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A New Diving Pliocene *Ardenna* Shearwater (Aves: Procellariidae) from New Zealand †

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Abstract: We report a new species of shearwater, *Ardenna buchananbrowni* sp. nov., from the Pliocene of New Zealand. It is both the smallest and oldest known diving member of the genus, demonstrating that this now abundant form of shearwater has had a long presence in southern oceans. *Ardenna buchananbrowni* sp. nov. is among the few extinct shearwaters described from the Southern Hemisphere and adds to an increasingly diverse seabird assemblage in the Pliocene of the region.

Keywords: biogeography; fossil; Piacenzian; Procellariiformes; Tangahoe Formation; Taranaki; Waipipian

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1. Introduction

Shearwaters (Procellariidae) are a diverse group of procellariiforms comprising three main lineages: the relatively large *Calonectris*, weighing 470–1060 g; the somewhat smaller *Ardenna*, weighing 320–950 g; and the notably smaller *Puffinus*, weighing 120–575 g [1–8].

Shearwaters contribute the greatest number of species to the Neogene procellariform fossil record [9], with the oldest unambiguous records dating back to the Middle Miocene [10]. The affinities of purported older species like *Puffinus raemdonckii* from the early Oligocene of Belgium remain unclear [10–12]. Shearwater fossils are concentrated in the Northern Hemisphere [9,13], with southern occurrences previously limited to modern or unidentified taxa from the Mio-Pliocene of South Africa [14,15], Peru [16], and Chile [17].

This situation has recently begun to change with the discovery of a globally important Pliocene seabird assemblage from Taranaki, Aotearoa New Zealand [18–23]. Procellariiforms from this locality already include *Ardenna davealleni*, a large gliding shearwater [18]. Here, we describe a smaller diving shearwater from the same assemblage.

2. Materials and Methods

The fossils described here come from Pliocene mudstone concretions and were mechanically prepared by their collectors. Based on their advanced degree of bone fusion, both specimens are osteologically mature. We compared the new fossils to other procellariiforms, including representatives of all clades of living shearwaters, using specimens housed at the Museum of New Zealand Te Papa Tongarewa (Te Papa; NMNZ, Wellington). We limited detailed comparisons to *Puffinus* and 'diving' species of *Ardenna* after initial morphological comparisons showed few similarities with larger 'gliding' species of shearwater (see [18]). Sexual size dimorphism was not considered as shearwaters show only limited differences, with males being larger on average [24–26]. To visualise anatomical differences, we summarised individual bone measurements of various living and extinct

shearwaters via principal component analysis (PCA) in R (v.4.3.2; [27]). All measurements were z-standardised (i.e., mean centred at 0 and standard deviation at 1) prior to analysis, and missing data were accounted for via mean value imputation. Considering the good preservation of the fossils, as well as the bone elements chosen for analysis (skull, humerus, and ulna; Table 1), we do not anticipate that damage and/or deformation will impact the results.Measurements (Tables 1 and 2; Supplementary File S1) were taken to the nearest 0.1 mm using Vernier callipers and include the following: Skull—S-C, culmen length, taken from the tip of the beak to the suture between the lacrimal and the frontonasal process; S-CL, cranium length; S-MFF, minimum interorbital width, taken between the supraorbital glands (fossae glandulae nasalis); S-MIF, minimum interorbital width including the supraorbital glands; S-PPW, cranium width, taken at the level of the paroccipital process; S-Q, quadrate height across the mandibular and otic processes; S-TL, total length, taken from the cerebellar prominence to the tip of the beak. Coracoid—C-SmW, mid-shaft width. Humerus—H-SmD, mid-shaft depth; H-SmW, mid-shaft width. Ulna—U-PW, proximal width. Osteological terms follow [28,29].

This published work and the nomenclatural act it contains have been registered in ZooBank, the online registration system for the International Code of Zoological Nomenclature. The ZooBank Life Science Identifier for this publication is http://zoobank.org/urn:lsid:zoobank.org:pub:7D76F702-3665-49FC-B0E1-43F2EC78CB76.

Table 1. Measurements (in mm) of the type specimens of *Ardenna buchananbrowni* sp. nov. (HOL = holotype NMNZ S.49931; PAR = paratype NMNZ S.49666), alongside mean values of measurements of specimens of *Puffinus* spp. and *Ardenna* spp. Abbreviations can be found in Section 2 of this paper; *n* indicates the number of specimens measured; an asterisk (*) indicates an estimated measurement from lightly damaged bones. See Supplementary File S1 for measurements of each specimen. The average weight (in grams) of living shearwaters was obtained from [25] and included for comparison.

