

Review

# Evolutionary and Biogeographical History of Penguins (Sphenisciformes): Review of the Dispersal Patterns and Adaptations in a Geologic and Paleoecological Context

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**Abstract:** Despite its current low diversity, the penguin clade (Sphenisciformes) is one of the groups of birds with the most complete fossil record. Likewise, from the evolutionary point of view, it is an interesting group given the adaptations developed for marine life and the extreme climatic occupation capacity that some species have shown. In the present contribution, we reviewed and integrated all of the geographical and phylogenetic information available, together with an exhaustive and updated review of the fossil record, to establish and propose a biogeographic scenario that allows the spatial-temporal reconstruction of the evolutionary history of the Sphenisciformes, discussing our results and those obtained by other authors. This allowed us to understand how some abiotic processes are responsible for the patterns of diversity evidenced both in modern and past lineages. Thus, using the BioGeoBEARS methodology for biogeographic estimation, we were able to reconstruct the biogeographical patterns for the entire group based on the most complete Bayesian phylogeny of the total evidence. As a result, a New Zealand origin for the Sphenisciformes during the late Cretaceous and early Paleocene is indicated, with subsequent dispersal and expansion across Antarctica and southern South America. During the Eocene, there was a remarkable diversification of species and ecological niches in Antarctica, probably associated with the more temperate climatic conditions in the Southern Hemisphere. A wide morphological variability might have developed at the beginning of the Paleogene diversification. During the Oligocene, with the trends towards the freezing of Antarctica and the generalized cooling of the Neogene, there was a turnover that led to the survival (in New Zealand) of the ancestors of the crown Sphenisciform lineages. Later these expanded and diversified across the Southern Hemisphere, strongly linked to the climatic and oceanographic processes of the Miocene. Finally, it should be noted that the Antarctic recolonization and its hostile climatic conditions occurred in some modern lineages during the Pleistocene, possibly due to exaptations that made possible the repeated dispersion through cold waters during the Cenozoic, also allowing the necessary adaptations to live in the tundra during the glaciations.

**Keywords:** Aves; phylogenies; paleobiogeography; penguins; Sphenisciformes



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## 1. Introduction

Penguins (Aves, Sphenisciformes) constitute a group of birds that are exclusively marine and flightless. All the species present extreme anatomical and physiological modifications directly related with the diving habit and the adaptations to cold-temperature waters [1,2]. From an evolutionary point of view, there is consensus to include the Sphenisciformes along with other aquatic birds in Aequornithes, and within this clade they are closely related to the Procellariiformes [3–6]. More precisely, the origin of penguins would be linked to a flying ancestor that secondarily would have lost the ability to fly as they became

excellent divers capable of traveling long distances ([7] and numerous later contributions) and reaching extreme depths [1,2,8].

The Sphenisciformes would have originated at the ends of the Cretaceous [9–13] in Zealandia [14] or Te Riu-a-Māui (Māori) or Tasmantis, lands that emerge today as New Zealand. Their appearance and diversification would be closely related to the extinction of the large marine reptiles that played the role of top predators in the southern oceans [15]. Later, these niches became vacant and were occupied by other vertebrates such as penguins in the Southern Hemisphere ([16] and references therein). Although no Cretaceous penguins are known, the fossil record is consistent with this idea. The oldest records of penguins correspond to forms that are morphologically archaic [11,17–20] that probably acquired a great size, a non-pneumatic skeleton, a flattening of the wing bones constituting propelling blades for diving, and an incipient widening and shortening of the tarsometatarsus, during the lower Paleocene.

These and other specializations for wing-propelled diving are already present in the Paleocene species (*Kupoupou stilwelli*, *Waimanu manneringi*, *Sequiwaimanu rosieae*, *Kumimanu biceae*, *Muriwaimanu tuatahi*, *Crossvallia waiparensis*, and *Crossvallia unienwillia*), although in the Eocene, forms with more extreme morphophysiological specializations are evident. In this regard, features such as the development of a blood plexus in the wing are observed early in the evolution of penguins (see details in [21]). This acquisition allowed them better thermal regulation during cold-water forays [22,23], as did the presence of highly modified feathers transformed into scales that cover the wings and substantially improve hydrodynamic skills during diving [24].

An increase in body size and a greater adaptation for diving in cold water would have conferred an important adaptive advantage in this context, since a greater body size implies a greater diving capacity, both in terms of depth reached and the duration of the dive [25]. The maximum expression of body size was achieved in the Eocene, when *Palaeudyptes klekowskii* reached more than two meters in height [26]. Although there is no consensus about how the size of Paleogene penguins should be calculated, several cases of giant species have been reported in Antarctica, South America, New Zealand, and Australia, covering almost all the areas where penguins are recorded. Thus, penguins reached their apogee with many shapes and an incredible diversity of sizes [27].

