongate, as in extant *Eudyptula*.

On the right quadrate of the immature individual, the attachment of m. adductor mandibulae externus pars profunda forms a well-developed ridge (Fig. 3). This origin varies between and within extant penguin species, ranging from a very weak ridge (in all examined *Megadyptes*, nearly all individuals of

*Aptenodytes*) to a strongly projected and rounded tubercle (in most individuals of *Spheniscus* and *Eudyptes*). We observed that a ridge is present in most extant *Eudyptula* specimens, but a more tubercle-like morphology occurs in few individuals of *Eudyptula m. minor*.

**Etymology.**—The species name honors New Zealand ornithologist Kerry-Jayne Wilson, in recognition of her many

**Table 1.** Skull measurements (in mm) of *Eudyptula wilsonae* sp. nov. compared to summaries of those from other *Eudyptula* taxa; expressed as mean  $\pm$  standard deviation (N), measured with digital calipers. See Supplemental Data for individual measurements and other data, including age class when known.

Accession details	NMNZ S.048854	NMNZ S.048855	Multiple	Multiple	Multiple	Multiple	Multiple
Taxon	<i>Eudyptula wilsonae</i> n. sp.	<i>Eudyptula wilsonae</i> n. sp.	<i>Eudyptula</i> extant spp.	<i>Eudyptula m. minor</i>	<i>Eudyptula m. minor</i>	<i>Eudyptula m. minor</i>	<i>Eudyptula m. novaehollandiae</i>
Age	adult	immature	multiple	multiple	adult	immature	multiple
Maximum length	92.6 (1)	79 (1)	91.4 $\pm$ 4 (81)	91.8 $\pm$ 2.8 (62)	91.8 $\pm$ 2.9 (59)	91.8 $\pm$ 0.5 (3)	90.2 $\pm$ 6.5 (19)
Width of internarial bar	4.2 (1)	4 (1)	4.3 $\pm$ 0.5 (84)	4.5 $\pm$ 0.4 (65)	4.5 $\pm$ 0.4 (59)	4.4 $\pm$ 0.6 (6)	3.8 $\pm$ 0.4 (19)
Minimum interorbital width	5.1 (1)	4.7 (1)	4.1 $\pm$ 0.8 (87)	4.0 $\pm$ 0.7 (68)	4.0 $\pm$ 0.7 (61)	4.1 $\pm$ 0.7 (7)	4.6 $\pm$ 0.9 (19)
Width between postorbital processes	34.6 (1)	33.3 (1)	38.8 $\pm$ 2.7 (83)	39.7 $\pm$ 1.6 (64)	39.6 $\pm$ 1.5 (60)	40.5 $\pm$ 2.4 (4)	36 $\pm$ 3.6 (19)

contributions to seabird conservation, particularly her cofounding of the West Coast Penguin Trust.

**Remarks.**—In extant penguins, most cranial sutures (e.g., frontal-parietal, interfrontal, parietal-supraoccipital, laterosphenoid-parietal, squamosal-laterosphenoid, and supraoccipital-exoccipital) are obliterated only after individuals attain adult size (unpublished data, DTK, 2022). The combination of nearly-adult skull length and open sutures leads us to infer that NMNZ S.048855 was fully fledged but not yet sexually mature, and thus a young-of-the-year. The cerebellar prominence is more ventrally and cranially oriented in the juvenile than the adult (Fig. 5). A more ventral orientation of this structure has been observed in juvenile penguins (Sosa and Acosta Hospitaleche, 2018; Plateau and Foth, 2021) (e.g., in the Emperor Penguin, *Aptenodytes forsteri* Gray, 1844). However, this difference is only observable in very young individuals, and the immature fossil skull is closely approaching adult size. Therefore, we believe it is more likely that the difference in orientation of the cerebellar prominence between the two skulls is due to postburial alteration of the immature skull.

## Phylogenetic analysis

The strict consensus of our analysis places *Eudyptula wilsonae* n. sp. inside a polytomy alongside extant *Eudyptula*, living and extinct *Spheniscus*, and the extinct *Inguza predemersus* Simpson, 1971 and *Madrynornis mirandus* (Fig. 6). This lack of resolution reflects both the paucity of cranial characters supporting the monophyly of *Eudyptula* and the partial or complete lack of skull data for several species within the polytomy (e.g., *Spheniscus muizoni* Göhlich, 2007 and *Inguza predemersus*). Nonetheless, the assignment of *Eudyptula wilsonae* n. sp. to *Eudyptula* is well supported based on their extremely similar skull shape, small size, and virtually identical codings. The only exception was character 108 (quadrate, attachment scar for m. adductor mandibulae externus, par profunda), which was coded ‘1’ (present as a tubercle) for *Eudyptula wilsonae* n. sp. but shows intraspecific variation within *Eudyptula m. minor* and so coded ‘0/1’ (present as a ridge / present as a tubercle).