Species	*n*	S-TL	S-CL	S-C	S-MIF	S-MFF	S-PPW	S-Q	C-SmW	H-TL	H-SmD	H-SmW	U-TL	U-PW	Weight
A. buchananbrowni sp. nov.	HOL PAR	84.4 * 86.0 *	38.0 40.2	46.4 * 46.0 *	8.6 8.4	3.7 3.1	- 16.9	- 8.7	3.9 3.4	80.2 -	3.3 3.1	5.9 6.6	72.0 -	8.1 8.5	- -
A. bulleri (Salvin, 1888)	5	89.1 ± 1.00	41.3 ± 0.44	47.8 ± 1.04	10.6 ± 0.46	4.8 ± 1.07	17.4 ± 0.78	10.3 ± 0.44	2.8 ± 0.16	98.3 ± 2.27	4.0 ± 0.09	5.0 ± 0.05	98.9 ± 2.08	8.0 ± 0.15	420
A. carneipes (Gould, 1844)	5	97.3 ± 3.09	44.4 ± 1.23	52.9 ± 1.95	10.4 ± 0.48	4.1 ± 0.72	20.7 ± 1.03	11.3 ± 0.25	3.5 ± 0.16	114.2 ± 3.05	4.5 ± 0.15	6.0 ± 0.11	113.9 ± 2.65	9.5 ± 0.21	700
A. creatopus (Coues, 1864)	3	96.3 ± 3.83	45.0 ± 0.38	51.6 ± 3.12	10.4 ± 0.72	3.6 ± 0.35	20.8 ± 1.35	11.5 ± 0.49	3.4 ± 0.06	113.2 ± 2.77	4.6 ± 0.06	5.7 ± 0.30	111.7 ± 2.97	9.5 ± 0.17	900
A. davealleni Tennyson & Mannering, 2018	1	105	50.2	54.8	10.8	3.8	-	-	-	121.8	5.2	6.5	117.7	9.7	-
A. gravis (O'Reilly, 1818)	1	102.5	46.2	56.3	10.4	1.8	20.2	10.8	3.8	120.9	4.6	6.3	117.7	9.8	830
A. grisea (Gmelin, 1789)	5	93.0 ± 1.18	42.5 ± 0.41	50.6 ± 1.04	9.3 ± 0.66	1.4 ± 0.41	19.5 ± 0.64	10.1 ± 0.31	3.8 ± 0.27	107.1 ± 2.33	4.0	7.0 ± 0.30	99.1 ± 2.39	10.3 ± 0.27	800
A. pacifica (Gmelin, 1789)	10	85.1 ± 4.7	39.9 ± 1.80	45.3 ± 3.11	8.7 ± 0.80	3.6 ± 0.49	17.7 ± 0.91	9.5 ± 0.66	2.8 ± 0.30	105.1 ± 6.28	3.8 ± 0.29	4.9 ± 0.42	107.8 ± 5.34	8.0 ± 0.87	435
A. p. chlororhynchus (Lesson, 1831)	5	81.9 ± 2.58	38.5 ± 1.12	43.3 ± 1.73	8.3 ± 0.82	3.4 ± 0.29	17.0 ± 0.60	8.9 ± 0.29	2.6 ± 0.27	99.9 ± 3.79	3.7 ± 0.25	4.6 ± 0.23	103.9 ± 3.89	7.4 ± 0.49	435
A. p. pacifica (Gmelin, 1789)	5	88.4 ± 4.15	41.2 ± 1.24	47.2 ± 3.08	9.1 ± 0.61	3.8 ± 0.60	18.4 ± 0.55	10.0 ± 0.42	2.9 ± 0.31	110.3 ± 2.64	3.9 ± 0.31	5.2 ± 0.39	111.7 ± 3.21	8.5 ± 0.87	435
A. tenuirostris (Temminck, 1836)	5	81.2 ± 0.92	40.7 ± 0.40	41.3 ± 0.69	8.1 ± 0.31	1.8 ± 0.64	17.9 ± 0.59	9.3 ± 0.15	3.6 ± 1.19	98.6 ± 2.85	3.9 ± 0.11	6.3 ± 0.36	92.7 ± 2.73	9.2 ± 0.24	550
P. assimilis Gould, 1838		65.4 ± 2.13	33.9 ± 0.89	31.5 ± 1.58	5.1 ± 0.39	2.2 ± 0.53	13.3 ± 0.50	7.7 ± 0.28	2.2 ± 0.15	60.1 ± 2.19	2.4 ± 0.13	4.0 ± 0.30	54.2 ± 1.97	6.2 ± 0.34	240
P. a. assimilis Gould, 1838	1	61.1	33.1	28.0	4.7	2.3	12.6	7.4	1.8	57.4	2.2	3.3	51.6	5.4	240
P. a. haurakiensis Fleming & Serventy, 1943	4	66.6 ± 1.74	34.6 ± 0.86	32.0 ± 1.04	5.4 ± 0.40	2.3 ± 0.74	13.4 ± 0.50	7.7 ± 0.34	2.2 ± 0.08	61.1 ± 1.73	2.5 ± 0.14	4.2 ± 0.22	54.8 ± 1.90	6.4 ± 0.21	240
P. a. kermadecensis Murphy, 1927	5	65.3 ± 1.34	33.5 ± 0.54	31.9 ± 1.14	5.0 ± 0.24	2.0 ± 0.40	13.4 ± 0.48	7.6 ± 0.25	2.2 ± 0.08	59.9 ± 2.37	2.5 ± 0.09	3.9 ± 0.11	54.2 ± 1.99	6.1 ± 0.11	240
P. elegans Giglioli & Salvadori, 1869	5	66.7 ± 2.05	36.3 ± 0.85	3-.5 ± 1.39	5.8 ± 0.21	1.3 ± 0.55	14.0 ± 0.59	7.9 ± 0.14	2.5 ± 0.09	64.1 ± 1.28	2.8 ± 0.05	4.5 ± 0.28	55.8 ± 1.79	6.9 ± 0.22	250