It has been proposed that large and robust penguins would have arrived at the Peruvian coasts through two successive colonizations from different areas. The first spread, from Antarctica, would have occurred by the middle Eocene, whereas the second colonization, from New Zealand, would have occurred by the end of the Eocene. According to this proposal, based on the Eocene record of Peruvian penguins [24,28], the presence of Antarctic forms in the middle Eocene in Chile [29] and Argentina [30] is also explained. This stage does not extend beyond the Oligocene. It is not possible to determine the causes or the exact mechanisms that caused these faunal changes, but the diversity of diving birds is inversely proportional to the diversity of marine mammals, especially odontocetes cetaceans. Giant penguins were extinguished where marine mammals became successful as the top predators in the oceans [31]. A new stage in the evolution of the group begins in the Neogene, which includes the appearance of modern forms closely related to living species [32,33]. Taxonomic and morphological diversification in living species is notably less than what was known in the past, and post-Pliocene species are almost entirely attributed to modern genera [34,35].

An example of the transition that occurred during the Neogene is the avian assemblage of Horcón, on the central coast of Chile, which reflects the existence of a mixed fauna during the Pliocene, connecting the seabird associations of the late Miocene with the modern regional avifauna [36]. However, the Cenozoic history of penguins seems to have been somewhat more complex than previously believed. The current avifauna would be the result of a series of successive colonizations and extinctions closely linked to the establishment and development of the ocean currents and the ecological dynamics of

species [35,37]. A recent analysis identified New Zealand (either exclusively or with South America) as the most likely ancestral area for crown clade penguins [38].

Despite being a group with a low current diversity (18 species), considering the species known from the fossil record, the Sphenisciformes are one of the best-known avian clades, with about 65 recognized species [6,39]. Likewise, the phylogenetic relationships have led to the proposition of various phylogenetic hypotheses, which have been possible due to the good state of preservation of many fossils and the deep and widely comparative studies of the morphological features among the described lineages. In recent years, extensive morphological knowledge and the consolidation of molecular analysis techniques have allowed phylogenetic approaches to reconstruct the evolution of penguins by integrating extant and extinct forms [17,19,32,33,35,36,40–43].

Some approaches have generated hypotheses where the influence of events such as those that occurred during the Neogene on the biogeographic patterns and the evolution of the Sphenisciformes niche are reconstructed; however, many scenarios only consider the current species [35,43]. In this sense, the richness of the penguin fossil record [6] allows the possibility of considering and integrating all the available information to propose broader approximations in a deep time approach.

Thanks to the vast amount of information available on the presence of species during the Cenozoic in several locations of the Southern Hemisphere and modern biogeographic analyses methodologies, it is possible to reconstruct geographical scenarios of evolution over time and to understand the influence of environmental and geological changes on the diversification of penguins. In particular, BioGeoBEARS [44,45] analysis allows the reconstruction of ancestral areas in a context of maximum likelihood and employs Bayesian modeling from a calibrated phylogeny. Some previous contributions have dealt with this topic (e.g., [28,35,38]). We focus our review on detecting ancestral areas of origin and describing the paleobiogeographical patterns of the Sphenisciformes lineage based on a broad and complete analysis of the Sphenisciformes fossil record and the most recently published phylogenetic proposal based on the total evidence for the group [32]. This approach allows us to visualize the speciation, dispersal, and extinction events that would have occurred throughout their evolutionary history, shedding more light on how the environmental changes that occurred throughout the Cenozoic could have influenced the evolution and diversification patterns of penguins. This gives us the possibility of comparing our own results with the previous proposals.

## 2. Materials and Methods

### 2.1. Fossil Record and Penguin Phylogenies

According to the available scientific literature and the Paleobiology Database, we consolidated a new biogeographical and temporal matrix, considering all the records for penguin species (Table 1). In this way, we recorded the time intervals according to their chronostratigraphic distribution range and encoded the presence (1) or absence (0) of the species in each geographical area. It should be mentioned that although a single occurrence is the only data for some fossil species (e.g., *Crossvallia unienwillia*), the stratigraphical range provided in Table 1 corresponds to the age of the level where the fossil was collected. The same criterion applies for species with multiple records (e.g., *Palaeudyptes klekowskii*), in which the stratigraphical range corresponds to the ages of the levels where it was reported. For species with an uncertain age, due to the lack of a strict stratigraphic control (i.e., *Marplesornis novaezealandiae*), the range includes a different-ages proposal. Table 1 includes the source of the data.

**Table 1.** Updated checklist of the fossil penguin species of the world ( $n = 65$ ), their occurrences, and stratigraphical ranges (SR) (in some cases, only an approximation is provided, corresponding to the age of the level where the fossil was collected).

