

Article

A New Giant Petrel (*Macronectes*, Aves: Procellariidae) from the Pliocene of Taranaki, New Zealand [†]

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Abstract: A new species of giant petrel, *Macronectes tinae* sp. nov., is described from the Pliocene deposits of South Taranaki, New Zealand. The holotype is a near complete skull and the paratype a fragmentary left humerus; both come from the Tangahoe Formation, dating from the late Pliocene (Piacenzian or “Waipipian”; age estimated as ca. 3.36–3.06 Ma). The new species of giant petrel is the first fossil *Macronectes* ever reported. It is morphologically similar to the two present-day *Macronectes* spp., but it was a smaller bird. The skull is diagnosed by its overall smaller size, a proportionately longer *apertura nasi ossea*, and potentially by a shorter *os supraorbitale*. The humerus is diagnosed from both species by a proportionately less deep shaft, a more prominent medial portion of the *epicondylus ventralis*, and a larger and fusiform *fossa medialis brachialis*. The Tangahoe Formation is proving to be a remarkable source of marine vertebrate fossils and an important piece of the puzzle in understanding the evolution and biogeography of seabirds.

Keywords: *Macronectes tinae* sp. nov.; Piacenzian; Procellariiformes; Tangahoe Formation; Waipipian



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1. Introduction

Giant petrels (*Macronectes* Richmond, 1905) are the largest birds in the family Procellariidae, identifiable by their heavyset body and beak. They are represented by two living species, *Macronectes giganteus* (Gmelin, 1789) and *M. halli* (Mathews, 1912) [1,2]. *Macronectes halli* was originally described as a subspecies of *M. giganteus*; its status as a separate species was only attained in the second half of the 20th century [3–5] (see also [6]).

Both species of giant petrels are distributed around the Southern Hemisphere, ranging from Antarctica to the subtropics [1,7]. They are fulmarine petrels, phylogenetically close to the fulmar species (*Fulmarus* Stephens, 1826), their sister taxa, and to the Cape petrel *Daption capense* (Linnaeus, 1758), Antarctic petrel *Thalassoica antarctica* (J.F. Gmelin 1789), and snow petrel *Pagodroma nivea* (G. Forster, 1777) [6].

Macronectes has no fossil representatives known so far, aside from the bones of undetermined taxa in Pleistocene and Holocene deposits (e.g., [8,9]). A skull and a humerus belonging to *Macronectes* were recently found in the Pliocene deposits of the Tangahoe Formation in New Zealand. The Tangahoe Formation is a sequence of alternating marine sandstones, siltstones, and shell beds, located in the sedimentary Whanganui Basin in the western portion of New Zealand’s North Island (see [10] for lithologic and stratigraphic descriptions of its fossiliferous sites in the western coastal section in South Taranaki). These deposits have been dated through biostratigraphic correlation and magnetostratigraphy at 3.36–3.06 Ma, late Pliocene [10–12].

In the present paper, we analyse those new *Macronectes* fossils, compare them to the skeletons of living giant petrels, and assign them to a new species based on their morphological characters: *Macronectes tinae* sp. nov.

2. Materials and Methods

The only two fossils known of the herein-described new species of giant petrel were recovered in the coastal deposits of South Taranaki. They consist of a fragmentary left humerus (proximal end not preserved) and a nearly complete skull, which in all likelihood belonged to distinct individuals because the humerus was found about 2 km south of the skull. The fossils are housed in the fossil vertebrate collection of the Museum of New Zealand Te Papa Tongarewa (NMNZ, Wellington, New Zealand) under the registration numbers NMNZ S.048502 (skull) and NMNZ S.048870 (humerus).

The fossils were compared to recent specimens of Procellariiformes in the NMNZ to determine their affinities. The osteological nomenclature used here follows [13–15]. After its identity as a giant petrel (*Macronectes* Richmond, 1905) was established (see Systematics section), a more detailed comparison with congeners was conducted. The common names of the bird species used herein follow [2].

