




## Article

# First Complete Wing of a Stem Group Sphenisciform from the Paleocene of New Zealand Sheds Light on the Evolution of the Penguin Flipper

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**Abstract:** We describe a partial skeleton of a stem group penguin from the Waipara Greensand in New Zealand, which is tentatively assigned to *Muriwaimanu tuatahi*. The fossil includes the first complete wing of a Paleocene penguin and informs on previously unknown features of the mandible and tibiotarsus of small-sized Sphenisciformes from the Waipara Greensand. The wing is distinguished by important features from that of all geologically younger Sphenisciformes and documents an early stage in the evolution of wing-propelled diving in penguins. In particular, the wing of the new fossil exhibits a well-developed alular phalanx and the distal phalanges are not flattened. Because the wing phalanges resemble those of volant birds, we consider it likely that the wing feathers remained differentiated into functional categories and were not short and scale-like as they are in extant penguins. Even though the flippers of geologically younger penguins may favor survival in extremely cold climates, they are likely to have been shaped by hydrodynamic demands. Possible selective drivers include a diminished importance of the hindlimbs in subaquatic propulsion, new foraging strategies (the caudal end of the mandible of the new fossil distinctly differs from that of extant penguins), or increased predation by marine mammals.

**Keywords:** Aves; evolution; fossil birds; *Muriwaimanu tuatahi*; Sphenisciformes; wing-propelled diving

## 1. Introduction

Penguins (Sphenisciformes) are flightless, wing-propelled diving birds, in which the forelimbs attained a flipper-like shape. In the extant species, the wing forms an essentially flat and stiff unit, which exhibits a strongly restricted motility of the carpal joint [1]. The distal wing muscles of crown group Sphenisciformes are greatly reduced [2] and most bony attachment structures are poorly developed. The wing feathers are, furthermore, greatly shortened and not differentiated into functional categories, such as primaries, secondaries, and coverts. However, even though penguins have a comparatively extensive fossil record that dates back to the earliest Cenozoic Era [3,4], little is known about the evolutionary transitions that occurred in the evolution of the penguin wing.

The Paleocene strata of the Waipara Greensand in New Zealand have, in particular, yielded a diverse array of stem group Sphenisciformes. These fossils represent the oldest known penguins and belong to several differently-sized species. The first two species that were scientifically described were assigned to the taxon *Waimanu*, the type species of which is *Waimanu manneringi* [5]. Another species assigned to *Waimanu* in the original description of this taxon [5] was transferred to the new taxon *Muriwaimanu* and is now classified as *M. tuatahi* [6]. *W. manneringi* is only known from pelvic elements and leg bones, whereas the original description of *M. tuatahi* was based on partial skeletons of two individuals [5]. The recently described *Sequiwaimanu rosieae* is likewise based on a well-preserved partial skeleton, which includes most of the major cranial and postcranial bones [6]. By contrast, two very large-sized penguins from the Waipara Greensand, *Crossvallia waiparensis* as well as an unnamed species [7,8], are only represented by leg bones.

These fossils yielded much new information on the skeletal morphology of the earliest stem group Sphenisciformes and show that Paleocene penguins differed from geologically younger species in numerous osteological features [3,6]. However, critical details remain unknown and this is particularly true for the distal bones elements of the wing, which are an integral part of the penguin flipper. Two of the wing phalanges, the phalanx proximalis digiti majoris and the phalanx digiti minoris, are preserved in a recently described new stem group penguin from the early to middle Paleocene of the Chatham Islands, New Zealand [9]. Of the sphenisciform species from the Waipara Greensand, however, only the major wing bones (humerus, ulna, radius, and carpometacarpus) of *M. tuatahi* and *S. rosieae* have been described so far [3,5,6].

Concerning other early Cenozoic stem group Sphenisciformes, largely complete wings are known for *Anthropornis* sp. and *Palaeudyptes gunnari* from the Eocene of Antarctica [10], *Icadyptes salasi* from the late Eocene of Peru [11,12], and *Kairuku grebneffi* from the late Oligocene of New Zealand [13]. Even though all of these taxa differ from extant penguins in plesiomorphic traits, their wings were already transformed into flattened, flipper-like structures. At least the late Eocene *Inkayacu paracasensis*, of which the distal wing elements are unknown, also had the characteristic feathers found in extant penguins [14].

Here, we describe a newly found partial skeleton from the Waipara Greensand, which includes the first complete wing of a Paleocene stem group penguin. The fossil is from a small-sized species and is tentatively assigned to *Muriwaimanu tuatahi*, which is the smallest sphenisciform species from the Waipara Greensand. This assignment is based on the similar shape and concordant dimensions of the wing elements of the new fossil and those of *M. tuatahi*. We note, however, that there exists some morphological variability in the *M. tuatahi*-sized Sphenisciformes from the Waipara Greensand and these fossils probably represent more than one species. In light of a pending revision of the fossil material, our study mainly focuses on the morphology of the wing bones, but, as detailed in the following, the new fossil also elucidates other previously unknown aspects of the osteology of Paleocene stem group Sphenisciformes.

## 2. Material and Methods

The fossil is deposited in the Canterbury Museum, Christchurch, New Zealand (CM). Use of open nomenclature follows the recommendations of Bengtson [15].