| Species                                   | Location                  | Epoch                | SR (Ma)   | Reference  |
|-------------------------------------------|---------------------------|----------------------|-----------|------------|
| <i>Kupoupou stikwelli</i>                 | New Zealand               | Paleocene            | 62.5–60   | [33]       |
| <i>Crossvallia waiparensis</i>            | New Zealand               | Paleocene            | ~61       | [20]       |
| <i>Muriwaimanu tuatahi</i> *              | New Zealand               | Paleocene            | 58–60     | [20]       |
| <i>Sequiwaimanu rosieae</i>               | New Zealand               | Paleocene            | ~61       | [19]       |
| <i>Waimanu manningi</i> *                 | New Zealand               | Paleocene            | 60.5–61.6 | [11]       |
| <i>Crossvalia unienwillia</i>             | Antarctica                | Paleocene            | 59.2      | [46,47]    |
| <i>Kumimanu biceae</i>                    | New Zealand               | Paleocene            | 60.5–61.6 | [17]       |
| <i>Kaika maxwelli</i>                     | New Zealand               | Eocene               | 55.8–49.3 | [48]       |
| <i>Perudyptes devriesi</i> *              | Peru                      | Eocene               | ~42       | [28,41]    |
| <i>Delphinornis gracilis</i> *            | Antarctica                | Eocene               | 41–34     | [49]       |
| <i>Delphinornis larsenni</i> *            | Antarctica                | Eocene               | 53–34     | [50]       |
| <i>Mesetaornis polaris</i> *              | Antarctica                | Eocene               | 53–34     | [49,51]    |
| <i>Anthropornis grandis</i> *             | Antarctica                | Eocene               | 53–34     | [52–54]    |
| <i>Anthropornis nordenskjöldi</i> *       | Antarctica                | Eocene               | 53–34     | [52,54]    |
| <i>Apros dokitos mikrotero</i>            | Antarctica                | Eocene               | 38–34     | [27]       |
| <i>Marambiornis exilis</i> *              | Antarctica                | Eocene               | 53–34     | [49,54]    |
| <i>Delphinornis arctowskii</i> *          | Antarctica                | Eocene               | 38–34     | [49,54]    |
| <i>Delphinornis wimani</i> * <sup>a</sup> | Antarctica                | Eocene               | 53–34     | [49,54]    |
| <i>Icadyptes salasi</i> *                 | Peru                      | Eocene               | 37.2–35.7 | [28]       |
| <i>Inkayaku paracacensis</i> *            | Peru                      | Eocene               | 37.2–35.7 | [24]       |
| <i>Marambiornopsis sobrali</i>            | Antarctica                | Eocene               | 37.8–41.1 | [51]       |
| <i>Pachydyptes ponderosus</i> *           | New Zealand               | Eocene               | 36–30     | [55]       |
| <i>Pachydyptes simpsoni</i>               | Australia                 | Eocene               | 38–36.5   | [56]       |
| <i>Palaeudyptes antarcticus</i> *         | New Zealand               | Eocene–Oligocene     | 38–28     | [42]       |
| <i>Palaeudyptes marplei</i>               | New Zealand               | Eocene               | 38–34     | [42]       |
| <i>Tommiornis mesetaensis</i>             | Antarctica                | Eocene               | 37.8–34   | [54,57]    |
| <i>Tommiornis minimum</i>                 | Antarctica                | Eocene               | 37.8–34   | [54,57]    |
| <i>Palaeudyptes gunnari</i> *             | Antarctica                | Eocene               | 55–34     | [30,54,58] |
| <i>Palaeudyptes klekowskii</i> *          | Antarctica                | Eocene               | 52–34     | [54,58,59] |
| <i>Kairuku waeawaeroa</i>                 | New Zealand               | Oligocene            | 34–27.3   | [60]       |
| <i>Archaeospheniscus lopdelli</i> *       | New Zealand               | Oligocene            | 27–25     | [55]       |
| <i>Archaeospheniscus lowei</i> *          | New Zealand               | Oligocene            | 27–25     | [55]       |
| <i>Kairuku grebneffi</i> *                | New Zealand               | Oligocene            | 27.3–25.2 | [42]       |
| <i>Kairuku waitaki</i> *                  | New Zealand               | Oligocene            | 27.3–34.5 | [42]       |
| <i>Korora oliveri</i>                     | New Zealand               | Oligocene            | 25–24     | [55]       |
| <i>Pakudyptes hakataramea</i>             | New Zealand               | Oligocene            | 25–24     | [55]       |
| <i>Platydyptes amiesi</i>                 | New Zealand               | Oligocene            | 26–24     | [55]       |
| <i>Platydyptes marplei</i> *              | New Zealand               | Oligocene–Miocene    | 27–22     | [55]       |
| <i>Platydyptes novaezealandiae</i> *      | New Zealand               | Oligocene            | 26–24     | [55]       |
| <i>Duniroornis parvus</i> *               | New Zealand               | Oligocene–Miocene    | 27–24     | [55]       |
| <i>Paraptenodytes robustus</i>            | Argentina                 | Oligocene–Miocene    | 25–22     | [61,62]    |
| <i>Arthrodytes andrewsi</i>               | Argentina                 | Oligocene–Miocene    | 25–22     | [61,62]    |
| <i>Eretiscus tonni</i> *                  | Argentina                 | Miocene              | 23–20.44  | [63]       |
| <i>Palaeospheniscus bergi</i> *           | Argentina                 | Miocene              | 23–20.44  | [64]       |
| <i>Palaeospheniscus biloculata</i> *      | Argentina                 | Miocene              | 23–20.44  | [65]       |
| <i>Palaeospheniscus patagonicus</i> *     | Argentina                 | Miocene              | 23–20.44  | [66]       |
| <i>Paraptenodytes antarcticus</i> *       | Argentina                 | Miocene              | 23–20.44  | [61]       |
| <i>Anthropodyptes gilli</i>               | Australia                 | Miocene              | 21–17.6   | [67]       |
| <i>Spheniscus muizoni</i> *               | Peru                      | Miocene              | 13–11     | [68]       |
| <i>Spheniscus urbinai</i> *               | Argentina, Chile,<br>Perú | Miocene              | 23–5      | [69]       |
| <i>Madrynornis mirandus</i> *             | Argentina                 | Miocene              | 11.4–9    | [70,71]    |
| <i>Pygoscelis calderensis</i>             | Chile                     | Miocene              | ~7.6      | [69,72]    |
| <i>Marpleornis novaezealandiae</i> *      | New Zealand               | Miocene–Pliocene     | 12.7–2.4  | [55]       |
| <i>Spheniscus megaramphus</i> *           | Chile, Peru               | Miocene–Pliocene     | 11.6–3.6  | [73,74]    |
| <i>Pseudaptenodytes macraei</i>           | Australia                 | Miocene–Pliocene     | 6.2–5     | [75]       |
| <i>Dege hendeyi</i>                       | South Africa              | Pliocene             | 5.3–3.6   | [76]       |
| <i>Inguza predemersus</i>                 | South Africa              | Pliocene             | 5         | [77]       |
| <i>Nucleornis insolitus</i>               | South Africa              | Pliocene             | 5         | [77]       |
| <i>Eudyptula calauina</i>                 | Chile                     | Pliocene             | 3.6–2.6   | [36]       |
| <i>Spheniscus chilensis</i>               | Chile                     | Pliocene             | 3.6–2.6   | [78]       |
| <i>Eudyptes atatu</i>                     | New Zealand               | Pliocene             | 3.3–3     | [38]       |
| <i>Tereingaornis moisleyi</i>             | New Zealand               | Pliocene             | 3–4       | [55]       |
| <i>Pygoscelis grandis</i> *               | Chile                     | Pliocene             | 5.3–3.6   | [67]       |
| <i>Pygoscelis tyreei</i>                  | New Zealand               | Pliocene–Pleistocene | 4–2       | [55]       |
| <i>Aptenodytes ridgeni</i>                | New Zealand               | Pliocene–Pleistocene | 4–2       | [55]       |