Table 1. *Cont.*

Species	*n*	S-TL	S-CL	S-C	S-MIF	S-MFF	S-PPW	S-Q	C-SmW	H-TL	H-SmD	H-SmW	U-TL	U-PW	Weight
P. gavia (Forster, 1844)	5	80.5 ± 2.37	37.3 ± 0.98	43.2 ± 1.57	7.4 ± 0.33	2.4 ± 0.41	14.9 ± 0.77	8.1 ± 0.47	3.2 ± 0.18	73.9 ± 0.96	3.2 ± 0.14	5.4 ± 0.21	64.2 ± 1.18	7.8 ± 0.18	365
P. huttoni Mathews, 1912	5	83.1 ± 1.80	36.7 ± 0.50	46.4 ± 1.55	7.6 ± 0.22	2.6 ± 0.41	15.3 ± 0.72	8.2 ± 0.23	3.0 ± 0.05	76.9 ± 1.47	3.0 ± 0.11	5.4 ± 0.15	69.1 ± 1.17	7.9 ± 0.24	350
P. lherminieri polynesiae Murphy, 1927	1	62.6	32.0	30.6	4.5	1.4	12.3	6.4	2.0	64.9	2.4	3.7	61.1	5.9	170
P. nativitatis Streets, 1877	3	71.6 ± 0.85	36.5 ± 0.93	35.1 ± 0.15	7.2 ± 0.11	3.4 ± 0.29	14.9 ± 0.85	7.9 ± 0.15	2.7 ± 0.25	79.3 ± 2.23	3.2 ± 0.10	5.0 ± 0.38	78.4 ± 1.60	7.8 ± 0.20	350
P. newelli Henshaw, 1900	1	78.3	37.8	40.5	7.0	2.6	16.2	8.8	3.0	78.9	3.3	5.6	74.9	8.1	384
P. puffinus (Brünnich, 1764)	3	79.8 ± 0.45	37.3 ± 0.72	42.5 ± 1.07	7.2 ± 0.29	2.1 ± 0.00	15.6 ± 0.11	8.7 ± 0.25	2.7 ± 0.06	78.7 ± 0.49	3.2 ± 0.23	5.4 ± 0.15	72.0 ± 0.84	8.3 ± 0.20	450
P. spelaeus Holdaway & Worthy, 1994	1	71.0	34.0	37.0	6.2	2.4	12.8	7.8	2.7	68.8	2.7	5.0	59.0	7.0	250

Table 2. Total lengths of humerus and ulna (in mm) of *Ardenna buchananbrowni* sp. nov., alongside those of *Puffinus* spp. and *Ardena* spp.