Non-destructive tomographic investigation was conducted using the DINGO thermal-neutron tomography facility located at the Australian Nuclear Science and Technology Organisation (ANSTO), Sydney, Australia [16]. Neutron tomography was conducted with a field of view of  $200 \times 200 \text{ mm}^2$ , yielding a reconstruction with cubic voxels of  $95.2 \mu\text{m} \times 95.2 \mu\text{m} \times 95.2 \mu\text{m}$ . Due to sample height, the specimen was scanned in two vertical parts. Each 11 h scan consisted of a total of 1200 equally-spaced angle shadow-radiographs obtained every  $0.15^\circ$  as the sample was rotated  $180^\circ$  about its vertical axis. To reduce anomalous noise, a total of three individual radiographs with an exposure length of 8 s were acquired at each angle [17] and individual radiographs were summed in post-acquisition processing in ImageJ v.1.51h. Tomographic reconstruction of the 16-bit

raw data was performed using Octopus Reconstruction v.8.8 (Inside Matters NV, Gent, Belgium), yielding virtual slices perpendicular to the rotation axis. A 3D model was uploaded to sketchfab (<https://sketchfab.com/3d-models/muriwaimanu-wing-cbfc37791ccd47108779889dcb4b16f0>).

### 3. Systematic Paleontology

Aves Linnaeus, 1758

Sphenisciformes Sharpe, 1891

cf. *Muriwaimanu* Mayr, De Pietri, Love, Mannering, and Scofield, 2017

cf. *Muriwaimanu tuatahi* Ando, Jones, and Fordyce, 2006

#### 3.1. Referred Specimen

CM 2018.124.4: partial skeleton in two blocks of matrix. The main specimen includes the mandible, right wing, left femur and tibiotarsus, synsacrum, partial pelvis, as well as several thoracic vertebrae and ribs (Figures 1 and 2). A much smaller second block contains a pedal phalanx and various fragmentary bones and was not part of this study; the proximal end of the left humerus and the left radius are preserved as isolated bones.

#### 3.2. Locality and Horizon

Waipara Greensand, Waipara River, Canterbury, New Zealand, site S1 of reference 6: Figure 1; 43°03'23.0" S, 172°35'57.0" E. The fossil was found 159 meters above mean sea level and stratigraphic correlations based on biostratigraphy and geochemistry [18] allowed an age estimate of 59–60 Ma (middle Paleocene/upper Teurian). The fossil was collected in 2017 by Leigh Love.

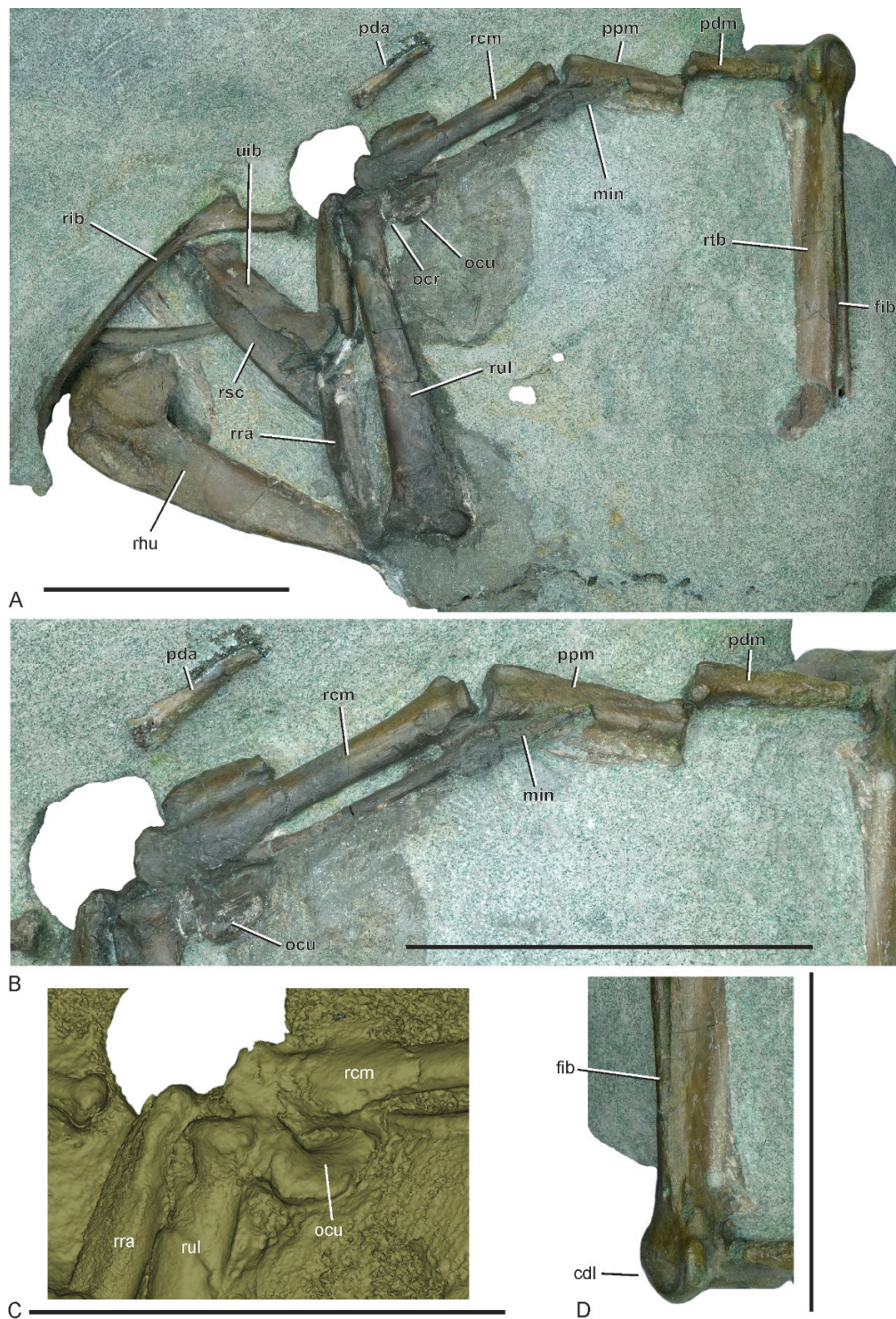
#### 3.3. Measurements (in mm, in Brackets the Dimensions of other *Muriwaimanu tuatahi* Specimens)