Measurements of the specimens (left humeri and skulls) were taken with a digital calliper (0.01 mm precision, rounded to the nearest 0.1 mm), except for the total length of the skull, which was taken with a metallic ruler, as it exceeded the length of the calliper. The following abbreviations are used for the measurements. Humerus: **DW**, distal width; **SbW**, shaft base width; and **SbD**, shaft base depth (measured from the ventral side). Furthermore, simple proportions were calculated to aid in the comparison, namely, [DW/SBW] and [SbW/SbD]. Skull: **FTD**, distance between *fossae temporalium*; **MFF**, minimum interorbital width (taken between the *fossae glandulae nasalis*); **MIF**, minimum interorbital width (including the *fossae glandulae nasalis*); **MUW**, maxillary unguis width; **NL**, nasal aperture (*apertura nasi ossea*) length; **NW**, nasal aperture (*apertura nasi ossea*) width; **PNW**, nasal process width (taken at the level of the *processus frontalis nasalis*); **PoW**, postorbital width (taken at the level of the *processus postorbitalis*); **PrW**, preorbital width (taken at the level of the *processus supraorbitalis* of the *os lacrimale*); and **TL**, total length (from the *prominentia cerebellaris* to the tip of the beak. Skull measurements follow [16], with the addition of MIF and MUW. The measurements can be found in the Supplementary Material (Table S1).

Principal component analyses (PCAs) were conducted in PAST (v.4.03; [17]) to aid in the visualisation of morphometric differences. Two analyses were conducted, one for measurements taken from the humerus and one for cranial measurements. The total length (TL) of the skull was excluded from the PCA, given the disproportionate effect it has on the results due to its higher order of magnitude. The results of the PCA analysis can be found in the Supplementary Material (skull: Table S2; humerus: Table S3).

List of comparative *Macronectes* spp. material measured: *Macronectes giganteus* (Gmelin, 1789): OR.028535, OR.030370, and OR.30745; *Macronectes halli* Mathews, 1912: OR.012449, OR.013563, OR.015278, OR.015606, OR.021100, and OR.026443; and *Macronectes* sp.: OR.014613, OR.015877, OR.015878, OR.017608, OR.025650, OR.028597, OR.029141, OR.029173, OR.030014, OR.030324, OR.030385, OR.030687, OR.031078, S.000704, S.000742, S.000744, S.000746, S.000748, S.000923, and S.000949.

3. Systematics

The fossil skull (Figure 1) is a clear indication of generic affinity, given the characteristic large bulbous bill shape, resulting from a wider and enlarged *corpus ossis premaxillaris* and a deeper proximal premaxilla (Figure 2; [16]). Furthermore, compared to other Procellariidae (including fulmars), the *apertura nasi ossea* (nasal aperture) is proportionately shorter (in relation to bill length) in *Macronectes* spp., and the region between the orbits and nasal aperture is more elongated [18].