Species	Specimen	H-TL	U-TL	H-TL/U-TL	Species	Specimen	H-TL	U-TL	H-TL/U-TL
A. p. chlororhynchus	OR.23001	101	105	0.95	*A. grisea*	OR.30973	107	99.2	1.08
A. p. chlororhynchus	OR.29670	96.1	101	0.95	*A. grisea*	OR.31127	106	98.5	1.08
A. p. pacifica	OR.16209	111	117	0.95	*A. tenuirostris*	OR.14992	99.7	92.6	1.08
A. p. chlororhynchus	OR.27271	106	110	0.96	*P. puffinus*	OR.26858	78.5	72.4	1.08
A. p. pacifica	OR.24045	108	112	0.96	*A. grisea*	OR.30667	106	97.4	1.09
A. bulleri	OR.29625	97.5	100	0.97	*P. a. haurakiensis*	OR.30200	61	56	1.09
A. p. chlororhynchus	OR.28942	97.7	100	0.97	*P. a. kermadecensis*	OR.23986	56.7	52	1.09
A. p. chlororhynchus	OR.29669	99.1	103	0.97	*P. puffinus*	OR.23335	79.3	72.5	1.09
A. p. pacifica	OR.27511	105	108	0.97	*P. a. kermadecensis*	OR.15912	61.4	56	1.10
A. p. pacifica	OR.27939	109	111	0.98	*P. a. kermadecensis*	OR.24279	59.5	54.2	1.10
A. bulleri	OR.29496	97.1	97.7	0.99	*P. huttoni*	OR.21463	77.6	70.6	1.10
A. bulleri	OR.24149	102	102	1.00	*P. huttoni*	OR.28605	75.6	68.8	1.10
A. bulleri	OR.26394	97.5	97.7	1.00	*P. puffinus*	OR.26859	78.4	71	1.10
A. bulleri	OR.29479	96.9	96.8	1.00	*A. buchananbrowni*	S.49931	80.2	72	1.11
A. carneipes	OR.26448	115	115	1.00	*P. a. assimilis*	OR.520-S	57.4	51.6	1.11
A. carneipes	OR.29207	112	112	1.00	*P. huttoni*	OR.29172	75.1	67.4	1.11
A. carneipes	OR.30170	111	111	1.00	*P. a. haurakiensis*	OR.31163	63.1	56.4	1.12
A. carneipes	OR.30277	118	117	1.00	*P. a. kermadecensis*	OR.15911	59	52.5	1.12
A. p. pacifica	OR.16208	110	110	1.00	*P. a. kermadecensis*	OR.23972	62.9	56.4	1.12
P. nativitates	OR.24682	78.2	78.4	1.00	*P. huttoni*	OR.30720	77.7	69.4	1.12
A. carneipes	OR.13608	116	115	1.01	*P. a. haurakiensis*	OR.20985	58.9	52.2	1.13
A. creatopus	OR.26623	115	114	1.01	*P. a. haurakiensis*	OR.31162	61.5	54.6	1.13
A. creatopus	OR.27754	110	108	1.01	*P. elegans*	OR.22082	65.4	57.8	1.13
P. nativitates	OR.19307	77.9	76.8	1.01	*P. huttoni*	OR.26395	78.5	69.5	1.13
A. creatopus	OR.27756	115	113	1.02	*P. elegans*	OR.26446	65	56.9	1.14
P. nativitates	OR.22142	81.9	80	1.02	*P. gavia*	OR.17253	75.2	65.8	1.14
A. davealleni	S.46316	122	118	1.03	*P. elegans*	OR.21865	64.6	56.3	1.15
A. gravis	OR.22144	121	118	1.03	*P. gavia*	OR.25696	74	64.4	1.15
P. newelli	OR.22764	78.9	74.9	1.05	*P. gavia*	OR.31071	73.1	63.3	1.15
A. tenuirostris	OR.29306	98.6	92.7	1.06	*P. gavia*	OR.30257	74.3	64.7	1.15
A. tenuirostris	OR.29471	102	96.3	1.06	*P. elegans*	OR.15621	63	54.2	1.16
A. tenuirostris	OR.30741	98.9	93.1	1.06	*P. gavia*	OR.17201	72.8	62.8	1.16
A. tenuirostris	OR.31128	94.1	88.6	1.06	*P. spelaeus*	S.28002	69.2	59.4	1.16
P. l. polynesiae	OR.27551	64.9	61.1	1.06	*P. elegans*	OR.22081	62.5	53.6	1.17
A. grisea	OR.30725	111	103	1.08	*P. spelaeus*	S.27981	68.8	59	1.17
A. grisea	OR.30972	105	97.4	1.08					

3. Systematic Palaeontology

Order Procellariiformes Fürbringer, 1888

The present fossils belong to Procellariiformes because of their straight, deeply grooved beaks, prominent dorsally opening nostrils, enlarged nasal glands above the eyes, and long, narrow wing bones.

Family Procellariidae Leach, 1820

The present fossils belong to Procellariidae because of their intermediate size (Diomedeidae are larger, Oceanitidae and Hydrobatidae smaller), gracile beaks, and dorsally projecting nostrils.

Genus *Ardenna* Reichenbach, 1853
Type species: *Procellaria gravis* O'Reilly, 1818.

***Ardenna buchananbrowni* sp. nov**. (Figures 1 and 2)
ZooBank reg.: urn:lsid:zoobank.org:act:A24C44F5-1969-4A6E-85F7-24B468BC5BCF
Holotype: NMNZ S.49931, partial articulated skeleton collected by Karl Raubenheimer, preserving the complete skull and premaxilla, posterior right mandible, sternum, furcula, right coracoid, a row of articulated thoracic vertebrae, four ribs, both humeri, right ulna, right radius, and several small unidentified fragments (Figure 1).
Type locality and horizon: Ohawe Beach, southern Taranaki, New Zealand (39°35.55′ S 174°12.45′ E). Tangahoe Formation. (Fossil Record Electronic Database FR Number Q21/F0175).
Age: Late Pliocene, Piacenzian/Waipipian; 3.36–3.06 Ma [30].
Paratype: NMNZ S.49666, partial skeleton preserving the complete skull and premaxilla, left quadrate, right coracoid, both humeri (missing their distal ends), right ulna, probable right radius, one vertebra, and several small unidentified fragments (Figure 2). This skeleton is similar in size to the holotype and was collected by John Buchanan-Brown at Waihi Beach, South Taranaki, New Zealand (39°36.13′ S 174°14.08′ E). Formation and age as for the holotype.
Etymology: The specific epithet honours John Buchanan-Brown, the discoverer of the paratype.
Diagnosis: Small species of shearwater differing from all procellariids except *Ardenna*, *Calonectris*, and *Puffinus* in having a thin elongate beak and long olecranon process of the ulna. Further differs from *Calonectris* and all species of *Ardenna* except *A. grisea* and *A. tenuirostris* in having a shallow brachial fossa on the humerus, a dorsoventrally flattened humeral shaft, and a humerus/ulna length ratio $\geq$ 1.05 (Tables 1 and 2). Differs from *Ardenna* in being smaller overall but is comparable to the largest members of *Puffinus*.