Humerus, length 105 (*M. tuatahi*, CM zfa 34: 109.6 [6]). Ulna, length, 76.2 (*M. tuatahi*, CM 2009.99.1: 77.5 [6]). Radius, ~76. Carpometacarpus, length, 49.2 (*M. tuatahi*, CM zfa 34: 49.5 [6]). Phalanx proximalis digiti majoris, length, 25.8. Phalanx distalis digiti majoris, length, 22.3. Phalanx digiti alulae, length, 19.0. Synsacrum, length, 133.6; Femur, length, 95.4 (*M. tuatahi*, CM 2009.99.1: 104.2 [6]). Tibiotarsus, length, 148.3.

#### 3.4. Taxonomic Remarks

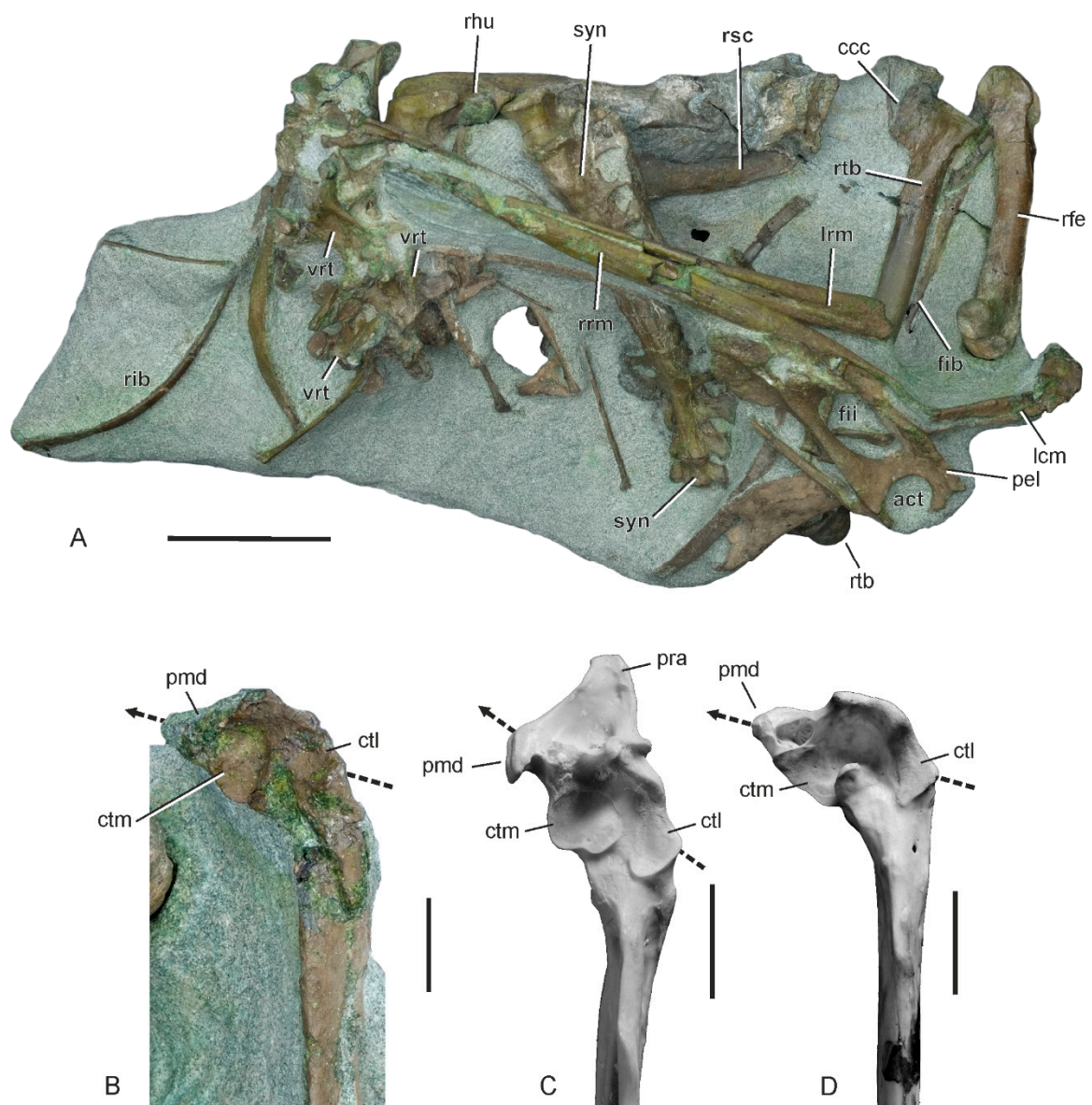
CM 2018.124.4 is tentatively assigned to *Muriwaimanu tuatahi*, but we note some differences to other *M. tuatahi*-like bones in the collection of the Canterbury Museum. The carpometacarpus of the new fossil, for example, is craniocaudally somewhat narrower and more gracile than that of CM zfa 34 (Figure 3B) and the femur to ulna ratio is 1.20 in the new fossil, whereas it is 1.34 in CM 2009.99.1. Whether these differences indicate intraspecific or sexual variation or whether they suggest distinctness on a species level will have to be determined once the small-sized penguins from the Waipara Greensand are subjected to a revision.