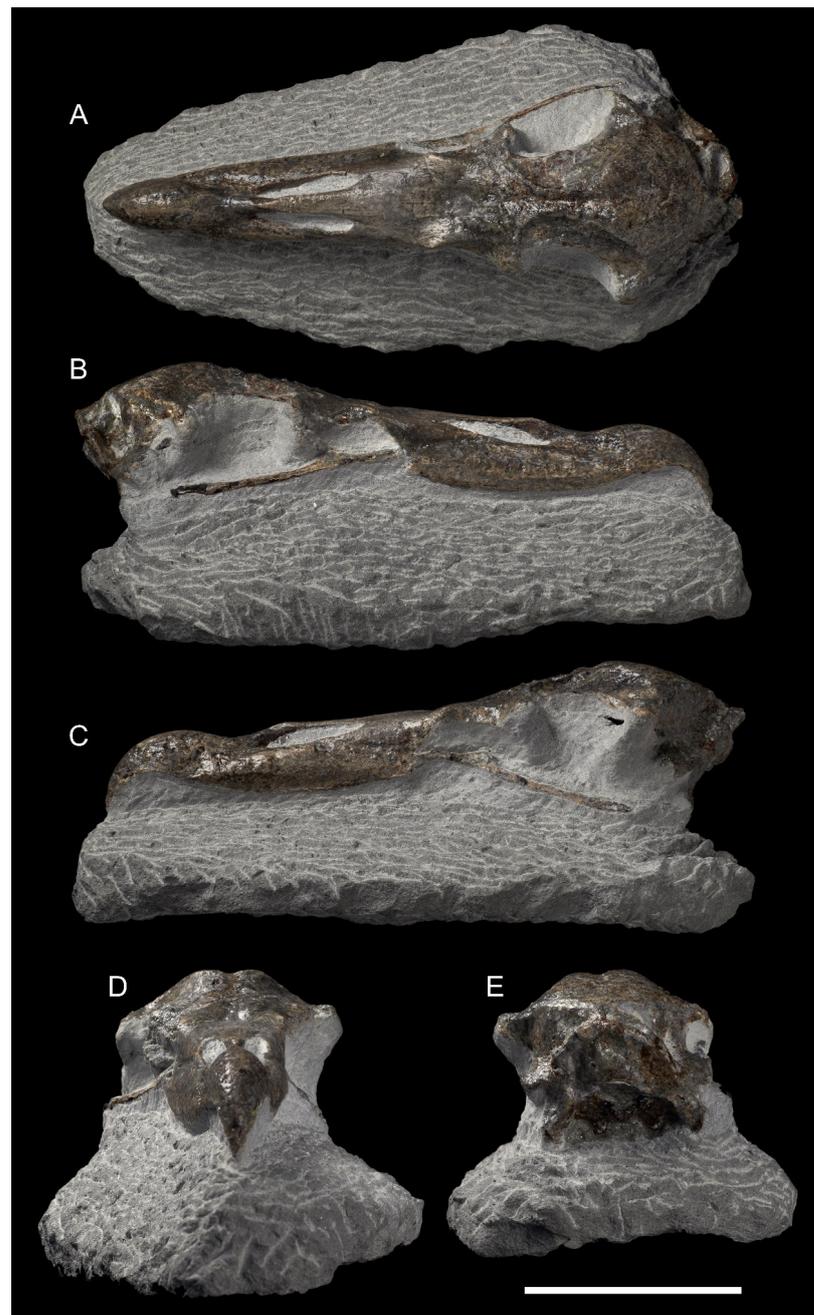


Figure 1. Skull (holotype, NMNZ S.048502) of *Macronectes tinae* sp. nov., partially embedded in matrix, in different views; scale bar = 5 cm. (A) Dorsal view. (B) Lateral view (right). (C) Lateral view (left). (D) Anterior view. (E) Caudal view.

The classification of the fossil humerus (Figure 3) in Procellariidae can be inferred based on: (1) the spur-like, extended *processus supracondylaris dorsalis* ([14]; the “ectepicondylar prominence” *sensu* [13]); and (2) the *epicondylus ventralis* (“ectepicondyle” *sensu* [13]; “convex bulge” *sensu* [19]) that craniocaudally slopes, forming a protrusion on the ventral margin [19]. It differs from larger Procellariiformes, such as *Diomedea* spp. and *Thalasarche* spp., by a greater expansion of the distal end of the humerus, a more proximally positioned *processus supracondylaris dorsalis* (ectepicondylar process), and a deeper *fossa medialis brachialis* (Figure 4).