Our results suggest that most synapomorphies uniting extant *Eudyptula* are soft-tissue characters, including: (20:3) iris bluish gray in color; (34:1) preocular region blue; (40:1) throat pattern white; (43:2) feathers of dorsum light bluish

gray; (57:1) flipper with small circular dot near tip of underside; and (65:3) feet white-pink.

In contrast, we identified only three osteological synapomorphies for *Eudyptula*: (98:1) lacrimal with ‘flange’ formed by laterally deflected and widened ventral extremity; (128:1) 12 synsacral vertebrae (also present in the stem penguin *Palaeospheniscus* and thus likely a reversal); and (154:1) coracoid fenestra incomplete (convergent in *Aptenodytes* and *Pygoscelis*). None of these characters can currently be scored for *Eudyptula wilsonae* n. sp., but they provide a benchmark to test its placement via future discoveries from the Tangahoe Formation.

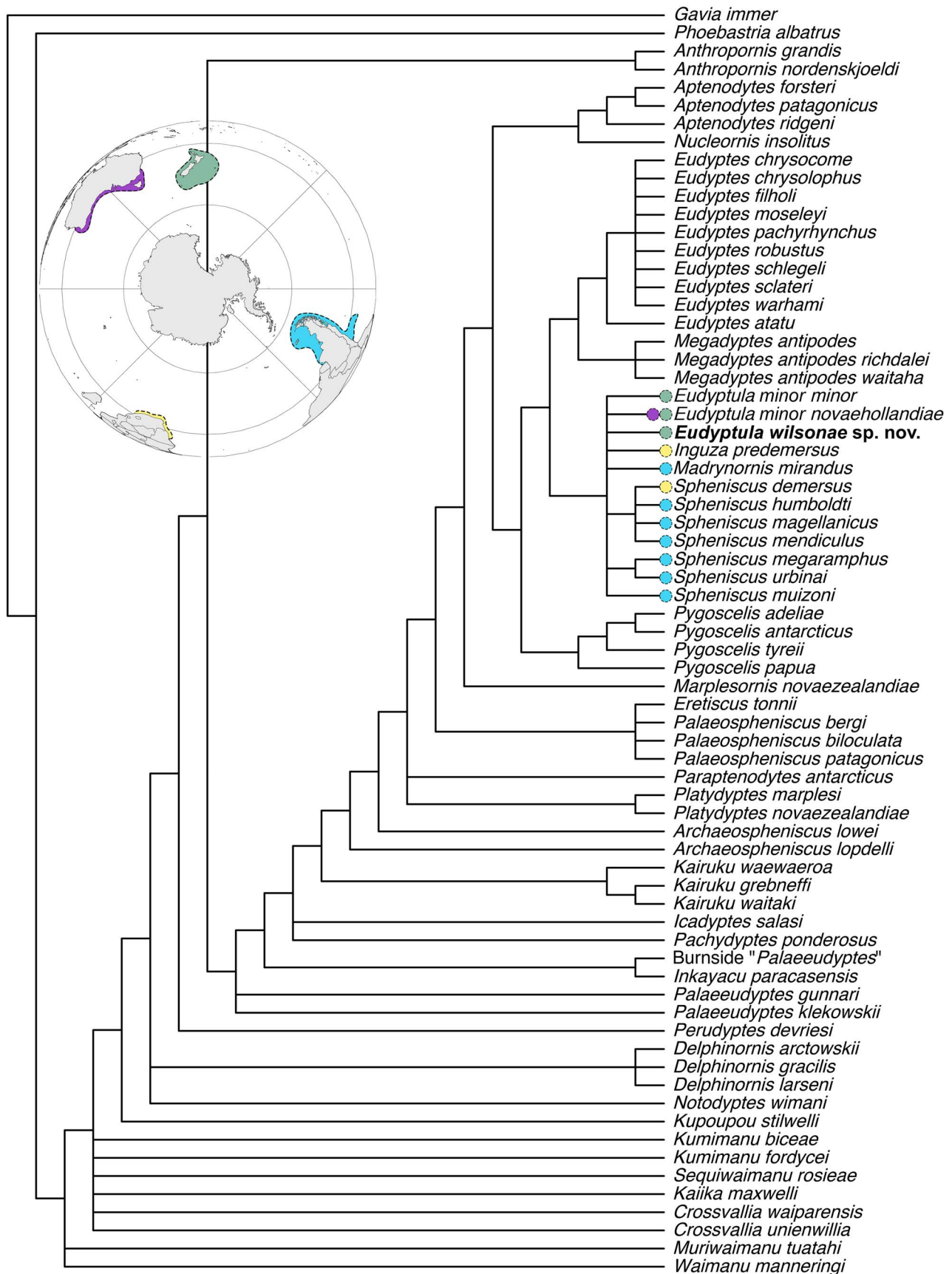
## Morphometrics

Maximum skull length and postorbital width were the major sources of variation in the dataset (Fig. 4.1). Principal component 1 explained 85.1% of the variation, with strong negative loadings for both maximum length and postorbital width. Principal component 2 explained 12.2% of the variation, with maximum length strongly positively loaded and postorbital width strongly negatively loaded. *Eudyptula m. novaehollandiae* skulls tend to be short and narrow, whereas those of *Eudyptula m. minor* tend to be longer and wider; however, this could partly reflect the immature status of some *Eudyptula m. novaehollandiae* skulls that were included in the study (Fig. 4.3, 4.4). The holotype (adult) skull of *Eudyptula wilsonae* n. sp. is proportionally narrower than any extant *Eudyptula* specimens measured here (Fig. 4.3). The skull of the paratype immature specimen is even narrower and most closely resembles the proportions of immature *Eudyptula m. novaehollandiae* (Fig. 4.2, 4.4).