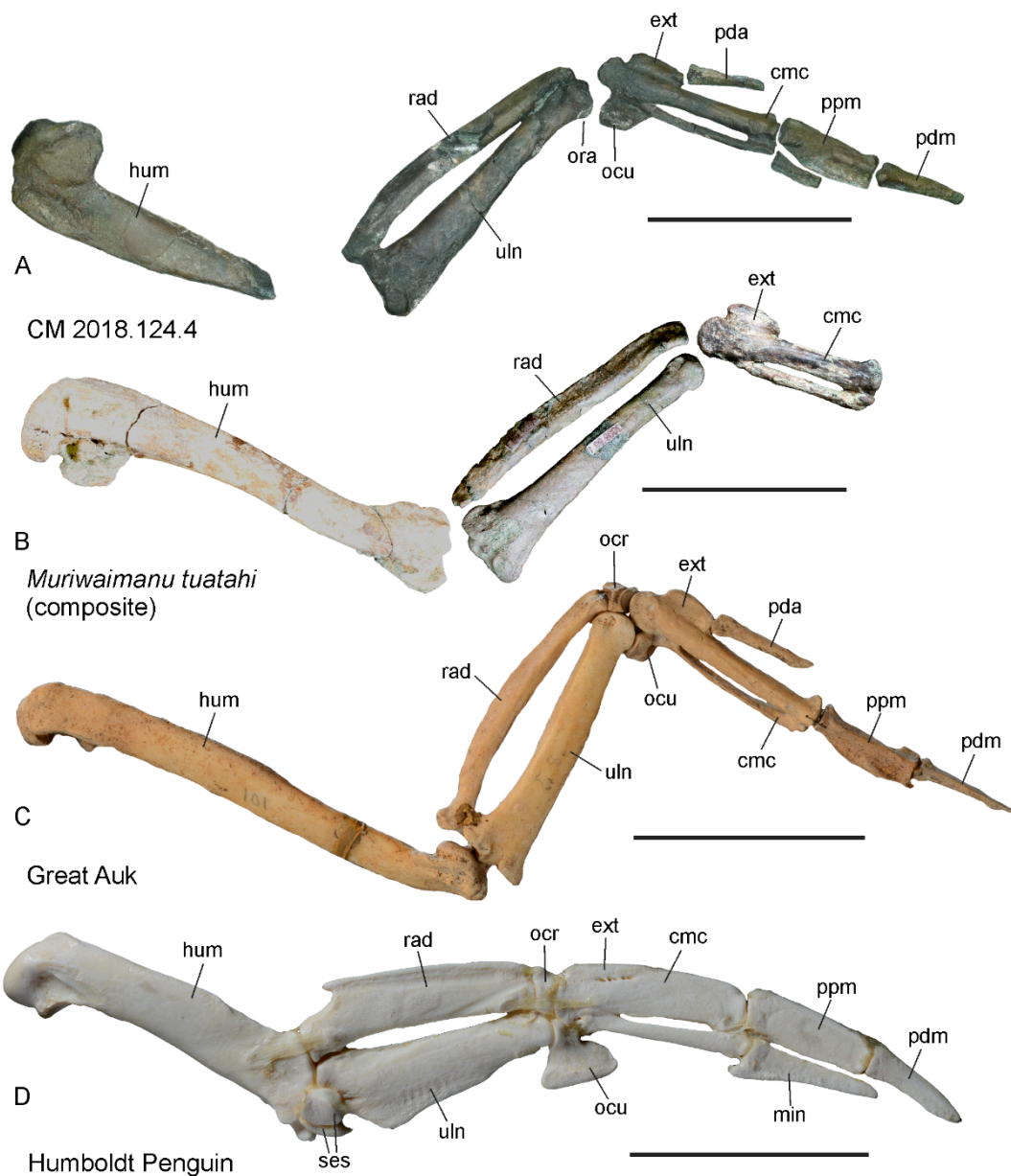


**Figure 1.** (A) Partial penguin skeleton from the Waipara Greensand in New Zealand (CM 2018.124.4, cf. *Muriwaimanu tuatahi*), view of exposed right wing and right tibiotarsus. (B) CM 2018.124.4, detail of wing skeleton. (C) Neutron tomography-based image of wrist joint. (D) Detail of distal end of the right tibiotarsus (craniolateral view) with distally-fused fibula. Abbreviations: cdl, condylus lateralis; fib, fibula; min, phalanx digiti minoris; ocr, os carpi radiale; ocr, os carpi ulnare; pda, phalanx distalis digiti alulae; pdm, phalanx distalis digiti majoris; ppm, phalanx proximalis digiti majoris; rcm, right carpometacarpus; rhu, right humerus; rib, rib; rra, right radius; rsc, right scapula; rtb, right tibiotarsus; rul, right ulna; uib, unidentified bone fragment (possible right ramus mandibulae). The scale bars equal 50 mm.





