

A new species of Pliocene shearwater (Aves: Procellariidae) from New Zealand

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ABSTRACT: We describe two partial but well-preserved Late Pliocene fossil skeletons from Taranaki, New Zealand, as a new species of seabird. In structure, these bones match those of a shearwater (Procellariiformes: Procellariidae) but the new taxon is distinguished from all known extant and extinct taxa by a unique combination of features. It was a gliding species as large as the largest species of extant shearwater. It represents the first pre-Pleistocene record of a new shearwater taxon from the western Pacific and helps reveal the history of shearwater evolution. Today, New Zealand has the greatest diversity of breeding shearwater species in the world, and the new fossil adds weight to other evidence that shearwaters have a long history in this region.

KEYWORDS: Procellariiformes, Procellariidae, shearwater, fossil, Pliocene, biogeography, New Zealand.

Introduction

Shearwaters are among the most diverse group of Procellariiformes (albatrosses, petrels, prions and shearwaters). Phylogenetic studies have found the shearwaters to be a monophyletic clade within the family Procellariidae (e.g. Heidrich *et al.* 1998; Nunn & Stanley 1998; Penhallurick & Wink 2004). Molecular studies suggest that the closest relative of the shearwater clade is the Kerguelen petrel *Lugensa brevirostris*, then successively more distantly the petrels *Procellaria*, *Bulweria* and *Pseudobulweria*, with other procellariid genera (prions *Pachyptila*, blue petrel *Halobaena caerulea*, the fulmars and the gadfly *Pterodroma* petrels) being even more distant (Nunn & Stanley 1998; Penhallurick & Wink 2004).

Within the shearwaters, there are three main clades: *Calonectris* (470–1060 g); all the other large shearwaters (320–950 g); and all the smaller (120–575 g) shearwaters (the Manx-group and little/Audubon's complex, as defined by Onley & Scofield 2007). *Calonectris* and all the smaller

shearwaters are sister taxa, and the other large shearwaters are sister to that clade (Austin 1996; Heidrich *et al.* 1998; Nunn & Stanley 1998; Austin *et al.* 2004; Penhallurick & Wink 2004; Onley & Scofield 2007).

The taxonomy of the shearwaters (Procellariidae) is controversial but we follow Dickinson and Remsen (2013), who recognised three genera: *Calonectris* for the streaked shearwater (*C. leucomelas*) and the Scopoli's shearwater (*C. diomedea* clade); *Ardenna* for all the other larger taxa – wedge-tailed shearwater (*A. pacifica*), Buller's shearwater (*A. bulleri*), pink-footed shearwater (*A. creatopus*), flesh-footed shearwater (*A. carneipes*), great shearwater (*A. gravis*), sooty shearwater (*A. grisea*) and short-tailed shearwater (*A. tenuirostris*); and *Puffinus* for the smaller taxa. Kuroda's (1954) pioneering work on shearwater relationships recognised *Calonectris* as distinct and placed all other species in the genus *Puffinus*, which he then divided into subgenera: *P. pacificus* and *P. bulleri* in *Thyellodroma*; *P. creatopus* and *P. carneipes* in *Hemipuffinus*;

P. gravis and the extinct *P. conradi* in *Ardenna*; *P. griseus*, *P. tenuirostris* and the Christmas shearwater (*P. nativitatis*) in ‘*Puffinus Neonectris*’; and all the smaller taxa in ‘*Puffinus Puffinus*’. Using a molecular phylogenetic analysis, Austin (1996) concluded that the *Puffinus* taxa of Kuroda fell into two distinct clades: all the larger taxa and all the smaller taxa (including *P. nativitatis*, which had previously been linked with *P. griseus* and *P. tenuirostris*). Using further DNA analysis, Heidrich *et al.* (1998) concluded that the two clades identified by Austin were not sister taxa, therefore supporting the conclusion that all three shearwater clades should be afforded generic rank.

Olson and Rasmussen (2001: 254) noted that ‘the species of shearwaters are marked by a progression from a primitive, aerially adapted condition (*Calonectris*) to increasing use of both the wings and feet for underwater propulsion ... in which the humerus becomes flattened, the forewing shortened ... the femur stouter and more curved ... and the tarsometatarsus more laterally compressed’. They considered that this progression was from *Calonectris* to the group containing *Ardenna pacifica*, *A. bulleri*, *A. creatopus* and *A. carneipes*, then to *A. gravis*, then to the *Puffinus* taxa.

Although New Zealand today is the centre of diversity for shearwaters, with nine (of a worldwide total of 42) breeding taxa (Dickinson & Remsen 2013), the pre-Late Pleistocene fossil record of Procellariiformes, including shearwaters, in the entire western Pacific is minimal (Warheit 2002; Henderson & Gill 2010; Worthy & Tennyson 2010). The discovery of pre-Late Pleistocene fossil procellariiform specimens in New Zealand can, therefore, add significant new knowledge about the history of this group.

New Zealand has one of the best fossil records worldwide for birds for the Late Pleistocene–Holocene (Worthy & Holdaway 2002). However, the pre-Late Pleistocene avian fossil record is poor, apart from penguin fossils and those from an Early Miocene lacustrine site in Otago (e.g. Simpson 1975; Fleming 1979: 75; Fordyce 1991; Worthy *et al.* 2007; Henderson & Gill 2010; Worthy & Tennyson 2010; Ksepka *et al.* 2012; Mayr *et al.* 2017).

The few pre-Late Pleistocene non-penguin New Zealand seabirds reported include: the Paleocene *Australornis lovei* described by Mayr & Scofield (2014); a Paleocene tropicbird described by Mayr & Scofield (2015); a fragmentary furcula of uncertain relationships named *Manu antiquus* from the Middle to Late Oligocene (see Worthy & Tennyson 2010); the Early Miocene diving petrel *Pelecanoides miokuaka* described by Worthy *et al.* (2007); an indeterminate Middle Miocene diving petrel (Scofield *et al.* 2006); two

pelagornithid taxa, possibly *Pelagornis miocaenus* from the Middle to Late Miocene (Scarlett 1972; Harrison & Walker 1976) and *Neodontornis stirtoni* from the Early Miocene to Pliocene (Howard & Warter 1969); another Pliocene pelagornithid of unclear affinities (McKee 1985); and a mid-Pliocene shearwater skull, also of uncertain affinities (Henderson & Gill 2010). Additionally, a tarsometatarsus from the Late Cretaceous or Early Paleocene may be from a seabird (Ksepka & Cracraft 2008).

The few seabirds described from the Pliocene of Taranaki, New Zealand, are the pelagornithid of unclear affinities mentioned above and a penguin (McKee 1988), although mention has been made of several others being found, including shearwaters (see McKee 1994; Henderson & Gill 2010; Worthy & Tennyson 2010: 331).

Many fossil species of procellariiform have been named and the most speciose clade of extinct taxa is the shearwaters (Warham 1996; Warheit 2002). Pre-Pleistocene shearwater fossils are widely distributed, but are found mainly in Miocene and Pliocene North Atlantic and North Pacific coastal deposits (Warheit 2002). Shearwater fossils of this age are surprisingly rare in the southern hemisphere, consisting of a range of modern or unidentified taxa from South Africa (Olson 1985a,b), the western South American coast (Hoffmeister *et al.* 2014) and the various unidentified fossils from New Zealand (see above). The earliest fossil species of shearwater globally is *Puffinus raemdonckii* (van Beneden, 1871) from the Early Oligocene of Belgium, however its true affinities are uncertain (van Beneden 1871; Brodkorb 1962; Olson 1985c; Mayr & Smith 2012). Several fossil species of shearwater are known from the Miocene through to the Holocene, with the earliest of these being *Puffinus micraulax* Brodkorb, 1963, from the Early Miocene of South Carolina, USA (Brodkorb 1963a).

Here we report on significant new shearwater fossils from the Pliocene of Taranaki, and compare them with all living and extinct shearwater taxa.

