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ARTICLE

A new fossil species of *Procellaria* (Aves: Procellariiformes) from the Pliocene of New Zealand

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Abstract. We describe a new *Procellaria* petrel species from the late Pliocene of Taranaki, New Zealand. The new species is most similar morphologically to the White-Chinned Petrel (*P. aequinoctialis*), Spectacled Petrel (*P. conspicillata*) and the Westland Petrel (*P. westlandica*). Compared with those taxa, the new species has a deeper and shorter premaxilla, longer coracoid and shorter wings, while its legs are a similar size. Today, New Zealand is the centre of global diversity of the genus, with four breeding species. This is the first fossil species of *Procellaria* to be described from New Zealand, attesting to a reasonably long history of this genus in the region.

Keywords. *Procellaria altirostris* sp. nov.; Petrel; Piacenzian; Procellariidae; Taranaki.

INTRODUCTION

New Zealand is a global centre of diversity for seabirds today, however this contrasts with its sparse pre-Pleistocene fossil record – while penguins are well represented, other seabirds are not (Gill *et al.,* 2010) – so the history of seabirds in the region is poorly understood. For instance, Procellariiformes are presently the most diverse group of seabirds in New Zealand (Gill *et al.,* 2010), but only three fossil pre-Pleistocene taxa are described: a Pliocene albatross (Mayr & Tennyson, 2020) and a shearwater (Tennyson & Mannering, 2018), both from Taranaki, and a Miocene diving petrel from St Bathans (Worthy *et al.,* 2007).

The Pliocene outcrops in the Taranaki region continue to produce a rich and globally significant fauna of marine vertebrates, including cetaceans, seals, fishes and other birds, the latest being a new species of penguin (McKee, 1994; Thomas *et al.,* 2020). Here we describe the latest discovery from Taranaki: a new procellariiform species.

MATERIAL AND METHODS

The new fossil was identified as a bird from the *Procellaria* genus and thus compared with all living members of this genus: White-Chinned Petrel (*P. aequinoctialis* Linnaeus, 1758), Spectacled Petrel (*P. conspicillata* (Gould, 1844)), Westland Petrel (*P. westlandica* Falla, 1946), Grey Petrel (*P. cinerea* (Gmelin, 1789)), and Black Petrel (*P. parkinsoni* G.R. Gray, 1862).

We measured 155 skeletons of *Procellaria* spp. deposited in the collections of the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ) and the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP). In order to compare the measurements of the different species with the fossil, we only measured beaks from skulls where the rhamphotecal plates were removed. Thus, the total sample size for individual measurements varies. For the principal component analysis (see below), we only used individuals that had all measurements, thus the PCA only includes a single *P. conspicillata* specimen. The primary comparative specimens used are listed in Appendix 1.

We took the following skeletal measurements (also see Fig. 1): **skull** minimum interorbital width; **premaxilla** maximum length from nasal hinge to tip, depth at the middle of the *apertura nasi ossea,* width at the middle of the *apertura nasi ossea;* **coracoid** maximum omal-sternal length; **humerus** maximum length, maximum proximal dorso-ventral width, maximum distal dorso-ventral width, mid-shaft dorso-ventral

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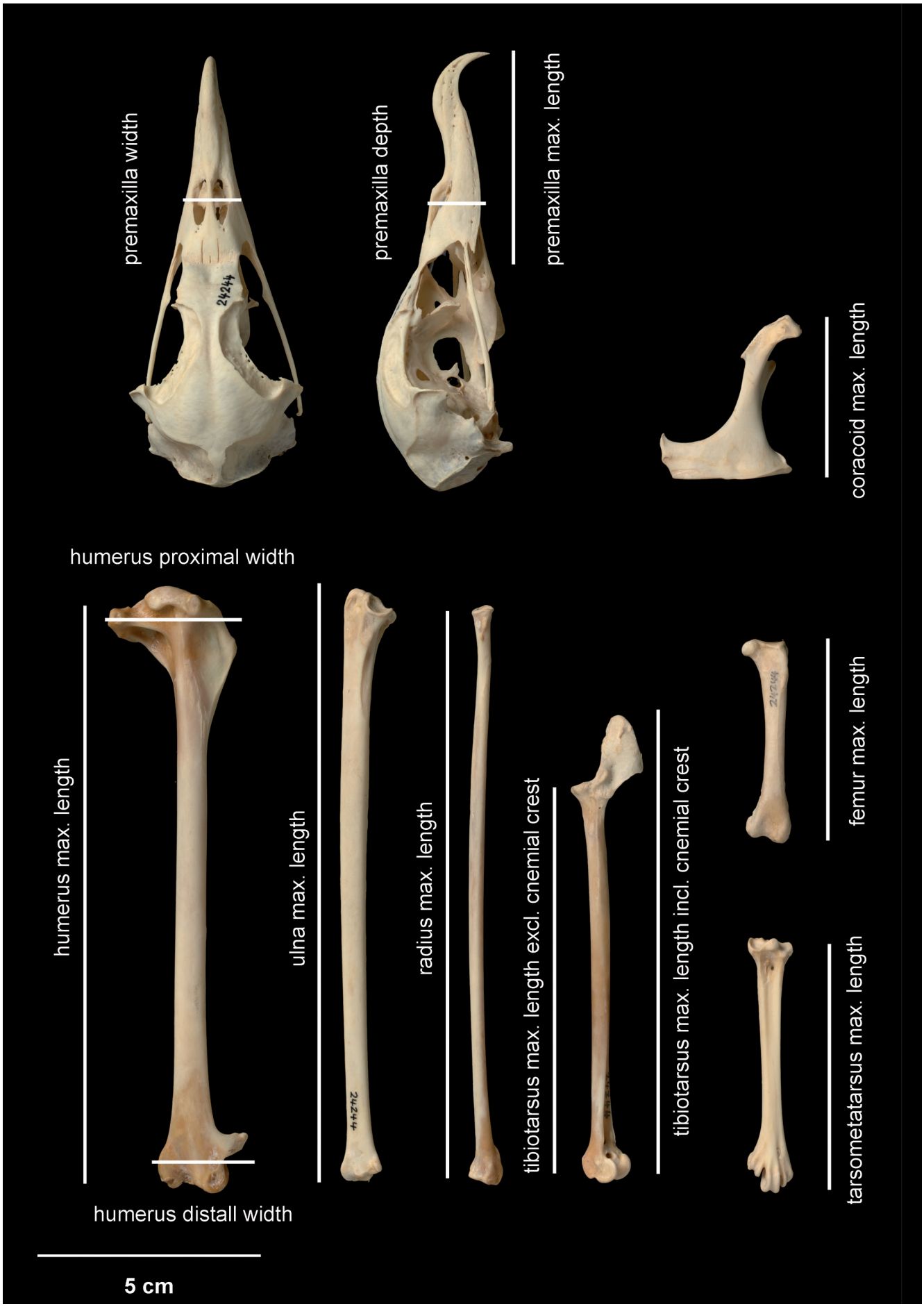

Figure 1. Plate illustrating how each bone element was measured.

width; **ulna** maximum length; **radius** maximum length; **femur** maximum length; **tibiotarsus** maximum length including cnemial crest, maximum length excluding cnemial crest; **tarsometatarsus** maximum length. Osteological nomenclature follows Baumel & Witmer (1993). All measurements were taken using vernier digital calipers (precison 0.01 mm) or a ruler (precision 0.1 mm) when skeletal elements were larger than 150 mm.