**Figure 2.** (A) Partial penguin skeleton from the Waipara Greensand in New Zealand (CM 2018.124.4, cf. *Muriwaimanu tuatahi*); view of the reverse side of the specimen shown in Figure 1. (B) *M. tuatahi* (CM 2018.124.4), caudal end of mandible in dorsal view. (C) *Aptenodytes patagonicus* (Sphenisciformes), caudal end of mandible in dorsal view. (D) *Fregata magnificens* (Suliformes, Fregatidae), caudal end of mandible in dorsal view. The dashed arrows connect the rostral margin of the cotyla lateralis with the processus medialis and indicate the different orientations of the caudal mandible relative to the longitudinal axis of the ramus. Abbreviations: act, foramen acetabuli; ccc, crista cnemialis cranialis; ctl, cotyla lateralis; ctm, cotyla medialis; fib, fibula; fii, foramen ilioischadicum; lcm, caudal end of left ramus mandibulae; lrm, left ramus mandibulae; pel, pelvis; pmd, processus medialis; pra, processus retroarticularis; rfe, right femur; rhu, right humerus; rib, rib; rrm, right ramus mandibulae; rsc, right scapula; rtb, right tibiotarsus; syn, synsacrum; vrt, vertebra. The scale bars equal 50 mm for (A) and 10 mm for (B–D).



**Figure 3.** (A) Reconstruction of the wing skeleton (right side) of CM 2018.124.4 (cf. *Muriwaimanu tuatahi*) with surrounding matrix digitally removed and bones reassembled. (B) Composite wing skeleton of *Muriwaimanu tuatahi* from the Waipara Greensand (humerus: CM 2010.108.3; ulna and radius: CM 2009.99.1, both left side, mirrored; carpometacarpus: CM zfa 34; left side, mirrored). (C) Wing of the flightless Great Auk, *Alca impennis* (Alcidae). The specimen lacks the phalanx digiti minoris. (D) Wing of the extant Humboldt Penguin, *Spheniscus humboldti*. Abbreviations: cmc, carpometacarpus; ext, processus extensorius (carpometacarpus); hum, right humerus; min, phalanx digiti minoris; ocr, os carpi radiale; ocr, os carpi radiale; ocu, os carpi ulnare; pda, phalanx digiti alulae; pdm, phalanx distalis digiti majoris; ppm, phalanx proximalis digiti majoris; rad, radius; ses, sesamoid bones associated with the tendon of musculus scapulotriceps; uln, ulna. Scale bars equal 50 mm.

### 3.5. Description and Comparisons

The proportions of the mandible indicate a long and narrow beak, which is also characteristic of other early Cenozoic stem group Sphenisciformes [6,11]. The mandibular symphysis exposes the ventral surface and the mandibular rami are closely appressed in their rostral sections. The caudal portions of both mandibular rami are broken and displaced. The caudal section of the left ramus

mandibulae is situated next to the rostral section of the right ramus mandibulae (at first sight, Figure 2A may give the impression of a continuous connection, but closer examinations clearly shows that the ventral surface of the rostral portion of the mandible is exposed, whereas the caudal portion is seen in dorsal view; the rostral and caudal mandibular sections are not connected by bone). The caudal section of the right ramus could not be unambiguously identified, but may be a bone fragment situated on top of the right radius (Figure 1A). For the first time, the caudal end of the mandible is preserved in a Paleocene penguin, with the dorsal surface of the caudal end of the left ramus mandibulae being well exposed. Unlike in the crown group (Figure 2C) and Eocene stem group Sphenisciformes [19,20], the mandible of CM 2018.124.4 lacks a retroarticular process and the processus medialis is proportionally larger and more pointed and is medially, rather than caudomedially, directed (amongst extant penguin, the caudomedial orientation of the processus medialis is less pronounced in *Eudyptula* and *Spheniscus* than in *Aptenodytes*). With regard to the above features and overall morphology, the caudal end of the mandible of CM 2018.124.4 actually more closely resembles the caudal end of the mandible of extant Fregatidae (frigatebirds; Figure 2D) than that of geologically younger Sphenisciformes.

In size and morphology, the humerus, ulna, radius, and carpometacarpus resemble the corresponding bones of the *Muriwaimanu tuatahi*-type material [5]. As noted above, however, the carpometacarpus is more gracile than that of other specimens assigned to *M. tuatahi* (Figure 3B). No sesamoid bones associated with the tendon of musculus scapulotriceps could be identified in the fossil. These sesamoids are located near the distal end of the humerus and are a derived characteristic of extant penguins (Figure 3D). Their first occurrence in the fossil record is in the late Eocene *Icadyptes salasi* [12]; sesamoid bones associated with the tendon of musculus scapulotriceps are also present in the late Oligocene *Kairuku grebneffi* [13].