Methods

Dave Allen collected one of the fossils in an Upper Pliocene concretion at Ohawe Beach, south Taranaki, in 2006. The specimen was found by splitting a mudstone concretion in half with a sledgehammer. Unfortunately, the counterpart of the concretion was not collected and it is unknown if there were further bones in it. Allen and Craig (then of the Institute of Geological and Nuclear Sciences) roughly prepared the specimen, with final preparation work by Al Mannering.

A second specimen was found in 2011 by Xavier Johnson, by splitting a concretion at Waihi Beach, about 1 km southeast of the first specimen, in similarly aged rocks (e.g. McKee 1985, 1988, 1994). Initial preparation was carried out by Alastair Johnson and it was completed by Al Mannering.

The relevant morphological characters of the new Taranaki specimens were compared with representatives of all procellariiform families and all key species within Procellariidae. Key references containing morphological characters were Chandler (1990), Kuroda (1953, 1954, 1955), Olson (2008, 2009) and Olson & Rasmussen (2001). Important species of procellariid not directly compared were Scopoli's shearwater (*Calonectris diomedea*) and Cape Verde shearwater (*C. edwardsii*), which were not available to us but are considered to be closely related to Cory's shearwater (*C. borealis*) (e.g. Olson 2008). We did not compare every species in the small-bodied shearwater clades because initial comparisons showed little similarity between these groups and the Taranaki fossil. Also, comparison was made with the extinct Late Miocene Mediterranean genus and species of the procellariid *Pterodromoides minoricensis* based on the description by Seguí *et al.* (2001).

Osteological terms are based on the work of Baumel and Witmer (1993) and Livezey and Zusi (2006); p = proximal, d = distal, L = left, R = right. Measurements were taken in millimetres (mm) using Vernier callipers. The primary comparative specimens used are listed in the Appendices. All are part of the Museum of New Zealand Te Papa Tongarewa (Te Papa) collection (NMNZ, including specimens with 'S' and 'OR' prefixes).

Systematic Palaeontology

Order PROCELLARIIFORMES

Family PROCELLARIIDAE

Leach, 1820

Ardenna Reichenbach, 1853

TYPE SPECIES: *Ardenna gravis* (O'Reilly, 1818)

Ardenna davealleni Tennyson & Mannering, sp. nov

Holotype: NMNZ S.45183: Partial skeleton (Fig. 1), collected by D. Allen, 8 October 2006.

DESCRIPTION OF HOLOTYPE: See Fig. 1 and Appendices 1 and 3. The specimen is a well-preserved individual, which was fossilised with some disturbance to the skeleton before burial, such that several key bones have been lost. It preserves 14

recognisable elements – one vertebra; pL humerus; most of the R humerus, although the shaft is damaged near the proximal end so an accurate length measurement could not be obtained; complete L ulna; most of the R ulna; most of both radii; complete L carpometacarpus; dR carpometacarpus; complete L manus phalanx p digitus major; complete L femur; pR femur; pL tarsometatarsus; dR tarsometatarsus – and four unidentified small fragments. Most bones are partially obscured because of the way they are lying or because other bones lie on top of them, and early preparation involved a roughly applied consolidant, which obscured some bone features and could not be removed by Mannering. The specimen lacks the skull, all but one vertebrae, all pectoral and pelvic elements, the outermost wing bones, both tibiotarsi and all but one of the phalanges. The specimen is osteologically mature, showing the degree of bone fusion expected in an adult.

Humerus (proximal end) with caput humeri undercut and overhanging the fossa pneumotricipitalis dorsalis slightly; capital shaft ridge extends to caput humeri; no tubercle on the cranial surface of the ventral margin of the bicapital area; crista deltopectoralis rounded in dorsal profile.

Humerus shaft with rounded cross section (rather than dorsoventrally flattened), with ratio of central shaft width to depth of 1.3. Distal end of the humerus, processus supracondylaris dorsalis (= ectepicondylar process) moderately sized; fossa m. brachialis medium depth. Ulna (proximal end), caudal surface of the shaft forms a prominent and continuous ridge to the tip of the proximal end. Femur shaft in medial view fairly curved (arched dorsally).

HOLOTYPE LOCALITY AND AGE: Ohawe Beach, south Taranaki, New Zealand (39°35.72' S, 174°12.90' E); Waipipian (3.0–3.6 Ma, Late Pliocene). (FR Number Q21/F0175.) Mollusc fossils in the concretion were identified as *Dosinia* sp. cf. *D. lambata* and *Maorimactra* sp. cf. *M. ordinaria* (B. Marshall, pers. comm., 2014). *Dosinia lambata* has a currently accepted age as ranging from Duntroonian (Late Oligocene) to Holocene, and *M. ordinaria* is also extant and its fossils are found as far back as the Opoitian (Pliocene) (B. Marshall, pers. comm., 2014). These age ranges are consistent with the Waipipian (Pliocene) age previously attributed to these deposits (e.g. McKee 1985, 1988, 1994). Minimum storm base wave depth indicates that the fossil bird's depositional water depth may have been 50 m or more (Peters & Loss 2012) in order for the skeleton to have remained partly intact. However, the presence of some of the mollusc species in 'life position' suggests a shallower depth, as