Analyses were carried out in R version 3.6.1 (R Core Team, 2017). Firstly, measurements were compared using descriptive statistics (mean, standard error and measurement range). Then, we carried out a principal component analysis (PCA) on the z-standardized measurements (mean centred at 0 and standard deviation at 1) that allowed us to detect whether the fossil would cluster together with one of the other species.

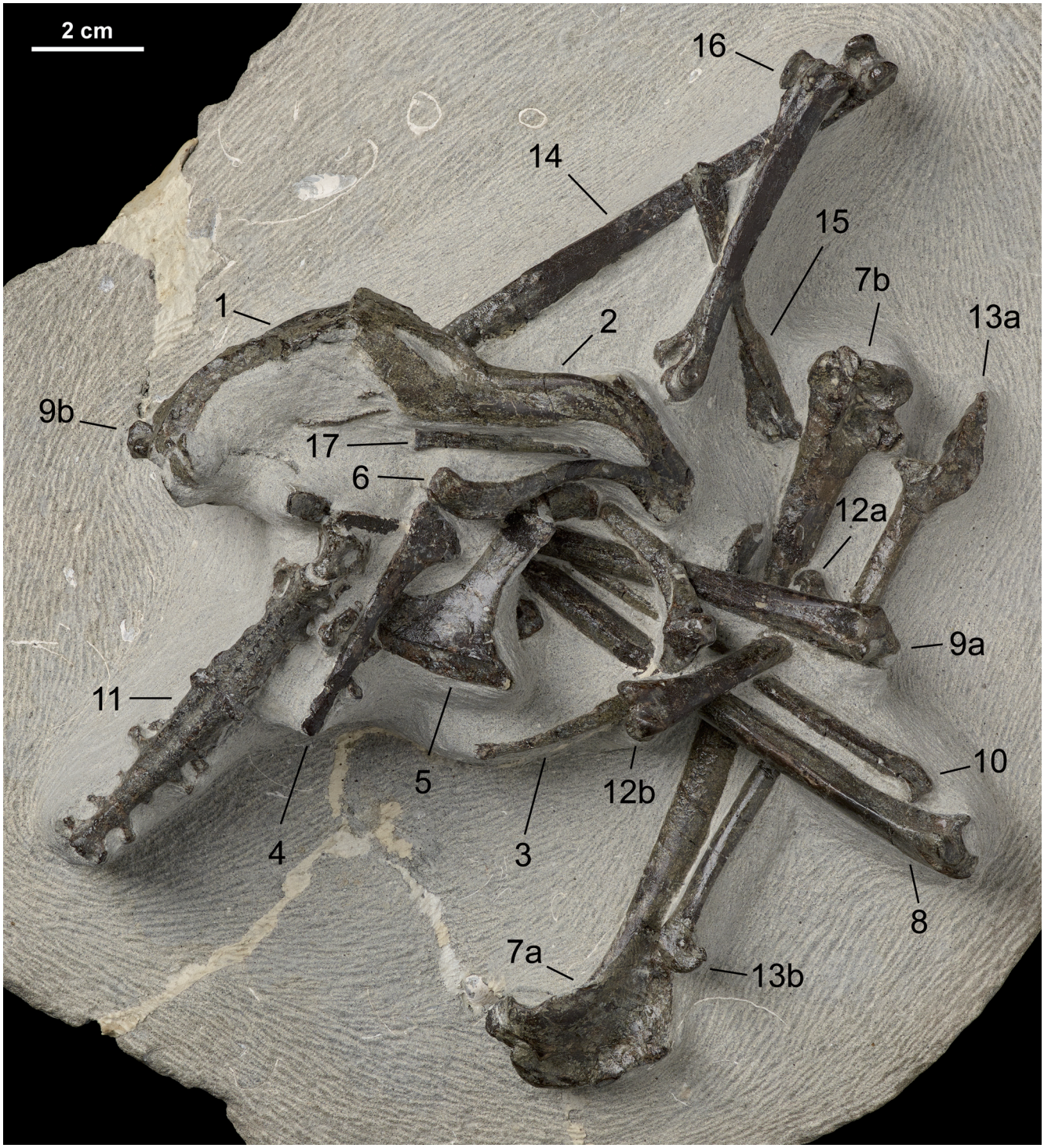

Figure 2. Pliocene fossil petrel *Procellaria altirostris* sp. nov., holotype NMNZ S.46691. Photo: Jean-Claude Stahl (Te Papa). (1) cranium; (2) premaxilla; (3) furcula; (4) right scapula; (5) left coracoid; (6) right coracoid; (7a) proximal right humerus; (7b) distal right humerus; (8) left ulna; (9a) proximal right ulna; (9b) distal right ulna; (10) right radius; (11) synsacrum; (12a) proximal left femur; (12b) distal left femur; (13a) proximal left tibiotarsus; (13b) distal left tibiotarsus; (14) right tibiotarsus; (15) left tarsometatarsus; (16) right tarsometatarsus; (17) pedal phalange.

RESULTS

Systematic Palaeontology
Order Procellariiformes Fürbringer, 1888
Family Procellariidae Leach, 1820
Procellaria Linnaeus, 1758
Procellaria altirostris sp. nov.
http://zoobank.org/urn:lsid:zoobank.org:act:093F56E5-D07E-44C3-8E75-059C486CB222

Etymology: From the unusually deep premaxilla in comparison to other members of the *Procellaria* genus.

Holotype: NMNZ S.46691; partial skeleton embedded, but largely exposed, in a concretion. Elements preserved: partial cranium (crushed) with premaxilla, furcula, both coracoids, right scapula, right humerus, both ulnae, right radius, synsacrum, left femur, both tibiotarsi, both tarsometatarsi but the left is missing both ends, one pedal phalange, and other fragments. The fossil is from a fully grown individual based on bone ossification (Fig. 2).

Type Locality, Type Horizon and Age: Ohawe Beach, south Taranaki, North Island, New Zealand (New Zealand Fossil Record Electronic Database Number Q21/F0175, Fig. 3). The fossil was found inside a marine mudstone concretion loose on the beach in 2015, and prepared by John Buchanan-Brown in the same year. The concretion is presumed to have eroded from an adjacent cliff in the Tangahoe Formation. This Formation is 3.0-3.4 Ma (local Waipipian stage, late Pliocene, Piacenzian; McKee, 1994; Naish *et al.,* 2005; Thomas *et al.,* 2020). Such concretions are thought to have formed on the ocean floor at a depth of up to 50 m or more (Tennyson & Mannering, 2018).

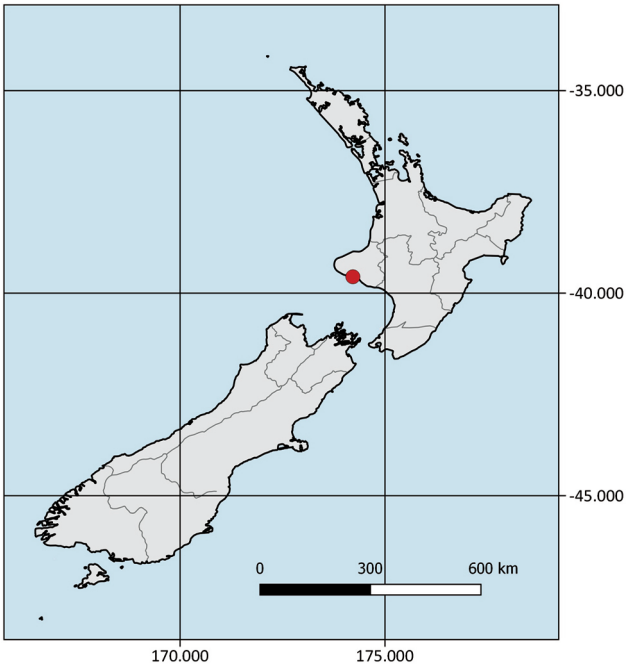

Figure 3. General location in Taranaki where the fossil was found.