Our PCA clusters the new fossils with *Ardenna* but still within the 95% confidence ellipse of *Puffinus*, reflecting their intermediate size and morphology (Figure 3A; Supplementary File S1). PC1 accounts for 78% of the variation and largely reflects size. By contrast, PC2 accounts for 12% of the variation and broadly separates diving shearwaters (*Puffinus*, *Ardenna grisea*, and *A. tenuirostris*) from gliding forms (other *Ardenna*), with the new species clustering with the divers. Overall, it falls closest to *A. tenuirostris*, but differs from the latter, like from all *Ardenna*, in having a shorter humerus and ulna (Table 2). For a comparison of size and morphology between diving shearwaters (*Puffinus*, *A. grisea*, and *A. tenuirostris*) and gliding *Ardenna*, see Supplementary File S2.

Description: The new fossils are small to medium-sized relative to other procellariiforms. The skull is elongate with a prominent supraoccipital. The beak is long and narrow, with prominent nasal openings, deep nasal sulci, and large supraorbital glands. The wing bones are long, slender, and straight. The head of the humerus slightly overhangs the dorsal pneumotricipital fossa. The humerus is noticeably flattened and bears a capital shaft ridge extending from the proximal shaft to the head. There is no tubercle on the cranial surface of the ventral margin of the bicipital area. The dorsal supracondylar process is moderately sized and tapers to a point, but is relatively straight and not clearly angled proximally. A ridge runs along the caudal surface of the ulna to the proximal tip, which forms a prominent olecranon process. The sternum is elongate and has a large keel with a convex ventral edge. The coracoid is short and stout, with a large acrocoracoid process. Neither specimen preserves the pelvic or leg elements, but the holotype includes a row of vertebrae and ribs.

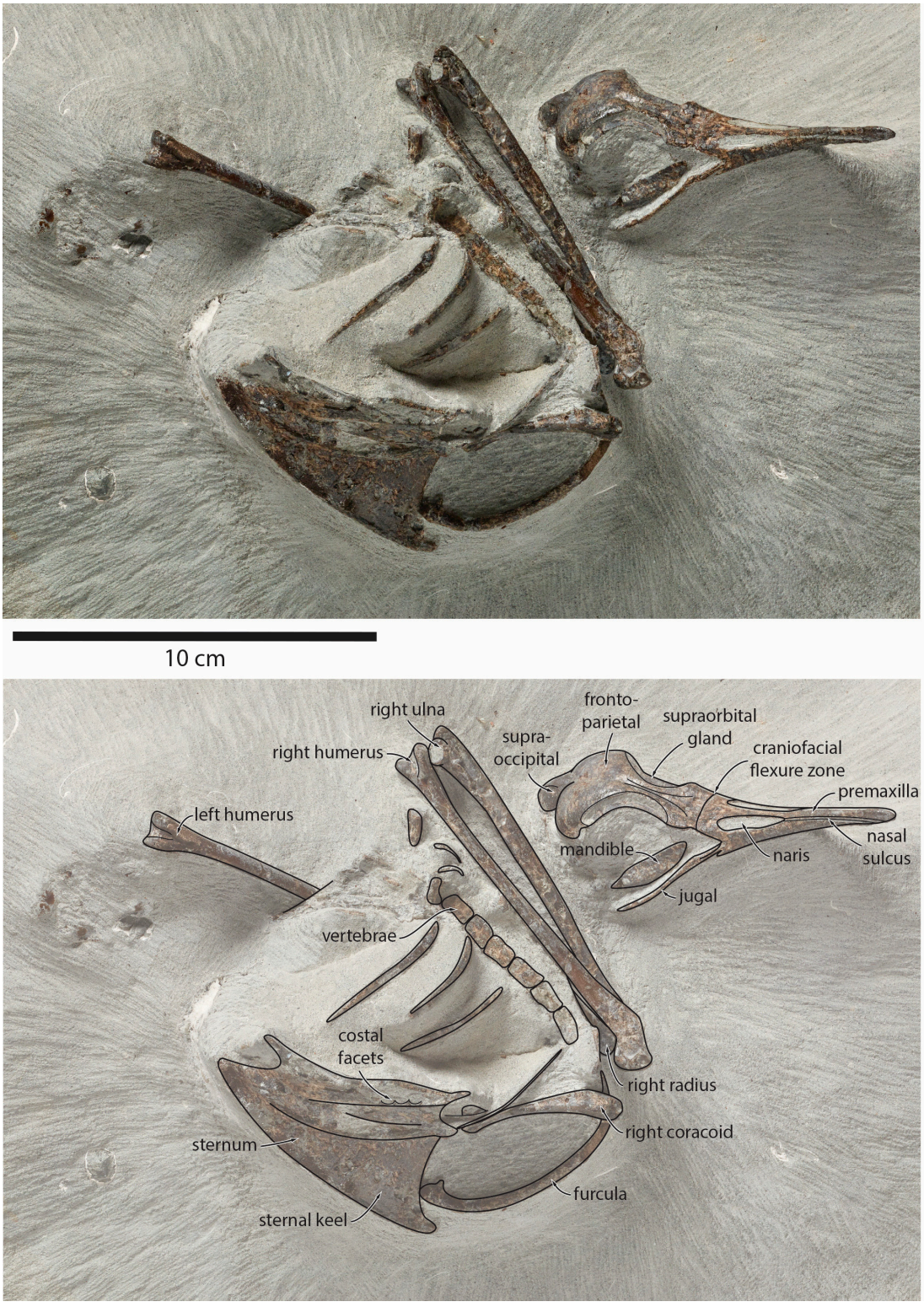

Figure 1. Pliocene fossil shearwater *Ardenna buchananbrowni* sp. nov. Photograph of holotype NMNZ S.49931 (**top**) and explanatory line drawing (**bottom**).