\* Species included in the paleobiogeographical analyses. <sup>a</sup> We agree with Jadwiszczak [52,78] regarding the prematurity of the new combination *Delphinornis wimani* [41] for a species that already transferred from *Notodyptes* to *Archaeospheniscus* [79]. However, we maintain the new name for this table in accordance with the phylogeny on which we have based our biogeographical analyses [32].

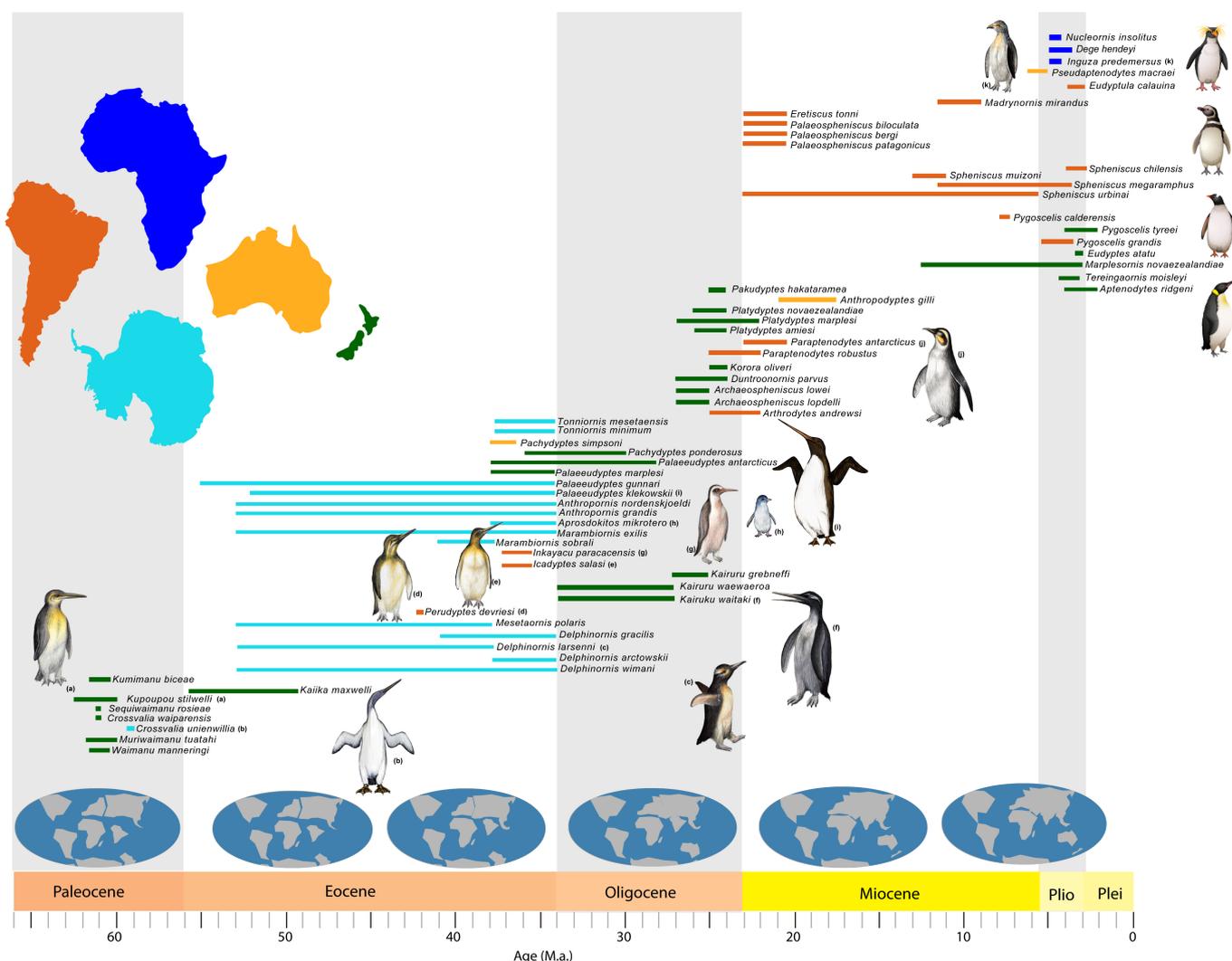
Data from 83 species (18 living and 65 fossil ones) were obtained. Given the need for a completely resolved and calibrated phylogeny to perform the BioGeoBEARS analysis, a review of the latest phylogenies proposed for Sphenisciformes was carried out. After considering the number of species included, the consistency of the calibrated ages, the degree of resolution, and the integration of multiple information sources, we applied the Bayesian total evidence phylogeny proposed by Gavryushkina et al. [32]. Another proposal, the Bayesian Markov Chain Monte Carlo (MCMC) framework for phylogenetic analysis, takes an extensive data source from molecular sequences derived from extant species and morphological traits from extant and fossil species. It also considers the stratigraphic intervals as the fossil occurrences. The phylogenetic proposal of Gavryushkina et al. considers the evolutionary affinities of penguins according to 202 morphological characters [42] derived from reasonably complete fossil specimens ( $n = 36$ ), together with molecular and morphological information from the 18 living species [32]. With this input, this approach estimates and dates species phylogenies. The Bayesian method integrates the fossil information under a new perspective, unlike other methods that only use fossils to calibrate nodes or established origin intervals. For our purposes, we used the maximum sampled-ancestor clade credibility tree (the MSACC tree). This tree is a summary tree derived from a posterior sample that maximizes the product of posterior clade probabilities (see details in [80], cited in [32]). Other biogeographical proposals discussed below are based on different phylogenetic approaches [38,43] and references cited therein).