Generic attribution: *Procellaria altirostris* sp. nov. is referred to *Procellaria* because it is a large petrel falling in the size range of *Procellaria* species and outside the size range of every other recent genus in Procellariiformes: all recent Diomedeidae are larger and all Hydrobatidae and Pelecanoididae are smaller. Within the family

Table 1. Measurements (in mm) of skeletal elements of the holotype of *P. altirostris* sp. nov., compared with measurements of other *Procellaria* species. For measurement details, see Methods.

Measurement	NMNZ S.46691	*P. aequinoctialis*	*P. westlandica*	*P. conspicilata*	*P. cinerea*	*P. parkinsoni*
skull						
min. intraorbital width	15	14.24 ± 0.09 (50)	14.4 ± 0.12 (35)	13.57 ± 0.22 (7)	13.76 ± 0.10 (37)	11.4 ± 0.15 (16)
premaxilla						
max. length	55.56	62.22 ± 0.34 (32)	59.62 ± 0.36 (29)	57.22 (1)	57.15 ± 0.26 (37)	49.48 ± 0.57 (15)
depth	14.52	11.96 ± 0.08 (34)	12.12 ± 0.11 (34)	11.95 (1)	9.95 ± 0.07 (38)	9.81 ± 0.13 (17)
width	13.5	13.76 ± 0.13 (34)	14.7 ± 0.17 (34)	14.23 (1)	12.42 ± 0.13 (38)	11.98 ± 0.21 (17)
coracoid						
max. length	41.99	37.93 ± 0.20 (27)	39.12 ± 0.15 (33)	38.92 ± 0.86 (2)	36.15 ± 0.15 (35)	33.35 ± 0.28 (17)
humerus						
max. length	143.22	150.71 ± 0.62 (29)	149.65 ± 0.48 (37)	151.22 ± 1.59 (4)	136.76 ± 0.44 (37)	130.06 ± 0.74 (17)
proximal width	32.26	32.34 ± 0.16 (29)	32.37 ± 0.15 (37)	31.77 ± 0.36 (4)	30.54 ± 0.15 (37)	28.19 ± 0.17 (17)
distal width	17.68	17.49 ± 0.07 (29)	17.12 ± 0.08 (36)	17.77 ± 0.22 (4)	16.4 ± 0.05 (37)	15.04 ± 0.10 (18)
shaft width	7.44	7.58 ± 0.05 (28)	7.44 ± 0.05 (37)	7.38 ± 0.07 (4)	7.41 ± 0.05 (37)	6.52 ± 0.06 (18)
ulna						
max. length	138.53	151.13 ± 0.50 (29)	149.91 ± 0.50 (37)	149.84 ± 0.67 (4)	135.09 ± 0.47 (36)	131.29 ± 0.84 (18)
radius						
max. length	132.95	147.57 ± 0.53 (29)	146.33 ± 0.52 (36)	146.08 ± 0.37 (4)	131.51 ± 0.45 (36)	128.19 ± 0.81 (18)
femur						
max. length	50.05	50.64 ± 0.30 (28)	50.9 ± 0.22 (31)	50.52 ± 0.67 (4)	48.62 ± 0.24 (34)	42.28 ± 0.48 (16)
tibiotarsus						
max. length incl. cnemial crest	116.56	114.01 ± 0.52 (27)	111.86 ± 0.40 (31)	114.48 ± 0.65 (4)	109.94 ± 0.35 (32)	94.89 ± 0.70 (14)
max. length excl. cnemial crest	99.53	99.5 ± 0.40 (30)	96.94 ± 0.33 (35)	99.43 ± 0.69 (4)	95.54 ± 0.33 (35)	82.36 ± 0.67 (14)
tarsometatarsus						
max. length	64.82	65.99 ± 0.31 (30)	63.65 ± 0.26 (34)	65.33 ± 0.16 (4)	61.66 ± 0.22 (35)	54.53 ± 0.45 (15)

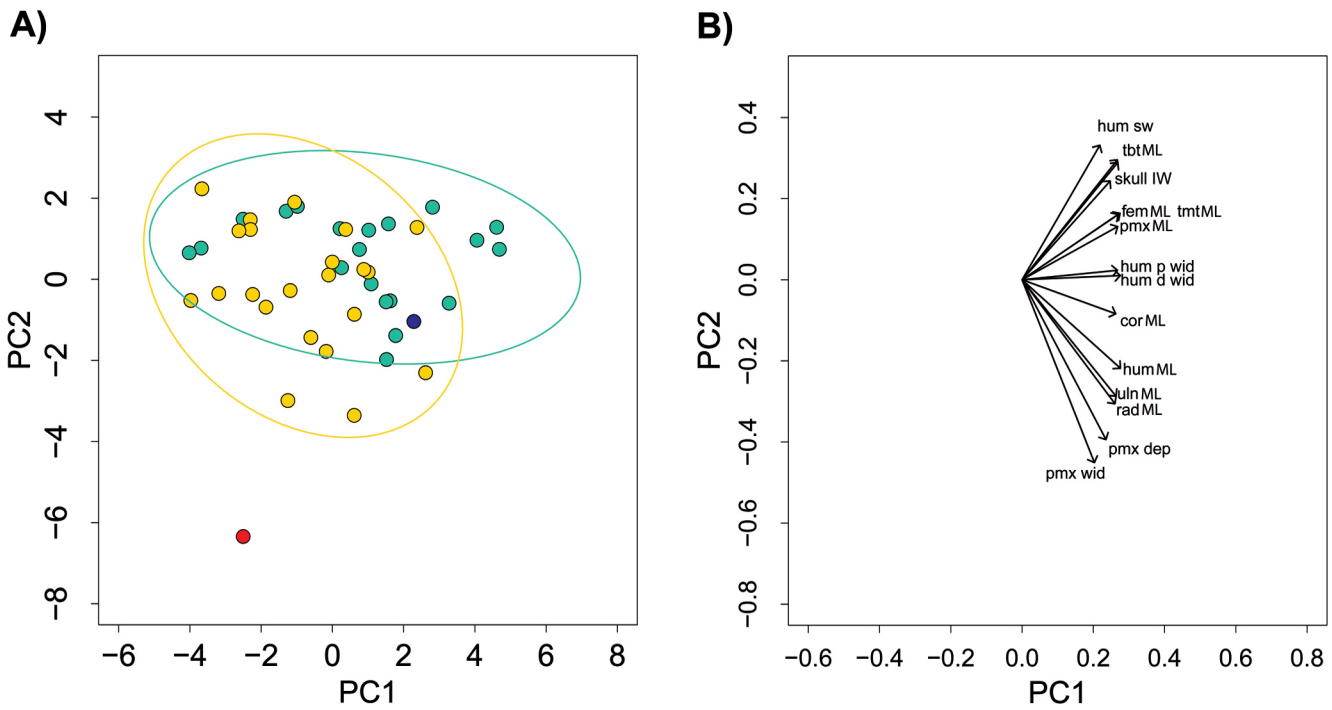

Figure 4. Principal component analysis for the skeletal measurements of the three *Procellaria* species that are most similar in morphology to the new species: *P. aequinoctialis, P. conspicillata* and *P. westlandica.* (A) Biplot of the first and second principal component scores. (B) Projection of the principal component vectors (loadings) of the tested parameters onto the PC1-PC2 biplot. Colours represent the different species: *P. aequinoctialis* = green; *P. conspicillata* = blue; *P. westlandica* = yellow; *P. altirostris* sp. nov. = red.