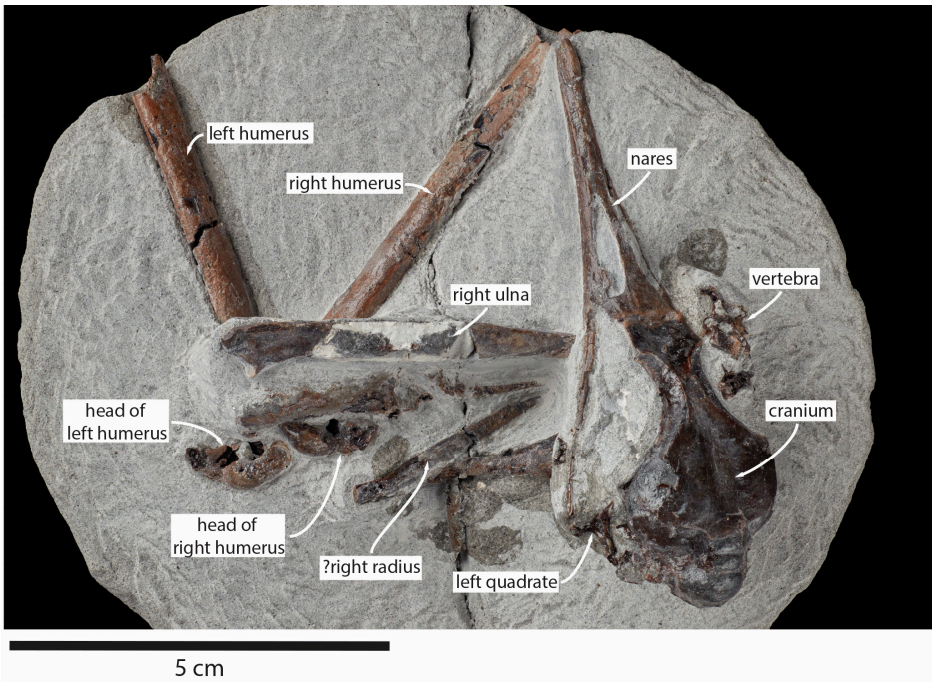

Figure 2. Pliocene fossil shearwater *Ardenna buchananbrowni* sp. nov. paratype NMNZ S.49666, with elements identified.