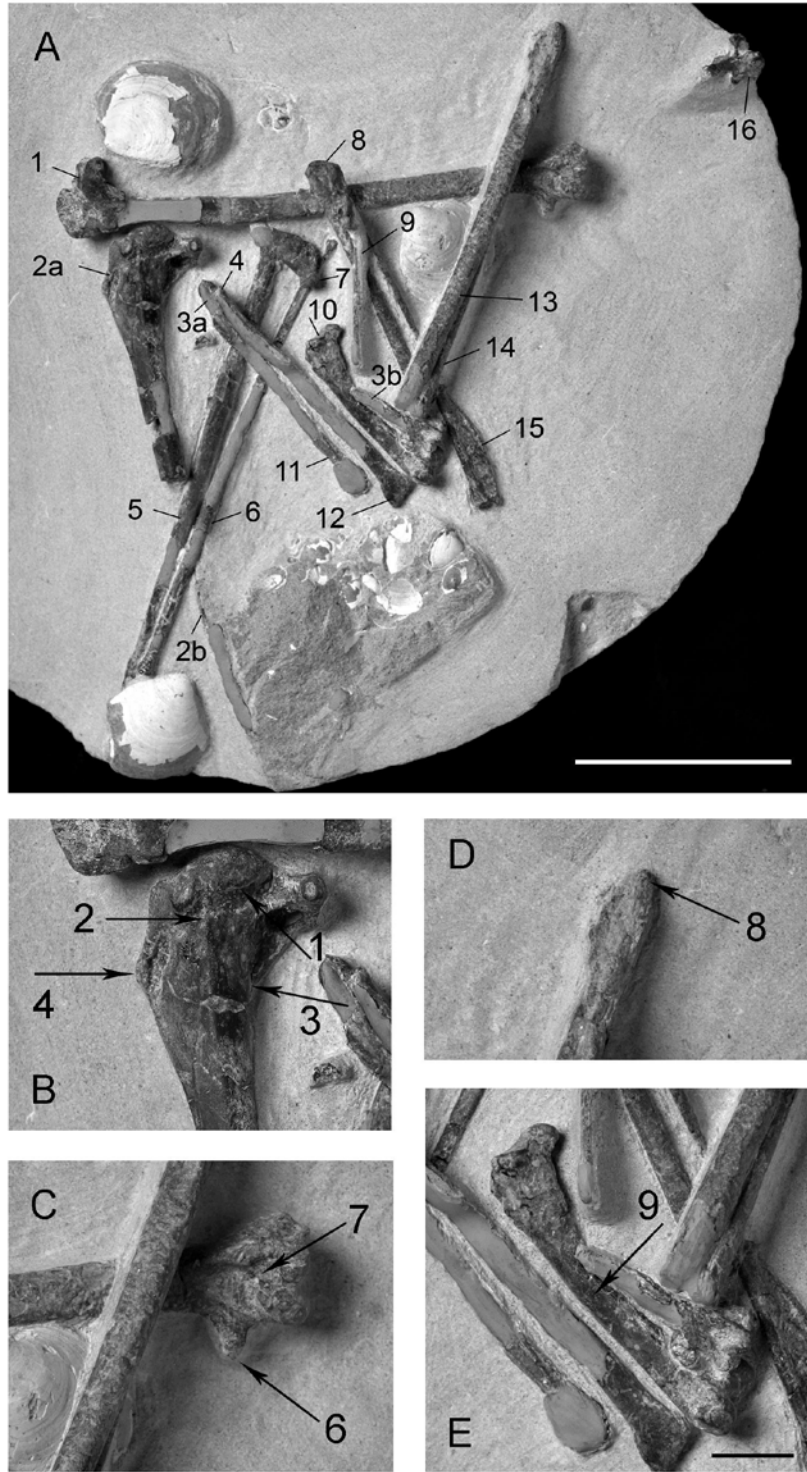


Fig. 1 Pliocene fossil shearwater *Ardenna davealleni* n. sp. holotype NMNZ S.45183. A, general view of the entire fossil: 1, right humerus; 2a, proximal end of the left humerus; 2b, distal end of the left humerus; 3a, distal end of the right tibiotarsus; 3b, ?Proximal end of the right tibiotarsus; 4, unidentified fragment; 5, left ulna; 6, left radius; 7, proximal end of the right femur; 8, left carpometacarpus; 9, distal end of the right carpometacarpus; 10, left femur; 11, unidentified fragment; 12, proximal end of the left tarsometatarsus; 13, right ulna, missing the distal end; 14, right radius; 15, left manus phalanx proximal digitus major; 16, vertebra. Scale bar is 5 cm. B, detailed view of the proximal end of the left humerus, showing Appendix 2 characters 1, 2, 3 and 4; character 3 is on the cranial surface of the bone at the arrowed point. C, detailed view of the distal end of the right humerus, showing Appendix 2 characters 6 and 7. D, detailed view of the proximal end of the right ulna, showing Appendix 2 character 8. E, detailed view of left femur, showing Appendix 2 character 9. Scale bar in B–E is 1 cm.

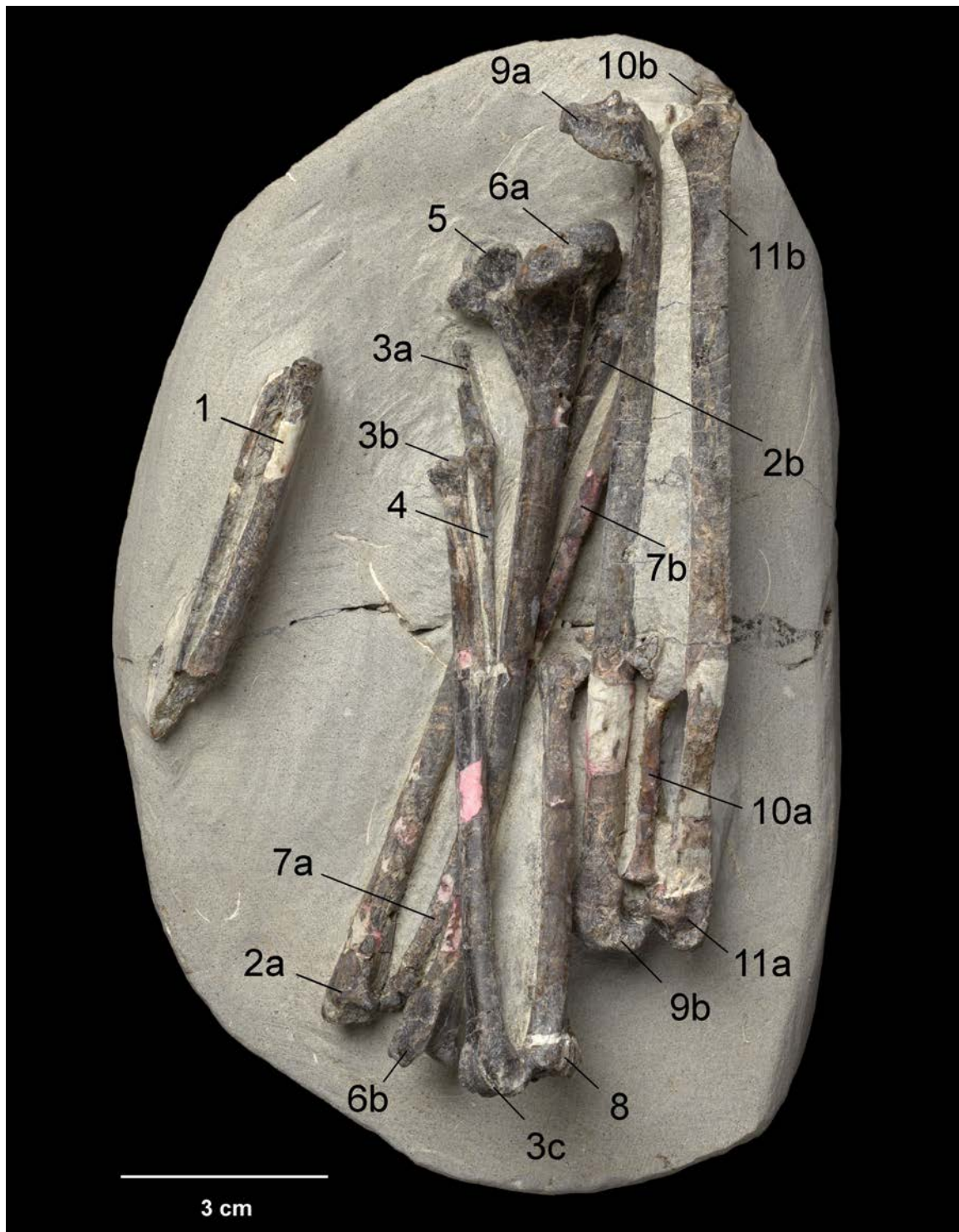


Fig. 2 Pliocene fossil shearwater *Ardenna davealleni* n. sp. paratype NMNZ S.46316. 1, left carpometacarpus; 2a, proximal end of the right ulna; 2b, distal end of the right ulna; 3a, cnemial crest of the proximal end of the right tibiotarsus; 3b, proximal end of the right tibiotarsus; 3c, distal end of the right tibiotarsus; 4, right fibula; 5, proximal end of the right carpometacarpus; 6a, proximal end of the right humerus; 6b, distal end of the right humerus; 7a, proximal end of the right radius; 7b, shaft of right radius; 8, left tarsometatarsus; 9a, proximal end of the left humerus; 9b, distal end of the left humerus; 10a, proximal end of the left radius; 10b, distal end of the left radius; 11a, proximal end of the left ulna; 11b, distal end of the left ulna.

specimens in the Te Papa collection (n = 185 'lots' for both mollusc species combined) were collected live between 4 m and 48 m (B. Marshall, pers. comm., 2015; see also McKee 1994).

ETYMOLOGY: The species name honours Dave Allen of New Plymouth, the collector and donor of the holotype.

SUGGESTED ENGLISH VERNACULAR NAME: Pom's shearwater, as requested by Dave 'Pom' Allen.

PARATYPE: NMNZ S.46316: Partial skeleton (Fig. 2), collected by X. Johnson, 6 June 2011.

DESCRIPTION OF PARATYPE: See Fig. 2 and Appendices 1, 3 and 4. This specimen is also a well-preserved individual, with 11 recognisable (mostly complete) elements: L humerus, missing the very proximal end; R humerus; both ulnae; both radii; L carpometacarpus, missing the proximal end; R carpometacarpus, with the distal end still embedded in matrix; R tibiotarsus; R fibula; and R tarsometatarsus. The specimen is osteologically mature and has the same morphological features described for the humeri and ulnae of the holotype. The relatively short cnemial crest of the tibiotarsus and the relatively laterally broad tarsometatarsus are consistent with that seen in some other species of *Ardenna*. As for the holotype, the partially intact skeleton indicates that the bird's remains were originally deposited in water 50 m deep or more, although deposition was possibly shallower than this (see above). This skeleton is from a bird very similar in size to the holotype.

PARATYPE LOCALITY AND AGE: Waihi Beach, south Taranaki, New Zealand (39°36.10' S, 174°14.05' E); Waipipian (3.0–3.6 Ma, Late Pliocene; McKee 1985, 1988, 1994).