Procellaridae, birds in the *Procellaria* genus are the largest, with the exception of *Macronectes* Richmond, 1905, which is similar in size to some albatross taxa. Based on the narrow and deep beak, the strongly hooked premaxilla and the prominent *pila supranasalis,* the genus *Procellaria* can be easily distinguished from almost all other genera within the Procellaridae; the exceptions being *Pterodroma* Bonaparte, 1856 and *Pseudobulweria* Mathews, 1936. Generally, *Pterodroma* taxa have a narrower and shorter beak than *Procellaria* taxa; moreover, as in all *Procellaria,* the fossil has a longer humerus than ulna, while *Pterodroma* taxa have longer ulnae than humeri (Tennyson & Mannering, 2018). The *apertura nasi ossea* of *Pseudobulweria* is smaller than in *Procellaria* taxa; moreover, the proximal end of the humerus of *Pseudobulweria* taxa lack the tubercle on the cranial surface of the ventral margin in the bicipital area (Tennyson & Mannering, 2018). The shape of the *apertura nasi ossea* and this humeral tubercle of the fossil are features found in *Procellaria* taxa (Tennyson & Mannering, 2018).

Differential diagnosis: *Procellaria altirostris* sp. nov. is identified as a member of the Procellariiformes by the beak having a sharply hooked tip, lateral furrows rostral of the nostrils (nasolabial grooves) and marked *supraorbital fossae* for nasal glands (*fossa glandulae nasalis*), *i.e.,* salt glands.

Procellaria altirostris sp. nov. is most similar to the White-Chinned Petrel (*P. aequinoctialis*), Spectacled Petrel (*P. conspicillata*) and Westland Petrel (*P. westlandica*). Compared with these taxa, the new species has a deeper and shorter premaxilla, a larger coracoid and shorter wings, while its legs are a similar size. It is slightly larger than the Grey Petrel (*P. cinerea*) and notably larger than the Black Petrel (*P. parkinsoni*). The Grey Petrel also differs in having a more slender beak (width and depth relative to length) than all other members of the genus. *Procellaria* species show minor sexual dimorphism in size, with males averaging a little larger (Marchant & Higgins, 1990; Warham, 1990). However, regardless of the sex of the fossil, it still falls outside the range of variation seen in other species (Table 1, Fig. 2, Fig. 4, Appendix 2).

Measurements: see Table 1, Fig. 1.

Distribution: The holotype is the only known specimen of *Procellaria altirostris* sp. nov. All members of the genus *Procellaria* travel thousands of kilometres at sea when foraging and/or migrating (Brooke, 2004), so we expect that *Procellaria altirostris* sp. nov. had similar behaviours and would have ranged widely in the seas around proto – New Zealand and probably been a long-distance migrant like other members of this genus (Brooke, 2004).

DISCUSSION

The discovery of a well-preserved specimen of a *Procellaria* petrel from the Pliocene adds important new knowledge about the history of this genus. Only two previous studies have identified this genus in Pliocene deposits and those were disarticulated remains: a single partial humerus from the early Pliocene of South Africa (Olson, 1985a) and three bones from the early Pliocene of North Carolina, USA (Olson & Rasmussen, 2001). No older fossils of the genus are known (Olson, 1985b). Otherwise

only much younger (Holocene) fossils have been documented (*e.g.,* Tennyson, 2020; Worthy & Jouventin, 1999).

This lack of a good fossil record for the genus has impaired more detailed analyses of its evolution. Our description of a Pliocene *Procellaria* provides further evidence to support the phylogeny proposed by Penhallurick & Wink (2004), which suggested that crown-group *Procellaria* taxa were already present in the Miocene.

While we can only speculate on the functional significance of the minor skeletal differences between *P. altirostris* sp. nov. and other members of the genus, the fossil species probably had similar feeding strategies to living *Procellaria*. For example, surface feeding and shallow diving, with a diet consisting mainly of fishes, cephalopods and crustaceans (Brooke, 2004). When compared with other *Procellaria,* the relatively short wings, particularly the short ulna compared with the humerus length, suggest that it may have been less of a glider (Kuroda, 1955), perhaps using diving more often as a feeding strategy.

Finally, while New Zealand today is the worldwide centre of diversity for species of procellariiforms, including *Procellaria* (Dickinson & Remsen, 2013), the new Pliocene fossil is the only evidence of *Procellaria* petrels being present in the country prior to the Late Pleistocene (Gill *et al.,* 2010) and demonstrates a longer history for the genus in the region.

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AUTHORS' CONTRIBUTION

Conceptualization: A.J.D.T.; Investigation: A.J.D.T., B.M.T.; Formal analysis: B.M.T.; Writing - Original draft: A.J.D.T., B.M.T.; Writing – Review & Editing: A.J.D.T., B.M.T.