## 2.2. Species Considered in the Present Analysis

The description of the first fossil penguin was followed by a great proliferation of new genera and species, which after some years were re-evaluated and, in many cases, dismissed or considered as synonyms. This work took, as a starting point, a complete review of the fossil record for the Sphenisciformes lineage (Table 1, Figure 1). Even though the list of penguin fossil species is much more extensive, rigorous analyses carried out over recent decades have established long synonymic lists of species and genera that are no longer considered valid. Table 1 follows the taxonomic arrangements proposed for Argentinian [63–71], Chilean [67,69,72,73,78,81], Peruvian [24,28,41,57,69,73], Antarctic [27,49–54,57–59], New Zealand [11,17,19,20,33,38,42,48,55,60], Australian [56,67,75], and African [76,77] taxa. This compilation is essential to obtain complementary information for the discussion and the palaeoecological analysis.

A particular case worth commenting on is that of *Eudyptula*. In this work, the traditional and most widely analyzed proposal, in which *Eudyptula minor* would be the only modern species of the genus *Eudyptula*, was adopted as input for the present analysis. According to that proposal, the diversity of *Eudyptula* forms is reflected in the six subspecies inhabiting Australia and New Zealand [2,82]. Other more recent proposals consider that *Eudyptula* would be constituted by *E. minor* and *E. novaehollandiae*, species of recent divergence [83,84] that have been accepted as such by the ornithological community [85]. The inclusion of *Eudyptula* as the only living species does not modify or bias our results. Further, the incorporation of extinct species was constrained by several additional factors, including taxonomic status, given that some taxa are currently synonyms or have been considered non-valid taxa in subsequent revisions, and their previous inclusion in a phylogeny.

On the other hand, *Spheniscus anglicus*, a species described from materials that presumably come from the Miocene Bahía Inglesa Formation of Chile [86], was excluded from this analysis due to serious irregularities. The material was bought and removed the country illegally, violating the laws for the protection of the paleontological heritage in Chile. In this context, the species' geographical and stratigraphic origin is not reliable. In addition, the characters used for its diagnosis are not adequate, and the proposal of a new species is unjustified. For these reasons, we decided to exclude *S. anglicus* from our analysis, a species that has never been listed or considered in any of the subsequent specialized scientific publications.



**Figure 1.** Updated chronostratigraphic distribution of fossil penguins of the world ( $n = 65$ ). Follow color key to geographical occurrence (see Table 1 for details): (a–k) indicates the species of penguin illustrations. On the right side (bottom-up), the living forms *Aptenodytes forsteri*, *Pygoscelis papua*, *Spheniscus magellanicus*, and *Eudyptes chrysolophus* are representatives of each genus. Penguins not at scale. Penguin illustration credits: Jacobo Sabogal.