MEASUREMENTS AND RATIOS OF HOLOTYPE AND PARATYPE BONES: See Appendices 3 and 4.

Diagnosis

The fossils are referred to the genus *Ardenna*. Compared with species of *Puffinus*, the humerus of the fossil species has a rounded shaft (rather than dorsoventrally flattened), a deeper fossa brachialis and a less proximally angled processus supracondylaris dorsalis, a larger ulna to carpometacarpus length ratio, a straighter femur shaft, and a relatively shorter cnemial crest on the tibiotarsus. Compared with species of *Calonectris*, the humerus of the fossil species has a more rounded profile to the crista deltopectoralis and a smaller

processus supracondylaris dorsalis, a larger humerus to ulna length ratio, a smaller ulna to carpometacarpus length ratio, a smaller ulna to manus phalanx p digitus major length ratio, and a longer cnemial crest.

The fossil species differs from all other species in the genus *Ardenna* by having a smaller ulna to manus phalanx p digitus major length ratio. It differs from *A. grisea* and *A. tenuirostris* in having a rounded humeral shaft, a deeper fossa brachialis, a relatively straighter femur shaft, a relatively shorter cnemial crest, and a less laterally flattened tarsometatarsus. The relative length of the cnemial crest is intermediate between that found in most species of *Ardenna* and that of *A. grisea* and *A. tenuirostris*. The species differs from *A. carneipes*, *A. creatopus* and *A. gravis* in having a more rounded crista deltopectoralis, and a smaller processus supracondylaris dorsalis. It differs from *A. pacifica*, *A. bulleri*, *A. carneipes* and *A. creatopus* in having a higher humerus to ulna length ratio. It differs from *A. pacifica*, *A. bulleri*, *A. carneipes*, *A. creatopus* and *A. gravis* in having lower ulna to carpometacarpus and ulna to femur length ratios, and in having a relatively longer cnemial crest. It differs from *A. bulleri* in having a less undercut caput humeri. It shares most characters with *A. bulleri*, but it is substantially larger than that species and is larger than all members of the genus except *A. gravis*. Its wing and leg bones are in the range of 14–24% longer than those of *A. bulleri*. It differs from fossil taxa of *Ardenna* primarily by a combination of size, proportions and age.

Further comparisons with living procellariiform taxa

See Figs 1 and 2 and Appendices 1, 3 and 4.

Using an analysis of some key characters, all procellariiform families and all other procellariid genera can be differentiated from all shearwaters by a range of morphological features (see Appendix 1). For example, shearwaters differ from all other procellariid genera by having a shallower fossa brachialis on the humerus. Aside from *Daption*, *Pagodroma*, *Bulweria* and *Pseudobulweria*, all other procellariid genera differ from shearwaters by having a raised tubercle on the cranial surface of the ventral margin of the bicipital area of the humerus. Additionally, fulmars do not have such ventrally prominent crista medialis hypotarsi on the tarsometatarsus and, while

shearwaters and many other procellariiforms have ventrally fused cristae hypotarsi, other genera – such as *Thalassoica*, *Lugensa* and *Pterodroma* – show no such fusion, with albatrosses having the most extreme condition, whereby the cristae hypotarsi remain widely separated. Furthermore, only some shearwaters and *Pagodroma* have a similarly rounded angle (point) to the crista deltopectoralis on the humerus as found in *Ardenna davealleni*, and *A. davealleni* differs from procellariid genera (other than some shearwaters) by having a fairly curved femur shaft.

Ardenna davealleni is one of the largest species of shearwater known. Based on *A. davealleni* having a femur of overall similar size to that of the gliding *Calonectris borealis*, we estimate that the species had a similar weight to the latter (see Campbell & Marcus 1992), which is about 605–1060 g (see Marchant & Higgins 1990; Onley & Scofield 2007). In comparison, *A. bulleri* weighs about 385–490 g (Marchant & Higgins 1990; Onley & Scofield 2007), which is only half the weight of *C. borealis*. It should be noted that shearwaters exhibit only very limited sexual size dimorphism, with males being larger on average (Marchant & Higgins 1990; Warham 1990).

Within the shearwaters, *Puffinus* species differ from species of *Calonectris* and most species of *Ardenna* in having a dorsoventrally flatter humeral shaft and a shallower fossa brachialis on the humerus. *Puffinus* species differ from other shearwaters in having a smaller processus supracondylaris dorsalis on the humerus. *Calonectris* and *Ardenna* have a larger ulna to carpometacarpus length ratio than *Puffinus*. Walker *et al.* (1990) found a similar relationship, where diving shearwater species had relatively longer outer wing bones. *Calonectris* species differ from species of *Ardenna* and *Puffinus* in having a straighter femur shaft. Additionally, *Calonectris* and *Ardenna* are all larger than taxa of *Puffinus*. The extant *C. diomedea* and extinct *C. wingatei* are similar in size to *A. davealleni*, whereas the extant *C. edwardsii* and extinct *C. kurodai* are smaller than *A. davealleni* (see Olson 2008, 2009).

In conclusion, *Ardenna davealleni* shares most features with the species of *Ardenna* evolved for gliding (*A. pacifica*, *A. bulleri*, *A. carneipes*, *A. creatopus*, *A. gravis*). *Ardenna davealleni* differs from living shearwater taxa that are the most accomplished diving species, i.e. the clade of small taxa (*Puffinus*) and *A. grisea* and *A. tenuirostris* (e.g. see Appendix 4), in having a rounded humeral shaft, a deeper fossa brachialis, a relatively straighter femur shaft, and a relatively shorter cnemial crest on the tibiotarsus.

Detailed comparisons with fossil shearwater taxa

For fossil shearwater taxa, Olson (2009: 468) concluded that *Puffinus micraulax* Brodkorb, 1963 (Early Miocene, South Carolina, USA), *P. inceptor* Wetmore, 1930 (Middle Miocene, California, USA), *P. calhouni* Howard, 1968 (Late Miocene, California), *P. barnesi* Howard, 1978 (Late Miocene, California), *P. felthami* Howard, 1949 (Early Pliocene, California), *P. kanakoffi* Howard, 1949 (Late Pliocene, California), *P. priscus* Miller, 1961 (Late Miocene, California) and *P. mitchelli* Miller, 1961 (Late Miocene, California) all belonged to ‘the more derived species of the genus *Puffinus*’ owing to their relatively flattened humerus. Using the taxonomy adopted in this paper, Olson’s definition would include species of *Puffinus*, together with *Ardenna grisea* and *A. tenuirostris* – all clearly separable from *A. davealleni*, which has a rounded humeral shaft (see Appendix 1). The humerus of *P. diatomicus* Miller, 1925 (Late Miocene, California) has a ‘flat shaft’ also (see Miller 1925). *Puffinus tedfordi* Howard, 1971 (Early Pliocene, Mexico) belongs to this diving group also based on its laterally flattened tarsometatarsus (Olson 2009). Miller (1961) and Chandler (1990: table 7) detailed the high degree of flattening in the humeri of *P. inceptor*, *P. calhouni*, *P. barnesi*, *P. felthami*, *P. kanakoffi*, *P. priscus* and *P. mitchelli*. Miller (1961) noted additionally that *P. inceptor* had features on the distal end of the humerus – the distal position of the dorsal condyle and the open intercondylar furrow – that set it aside from all other species of shearwater. *Ardenna davealleni* differs from *P. inceptor* in this way also.

Puffinus nestori Alcover, 1989 (Late Pleistocene, Pityusae Islands, Spain), *P. holeae* Walker, Wragg & Harrison, 1990 (Late Pleistocene, Canary Islands, Spain) and *P. olsoni* McMinn, Jaune & Alcover, 1990 (Holocene, Canary Islands) are all part of *Puffinus* (Heidrich *et al.* 1998), as defined in this paper, so are not closely related to *Ardenna davealleni*. *Puffinus spelaeus* Holdaway & Worthy, 1994, from the Holocene of New Zealand, differs substantially from *A. davealleni* as it is a close relative of *P. gavia* (see Tennyson & Shepherd 2017).