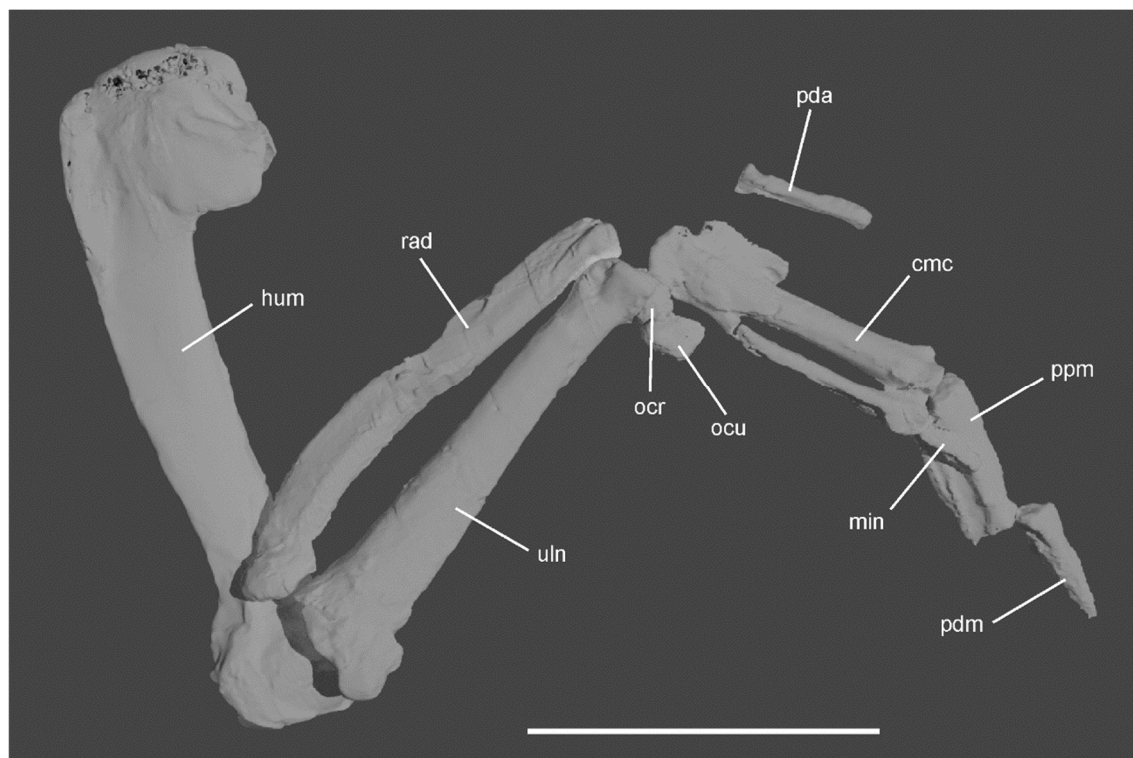
The phalanx digiti alulae, which was for the first time preserved in an early Cenozoic penguin, is detached from the carpometacarpus and is well developed (Figures 1A and 4). In crown group Sphenisciformes, this phalanx is fused with the carpometacarpus. However, based on the presence of an articular facet on the alular metacarpal of the carpometacarpus, it was hypothesized that the late Eocene *Icadyptes salasi* had an unfused phalanx digiti alulae [12]. In the late Oligocene *Kairuku grebneffi*, by contrast, the phalanx already seems to have been fused with the carpometacarpus [13].

The phalanx proximalis digiti majoris exposes its dorsal surface. Unlike in crown group Sphenisciformes, the bone is not dorsoventrally flattened, and it is furthermore craniocaudally wider and less elongated than in extant penguins. The phalanx proximalis digiti majoris of CM 2018.124.4 is also craniocaudally wider than that of the recently described *Kupoupou stilwelli* from the late early to middle Paleocene of Chatham Island. Whereas the phalanx proximalis digiti majoris has an essentially flat surface in crown group Sphenisciformes, it exhibits a shallow fossa dorsalis and a pila cranialis in the fossil. The facies articularis metacarpalis is a shallow cotyla. The phalanx distalis digiti majoris is likewise barely flattened and has a similar shape to the corresponding phalanx of volant birds.

The phalanx digiti minoris is not greatly elongated as it is in extant penguins, in which it surpasses the phalanx proximalis digiti majoris in length. In CM 2018.124.4 this phalanx measures only 50% of the length of the phalanx proximalis digiti majoris. Even though this phalanx is also proportionally shorter in Eocene and Oligocene stem group Sphenisciformes, it already measures 60% of the length of the phalanx proximalis digiti majoris in *Kairuku grebneffi* [13] and 65% in *Icadyptes salasi* [12]. Unfortunately, the bone surface of the phalanx is damaged in the fossil, so that further details were not clearly visible. Unlike in *Kupoupou stilwelli*, however, the caudal margin of the bone does not form a proximally directed process (see [9] (figure 6)).

Osteological details of the carpal bones were not well visible in the fossil. The os carpi ulnare (Figure 1A–C) is proportionally smaller and less flattened than in crown group Sphenisciformes, in which it forms a large, plate-like structure of subtriangular shape. The os carpi radiale is situated between the distal end of the ulna and the os carpi ulnare (Figure 4) and no details of its morphology are discernible.