In short, despite not being included in the present biogeographical analysis, the information derived from all the species was not included in phylogenetic proposal of Gavryushkina et al. [32], which provided complementary information on the presence and diversity in the continental areas considered, allowing the enrichment of aspects of the discussion. The details of the fossil species considered here, and those included in our analysis, are provided in Table 1.

### 2.3. Paleobiogeographical Analyses

The biogeographic regions established for the analysis were chosen based on the extant and ancient distribution of Sphenisciformes species, as well as on geological and climatic criteria. Thus, we established six biogeographic regions or areas: north-central South America, including Galapagos (from 23° S), southern South America, southern Africa, Antarctica, Australia, and New Zealand, unlike the nine [28], ten [35], or the twelve [38] areas included in other contributions. For analysis, we proposed a flexible scenario for the dispersal events among the various study areas. This criterion was determined by the proximity and distances among the six areas and their geological histories linked to the

fragmentation and drift of Gondwana since the Cretaceous and, later, during the Paleogene and the Neogene [87,88]. These drift processes triggered the oceanographical evolution of marine currents [89], which are key factors in the dispersal possibilities for penguins. Likewise, the possibilities for the colonization of areas were established based on the long-distance swimming characteristics observed in current penguins, which were presumably present in Paleogene forms according to fossil distribution since the Paleogene [33]. Given the outstanding dispersal and marine movement capacity reflected in modern species, as well as the Southern Hemisphere distribution of the fossil and modern species, a matrix of the probability of colonization was adjusted to 1 with respect to the studied areas.

In accordance with the BioGeoBEARS analysis [44], we carried out the evaluation of three models: Dispersal—Extinction Cladogenesis (DEC); a likelihood version of the Dispersal—Vicariance model (DIVALIKE); and a likelihood version of the BayArea model (BAYAREALIKE). The DEC model considers and emphasizes changes in the range of distribution in speciation events (cladogenesis). Under that model, during events a descendant lineage will always occupy a single region of the ancestral area, considering sympatry or vicariance. The DIVALIKE model allows a daughter lineage to retain more than a single geographical region of ancestral occupation during the vicariant event. This model does not allow a daughter lineage to inherit a small rank that is sympatric to the rank of another descendant lineage. Conversely, the BAYAREALIKE model does not emphasize geographic range variation at speciation events; instead, it estimates range changes along speciation events through range expansion—contraction dynamics. We assessed these models including the Jump-dispersal (+J) parameter [44,90]. This parameter allows evolutionary founding events, where an emerging novel lineage disperses outside of the area(s) occupied by its ancestor during the speciation process.

All the models were compared, considering the *p*-value for the LRT (Likelihood Ratio Test) and the value of the AIC for each evaluated scenario [91]. The estimation models using the methodologies derived from BioGeoBEARS have been applied to various bird taxa, and despite receiving criticism for the inclusion of the parameter J (the founder effect) [92], these models have been reevaluated, reinforcing, and supporting the validity of the models [93]. Thus, we incorporated founder-event speciation (+J), which results in a process that is important in island systems for birds, considering the importance of transcontinental colonization events during different bird clades diversification, and especially for penguins [35]. Specifically, models that included the +J parameter have been broadly consistent in explaining the colonization processes in biogeographic and macroevolutionary studies. Examples are the contributions on several lineages of modern birds, including the Megapodidae family within Galliformes [94], Thraupidae (Coerebinae) [90], Motacillidae [95], Coraciiformes [96], Trogoniformes [97], Rallidae [98], and those studies on fossil lineages, such as Coelurosauria clade [99], and mammals, such as horses (Equinae) [100]. With particular reference to penguins, previous works analyzed the crown group species [35] as well as fossil representatives [38]. In line with these works and the life-history traits of penguins, we considered that the +J parameter would be associated with Sphenisciformes macroevolutionary process, due to the remarkable oceanic dispersion capacity evidenced by modern and ancient forms [77,101,102]. The statistical analyses were performed using the software RASP powered by R software [103].

### 3. Results and Discussion

#### 3.1. Paleogene History of Penguins

According to the results obtained here, the best model was the BAYAREALIKE + J, which provided the statistical support with the lowest AICc value and the highest AICw, compared to the other models (Figures S1–S6, Tables 2 and S1); there are significant differences between the BAYAREALIKE + J and BAYAREALIKE model scenarios (Table S2). Similar results were obtained in previous contributions [38], although in other analyses the selected model was DIVALIKE + J [35]. As we expected, our results confirmed the relevance of the +J parameter (founder events) to explain the biogeographical history