Puffinus conradi Marsh, 1870 (Middle Miocene, Maryland, USA) is in the subgenus *Ardenna* as a close relative of *A. gravis* (Wetmore 1926; Kuroda 1954: 114; Olson 1985c, 2009), therefore we refer it to the genus *Ardenna* following the taxonomy used in this paper. *Ardenna conradi* could, therefore, be a close relative of *A. davealleni*. Unfortunately, *A. conradi*

is known by only the ‘distal two-fifths of a left humerus’ (Wetmore 1926). Nevertheless, *A. conradi* differs from *A. davealleni* in having only a ‘slight’ processus supracondylaris dorsalis (Wetmore 1926), whereas *A. davealleni* has a moderately sized process (see Appendix 1). In fact, the broader ectepicondylar region of *A. conradi* is less developed than in *A. gravis* (see Wetmore 1926), yet this region of *A. davealleni* closely resembles that of *A. gravis*. The dorsoventral width of the distal end of the *A. conradi* holotype measures 13.4 mm (Wetmore 1926), so it is narrower than that of *A. davealleni* at 14.2 mm, yet the dorsoventral diameter of the shaft of the *A. conradi* holotype at the ‘upper end’ measures 7.1 mm (Wetmore 1926), which is similar to the mid-shaft width of *A. davealleni*, at 7.0 mm. This indicates a proportional shape difference between the species. The greater age of *A. conradi* and its location on the Atlantic Ocean also argue against it and *A. davealleni* being conspecific.

Puffinus aquitanicus (Milne-Edwards, 1874) (Middle Miocene, France) is based on a damaged humerus (Milne-Edwards 1874) that was initially considered similar to *Calonectris borealis* or *Fulmarus* (according to Kuroda 1954: 114; see Tennyson 2010 for an explanation of the current names for these taxa), but it has a more elongated fossa brachialis than that found in *Calonectris* and a stouter shaft (Olson 2009). *Puffinus aquitanicus* is somewhat smaller than *Ardenna davealleni*, having an estimated total humeral length of *c.* 112 mm, shaft depth of 4.5 mm, shaft width of 5.5 mm and distal breadth of *c.* 12 mm (estimated here) (Milne-Edwards 1874). This compares with 121.4 mm, 5.6 mm, 7.0 mm and 14.2 mm, respectively, for *A. davealleni*. The true affinities of *P. aquitanicus* remain unresolved, but its size, age and European location argue against it being conspecific with *A. davealleni*.

A second shearwater species named from the same location in the same article, *Puffinus antiquus* (Milne-Edwards, 1874) (Middle Miocene, France), is based on the proximal end of a humerus (Milne-Edwards 1874; Brodkorb 1963b). Milne-Edwards’s description (1874) does not clearly distinguish this species from many other shearwaters, but he considered the humerus to be only slightly stouter than that of a Cape petrel (*Daption capense*), yet the humerus of *Ardenna davealleni* is considerably larger than that of a Cape petrel. The size, European location and older age of *Puffinus antiquus* argue against it being closely related to *A. davealleni*.

According to Olson (2009), *Puffinus gilmorei* Chandler, 1990 (Late Pliocene, California) was correctly assigned by

Chandler (1990) to the ‘subgenus *Thyellodroma*’ (i.e. sister taxon to *Ardenna pacifica* and *A. bulleri*). Therefore, we assign *P. gilmorei* to *Ardenna* following the taxonomy used in this paper. Chandler (1990) noted that *A. gilmorei* differed from *A. pacifica*, *A. bulleri* and *A. carneipes* in having a more broadly undercut surface below the humeral head, but the shape of this surface in *A. davealleni* is similar to that in *A. pacifica* and *A. carneipes*. *Ardenna gilmorei* is considerably smaller than *A. davealleni*, having a humerus 96.7 mm long, a humerus shaft 3.8 mm deep × 5.6 mm wide, a humeral distal breadth of 8.1 mm and a humeral width at the processus supracondylaris dorsalis of 10.1 mm (Chandler 1990), compared with 121.8 mm, 5.6 mm, 7.0 mm, 14.2 mm and 13.4 mm, respectively, for *A. davealleni*. The femur of *A. gilmorei* is similarly small: length 35.1 mm, proximal breadth 7.5 mm, shaft depth 3.3 mm, shaft width 3.3 mm and distal breadth 7.2 mm (Chandler 1990). This compares with *A. davealleni* measurements of 44.1 mm, 10.2 mm, *c.* 4.5 mm, *c.* 4.4 mm and 10.7 mm, respectively. Therefore, *A. gilmorei* is a similar size to *A. bulleri* (see Appendix 3) and we conclude that it and *A. davealleni* are not conspecific.

Puffinus pacificoides Olson, 1975 (Pleistocene, St Helena) ‘belongs to the *pacificus-bulleri* species group’ (Olson 1975). *Puffinus pacificoides* should, therefore, be attributed to *Ardenna* using the taxonomy followed in this paper. Measurements for *A. pacificoides* femora are: length 32.8–36.3 mm, proximal breadth 8.0–8.7 mm, shaft width 3.5 mm and distal breadth 7.8 mm (Olson 1975). This compares with measurements for *A. davealleni* of 44.1 mm, 10.2 mm, *c.* 4.4 mm and 10.7 mm, respectively. Therefore, *A. pacificoides* was a substantially smaller bird than *A. davealleni* (see Appendix 3). Olson noted that the femur of *A. pacificoides* differs from that of *A. pacifica* and *A. bulleri* by having a much more pronounced trochanteric ridge, which is longer and bulges out further laterally. Also, the head of the femur is distinctly flatter and less bulbous in *A. pacificoides* (see Olson 1975). In *A. davealleni*, the femora are partly obscured in the surrounding matrix, but the femoral shape appears to be very similar to that in *A. pacifica* and *A. bulleri*. Similarly, Olson notes a range of features of the tarsometatarsus of *A. pacificoides* that differ from those found in *A. pacifica* and *A. bulleri*. *Ardenna davealleni* differs from *A. pacificoides* in these tarsometatarsus features, being more similar to all living *Ardenna* species. The humeral condyles of *A. pacificoides* were considered more delicate than those of *A. bulleri* and more similar to those of *A.*

pacifica (see Olson 1975). In size, the humeral condyles of *A. davealleni* resemble those of *A. bulleri* more closely than those of *A. pacifica*. The humeral shaft of *A. davealleni* is stouter than that in *A. bulleri*, and in this way more closely resembles the humerus of *A. pacifica* and *A. pacificoides* (see Olson 1975). Since the initial description, fossils of a species similar to *A. pacificoides* have been reported from an Early Pliocene deposit in North Carolina (Olson & Rasmussen 2001).

Finally, comparisons with *Puffinus raemdonckii* (van Beneden, 1871) of the Early Oligocene of Belgium are hampered by the fact that the type material has apparently been lost, and so the true relationships between the species and *Ardenna davealleni* remain unclear (Brodkorb 1962; Olson 1985c; Mayr & Smith 2012). However, the lectotype of the species is a c. 10 cm long humerus (missing the proximal end) (van Beneden 1871; Brodkorb 1962), which is smaller than the humerus of *A. davealleni*. In addition, the much greater age of *P. raemdonckii* argues against it being closely related to *A. davealleni*.

Various other Miocene and Pliocene '*Puffinus*' remains have been noted in the literature but not assigned to a taxon (e.g. Howard 1968; Olson 1985a,b; Howard & Barnes 1987; Chandler 1990; Olson & Rasmussen 2001; Hoffmeister *et al.* 2014). The only described Pliocene New Zealand shearwater (a skull) is from a slightly older deposit than the Taranaki fossil and is from a smaller species, closer in size to *Ardenna pacifica*, but its true generic affinities remain undetermined (Henderson & Gill 2010).

Note that the Late Miocene *Pterodromoides minoricensis* is considerably smaller than *Ardenna davealleni* and has cranial, coracoid and humeral features most similar to those of fulmarine petrels. Therefore, it is not closely related to shearwaters (Seguí *et al.* 2001).