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APPENDIX 1

List of the comparative specimens measured. All specimens are either part of the Museum of New Zealand Te Papa Tongarewa collection (NMNZ, including specimens with'S'and 'OR'prefixes) or the collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Museum	Registration	Taxa	Skull	premaxilla	premaxilla	premaxilla	coracoid	humerus	humerus	humerus	humerus	ulna	radius	femur	tibiotarsus	tibiotarsus	tarsometatarsus
			min. intraorbital width	max. length	depth	width	max. length	max. length	proximal width	distal width	shaft width	max. length	max. length	max. length	max. length incl. cnemial crest	max. length excl. cnemial crest	max. length
Te Papa	S.046691	altirostris	15	55,56	14,52	13,5	41,99	143,22	32,26	17,68	7,44	138,53	132,95	50,05	116,56	99,53	64,82
MZUSP	MZUSP 87937	aequinoctialis	14,6				40,07	152,1	33,43	17,2	7,87	149,62	145,2	51,35	115,48	101,4	66,26
MZUSP	MZUSP 113761	aequinoctialis	14,01														
MZUSP	MZUSP 113915	aequinoctialis	14,42														
MZUSP	MZUSP 113917	aequinoctialis	14,56														
MZUSP	MZUSP 113918	aequinoctialis	14,98														
MZUSP	MZUSP 113919	aequinoctialis	14,11														
MZUSP	MZUSP 113920	aequinoctialis	12,7														
MZUSP	MZUSP 113921	aequinoctialis	14,05														
MZUSP	MZUSP 113922	aequinoctialis	15,22														
MZUSP	MZUSP 113923	aequinoctialis	13,75														
MZUSP	MZUSP 113926	aequinoctialis	14,65														
MZUSP	MZUSP 113929	aequinoctialis	14,38														
MZUSP	MZUSP 113930	aequinoctialis	14,26														
MZUSP	MZUSP 113932	aequinoctialis	13,18														
MZUSP	MZUSP 113933	aequinoctialis	13,37														
MZUSP	MZUSP 114258	aequinoctialis	13,83		12,18	13,61	38,26	150,14	31,98	17,91	7,91	152,06	149,83	51,15	115,39	100,7	66,19
Te Papa	OR.21098	aequinoctialis	14,41	63,8	11,68	13,95											
Te Papa	OR.21096	aequinoctialis	13,77	62,67	12,05	14,18											
Te Papa	OR.21097	aequinoctialis	14,54	60,76	12,67	14,27											
Te Papa	OR.28949	aequinoctialis	12,87		10,69	12,66											
Te Papa	OR.18904	aequinoctialis	13,86	60,68	11,43	13,47	37,26	149,13	31,53	17,2	7,01	149,15	145,43	50,99		101,03	65,01
Te Papa	OR.21095	aequinoctialis	13,8				38,2	153,5	32,52	17,49	7,52	151,9	148,98	51,21	113,08	99,02	66,11
Te Papa	OR.21841	aequinoctialis	14,57	60,62	12,2	13,32	36,5	155	31,56	17,27	7,23	153,5	151,14		117,92	102,98	69
Te Papa	OR.26612	aequinoctialis	14,08	64,03	12,49	13,1											
Te Papa	OR.608	aequinoctialis	14,62	63,15	12,71	13,67	39,05	151,5	33,93	17,96		150,43	146,37			98,21	64,08
Te Papa	OR.542-S	aequinoctialis	14,38	60,81	11,52	13,56								48,61	107,29	94,45	63,34
Te Papa	OR.543-S	aequinoctialis	13,09	60,76	11,7	13,9											
Te Papa	OR.16054	aequinoctialis	14,91	66,21	12,66	14,22		158	33,83	18,36	7,89	156	152,8	53,78	115,7	101,94	68,03
Te Papa	OR.25171	aequinoctialis	15,39	63,5	12,1	13,58	38,46	151,3	32,19	17,82	7,6	153	149,56	50,01		100,6	65,11
Te Papa	OR.29968	aequinoctialis	12,81	59,71	11,94	14,21		146,66	31,71	16,8	7,2	148,86	145,86	49,83	111,82	97,16	65,52
Te Papa	OR.19809	aequinoctialis	15,15	61,94	11,66	13,5	37,35	152,1	30,93	16,96	7,68	152,13	148,44	50,02	115,92	100,51	68,03
Te Papa	OR.22411	aequinoctialis	15,2	59,52	11,7	13,28	35,61	142,58	31,57	16,76	7,66	145,94	142,56	47,04	111,05	96,83	62,87
Te Papa	OR.22077	aequinoctialis	14,48	62,26	11,61	12,53	37,47	152,41	31,94	17,67	7,72	154	150,95	50,7	115,47	100,37	68,11
Te Papa	OR.21108	aequinoctialis	14,03	64,77	12,09	14,09	38,05	147,39	31,47	17,25	7,61	148,2	145,28	49,58	114,94	100,25	66,27