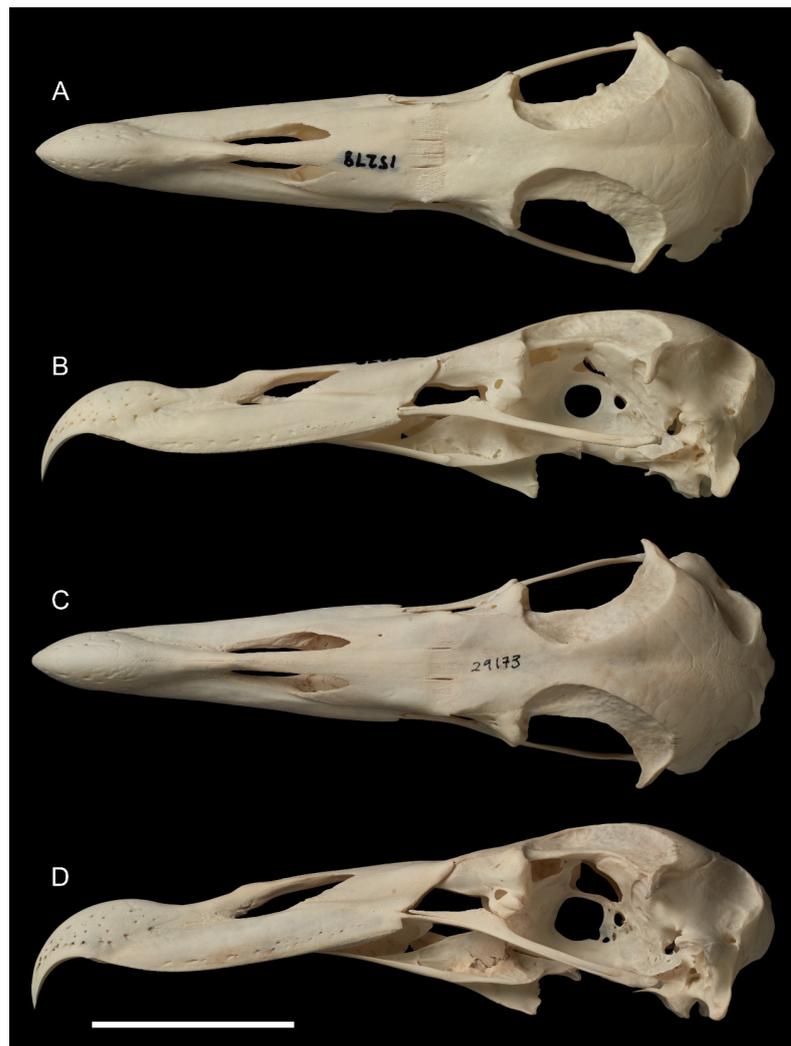


Figure 2. Skulls (except mandible) of *Macronectes* spp.; scale bar = 5 cm. (A,B) *M. giganteus*, NMNZ OR.015278. (C,D) *M. halli*, NMNZ OR.029173.



Figure 3. Left humeri of *Macronectes* spp. in cranial view; scale bar = 5 cm. (A) *Macronectes tinae* sp. nov., paratype NMNZ S.048870 (proximal end not preserved). (B) *M. giganteus*, NMNZ OR.029141. (C) *M. halli*, NMNZ OR.029173.

The defining feature of the humerus in the genus *Macronectes* is, unfortunately, at the proximal end: a weakly developed second (dorsal) *fossa pneumotricipitalis* [19]. Nevertheless, the dorsal end of the fossil humerus (Figure 3) bears a closer resemblance to *Macronectes* spp. than to other Procellariidae, including fulmars (the sister taxa; [6]) and other fulmarine petrels, which are much smaller birds overall. However, it is notable that, like the fossil, smaller fulmarine petrels have a slightly more oval *fossa medialis brachialis* and a more bulbous *epicondylus ventralis* (Figure 4). The position and general shape of the condyles are the same in the fossil and the two modern species of *Macronectes* (Figure 4). It is worth noting, however, that the humeri of modern *Macronectes* spp. have a proportionately shorter and wider distal end compared with the fossil and other fulmarine petrels (Figure 4).

The fusion of cranial and humeral elements (lacking visible sutures) indicates that these bones belonged to adult individuals. The differences in the size, proportions, and morphological structures of the fossils in comparison to living congeners allow the description of a new species (see below for a detailed comparison).