In summary, many fossil shearwater taxa align with the genus *Puffinus* rather than *Ardenna*, owing to their relatively flattened humerus or their particularly laterally flattened tarsometatarsus, so are not closely related to *A. davealleni*. Other fossil shearwater species differ from *A. davealleni* primarily through a combination of differences in humeral shape and size, and the fact that they occur in different eras.

Discussion

The discovery of a new species of *Ardenna* shearwater from the Pliocene adds important new knowledge about the history of this group. Although a few Pliocene shearwaters have been described before (*Puffinus tedfordi*, *P. felthami*, *P. kanakoffi* and *A. gilmorei*), all were found in the eastern Pacific (Howard 1949, 1971; Chandler 1990). While New Zealand today is the worldwide centre of diversity for species of shearwater (Dickinson & Remsen 2013), *A. davealleni* provides the only clear record of a shearwater genus for the region prior to the Late Pleistocene (Tennyson 2010) and demonstrates a long history for the genus in the western Pacific. Many southern hemisphere shearwater species migrate to the northern hemisphere in their non-breeding season (e.g. Marchant & Higgins 1990), so it is possible that northern hemisphere fossils represent such migrants (e.g. the southern nesting *A. grisea* has been reported from an English archaeological deposit; Harrison 1980).

Ardenna davealleni was a large species, structurally most similar to the much smaller *A. bulleri*, which breeds only in New Zealand (Marchant & Higgins 1990). It is possible that *A. davealleni* is an ancestral form of this extant species. Based on the behaviour of *A. bulleri* and its close relatives, *A. davealleni* was presumably more of a gliding species than a diving bird.

Using a molecular clock, Penhallurick and Wink (2004) considered that *Calonectris* shearwaters separated from other shearwater clades c. 13.8 million years ago, and that *Puffinus* and *Ardenna* diverged c. 10.4 million years ago. Gómez-Díaz *et al.* (2006) considered the *Calonectris* and '*Puffinus*' shearwaters to have separated 9 million years ago, but Olson (2009) noted that this may simply reflect the oldest divergence between the crown clades because the oldest '*Puffinus*' fossil is Oligocene and the oldest *Calonectris* fossil is Middle Miocene. Our finding of a Pliocene *Ardenna* shearwater (combined with the Californian Pliocene record of *A. gilmorei*), well differentiated from species of *Calonectris* and *Puffinus*, adds weight to the theory of an early divergence of the three shearwater genera.

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Nomenclatural act

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 the taxon in this publication is <http://zoobank.org/urn:lsid:zoobank.org:act:3F25CA99-540F-41E5-AD3B-DA533EC2E6C2>.

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Appendix 1: Data matrix of scored morphological characters of Procellariiformes as described in Appendix 2

Species	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Ardenna davealleni</i> n. sp. S.45183 and S.46316	1	1	1	1	0	2	1	1	2	1	2	2	3	4
<i>Phoebastria</i> , e.g. <i>P. immutabilis</i>	0	0	0	2	0	2	2	0	0	1	5	5	5	5
<i>Macronectes</i> , e.g. <i>M. halli</i>	1	1	0	2	0	2	0	0	0	2	4	4	3	5
<i>Fulmarus</i> , e.g. <i>F. glacialisoides</i>	2	1	0	2	0	2	0	0	0	1	3	2	2	4
<i>Thalassoica antarctica</i>	2	1	0	2	0	2	0	0	1	1	3	2	1	3
<i>Daption capense</i>	2	1	1	2	0	2	0	1	1	1	3	2	2	3
<i>Pagodroma nivea</i>	2	1	1	1	0	2	0	0	1	2	2	2	1	3
<i>Lugensa brevirostris</i>	2	2	0	3	0	2	0	1	1	0	3	3	3	3
<i>Pterodroma</i> , e.g. <i>Pt. macroptera</i>	2	0	0	2	0	3	0	1	1	0	3	3	3	2–4
<i>Halobaena caerulea</i>	2	0	0	2	0	2	0	1	1	1	2	2	2	2
<i>Pachyptila</i> , e.g. <i>P. vittata</i>	2	0	0	2	0	2	0	1	1	1	2	3	2	1–2
<i>Bulweria</i> , e.g. <i>B. bulwerii</i>	2	1	1	2	0	2	0	1	0	0	3	3	4	2
<i>Procellaria</i> , e.g. <i>P. parkinsoni</i>	1	1	0	2	0	3	0	1	1	1	3	3	3	4
<i>Pseudobulweria</i> , e.g. <i>P. rostrata</i>	1	1	1	2	0	3	0	1	0	1	3	3	–	2–3
<i>Calonectris borealis</i>	1	1	1	2	0	3	1	1	1	1	3	3	3	4
<i>Calonectris leucomelas</i>	1	1	1	2	0	3	1	1	1	1	3	3	3	4
<i>Ardenna pacifica</i>	1	1	1	1	0	2	1	1	2	0	3	4	4	4
<i>Ardenna bulleri</i>	2	1	1	1	0	2	1	1	2	1	2	3	3	4
<i>Ardenna carneipes</i>	1	1	1	2	0	3	1	1	2	1	2	3	3	4
<i>Ardenna creatopus</i>	1	1	1	2	0	3	1	1	2	1	2	3	3	4
<i>Ardenna gravis</i>	1	1	1	2	0	3	1	1	2	1	2	3	3	4
<i>Ardenna grisea</i>	1	1	1	1	1	2	2	1	3	2	2	3	3	4
<i>Ardenna tenuirostris</i>	1	1	1	1	1	2	2	1	3	2	2	3	3	4
<i>Puffinus nativitatis</i>	1	1	1	1	1	1	2	1	3	1	1	3	3	3
<i>Puffinus puffinus</i> *	1	1	1	1	1	1	2	1	4	2	1	2	2	3
<i>Puffinus assimilis</i> *	1	1	1	1	1	1	2	1	4	2	1	2	2	1–2
Northern storm petrel*, e.g. <i>Oceanodroma leucorhoa</i>	2	2	1	0	0	0	0	0	0	1	1	1	2	1
Southern storm petrel*, e.g. <i>Nesofregatta fuliginosa</i>	2	2	1	2	0	0	0	0	1	1	0	0	0	1
<i>Pelecanoides</i> , e.g. <i>P. urinatrix</i>	2	2	1	0	1	0	2	1	2	3	0	1	0	1

*Manx-type shearwater group, little/Audubon's shearwater complex and northern and southern storm petrel groups follow Onley & Scofield (2007).

Appendix 2: List of morphological characters of Procellariiformes used in this analysis

The list comprises a mix of newly derived characters and those from Kuroda (1953, 1954, 1955), Chandler (1990), Olson & Rasmussen (2001) and Olson (2008, 2009). Ratio groups were chosen to demonstrate proportional differences between taxa. The positions of most characters are shown in Fig. 1. Character scores for *Ardenna davealleni* n. sp. NMNZ S.45183 and/or NMNZ S.46316 are shown in **bold**.