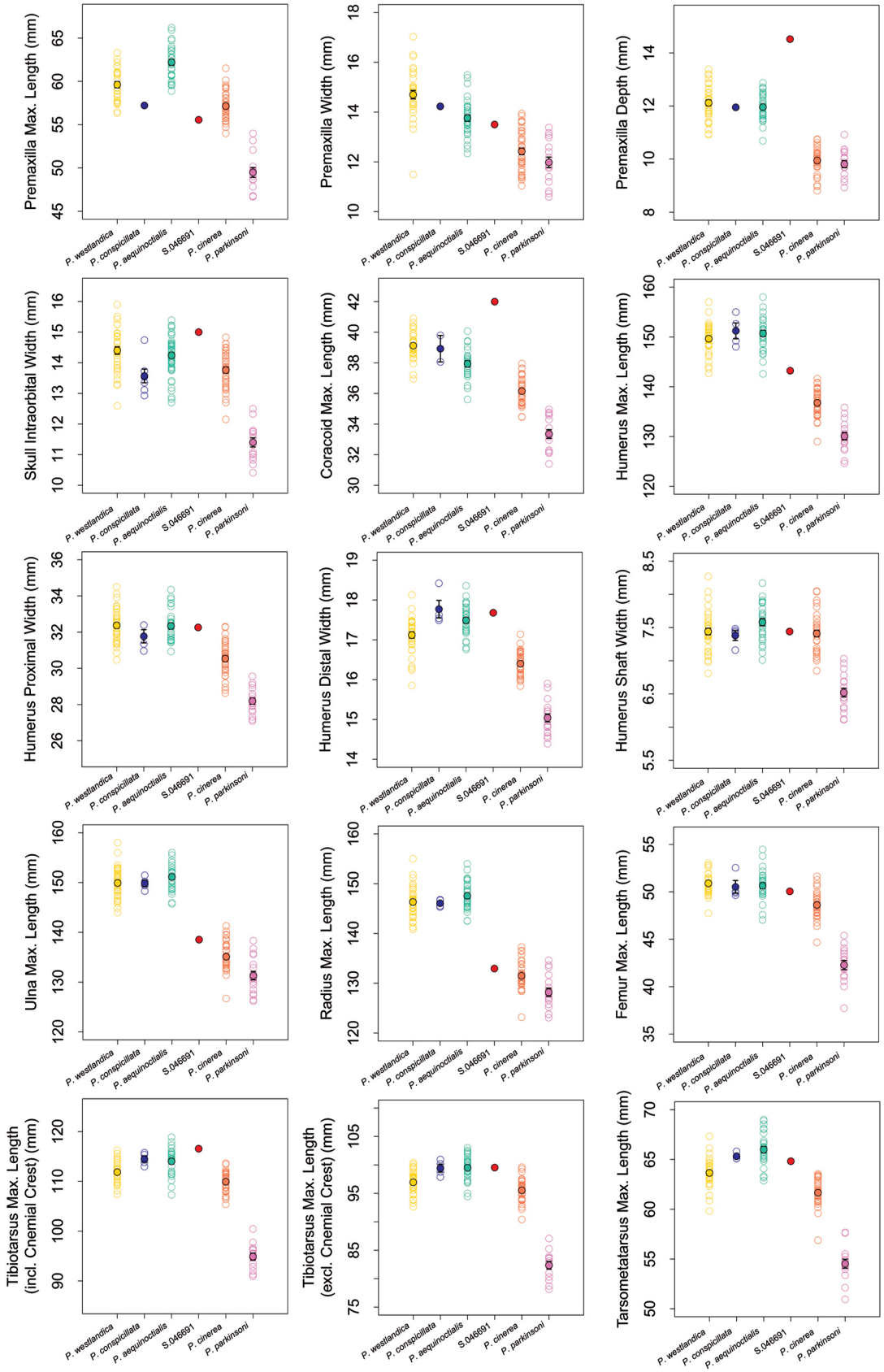
Museum	Registration	Taxa	Skull	premaxilla	premaxilla	premaxilla	coracoid	humerus	humerus	humerus	humerus	ulna	radius	femur	tibiotarsus	tibiotarsus	tarsometatarsus
			min. intraorbital width	max. length	depth	width	max. length	max. length	proximal width	distal width	shaft width	max. length	max. length	max. length	max. length incl. cnemial crest	max. length excl. cnemial crest	max. length
Te Papa	OR.22078	aequinoctialis	14,43	61,55	12,05	14,01	39,39	151,32	32,5	17,75	7,88	152,51	148,35	52,68	117,25	102,34	67,65
Te Papa	OR.21863	aequinoctialis	14,7	62,69	12,34	13,82	38,05	151,58	32,56	18,1	7,7	150,15	146,22	49,99	114,3	99,68	66,58
Te Papa	OR.15931	aequinoctialis	13,41	59,6	11,44	14,46	37,22	147,14	31,71	17,17	7,3	147,69	144,3	49,74	110,22	97,42	63,2
Te Papa	OR.25169	aequinoctialis	14,56	64,76	12,53	15,49	37,36	150,68	32,45	17,79	7,78	151,31	147,02	51,68	114,09	98,85	65,73
Te Papa	OR.536-S	aequinoctialis	14,29	62,09	12,39	13,48	37,62	149,68	31,47	17,39	7,32	152,17	148,37	50,04	112,03	98,37	66,17
Te Papa	OR.535-S	aequinoctialis	13,98	59,92	11,47	13,11	36,51	146,51	31,42	17,31	7,4	148,69	145,48	50,76	111,53	97,42	65,38
Te Papa	OR.17184	aequinoctialis	14,61	59,95	11,95	14,63	36,34	144,99	31,59	16,93	7,44	145,73	142,51	47,58	108,82	95	63,19
Te Papa	OR.17185	aequinoctialis	14,42	58,89	11,18	12,34	38,33	148,59	31,81	17,54	7,12	150,93	146,67	49,81	111,41	96,97	64,84
Te Papa	OR.25170	aequinoctialis	14,15	63,6	11,79	13,18	38,42	154	34,35	17,38	7,78	155,5	150,66	51,74	118,88	102,55	68,54
Te Papa	OR.23463	aequinoctialis	14,92	62,7	12,44	15,15	38,85	148,67	33,6	17,22	7,97	148,59	144,87	51,19	116	102,14	65,88
Te Papa	OR.22506	aequinoctialis	14,28	62,8	12,87	15,38	37,77	151,62	32,73	17,72	8,17	150,26	146,05	52,18	114,53	100	65,52
Te Papa	OR.25172	aequinoctialis	13,99	61,97	12	13,48	37,1	150,74	32,86	17,64	7,42	152,03	148,72	50	114,58	98,76	65,35
Te Papa	OR.23529	aequinoctialis	14,53	63,18	11,93	14,08	39,39	149,92	32,32	17,62	7,5	150,46	146,57	50,14	114,38	99,31	66,7
Te Papa	OR.30424	aequinoctialis	14,99	64,94	11,74	12,87	39,43	156	32,49	17,56	7,35	156	154	54,47	115,32	99,86	68,89
Te Papa	OR.25633	aequinoctialis	14,26	65,92	11,53	13,77	38,14	154	33,58	17,93	7,6	154,5	150,86	51,5	116,67	101,91	66,88
Te Papa	OR.25634	aequinoctialis	14,53	61,43	11,95	13,61	37,99	153,32	31,72	17,46	7,55	151,36	146,57	50,18	114,14	98,92	65,24
Te Papa	OR.12035	cinerea					36,6	141,64	30,56	16,54	7,37	140,21	136,44				
Te Papa	OR.16486	cinerea	13,23	55,13	8,81	12,94	34,48	134,22	28,95	16,01	7,3			49,25	108,2	93,99	61,36
Te Papa	OR.18136	cinerea	14,22	58,04	10,14	12	35,4	135,7	31,13	16,47	8,05	132,54	128,53	48,15	109,8	94,95	
Te Papa	OR.21862	cinerea	13,19	57,27	10,34	11,39	37,62	138,89	32,27	16,28	7,19	133,9	131,13	50,84		96,33	61,55
Te Papa	OR.607-S	cinerea	12,7	55,45	10,25	11,94		134,78	29,77	16	7,19	131,41	128,77				
Te Papa	OR.791-S	cinerea			9,94	12,83										96,42	60,53
Te Papa	OR.853-S	cinerea	13,49	59,16	9,8	11,99											61,73
Te Papa	OR.602-S	cinerea					36,86	138,46	31,49	16,5	8,04	135,18	131,99				
Te Papa	OR.24981	cinerea	14,48	57,55	10,21	12,03		137,23	30,6	16,17	7,14	132,81	130,32	48,36	109,26	95,33	63,35
Te Papa	OR.26232	cinerea	12,98	56,32	9,88	12,61	36,58	138,93	31,63	16,76	7,41	133,86	131,2	47,75		96,29	61,01
Te Papa	OR.25168	cinerea	14,14	56,83	10,18	12,6											
Te Papa	OR.24975	cinerea	13,7	56,8	10,22	11,7	35,35	137,7	28,8	16,05	7,14	134,45	131,58	49,41	110,8	96,1	60,76
Te Papa	OR.24662	cinerea	14,05	61,52	10,62	13,85	35,25	135,9	28,63	16,4	7,45	134,13	130,5	47,85	109,95	96,02	60,21
Te Papa	OR.24972	cinerea	13,75	54,72	8,97	12,65	37,25	139,74	30,65	16,1	7,63	137,57	133,07	48,55	110,95	99,59	61,67
Te Papa	OR.24664	cinerea	14,83	55,98	9,7	12,1	35,75	140,82	29,95	16,44	7,87	137,27	133,79	48,67	111,76	97,21	63,28
Te Papa	OR.24663	cinerea	13,79	59,26	10,75	13,62	37,3	139,86	30,7	16,55	7,54	137,46	134,42	50,62	111,43	96,36	63,18
Te Papa	OR.24974	cinerea	13,58	55,95	9,84	13,94	35,11	135,21	30,17	16,45	7,11	134,14	130,41	48,89	110,48	95,63	62,57
Te Papa	OR.17183	cinerea	12,15	55,48	9,74	11,44	35,43	134,07	29,6	15,84	7,63	132,26	128,72	48,21	108	93,83	61,94
Te Papa	OR.12475	cinerea	13,11	55,74	9,32	12,2	35,74	134,44	30,38	15,96	7,06	135,29	132,04	44,67	110,63	95,02	61
Te Papa	OR.12474	cinerea	13,39	56,6	10,45	13,23	36,16	135,72	29,18	16,28	7,16	134,04	129,98	48,88	110,9	96,6	63,34
Te Papa	OR.12248	cinerea	13,45	56,87	9,27	11,88	36,7	137,09	29,9	16,29	6,85	134,03	130,71	47,81	110,64	94,79	61,41
Te Papa	OR.24089	cinerea	13,77	59,36	9,9	11,28	36,91	139,56	32,3	16,69	7,81	139,53	136,56	48,94	112,29	97,4	63,55
Te Papa	OR.24153	cinerea	13,8	60,13	10,73	13,65	37,2	138,15	30,9	17,14	7,3	133,67	129,81	49,2	110,8	95,35	61,8
Te Papa	OR.24215	cinerea	14,62	57,32	10	13,26	35,46	137,88	30,78	16,73	7,69	138,5	134,65	49,99	111,71	97,53	62,92