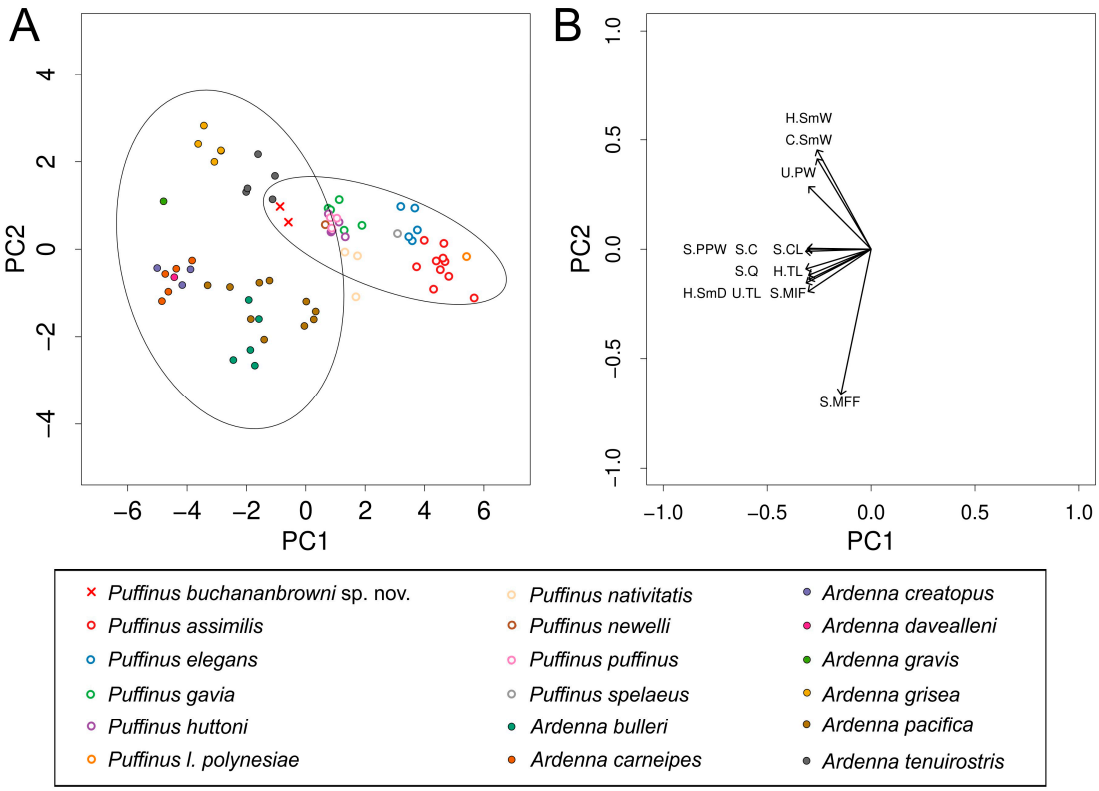

Figure 3. Results of principal component analysis of skeletal measurements of *Ardenna buchananbrowni* sp. nov., *Puffinus* spp., and *Ardena* spp. (see Supplementary File S1 for specimen list and measurements). (**A**) Biplot of first and second principal component scores, with 95% confidence ellipses for each genus. *A. buchananbrowni* sp. nov. is represented by red crosses; closed circles represent *Ardenna* spp., and open circles represent *Puffinus* spp. (each colour represents one species). (**B**) Projection of principal component vectors (loadings) of tested parameters on to PC1–PC2 biplot.

4. Discussion

In light of their morphology, supported by the PCA results, we parsimoniously interpret these fossils as a new diving species of *Ardenna*. Below, we provide more specific comparisons with other taxa and discuss the history of the group in New Zealand.

4.1. Convergent Evolution of Diving Adaptations

Puffinus and diving species of *Ardenna* convergently evolved a suite of adaptations for underwater propulsion, including flattened humeri, a shortened forewing, a stouter and more curved femur, and a more laterally compressed tarsometatarsus ([31] p. 254). *Ardenna buchananbrowni* sp. nov. shares many of these features and, thus, highlights the antiquity of this convergent trend.

Other potentially relevant characters in this context include the elongate sternum of the holotype, which recalls that of diving shearwaters [24,32]. Specifically, the ratio of its humerus to sternal keel lengths (84.4:69.1 = 1.22) falls within the range of *Puffinus* (1.17–1.28) and is only just below that of diving *Ardenna* (1.38–1.53), with the gliding species of *Ardenna* showing notably higher values (1.74–2.08) ([24] pp. 85–86). The sternal keel of the holotype also appears to protrude anteriorly just beyond the spina externa, as also only found in diving shearwaters and, especially, *Puffinus* ([24] pp. 108, 158); however, damage to the bone makes the exact extent of the projection hard to discern. Finally, our new fossils have a relatively thin beak and smooth nasal tubes that open more dorsally than in gliding species of *Ardenna*, but resemble those of *Puffinus* spp., *A. grisea*, and *A. tenuirostris* ([24] pp. 107, 128, 130).

4.2. Comparisons with Other Shearwater Fossils

The discovery of a third Pliocene species of *Ardenna* helps to elucidate the history of this genus. In the past, fossils of diving shearwaters have generally been assigned to *Puffinus*. Many of them are fragmentary, however, and were described when *Ardenna* was considered a junior synonym of *Puffinus* (e.g., [33]). As a result, the assignment of many *Puffinus* fossils should be considered tentative.

Two extinct species of shearwater have been described from New Zealand: *P. spelaeus* from the Holocene [34] and *A. davealleni* from the Pliocene [18]. Neither closely resembles *A. buchananbrowni* sp. nov., with *P. spelaeus* being notably smaller and *A. davealleni* being both notably larger and a gliding species (Table 1). A record of Pliocene '*Puffinus*' from near Taihape, from similarly aged deposits as those that yielded *A. buchananbrowni* sp. nov., remains unnamed [35].

Some southern shearwater species migrate between hemispheres in their non-breeding season (e.g., [25]) and have even been reported from northern archaeological deposits (e.g., [36–38]). As a result, and despite the vast distances involved, it is crucial to compare *A. buchananbrowni* sp. nov. to northern shearwater fossils.

Comparisons with *Puffinus raemdonckii* (van Beneden, 1871) from the early Oligocene of Belgium are hampered by the loss of the type material [10–12]. The lectotype is a c. 10 cm long humerus missing the proximal end [11,39], which is markedly longer than the humerus of *A. buchananbrowni* sp. nov. (80.2 mm).

Puffinus antiquus (Milne-Edwards, 1874) from the Middle Miocene of France is based on the proximal end of a humerus [40,41]. Its original description does not clearly distinguish this species from many other shearwaters, but suggests that the humerus is slightly stouter than that of the Cape petrel *Daption capense* (Linnaeus, 1758), which indicates that *P. antiquus* was slightly larger than *A. buchananbrowni* sp. nov. (see [42]). The far older age of *P. antiquus* also argues against close affinities with *A. buchananbrowni* sp. nov.