- 1 Humerus, proximal end, caput humeri undercut and overhangs fossa pneumotricipitalis: not at all (0); **slightly (1)**; considerably (2). The characters of the proximal end of the humerus described by Seguí *et al.* (2001) are directly linked with characters 1 and 2 in this paper.
- 2 Humerus, proximal end, capital shaft ridge: does not extend to caput humeri (0); **extends to caput humeri (1)**; extends to tuberculum dorsale (2).
- 3 Humerus, proximal end, bicipital area, tubercle on the cranial surface of the ventral margin: raised (0); **not present, or only slightly raised (1)**.
- 4 Humerus, proximal end, crista deltopectoralis: very low rounded angle (0); **rounded angle (1)**; sharper angle/point (2); sharper point with strongly concave outline distal of point (3).
- 5 Humerus shaft: **rounded, with ratio of central shaft width to depth <1.5 (0)**; dorsoventrally flattened, with ratio of central shaft width to depth >1.5 (1). Character 5 is also associated with the ventral epicondylar area being expanded. Note that this character does not separate all other shearwaters from *Calonectris* (*contra* Mourer-Chauviré & Geraads 2010) and a flattened humerus shaft is not an apomorphy of shearwaters (*contra* Seguí *et al.* 2001), although this feature is found in all *Puffinus* as defined in this paper.
- 6 Humerus, distal end, processus supracondylaris dorsalis (= ectepicondylar process): small (0); moderately sized, angled distinctly proximally (1); **moderately sized but projects straight (2)**; large straight process (3).
- 7 Humerus, distal end, fossa m. brachialis: deep (0); **medium depth (1)**; shallow (2).
- 8 Proximal end of the ulna, caudal surface of the proximal shaft forms a prominent and continuous ridge to the tip of the proximal end: absent (0); **present (1)**.
- 9 Femur shaft medial view: fairly straight (0); slightly curved (1); **fairly curved (2)**; very curved (3); extremely curved (4). Curvature is arching dorsally.
- 10 Ratio of humerus length to ulna length: <0.98 (0); **0.98–1.04 (1)**; 1.05–1.19 (2); >1.19 (3). Kuroda (1955) considered gliding species to have a longer ulna than humerus.
- 11 Ratio of ulna length to carpometacarpus length: <1.58 (0); 1.59–1.79 (1); **1.80–1.94 (2)**; 1.95–2.24 (3); 2.25–2.45 (4); >2.45 (5).
- 12 Ratio of ulna length to manus phalanx proximal digitus major length: <2.69 (0); 2.69–3.25 (1); **3.26–3.65 (2)**; 3.66–4.19 (3); 4.20–4.73 (4); >4.73 (5).
- 13 Ratio of ulna length to femur length: <1.61 (0); 1.61–2.09 (1); 2.10–2.44 (2); **2.45–3.07 (3)**; 3.08–3.39 (4); >3.39 (5).
- 14 Overall size (length): very small, <26 cm long (1); small, 26–32 cm long (2); medium, 33–41 cm long (3); **large, 42–55 cm long (4)**; very large, >74 cm long (5) (scores based on Onley & Scofield 2007 plates).

Appendix 3: Measurements of Procellariidae bones and ratios of these bones

Measurements are total lengths in millimetres. Abbreviations: Hum = humerus, Uln = ulna, Rad = radius, Cmc = carpometacarpus, Man = manus phalanx proximal digitus major, Fem = femur. Data for *Ardenna* species based on means presented in Appendix 5.

Taxa	Hum	Uln	Rad	Cmc	Man	Fem	Hum/Uln	Uln/Cmc	Uln/Man	Uln/Fem
<i>Ardenna davealleni</i> n. sp. NMNZ S.45183	–	113.4	111.4	62.9	31.8	44.1	–	1.81	3.57	2.57
<i>Ardenna davealleni</i> n. sp. NMNZ S.46316	121.8	117.7	112.8	–	–	–	1.03	–	–	–
<i>Phoebastria immutabilis</i> OR.22147	254	254	251	99.4	49.3	71.9	1.00	2.56	5.15	3.53
<i>Macronectes halli</i> OR.28597	257	242	235	101.8	56.3	91.3	1.06	2.34	4.30	2.65
<i>Fulmarus glacialis</i> OR.29079	115.0	111.7	109.0	55.5	31.4	50.5	1.03	2.01	3.56	2.21
<i>Thalassoica antarctica</i> OR.27407	85.6	85.9	83.5	43.9	25.2	43.3	1.00	1.96	3.41	1.98
<i>Daption capense</i> OR.29529	83.3	81.9	79.8	40.7	22.8	37.1	1.02	2.01	3.59	2.21
<i>Pagodroma nivea</i> OR.11947	78.5	73.4	71.5	39.3	21.7	41.8	1.07	1.87	3.38	1.76
<i>Lugensa brevirostris</i> OR.29066	77.5	82.1	80.5	39.8	21.0	32.4	0.94	2.06	3.91	2.53
<i>Pterodroma macroptera</i> OR.27820	109.5	113.1	110.5	54.1	28.4	39.8	0.97	2.09	3.98	2.84
<i>Halobaena caerulea</i> OR.17591	61.4	59.0	57.5	31.8	17.3	25.8	1.04	1.86	3.41	2.29
<i>Pachyptila vittata</i> OR.27311	61.0	61.4	59.5	32.2	16.2	26.2	0.99	1.91	3.79	2.34
<i>Bulweria bulwerii</i> OR.22145	60.4	62.4	61.1	30.0	16.2	19.2	0.97	2.08	3.85	3.25
<i>Procellaria parkinsoni</i> OR.25953	129.8	130.6	127.9	63.6	33.2	43.9	0.99	2.05	3.93	2.97
<i>Pseudobulweria rostrata</i> OR.23900	109.0	108.5	106.6	51.7	27.1	–	1.00	2.10	4.00	–
<i>Calonectris borealis</i> OR.27733	128.2	128.8	126.1	62.9	33.4	43.9	1.00	2.05	3.86	2.93
<i>Calonectris leucomelas</i> OR.29195	112.6	114.1	110.8	54.9	29.3	39.1	0.99	2.08	3.89	2.92
<i>Ardenna pacifica</i>	102.5	106.8	103.9	52.3	25.5	34.1	0.96	2.04	4.20	3.13
<i>Ardenna bulleri</i>	96.6	97.7	94.6	50.4	25.3	35.4	0.99	1.94	3.86	2.76
<i>Ardenna carneipes</i>	112.6	113.1	107.9	59.2	29.5	40.7	1.00	1.91	3.83	2.79
<i>Ardenna creatopus</i>	114.3	112.3	108.7	59.7	29.9	41.8	1.01	1.88	3.82	2.69
<i>Ardenna gravis</i>	119.8	117.6	113.9	61.7	30.2	39.9	1.03	1.91	3.89	2.84
<i>Ardenna grisea</i>	107.1	100.3	96.5	55.7	27.4	39.8	1.07	1.80	3.66	2.51
<i>Ardenna tenuirostris</i>	97.9	92.2	90.0	49.7	24.3	35.7	1.06	1.86	3.80	2.59
<i>Puffinus nativitatis</i> OR.24682	78.2	78.3	75.3	45.1	21.0	28.4	1.00	1.74	3.73	2.76
<i>Puffinus puffinus</i> OR.26859	78.4	70.8	68.3	42.5	21.2	30.7	1.11	1.66	3.34	2.31
<i>Puffinus assimilis</i> OR.23972	62.8	56.4	54.3	33.1	16.4	24.9	1.11	1.70	3.44	2.27
<i>Oceanodroma leucorhoa</i> OR.19320	31.9	32.2	30.8	18.1	10.2	14.7	0.99	1.78	3.16	2.19
<i>Nesofregatta fuliginosa</i> OR.27482	31.2	30.9	29.7	20.5	12.9	21.3	1.01	1.51	2.40	1.45
<i>Pelecanoides urinatrix</i> OR.28939	43.6	34.7	32.1	25.0	11.7	23.8	1.26	1.39	2.97	1.46

Appendix 4: Measurements of legs bones of *Ardenna davealleni* n. sp. paratype NMNZ S.46316 compared with other *Ardenna* shearwater species

Measurements are maximum lengths in millimetres. Where known, sex is shown as M = male, F = female. The tibiotarsus (tbt) measurements are presented with and without the cnemial crest. The proportion of the cnemial crest to the full length of the tibiotarsus is presented as % crest length. Tmt = tarsometatarsus.