Museum	Registration	Taxa	Skull	premaxilla	premaxilla	premaxilla	coracoid	humerus	humerus	humerus	humerus	ulna	radius	femur	tibiotarsus	tibiotarsus	tarsometatarsus
			min. intraorbital width	max. length	depth	width	max. length	max. length	proximal width	distal width	shaft width	max. length	max. length	max. length	max. length incl. cnemial crest	max. length excl. cnemial crest	max. length
Te Papa	OR.19305	cinerea	14,61	59,56	10,24	12,18	37,95	140,73	31,9	16,64	7,14	141,29	137,26	51,28	113,64	99,29	63,43
Te Papa	OR.792-S	cinerea	13,33	55,78	10,24	11,36	35,69	136,54	29,57	16,14	7,37	135,1	132,04	48,43	111,32	97,1	62,08
Te Papa	OR.918-S	cinerea	12,8	58,4	10,1	12,83	36,48	137,29	31,27	16,71	7	136,44	133	51,64	113,41	98,79	62,76
Te Papa	OR.24977	cinerea	14,24	58,55	10,01	13,14	37,64	138,88	31,05	16,09	7,51	139,43	135,77	49,6	109,91	95,87	60,74
Te Papa	OR.24976	cinerea	14,39	56,56	9,8	11,28	35,21	139,69	31,4	16,91	7,31	137,11	133,88	49,61	110,64	95,76	62,42
Te Papa	OR.24980	cinerea	13,15	56,97	10,05	13,38	35,4	135,48	30,26	16,27	7,42	133,55	129,79	48,71	108,9	93,91	61,28
Te Papa	OR.24978	cinerea	13,87	58,1	10,02	12,65	36,2	136,83	30,22	16,26	7,13	134,48	131,8	49,79	111,94	97,08	63,28
Te Papa	OR.24982	cinerea	14,32	57,1	9,73	12,9	35,37	135,4	30,67	16,31	7,42	133,3	130,09	46,38	107,9	93,74	59,59
Te Papa	OR.24511	cinerea	13,85	56,97	10,54	11,69	36,58	134,78	30,48	16,7	7,31	133,29	130,33	47,19	108,05	93,94	60,81
Te Papa	OR.24614	cinerea	14,06	57,05	10,25	13,59	36,54	136,64	30,81	16,4	7,48	136,24	132,02	49,21	111,57	96,19	61,82
Te Papa	OR.24512	cinerea	13,97	57,69	9,88	12,5	36,58	138,64	30,24	16,65	7,54	133,93	130,63	48,34	108,64	94,08	61,91
Te Papa	OR.24510	cinerea	13,57	57,35	9,92	11,95	36,21	134,36	30,9	16,13	7,91	138,78	128,4	47,51	106,42	92,59	60,8
Te Papa	OR.24659	cinerea	13,77	55,4	9,02	11,6	34,46	132,82	30,02	16,25	7,03	133,54	129,87	47,45	106,76	93,06	60,9
Te Papa	OR.24432	cinerea	13,81	53,99	10,06	11,47	35,88	132,71	30,66	16,57	7,5	132,87	130,45	47,8	108,75	95,04	61,3
Te Papa	OR.24983	cinerea	14,5	56,49	9,94	13,15	36	134,29	30,84	16,68	7,63	135,1	131,12	46,75	107,06	92,21	61,01
Te Papa	OR.28850	cinerea	14,4	57,16	9,4	11,04	35,87	128,98	31,53	16,34	7,57	126,71	123,18	47,41	105,41	90,4	56,88
MZUSP	MZUSP 113526	conspicillata	12,93				38,06	148,04	32,39	17,63	7,16	148,29	145,34	50,01	113,83	98,75	65,11
MZUSP	MZUSP 113543	conspicillata	13,73					152,62	31,35	17,49	7,43	150,21	146,67	49,9	115,37	100,17	65,09
MZUSP	MZUSP 113688	conspicillata	13,54					149,22	30,96	17,54	7,48	149,4	145,54	49,65	112,96	97,86	65,31
MZUSP	MZUSP 113924	conspicillata	13,11														
MZUSP	MZUSP 113927	conspicillata	13,35														
MZUSP	MZUSP 113934	conspicillata	13,56														
MZUSP	MZUSP 99377	conspicillata	14,74	57,22	11,95	14,23	39,79	155	32,39	18,42	7,45	151,46	146,79	52,54	115,75	100,94	65,8
Te Papa	OR.18907	parkinsoni	10,41	49,02	9,43	11,4	31,4	124,61	27,32	14,86	6,28	126,4	123,77	40,01	92,84	79,71	53,37
Te Papa	OR.18906	parkinsoni	11,75	48,71	9,69	12,18	32,17	128,93	27,61	14,82	6,6	128,48	125,76	41,04	94,61	82,23	54,66
Te Papa	OR.17258	parkinsoni	11,55		8,93	10,59	33,42	132,37	28,3	14,53	6,12	133,52	130,21	44,61	95,46	83,55	53,96
Te Papa	OR.793-S	parkinsoni	10,83	53,18	10,03	11,86				15,52	7,03	136,73	133,23				57,6
Te Papa	OR.25953a	parkinsoni	10,68	53,98	10,37	11,2	33,17	129,72	28,19	14,68	6,11	130,88	128,07	42,9			
Te Papa	OR.19283	parkinsoni	11,08	46,69	9,14	11,8	32,18	129,47	27,7	14,39	6,44	131,05	128,28	41,83	94,79	82,81	55,51
Te Papa	OR.18969	parkinsoni	11,32	46,71	9,25	10,73	32,29	127,58	27,17	14,67	6,45	126,19	123,09	41,96	92	80,3	54,23
Te Papa	OR.27276a	parkinsoni			10,29	13,07	33,73	131,52	28,09	15,05	6,49	130,8	128,6	43,5	96,18	83,65	54,83
Te Papa	OR.24247	parkinsoni	11,02	46,78	10,25	11,98	32,96	129,1	28,59	14,58	6,41	127,66	125,19				
Te Papa	OR.27119a	parkinsoni					34,75	135,82	29,56	15,2	6,55	138,32	134,62	43,78			
Te Papa	OR.29637	parkinsoni	12,33	49,56	10,36	11,74	34,67	130,58	29,08	15,9	6,88	131,64	127,73	43,18	95,58	83,09	54,22
Te Papa	OR.18905	parkinsoni	12,5	49,47	9,25	10,82	33,33	128,67	29,19	14,81	6,68	129,48	126,58	41,19	96,64	83,62	54,22
Te Papa	OR.19282	parkinsoni	11,79	48,63	10,92	12,59	32,1	127,3	27,91	15,3	6,78	130,04	127,26	37,73	90,96	78,16	52,12
Te Papa	OR.18968	parkinsoni	11,67	47,84	9,25	13,17	32,28	125,09	27,09	15,14	6,96	127,37	123,74	40,57	91,3	78,7	50,94
Te Papa	OR.19298	parkinsoni	11,74	50,16	9,88	11,8	34,76	130,41	28,45	14,96	6,41	130,57	126,88	42,02	93,57	81,01	54,42
Te Papa	OR.19781	parkinsoni	11,01	52,08	9,71	12,4	34,29	134,66	28,06	15,23	6,3	135,51	131,65	44,05	97,76	85,24	55,25
Te Papa	OR.24236	parkinsoni	10,92	49,72	10,04	12,98	34,57	131,55	27,95	15,2	6,69	132,88	129,15	42,76	96,32	83,87	54,9