**Figure 4.** Neutron tomography-based reconstruction of the right wing of CM 2018.124.4 (cf. *Muriwaimanu tuatahi*). Abbreviations: cmc, carpiometacarpus; hum, humerus; min, phalanx digiti minoris; ocr, os carpi radiale; ocu, os carpi ulnare; pda, phalanx digiti alulae; pdm, phalanx distalis digiti majoris; ppm, phalanx proximalis digiti majoris; rad, radius; uln, ulna. The scale bar equals 50 mm.

Elements of the pelvic girdle preserved in the specimen include the synsacrum and the caudal portion of the left side of the pelvis. A synsacrum is also part of the *M. tuatahi*-type material [5] and in CM 2018.124.4 it consists of 12 or 13 fused synsacral vertebrae. As far as comparisons are possible, the pelvis closely resembles that of *Waimanu manneringi* [5]. As in crown group Sphenisciformes, the ilium and synsacrum are not co-ossified.

Whereas the femur is preserved in the *Muriwaimanu tuatahi* fossils described in the original description of the species [5], the tibiotarsus has not yet been described. In its proportions and the shapes of the proximal and distal ends, the tibiotarsus of CM 2018.124.4 resembles that of *Waimanu manneringi* and *Sequiwaimanu rosieae*. However, a notable feature of the new fossil is the fact that the distal end of the fibula is co-ossified with the tibiotarsus, which does not occur in extant penguins and has not been reported from any other fossil sphenisciform taxon.

As in other Paleocene stem group Sphenisciformes, no patella is preserved in CM 2018.124.4. This is particularly notable, because the right femur and tibiotarsus are preserved in close association and appear to have been embedded in an articulated state.

#### 4. Discussion

The new Paleocene stem group penguin CM 2018.124.4 (cf. *Muriwaimanu tuatahi*) has a more plesiomorphic wing morphology than all geologically younger Sphenisciformes, of which the corresponding wing bones are known. In particular, the alular phalanx is well developed and the phalanges of the major digit are not flattened so that the bones of the hand section of CM 2018.124.4 are strikingly similar to those of volant birds. Even though the greatly abbreviated ulna and radius and the thickened bone walls of the major limb elements clearly show that the fossil species already lost its flight capabilities, it must have used its wings in a different way than extant penguins.



Penguins are the only avian group in which a phalanx for the alular digit is absent. Ontogenetic evidence suggests that this phalanx is co-ossified with the carpometacarpus, and from the presence of a facies articularis alularis of the carpometacarpus it was concluded that some stem group Sphenisciformes had a free alular phalanx [12]. However, the actual development of this phalanx in early Cenozoic penguins remained unknown and in juvenile crown group Sphenisciformes it is a vestigial, splint-like rudiment (see [12] (figure 15)). CM 2018.124.4 not only provides the first direct evidence for the presence of a freely movable phalanx digiti alulae in stem group Sphenisciformes, but also reveals that this phalanx is of similar length and proportions to that of volant birds with a functional alula.

In flying birds, the alula functions as a vortex generator at high angles of attack, especially during start and landing [21,22]. In all extant birds except penguins, the alular phalanx bears well-developed feathers and usually there are four alular remiges [23]. The well-developed alular phalanx of CM 2018.124.4 suggests the presence of such remiges since the bone is unlikely to have maintained its full length if the alula feathers were greatly reduced. In turn, this indicates that the wing feathers of at least the hand section of the fossil species were differentiated into functional groups and were distinguished from the short, scale-like feathers of crown group Sphenisciformes. The close resemblance of the phalanges of the major wing digit (phalanx proximalis digiti majoris and phalanx distalis digiti majoris) to the corresponding wing elements of volant birds also suggests that the primaries of the fossil species were better developed than in extant penguins.

Based on the morphology of the articular surfaces of the distal end of the ulna, it was hypothesized that the wings of Paleocene stem group Sphenisciformes could be folded to a greater degree than those of extant penguins and did not form stiff flippers [6]. This assumption appears to be supported by the fact that the wrist of CM 2018.124.4 is preserved in a deflected position, with the hand section forming an angle of almost 90° with the ulna (Figures 1A and 4). Such a high degree of flexion is not possible in crown group Sphenisciformes, in which the longitudinal axis of the hand section is much more in line with that of the humerus and ulna (Figure 3D). Certainly, however, some caution is appropriate in the interpretation of the relative position of the wing bones of the fossil, which were embedded in an advanced state of decay.

In any case, we conclude that *Muriwaimanu*-like stem group Sphenisciformes did not yet have flippers and differed from extant Sphenisciformes in wing beat kinematics. As in auks, the hand section of Paleocene stem group Sphenisciformes was probably kept in a flexed position during the propulsive stroke, whereas it is extended in penguins [1,24]. In the proportions of the ulna, radius, and the bones of the hand section, the wing of CM 2018.124.4 most closely resembles the extinct Great Auk, *Alca impennis* (Alcidae, Figure 3C). In this flightless species, the ulna and radius are greatly abbreviated, but the distal wing elements do not differ from those of volant auks in their proportions. With regard to its humerus morphology, *Muriwaimanu* is distinct from *A. impennis* and other Alcidae and exhibits the characteristic derived features found in other penguins, including a globose humerus head and a very large pneumatic foramen.