Taxa	Tbt + crest	Tbt – crest	%crest length	Tmt
<i>Ardenna davealleni</i> n.sp.				
NMNZ S.46316	108.0	90.8	15.9	60.7
<i>Ardenna pacifica</i>				
OR.16209	88.8	77.3	13.0	54.7
OR.21455 M	80.1	70.2	12.4	49.4
OR.23001 F	78.2	68.6	12.3	48.0
OR.28441 F	82.1	72.2	12.1	50.7
OR.29669 M	78.4	68.4	12.8	48.7
OR.29670 F	79.2	69.0	12.9	48.4
Mean	81.1	71.0	12.6	50.0
<i>Ardenna bulleri</i>				
OR.29075	81.8	71.1	13.1	50.1
OR.29479 F	82.4	71.3	13.5	49.9
OR.29496 M	81.6	70.5	13.6	51.7
OR.29625 M	80.8	69.5	14.0	48.6
OR.29723 M	82.9	71.5	13.8	49.7
OR.29993	82.3	71.9	12.6	49.4
Mean	82.0	71.0	13.4	49.9
<i>Ardenna carneipes</i>				
OR.15924	88.0	75.6	14.1	53.4
OR.24666	93.4	80.3	14.0	56.6
OR.26223	95.4	82.9	13.1	57.7
OR.26447	94.5	80.6	14.7	58.3
OR.29119	89.6	76.7	14.4	54.8
OR.29207 M	90.5	77.0	14.9	53.9
Mean	91.9	78.9	14.2	55.8

Taxa	Tbt + crest	Tbt – crest	%crest length	Tmt
<i>Ardenna creatopus</i>				
OR.26623 F	94.7	81.7	13.7	56.3
OR.27754	91.7	78.7	14.2	54.0
OR.27755	95.0	81.3	14.4	56.7
OR.27756	96.2	82.4	14.3	56.3
Mean	94.4	81.0	14.2	55.8
<i>Ardenna gravis</i>				
OR.22144	105.3	89.8	14.7	60.9
<i>Ardenna grisea</i>				
OR.13311 F	100.3	80.2	20.0	53.7
OR.13312 F	106.0	85.2	19.6	57.2
OR.15619 M	105.2	85.7	18.5	56.8
OR.15620 M	103.8	85.7	17.4	58.5
OR.15922 M	106.1	86.1	18.9	57.9
OR.29656 M	102.4	84.0	18.0	56.6
Mean	104.0	84.5	18.7	56.8
<i>Ardenna tenuirostris</i>				
OR.14987 M	94.5	77.9	17.6	52.2
OR.15908	90.9	75.3	17.2	49.7
OR.25134	89.4	74.0	17.2	47.5
OR.25557	95.9	79.5	17.1	52.0
OR.29306	94.1	77.8	17.3	51.3
OR.29471 F	97.9	81.1	17.2	53.5
Mean	93.8	77.6	17.3	51.0

Appendix 5: Measurements of *Ardenna* shearwater bones and ratios of these bones

Measurements are total lengths in millimetres. Where known, sex is shown as M = male, F = female. Abbreviations: Hum = humerus, Uln = ulna, Rad = radius, Cmc = carpometacarpus, Man = manus phalanx proximal digitus major, Fem = femur.

Taxa	Hum	Uln	Rad	Cmc	Man	Fem	Hum/ Uln	Uln/Cmc	Uln/Man	Uln/Fem
<i>Ardenna pacifica</i>										
OR.16209	110.9	116.7	113.4	57.0	29.2	36.9	0.95	2.05	4.00	3.16
OR.21455 M	103.1	105.5	103.0	52.3	26.1	34.2	0.98	2.02	4.04	3.08
OR.23001 F	101.0	105.5	103.1	50.7	24.3	32.7	0.96	2.08	4.34	3.23
OR.28441 F	104.3	109.3	106.1	53.4	24.7	35.0	0.95	2.05	4.43	3.12
OR.29669 M	99.2	102.7	99.8	50.2	24.2	32.5	0.97	2.05	4.24	3.16
OR.29670 F	96.5	101.1	98.2	50.4	24.4	33.1	0.95	2.01	4.14	3.05
Mean	102.5	106.8	103.9	52.3	25.5	34.1	0.96	2.04	4.20	3.13
<i>Ardenna bulleri</i>										
OR.29075	97.5	98.0	94.9	50.2	24.4	34.8	0.99	1.95	4.02	2.82
OR.29479 F	96.9	96.8	93.9	48.8	25.0	35.8	1.00	1.98	3.87	2.70
OR.29496 M	97.4	97.6	94.5	52.4	26.6	35.5	1.00	1.86	3.67	2.75
OR.29625 M	97.7	100.2	97.3	50.2	24.5	34.4	0.98	2.00	4.09	2.91
OR.29723 M	96.7	98.2	94.2	51.9	26.5	35.5	0.98	1.89	3.71	2.77
OR.29993	93.5	95.6	92.6	49.1	25.0	36.5	0.98	1.95	3.82	2.62
Mean	96.6	97.7	94.6	50.4	25.3	35.4	0.99	1.94	3.86	2.76
<i>Ardenna carneipes</i>										
OR.15924	106.3	107.2	103.4	56.2	27.9	39.6	0.99	1.91	3.84	2.71
OR.24666	114.7	115.0	111.8	60.8	30.5	41.2	1.00	1.89	3.77	2.79
OR.26223	116.1	117.0	103.7	60.6	29.9	41.5	0.99	1.93	3.91	2.82
OR.26447	113.8	114.2	110.7	59.9	30.3	41.7	1.00	1.91	3.77	2.74
OR.29119	112.8	113.5	109.8	59.1	29.0	39.4	0.99	1.92	3.91	2.88
OR.29207 M	111.6	111.6	108.2	58.6	29.4	–	1.00	1.90	3.80	–
Mean	112.6	113.1	107.9	59.2	29.5	40.7	1.00	1.91	3.83	2.79
<i>Ardenna creatopus</i>										
OR.26623 F	114.6	114.2	110.6	59.2	29.4	41.5	1.00	1.93	3.88	2.75
OR.27754	110.0	108.3	105.2	57.1	28.9	40.5	1.02	1.90	3.74	2.67
OR.27755	114.5	113.7	109.9	61.7	30.3	43.4	1.01	1.84	3.75	2.62
OR.27756	114.8	112.8	109.2	60.8	30.9	41.7	1.02	1.86	3.90	2.71
OR.29584	118.2	–	–	–	–	–	–	–	–	–
OR.29585	113.8	–	–	–	–	–	–	–	–	–
Mean	114.3	112.3	108.7	59.7	29.9	41.8	1.01	1.88	3.82	2.69

Taxa	Hum	Uln	Rad	Cmc	Man	Fem	Hum/ Uln	Uln/Cmc	Uln/Man	Uln/Fem
<i>Ardenna gravis</i>										
OR.22144	120.8	117.6	113.9	61.7	30.2	41.4	1.03	1.91	3.89	2.84
OR.30073 F	118.8	–	–	–	–	38.3	–	–	–	–
Mean	119.8	–	–	–	–	39.9	–	–	–	–
<i>Ardenna grisea</i>										
OR.13311 F	102.6	93.8	89.8	52.6	26.5	39.1	1.09	1.78	3.54	2.40
OR.13312 F	108.9	103.0	99.6	56.5	28.0	39.7	1.06	1.82	3.68	2.59
OR.15619 M	107.4	100.2	96.1	56.4	27.5	40.8	1.07	1.78	3.64	2.46
OR.15620 M	107.0	102.0	98.5	56.6	27.6	38.7	1.05	1.80	3.70	2.59
OR.15922 M	109.3	103.6	99.9	58.0	28.3	40.8	1.06	1.79	3.66	2.54
OR.29656 M	107.1	98.9	95.2	54.3	26.5	39.7	1.08	1.82	3.73	2.49
Mean	107.1	100.3	96.5	55.7	27.4	39.8	1.07	1.80	3.66	2.51
<i>Ardenna tenuirostris</i>										
OR.14987 M	99.0	93.7	90.5	50.8	24.9	37.0	1.06	1.84	3.76	2.53
OR.15908	94.2	87.9	83.7	47.5	22.5	33.7	1.07	1.85	3.91	2.61
OR.25134	91.2	86.8	84.3	46.6	22.7	33.4	1.05	1.86	3.82	2.60
OR.25557	102.6	95.7	92.4	51.0	25.3	37.0	1.07	1.88	3.78	2.61
OR.29306	98.4	92.7	89.6	49.7	24.1	37.0	1.06	1.87	3.85	2.51
OR.29471 F	101.8	96.3	93.3	52.3	26.0	36.3	1.06	1.84	3.70	2.65
Mean	97.9	92.2	90.0	49.7	24.3	35.7	1.06	1.86	3.80	2.59