Museum	Registration	Taxa	Skull	premaxilla	premaxilla	premaxilla	coracoid	humerus	humerus	humerus	humerus	ulna	radius	femur	tibiotarsus	tibiotarsus	tarsometatarsus
			min. intraorbital width	max. length	depth	width	max. length	max. length	proximal width	distal width	shaft width	max. length	max. length	max. length	max. length incl. cnemial crest	max. length excl. cnemial crest	max. length
Te Papa	OR.289617	parkinsoni	11,79	49,62	10,06	13,38	34,96	133,72	28,91	15,8	6,21	135,76	133,66	45,39	100,45	87,06	57,68
Te Papa	OR.21422	westlandica	14,69	60,88	12,87	14,24	40,4	149,98	32,54	17,18	7,49	148,43	144,33				63,92
Te Papa	OR.22084	westlandica	14,63	58,26	11,82	14,72	38,95	144,04	30,86	16,33	7,14	143,99	141,29				
Te Papa	OR.21423	westlandica	13,93		12,15	15,61	39,45	149,9	34,12		7,31	149,06	144,37	51,89		98,08	64,38
Te Papa	OR.21424	westlandica	15,9	59,24	11,73	14,61	38,91	149,5		17,2	7,4	150,2	146,57	51,52		99,6	63,46
Te Papa	OR.21106	westlandica	14,35	58,56	12,29	15,05	39,89	151,68	33,1	17,21	8,27	152,82				96,35	
Te Papa	OR.21094	westlandica					38,82	155	32,91	17,1	7,09	150,94	147,81	51,46		97,62	64,66
Te Papa	OR.24272	westlandica	15,26		12,64	17,03	40,63	150,21	32,9	17,46	7,94	148,28	145,25	50,2	112,52	97,43	64,09
Te Papa	OR.11494	westlandica	14,44														
Te Papa	OR.838-S	westlandica					38,61	150,94	33,3	17,3	7,73	148,63	145,69		111,4	96,6	62,5
Te Papa	OR.15900	westlandica	13,84		12,24	15,73	39,91	146,4	32,22	17,02	7,38	146,7	142,16	50,38	109,22	93,83	60,87
Te Papa	OR.599-S	westlandica					38,6		32,61					50,56			
Te Papa	OR.11511	westlandica	12,59	56,32	10,94	14,32	37,95	144,98	32	16,52	6,98	147,46	143,7	50,93	111,04	96,07	63,1
Te Papa	OR.22968	westlandica						151,72	31,87	16,96	7,52	158	155		114,99	99,37	66,13
Te Papa	OR.22933	westlandica	14,4	57,49	10,92	13,51		148,52	32,04	16,97	6,81	151,83	147,81	49,38	112,81	98,38	63,15
Te Papa	OR.22085	westlandica	13,27		11,34	13,32	38,53	150,38	31,87	16,9	7	151,13	146,9	51	112,29	95,52	63,54
Te Papa	OR.23766	westlandica	14,32	59,27	12,38	11,49		149,35	32,5	17,43	7,54	153,5	151,19	50,02	109,16	93,94	62,31
Te Papa	OR.28672	westlandica	14,39	62,2	12,1	13,98	40,19	151,29	31,48	17,3	7,07	151,27	147,12	51,32	112,42	97,88	64,85
Te Papa	OR.23155	westlandica	14,24		12,65	13,73		150,31	32,62	16,75	7,39	151,74	146,7		111,73	97,53	
Te Papa	OR.23151	westlandica	13,45	57,41	11,1	14,39		142,7	31,15	15,85	7,2	144,87	140,85		108,15	92,64	59,82
Te Papa	OR.19299	westlandica	14,97	61,78	13,04	14,98	38,66	152	31,95	17,27	7,14	150	148	51,88	114,52	99,74	64,34
Te Papa	OR.21091	westlandica	13,6	60,13	11,4	15,34	38,9	148,14	31,37	16,74	7,49	150,47	145,83	50,36	109,88	95,91	63,46
Te Papa	OR.19281	westlandica	14,95	61,08	12,84	15,78	38,92	146,9	34,5	17,36	8,04	145,8	142,33	51,52	110,85	95,91	63,19
Te Papa	OR.19311	westlandica	14,96	60,86	13,38	14,69	39,92	152,82	33,45	17,78	7,42	150,84	147,45	52,58	116,27	100,37	67,33
Te Papa	OR.21499	westlandica	14,97	57,47	11,96	14,41	36,94	149,63	30,47	16,28	7,32	152,85	149,63	51,92	112,35	97,74	65,09
Te Papa	OR.21466	westlandica	15,42	62,58	13,17	14,85	38,35	150,21	32,38	17,14	7,58	148,45	145,12	52,8	112,42	97,25	63,9
Te Papa	OR.21099	westlandica	14,87	60,68	11,37	15	38,83	146,07	32,74	17,47	7,6	146,33	143,21	49,67	107,42	93,27	62,57
Te Papa	OR.21092	westlandica	14,37	57,7	12,07	16,3	37,21	150,95	31,87	17,31	7,65	152,75	148,88	52,78	115,58	100,13	65,62
Te Papa	OR.21093	westlandica	14,84	58,53	12,11	14,81	39,3	148,58	31,75	17,43	7,52	148,02	145,12	50,42	111,04	96,17	63
Te Papa	OR.27314	westlandica	14,49	60,97	12,49	14,3	39,76	148,35	33,27	17,48	7,48	147,37	144,45	50,24	113,19	97,7	64,07
Te Papa	OR.27409	westlandica	14,04	57,54	12,52	14,4	38,85	152,17	31,33	16,88	7,83	152,35	149,18	47,74	109,79	94,75	61,36
Te Papa	OR.24271	westlandica	13,92	60,97	11,7	13,51	40,33	157	33,91	17,45	7,53	156	151,83	49,88	114,59	98,76	64,61
Te Papa	OR.24244	westlandica	13,72	56,51	11,78	14,94	39,35	148,21	32,4	17,11	7,13	146,21	142,19	49,62	114,13	98,05	63,66
Te Papa	OR.13566	westlandica	13,3	63,3	12,06	16,24	38,26	152,45	32,83	17,59	7,65	153,03	150,02	49,9	110,27	96,15	65,62
Te Papa	OR.13594	westlandica	14,13	58,89	11,86	14,8	38,97	150,84	32,72	17,13	7,4	151,4	146,62	52,81	113,71	98,02	63,32
Te Papa	OR.22668	westlandica	13,79	57,8	11,62	14,92	39,47	149,63	31,57	17,06	7,2	149,77	146,76	50,04	109,5	94,71	62,96
Te Papa	OR.23734	westlandica	15,25	61,09	12,25	14,61	39,02	143,61	31,89	16,24	7,37	146,68	143,34	50,11	109,15	94,88	61,38
Te Papa	OR.23725	westlandica	14,35	61,73	11,95	14,1	39,4	151,45	33,42	17,43	7,7	152,58	149,2	51,29	111,96	97,75	64,26
Te Papa	OR.23121	westlandica	14,86	58,93	12,22	14,66	38,94	149,41	31,41	17,45	7,58	149,45	147,13	50,76	111,12	97,11	63,18
Te Papa	OR.23306	westlandica	15,51	60,68	13,21	15,53	40,9	151,91	32,32	18,13	7,36	147,37	144,96	53,01	114,13	97,79	64,23

APPENDIX 2

Means (solid symbols) and standard errors (error bars) of each of the 15 skeletal measurements used for the fossil description for each *Procellaria* species. Open symbols represent the individual measurements. Colours represent different species: yellow = *P. westlandica*; blue = *P. conspicillata*; green = *P. aequinoctialis*; red = *P. altirostris* sp. nov.; orange = *P. cinerea*; pink = *P. parkinsoni*.



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