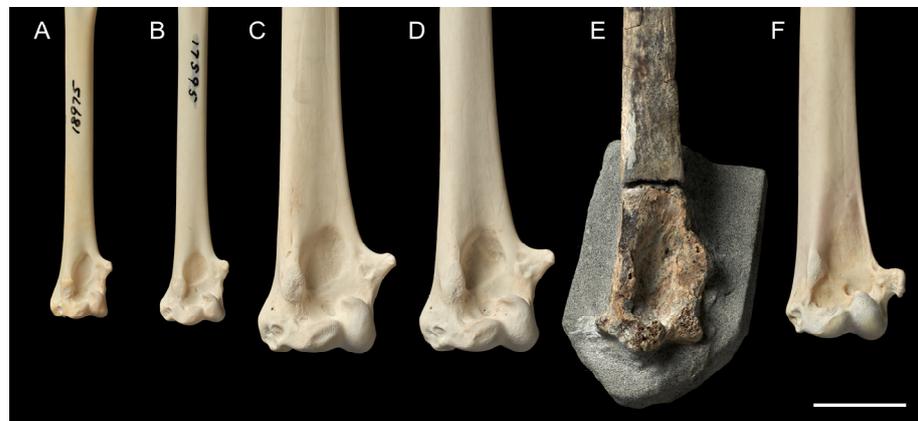


Figure 4. Detail of proximal end of the left humeri of selected Procellariiformes in cranial view; scale bar = 2 cm. (A) Antarctic petrel *Thalassoica antarctica* (Gmelin, 1789), NMNZ OR.018975. (B) Antarctic fulmar *Fulmarus glacialis* (Smith, 1840), NMNZ OR.017595. (C) *Macronectes giganteus*, NMNZ OR.029141. (D) *Macronectes halli*, NMNZ OR.029173. (E) *Macronectes tinae* sp. nov., paratype NMNZ S.048870. (F) Indian yellow-nosed albatross *Thalasarche carteri* (Rothschild, 1903), NMNZ OR.028477.

Order Procellariiformes Fürbringer, 1888

Family Procellariidae Leach, 1820

Genus *Macronectes* Richmond, 1905

Macronectes tinae sp. nov.

(Figure 1, Figure 3A, Figure 4E)

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Holotype: NMNZ S.048502 (col. Alastair Johnson, 2017): largely complete skull (Figure 1).

Paratype: NMNZ S.048870 (col. Alastair Johnson, 2019): left humerus, fragmentary, only the shaft and distal end remaining (Figure 3A). The shaft is to be broken near where the *crista deltopectoralis* would terminate.

Type locality and stratum: New Zealand, North Island, southern Taranaki, Hāwera. Tangahoe Formation. The holotype and paratype were surface collected as beach boulders and do not have an exact Fossil Record Electronic Database number, but see Q21/f0002 for nearby location.

Age: Late Pliocene, Piacenzian (“Waipipian Stage” in the New Zealand scale): constrained to 3.36–3.06 Ma, based on the oxygen isotope stage and magnetic polarity data [10].

Etymology: The specific epithet honours Tina King, the late partner of fossil collector Alastair Johnson. This giant petrel skull was her favourite fossil, hence the homage.

Measurements: Skull: FTD = 7.2 mm; MFF = 6.9 mm; MIF = 20.5 mm; MUW = 12.6 mm; NL = 23.1 mm; NW = 4.5 mm; PFNW = 22.2 mm; PoW = 48.8 mm (estimate); PrW = 34.9 mm

(estimate); TL = 148 mm. Humerus: total (preserved) length = 166 mm; DW = 26.8 mm; SbW = 14.7 mm; SbD = 6.8 mm.

Diagnosis: Skull: overall smaller size; proportionately longer *apertura nasi ossea*; apparently shallower *os supraoccipitale*. Humerus: shaft proportionately craniocaudally less deep, with more delicate appearance than congeners; medial portion of *epicondylus ventralis* more prominent; *fossa medialis brachialis* proportionately larger, elongated, and nearly fusiform.

Differential diagnosis: There is little intraspecific and interspecific variation in the skull and humerus morphology between *M. giganteus* and *M. halli* ([16,18]; this study: Table S1), barring sexual dimorphism (males are larger; [16,20,21]) and the slightly smaller average size of *M. halli* (the size range of the two species completely overlap; [1,7]). That is to be expected from taxa with little genetic distinction [6]. As such, morphological comparisons can be made between *M. tinae* sp. nov. and both living *Macronectes* spp. simultaneously.

Skull: The skull of *M. tinae* sp. nov. (Figure 1) is smaller than all *Macronectes* spp. in the NMNZ collection (Table S1) and can be instantly diagnosed by its size. Barring the size difference, almost all other structures are the same as in living *Macronectes* spp. (Figure 2), with two exceptions: the *fossa temporalium* and the *os supraoccipitale*.