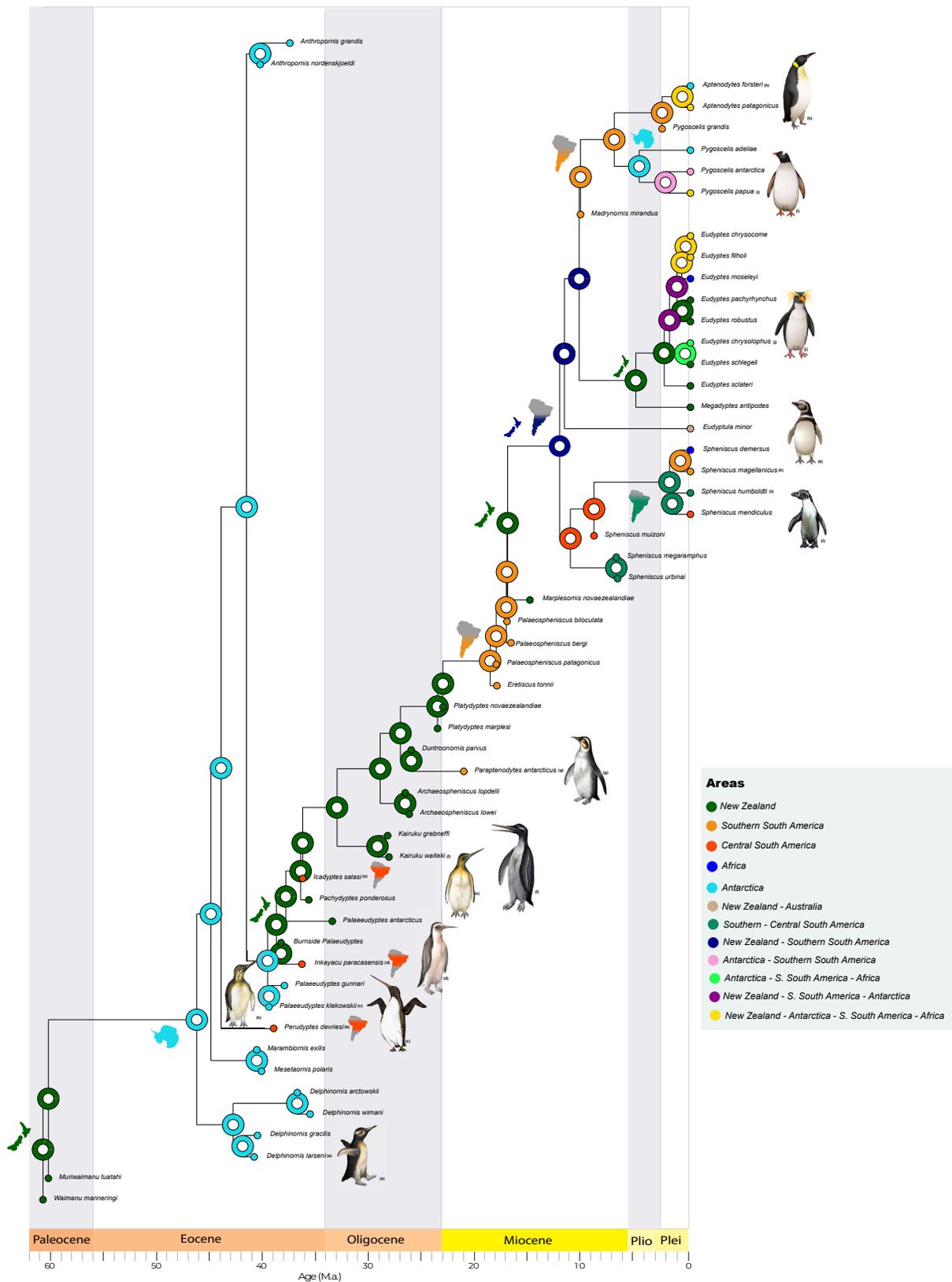
of penguins, a clade with a presumably well-established dispersal capacity due the early development of adaptive traits to navigate across marine environments; this is supported by the analyses of Paleogene forms, including those of *Waimanu* [11]. In addition, the BAYAREALIKE + J, as a better model, provides support for the importance of geographical expansion–contraction dynamics to explain the evolutionary patterns of Sphenisciformes. The Cenozoic cooling trends triggered many biotic expansions–contractions in Southern Hemisphere continents, which influenced the dispersal processes and possibly the speciation and extinction patterns.

**Table 2.** Summary of results for all six models evaluated under the six-area regime. Models with +J indicate those allowing for founder effect dispersals. The best-supported model is shown in bold. *p* is the number of parameters.

| Model                  | LnL           | <i>p</i> | AICc         | AICc wt.              |
|------------------------|---------------|----------|--------------|-----------------------|
| DEC                    | −139.9        | 2        | 284          | $2.6 \times 10^{-6}$  |
| DEC + J                | −133          | 3        | 272.5        | $8 \times 10^{-4}$    |
| DIVALIKE               | −151.4        | 2        | 307.1        | $2.5 \times 10^{-11}$ |
| DIVALIKE + J           | −143.7        | 3        | 294          | $1.8 \times 10^{-8}$  |
| BAYAREALIKE            | −150.2        | 2        | 304.6        | $8.9 \times 10^{-11}$ |
| <b>BAYAREALIKE + J</b> | <b>−125.9</b> | <b>3</b> | <b>258.3</b> | <b>1.00</b>           |