*Muriwaimanu tuatahi* is one of the oldest and, phylogenetically, most early-diverging stem group representatives of the Sphenisciformes known so far [3,5,6]. The new fossil is about 23–24 million years older than previously known penguin wings with sufficiently complete distal sections, that is, fossils of *Anthropornis* and *Icadyptes* from the late Eocene (36 Ma) of Antarctica and Peru, respectively [10,11]. In these taxa, the hand section already shows the flipper-like morphology characterizing the crown group representatives, which suggests that the distinctive paddle-shaped wing of penguins evolved between the late Paleocene and the late Eocene.

It is not unexpected to find a plesiomorphic wing morphology in one of the earliest penguins. However, it is less trivial to scrutinize the reasons for the presence of highly advanced flippers in all geologically younger species. There were, and still are, other evolutionary successful groups of wing-propelled diving birds with forelimb morphologies similar to that of *Muriwaimanu*, such as auks and the extinct penguin-like Plotopteridae, which occurred in the North Pacific from the late Eocene to the early Miocene [4]. Accordingly, there must have been strong selective forces in the evolution

of penguins, which shaped their forelimb morphology and led to the extinction of species with less specialized wings.

The small, scale-like feathers of extant penguins have an insulating function [25]. Hence, it is conceivable that a reduction of the distal forelimb muscles as well as the formation of a uniformly feathered integument constitute adaptations for foraging in cold waters, because it is energetically favorable to concentrate muscle mass near the trunk in order to minimize heat loss through the vasculature supplying these muscles. However, with more specialized, and more “modern-type” wings being present in the ca. 35 million-years-old *Icadyptes* and *Anthropornis*, the evolution of a penguin flipper seems to have preceded the formation of the Antarctic Circumpolar Current, which induced cooling of the sea surface temperatures and is dated at about 33–34 million years ago [26]. Even though the flipper-like penguin wing may well constitute an exaptation for survival in cold climates, we concur with previous observations [27] that climatic cooling of the Antarctic Region was probably not a major driver in its formation.

The differences in the shape and orientation of the caudal end of the mandible as well as the absence of a retroarticular process indicate that Paleocene stem group Sphenisciformes had a different feeding ecology than more crownward penguins. This is also suggested by the fact that CM 2018.124.4 and other early Cenozoic stem group Sphenisciformes featured extremely long and pointed beaks [6,11]. Possibly, there existed a functional correlation between the length of the beak and the shape of the caudal end of the mandible (which is unknown in other long-beaked species), and it was assumed that the diet of early Cenozoic Sphenisciformes included larger prey items than those taken by crown group penguins [3]. A transition in the feeding ecology of penguins may have been related to the formation of the Antarctic Circumpolar Current, which was critical for the evolution of notothenioid fishes and krill [28,29], both of which today constitute a major part of the diet of Antarctic and Subantarctic penguins. However, long, spear-like beaks occur in penguins with flipper-like wings, such as *Icadyptes* [11], so that differences in foraging strategies probably did not account for the transformation of the forelimbs into stiff paddles.

In extant penguins, the feet only have a steering function in subaquatic locomotion, but the very long fibula of CM 2018.124.4, whose distal end is co-ossified with the tibiotarsus, suggests that the legs of Paleocene stem group Sphenisciformes played a greater role in aquatic locomotion. Fusion of the distal end of the fibula and the tibiotarsus is a characteristic feature of birds with a strongly developed leg musculature and, in addition to raptorial birds, it occurs in foot-propelled divers, such as the Phalacrocoracidae. That Paleocene stem group Sphenisciformes may have used their feet for underwater locomotion was also deduced by earlier authors from the morphology of the tarsometatarsus of these birds [3,6]. The formation of a flipper-like forelimb may have been correlated with a diminished importance of the hindlimbs in subaquatic propulsion and it is well possible that the stem species of penguins used both its wings and hindlimbs for underwater locomotion, as do extant Sulidae [30].

Finally, we note that the first occurrences of more specialized (more “modern-type”) penguin flippers coincided with those of the earliest stem group cetaceans in the Southern Hemisphere, which were reported from the middle Eocene of Antarctica and Peru [31,32]. These toothed species may well have preyed on penguins and it is conceivable that dispersal of stem group cetaceans into the Subantarctic and Antarctic regions resulted in an increased selective pressure on the escape strategies of penguins. However, if predation pressure by cetaceans played a role in the evolution of the penguin flipper, it is difficult to understand why pteropterids and auks, with less specialized, *Muriwaimanu*-like wings, coexisted with cetaceans in the North Pacific [33]. Earlier analyses did not identify a correlation between the diversity of stem group cetaceans and stem group penguins [33], but the fossil record of both groups is continuously improving for the Subantarctic and Antarctic regions and future studies may provide new insights into competitive interactions.

Even though it is not possible to identify a single evolutionary driver for the evolution of paddle-shaped wings in penguins, the wing of CM 2018.124.4 documents an early stage in the evolution

of wing-propelled diving in penguins. As such, the specimen will be of significance in future studies addressing the evolution of one of the most aberrant forelimb morphologies found in birds. Other Paleocene stem group Sphenisciformes from the Waipara Greensand probably had a similar wing morphology, even though future findings may eventually reveal species that are even closer to that of the flying ancestor of penguins.

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