According to the PCA, PC1 explains circa 55% of variance, PC2 26%, and PC3 8% (Table S2). PC1 values are strongly related to almost all measurements, except FTD (distance between *fossae temporalium*); larger values of PC1 mean larger sizes. PC2 is mostly related to FTD, with larger PC2 values indicating larger FTD. PC3 is related to MFF (minimum interorbital width) and NL (length of the nasal aperture); larger PC3 values indicate larger MFF, but smaller NL. In a PC1 × PC2 plot (Figure 5B), there is not much difference between *M. tinae* sp. nov. and living *Macronectes* spp. (which greatly overlap). However, a PC1 × PC3 plot (Figure 5C) shows *M. tinae* sp. nov. is separated from the two recent species due to its low PC3 value (potentially due to NL).

The length of the nasal aperture (Table S1) of *M. tinae* sp. nov. is roughly the same as in living giant petrels, making it proportionately larger in the fossil (in relation to the rest of the skull).

Furthermore, the *os supraoccipitale* (supraoccipital bone) of *M. tinae* sp. nov. (Figure 1) is apparently shallower than in living *Macronectes* spp., even considering the smallest specimens of the latter. The depth of this bone in *M. tinae* sp. nov. is likely somewhere between 1/2 and 2/3 of the depth observed in recent *Macronectes* spp. (Figure 2) and could be an important diagnostic feature. However, due to the light deformation of the fossil, this cannot be stated with precision, and no reliable measurements could be taken from this bone to include in the PCA. As such, this must remain as a qualitative comparison for the moment.

Finally, the *crista nuchalis transversa* is apparently more prominent in *M. tinae* sp. nov. than in its living congeners, although this feature might have been exacerbated in the present fossil due to preservation (caudal end of skull lightly crushed; Figure 1).

Humerus: The humerus of *M. tinae* sp. nov. is about as big as the smallest *Macronectes* spp. in the NMNZ collection (e.g., NMNZ OR.015606; Table S1). The distal end of the fossil is more delicate than that of living *Macronectes* spp., with its shaft being proportionately less deep (Figure 3; Table S1: larger [SbW/SbD] measure in *M. tinae* sp. nov.). According to the PCA, PC1 explains 81% of variance and PC2 17% (Table S3). Larger PC1 values mean greater W, SbW, and SbD, while larger PC2 values mean greater SbW and SbD (thicker shaft), but lower W (smaller distal end). By plotting PC1 × PC2 (Figure 5A), it is clear that *M. tinae* sp. nov. is separated from the two recent species (which largely overlap) due to its different proportions, as explained above.

The base of the *processus supracondylaris dorsalis* of the fossil has the same shape as found in living *Macronectes* spp., but its spur-like extension is broken off (Figure 3A). Likewise, the *condylus dorsalis* (dorsal/external condyle), *condylus ventralis* (ventral condyle), and *epicondylus ventralis* (ventral epicondyle) are all worn, but what remains of them has similar shapes to the equivalent condyles found in the living species (Figure 3). The

expected that *M. tinae* sp. nov. had a generally similar anatomy and habits to its congeners, the present-day giant petrels (Figure 6).



Figure 6. Artistic reconstruction of *Macronectes tinae* sp. nov. in its palaeoenvironment. Illustration by Simone Giovanardi, © Te Papa (CC-BY 4.0). A darker plumage was chosen for the reconstruction because a darker colouration in giant petrels seems to be related to warmer regions [7], as Taranaki had warmer temperatures during the Pliocene [22].

All evidence from the size of the fossils (Table S1) suggests that individuals of *M. tinae* sp. nov. had smaller bodies than both *M. halli* and *M. giganteus* (including the smaller-bodied potential subspecies *M. g. solanderi* (Mathews, 1912) from the southern Atlantic [23], which is currently not accepted as a separate taxon [2]). The slenderer and more delicate humerus is also an indication that members of *Macronectes* in the Pliocene had not yet achieved the bulk of recent species (the largest birds among the Procellariidae) and that the ancestors of *Macronectes* were smaller, as might be predicted because their closest relatives are much smaller. One possible reason for the smaller size of the fossil species is that the species occupied relatively warm waters, in a similar way to the *Diomedea exulans* group *sensu lato*, where the smaller taxa occupy more northern breeding sites [24]. The average temperatures of the Tangahoe Formation palaeoenvironment were higher than in the present [22]. However, while living *Macronectes* spp. generally nest in the subantarctic, both species range into tropical waters, particularly as juveniles [7].