## Discussion

**Zealandian origins of little penguins.**—The Pliocene age of *Eudyptula wilsonae* n. sp. supports a Zealandian origin of little penguins as proposed by recent biogeographic analyses (Thomas et al., 2020; Cole et al., 2022). The age of these fossils also precedes the proposed molecular divergence between *Eudyptula minor minor* and *Eudyptula m. novaehollandiae* at 1.34 Ma (95% HPD = 0.48–2.26 Ma; Cole et al., 2022). Provided that the estimated divergence date is accurate, *Eudyptula wilsonae* n. sp. could plausibly be ancestral to both of the living little penguin species inhabiting Australia and New Zealand today.





**Figure 6.** Strict consensus of most parsimonious trees. Evolutionary relationships for *Eudyptula wilsonae* n. sp. described in this study were not fully resolved. Instead, *Eudyptula wilsonae* n. sp. is placed in a clade with extant and fossil *Spheniscus*, *Inguza predemersus* and *Madrynornis mirandus*. Location information for species in this clade are identified with colored symbols: green = New Zealand; purple = Australia; blue = South America, Falkland Islands, and Galápagos Islands; yellow = South Africa.

Whereas a Zealandian origin for crown *Eudyptula* is increasingly well supported, the dispersal of stem *Eudyptula* to Zealandia remains an open question, obscured in part by the unstable phylogenetic positions of *Inguza predemersus* from the Pliocene of Africa and *Madrynornis* from the Miocene of South America. Previous analyses (Thomas et al., 2020; Cole et al., 2022) favored dispersal from Africa to New Zealand due to *Inguza* Simpson, 1971 being recovered as sister taxon to *Eudyptula*. Intriguingly, a single vertebra supports the presence of a small penguin within the size range of *Eudyptula* in the Miocene of South Africa (Thomas and Ksepka, 2013). In this scenario, the South Atlantic Gyre could plausibly have facilitated the eastward dispersal of the ancestors of the *Inguza-Eudyptula* clade from South America to Africa (Ksepka and Thomas, 2012), followed by a further eastward dispersal from Africa to Zealandia via the Antarctic Circumpolar Current. Regardless of the pathway, *Eudyptula wilsonae* n. sp. minimally dates the arrival of little penguins in Zealandia to the Pliocene.

**Beak evolution in seabirds.**—Apart from a slightly narrower skull, *Eudyptula wilsonae* n. sp. is almost indistinguishable from its extant relatives. In this, the species notably contrasts with some other Pliocene seabirds from the Tangahoe Formation, which show skull proportions that are substantially different from those of closely related extant taxa. For example, the stem crested penguin *Eudyptes atatu* Thomas, Tennyson, Scofield, and Ksepka (2020) in Thomas et al. (2020) has a substantially slenderer mandible than all extant *Eudyptes* and might have been less reliant on planktonic prey (Thomas et al., 2020). Likewise, the probable stem albatross *Aldiomedes angustirostris* Mayr and Tennyson, 2019 is smaller and has a more mediolaterally compressed beak than any living albatrosses and was likely more piscivorous (Mayr and Tennyson, 2019). Future studies might explore the coevolution of the marine environment and seabird skull structure in a Zealandian context.

**Body size.**—*Eudyptula wilsonae* n. sp. was likely the same size as extant *Eudyptula* (~1 kg; Stonehouse, 1967). It is thus the smallest crown penguin fossil ever described and shows that the lower body size bound for crown penguins had been reached by at least the Pliocene, when sea surface temperatures were several degrees warmer than today (Burke et al., 2018). This, in turn, suggests a deep-time thermal tolerance that mirrors the latitudinal temperature range occupied by little penguins today.

## Conclusions

We describe fossils of *Eudyptula* from the late Pliocene of New Zealand, which show that little penguins have been part of this globally famous seabird biodiversity hotspot for at least three million years. Further discoveries and better-resolved phylogenies are needed to establish when and from whence the ancestors of *Eudyptula* first arrived in the New Zealand region. The fossils described here show that both the cranial morphology and body size of little penguins have remained largely unchanged since the Pliocene, despite substantial environmental changes in the region over the past three million years.

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## Declaration of competing interests

The authors do not have competing interests to declare.

## Data availability statement

Measurements from modern and fossil penguin skulls, R code and data for comparing mean annual sea-surface temperatures at penguin breeding colonies, and morphological characters used for phylogenetic analysis are available from Zenodo (<https://doi.org/10.5281/zenodo.7452334>).

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