Several diving shearwaters with flattened humeri and/or tarsometatarsi are known from the Mio-Pliocene of the United States [43–46]. Among the latter, Early Miocene *Puffinus micraulax* Brodkorb, 1963 is smaller than *A. buchananbrowni* sp. nov.; it is only known from the coast of the Atlantic Ocean, and considerably predates the New Zealand fossil [12,42,47]. *Puffinus inceptor* Wetmore, 1930 from the Middle Miocene of California differs from *A.*

buchananbrowni sp. nov. in the distal position of its dorsal condyle on the humerus and open intercondylar furrow [44,48]. *P. inceptor* is probably also larger than *A. buchananbrowni* sp. nov. (see [42]). *Puffinus calhouni* Howard, 1968, *P. barnesi* Howard, 1978, *P. priscus* Miller, 1961, and *P. diatomicus* Miller, 1925 from the Late Miocene of California were described based on crushed or rather fragmentary material and are similar to *A. buchananbrowni* sp. nov. in size, but predate it [43–45,49–52]. *Puffinus mitchelli* Miller, 1961 and P. *felthami* Howard, 1949 from the Late Miocene and Early Pliocene of California are considerably larger than *A. buchananbrowni* sp. nov. [42,44,49]. *Puffinus kanakoffi* Howard, 1949 from the Late Pliocene of California has different humeral proportions to *A. buchananbrowni* sp. nov., with a humeral shaft width & depth of 5.3–5.7 & 3.3–3.7 mm versus 5.9–6.6 & 3.1–3.3 mm (Table 1; [45,49]). *Puffinus tedfordi* Howard, 1971 from the Early Pliocene of Mexico is only represented by partial tarsometatarsi and, thus, currently cannot be directly compared with *A. buchananbrowni* sp. nov. despite its potentially similar size [42,46]. *P. tedfordi* has, however, been noted for its unusually robust anatomy and, furthermore, still predates our material by about two million years [42]. Pending the discovery of further material, we, hence, consider these taxa to be different.

Puffinus nestori Alcover, 1989, *P. holeae* Walker, Wragg & Harrison, 1990, and *P. olsoni* McMinn, Jaune & Alcover, 1990 from the Pleistocene and Holocene of Spain all come from younger deposits than *P. buchananbrowni* sp. nov. [2,53–55]. Additionally, *P. nestori* and *P. holeae* are larger species than *P. buchananbrowni* sp. nov. [53,55], and *P. olsoni* is smaller than *P. buchananbrowni* sp. nov. [54]. Various other Miocene and Pliocene '*Puffinus*' remains have been described but not assigned to species (e.g., [14,15,17,31,45,50,52]).

All other extinct shearwaters clearly differ from *A. buchananbrowni* sp. nov. because they resemble either *Calonectris* or the gliding forms of *Ardenna* (see [18]). These fossils include *Calonectris kurodai* Olson, 2009 (Middle Miocene, Chesapeake Bay, east coast of USA), *C. krantzi* Olson and Rasmussen, 2001 (Early Pliocene, Lee Creek Mine, NC, USA), *C. wingatei* Olson, 2008 (Middle Pleistocene, Bermuda), *Ardenna conradi* (Marsh, 1870) (Middle Miocene, MD, USA), "*Puffinus*" *aquitanicus* Milne-Edwards, 1874 (Middle Miocene, France), *Ardenna gilmorei* (Chandler, 1990) (Late Pliocene, San Diego, CA, USA), and *Ardenna pacificoides* (Olson, 1975) (Pleistocene, Saint Helena).

4.3. Shearwater Evolution in Zealandia

New Zealand today is a centre of shearwater diversity with nine of a global total of 42 species breeding there [7]. Resident species include the wedge-tailed shearwater, *A. pacifica*; Buller's shearwater, *A. bulleri*; the sooty shearwater, *A. grisea*; the pale-footed shearwater, *A. carneipes*; the fluttering shearwater, *P. gavia*; Hutton's shearwater, *P. huttoni*; the little shearwater, *P. assimilis*; and the subantarctic little shearwater, *P. elegans* [8].

Ardenna davealleni and *A. buchananbrowni* sp. nov. from the Pliocene provide a glimpse of the past diversity of shearwaters in New Zealand and evince their relatively long history in the South Pacific. More broadly, they also add to earlier undescribed records of extinct southern shearwaters from South Africa and western South America [14–17].

Ardenna buchananbrowni sp. nov. is both the earliest diving member and one of the smallest representatives of the genus *Ardenna* (the smallest among the diving *Ardenna* spp.). Modern diving *Ardenna*—*A. grisea* and *A. tenuirostris*—are key members of the marine community and two of the most abundant seabirds globally [56]. The new species provides the first evidence that *Ardenna* shearwaters have had a diving form for at least 3 million years. Details about the evolution of *A. grisea* and *A. tenuirostris* remain poorly known, but the discovery of *A. buchananbrowni* sp. nov. either suggests that the living species evolved from a smaller diving ancestor or that diving *Ardenna* species were more diverse in the past. *Puffinus* and *Ardenna* are estimated to have diverged at least 10.4 million years ago based on molecular data [5] but fossils indicate that this divergence apparently occurred by the Middle Miocene [12,18,24,48]. Therefore, any Pliocene shearwater species should already be well differentiated into their respective genera.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/taxonomy4020012/s1, File S1: Data used and results from PCA analysis; measurements in mm. Abbreviations can be found in the Materials and Methods section of this paper; File S2. Comparative image of bone elements of three recent shearwater species.

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