Giant petrels are more littoral birds than other Procellariidae and, notably, are the only species in the family that can effectively stand and walk on land [1,25]. On land, they tend to be gregarious opportunistic scavengers and predators, depending largely on seal and penguin colonies on the shore for both carcasses and chicks [7,20,26,27]. Giant petrels also prey upon other seabirds, and hunt cephalopods and fish near the water surface, also taking krill to feed their chicks [1,25,28,29]. The diet of females has a larger proportion of fish, cephalopods, and crustaceans [27].

The Tangahoe Formation in Taranaki represents a coastal palaeoenvironment [10] suitable for giant petrels. It contains fossils of colonial mammals and seabirds that would have provided a ready food source for them (Figure 6), such as the monk seal *Eomonachus belegaerensis* (Rule et al., 2020) and the dawn crested penguin *Eudyptes atatu* (Thomas, Tennyson, Scofield & Ksepka, 2020) [30,31].

The seabird fauna of the Tangahoe Formation is starting to be studied in more depth and is proving to be quite diverse. Besides the penguin, there are fossils of three other

Procellariiformes: Pom's shearwater *Ardenna davealleni* (Tennyson & Mannering, 2018), the deep-billed petrel *Procellaria altirostris* (Tennyson & Tomotani, 2021), and Alastair's albatross *Aldiomedes angustirostris* (Mayr & Tennyson, 2020) [32–34]. The fossils of all three species were found in the same outcrops as the penguins, seals, and the presently described giant petrel. There are also undescribed Pelagornithidae fossils [2,35], an extinct family of seabirds.

Macronectes tinae sp. nov. is the first pre-Quaternary fossil giant petrel ever reported. The location where the fossils were found in New Zealand is within the species' present at-sea distribution [7]; therefore, *Macronectes tinae* sp. does not have clear biogeographical implications.

It has been speculated [36] that *Macronectes* originated in the late Oligocene. Fulmar species (*Fulmarus* spp.), the sister taxa of *Macronectes*, have a fossil record spanning back to the middle Miocene of California, USA (ca. 16.0–15.2 Ma; [37–39]), *Fulmarus hammeri* (Howard, 1968) and *F. miocaenus* (Howard, 1984); this would imply that *Fulmarus* and *Macronectes* had already split before that date. One molecular estimate put the divergence of these two genera at around 7.8 Ma, while the divergence between the clades *Fulmarus*+*Macronectes* and *Thalassoica*+*Pagodroma* was estimated at around 15.9 Ma [6]. Another molecular study put the divergence date between *Macronectes* and *Fulmarus* at 1.8 Ma [40]. The presence of *Macronectes tinae* sp. nov. in the Pliocene and the *Fulmarus* species in the Miocene indicate that both molecular studies have underestimated the divergence dates.

No fossils of *Pagodroma*, *Thalassoica*, or *Daption* are known, but a Fulmarinae gen et sp. indet. from the Pliocene of South Africa is considered to be closely related to *Daption* [41] (see also the fossil Procellariidae gen. et sp. Indet. Mentioned by [42]). *Daption* is the sister clade to all other fulmarine petrels, with an estimated divergence from them at circa 26.2 Ma [6], so that fossil does not add much information.

5. Conclusions

A new species of extinct giant petrel, *Macronectes tinae* sp. nov., from the late Pliocene (Piacenzian) of Taranaki, New Zealand, is described herein. The Tangahoe Formation continues to provide outstanding seabird fossils and is becoming an important piece of the puzzle to understand the evolution and biogeography of seabirds in New Zealand and beyond. New Zealand, in particular, is considered a global centre of procellariiform diversity [43], a status that was probably already in place in the late Pliocene.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/taxonomy3010006/s1>, Table S1: Specimen measurements; Table S2: PCA results (skull); Table S3: PCA results (humerus).

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Data Availability Statement: All data can be found within the article and its Supplementary Materials.

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Conflicts of Interest: The authors declare no conflict of interest.

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