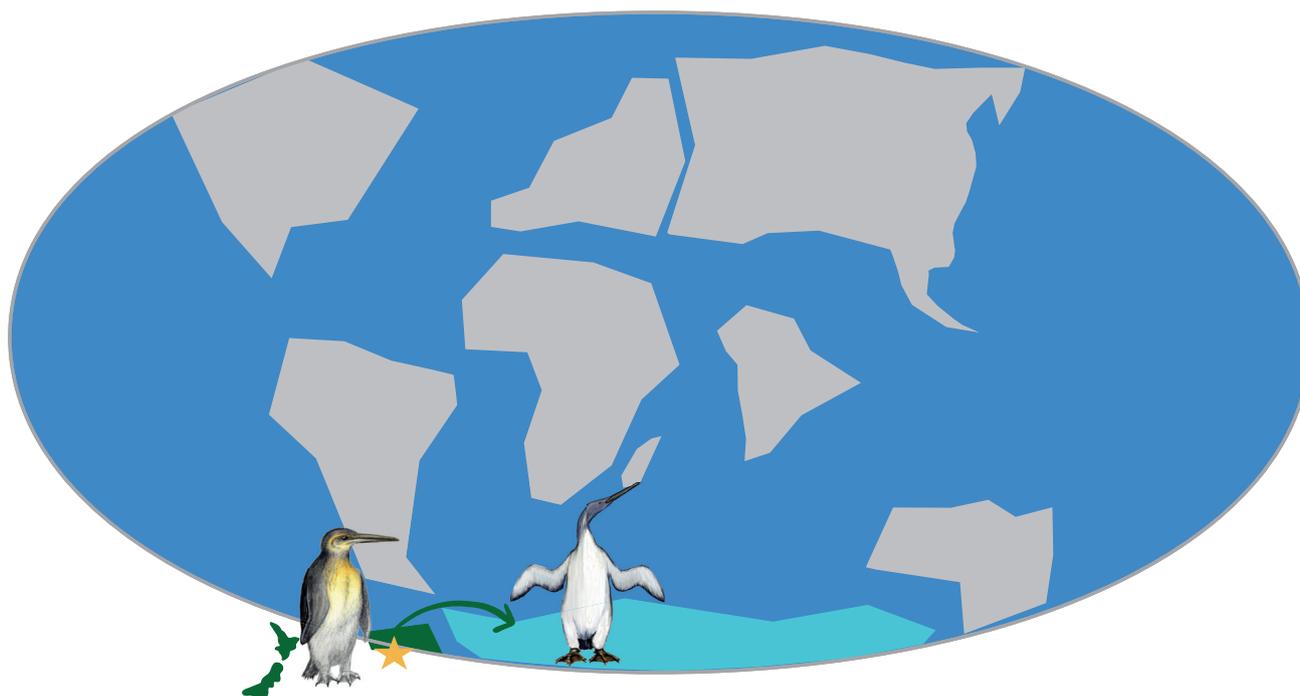
In general terms, all the models pinpoint and concur with a center of origin for Sphenisciformes in New Zealand (Figures S1–S6). These results are consistent with previous estimates based on fossil findings, which also estimate the origin of the lineage towards the late Cretaceous [9–13]. This is a logical proposal given the high diversification and specialization already present in the Paleocene. The oldest records for penguins correspond to the Paleocene and are concentrated in New Zealand [17–20,104].

The results of our analysis pinpoint New Zealand as the most likely ancestral area, and secondly points to Antarctica with slightly lower probabilities (Figure 2; see the Supplementary Materials for details). It is noteworthy that New Zealand’s importance as a center of origin is strongly supported by a high concentration of records, many of them being the oldest penguin records reported to date [6,19,20,104] (Figure 1, Table 1). It should be noted that New Zealand’s geographical proximity to the Antarctic territory during the Upper Cretaceous and the early Paleogene provides some evidence of the significance of both continents during the initial diversification of the group. Findings for the Chatham Islands, and specifically associated with the Takatika Grit, show that since the Upper Cretaceous (c.83–79 Ma) Zealandia began to present a progressive rupture with respect to West Antarctica [14,87,105], continuing until the Eocene with respect to the eastern Antarctic region [106]. At the end of this stage, Zealandia would have experienced a strong marine transgression [107,108]. This process might explain the notable radiation and rapid diversification of penguins during the Eocene for Antarctica, as compared with New Zealand. The abundant fossil record of Seymour Island (Antarctica) strongly supports this idea. In this sense, the wider Antarctic territory would have offered greater opportunities, in terms of colonization of new niches and thus the generation of diverse processes of speciation, due to geographic isolation.



**Figure 2.** Ancestral range estimation for Sphenisciformes based on results of high percentages for nodes considering the BAYAREALIKE + J scenario and using the six-area regime as shown in map of biogeographic areas powered in BioGeoBEARS. (a–l) indicates the species of penguin illustrations. Follow the color key for the cases of presence in more than one area. For details see the Supplementary Materials. Penguin illustration credits: Jacobo Sabogal.

Our results, like previous findings [28,38], allow us to postulate New Zealand as a probable main ancestral territory. In addition, it is important to consider the geographical proximity between New Zealand and Antarctica during the Paleogene; both territories during the Paleocene-Eocene climatic optimum would have presented very similar environmental conditions at the continental level, with cold temperate environments that would have presented periods of fluctuation towards warm temperate climates during the Early Eocene Climatic Optimum (EECO). This would have made it possible to configure humid temperate forest biomes, with tropical floristic components during several Paleogene intervals [109–111]. Likewise, marine estimates show significant warming of Pacific waters from the upper Paleocene to the middle Eocene [46,112,113]. This paleoenvironmental context could have favored the dispersal between New Zealand and Antarctica, given the importance that oceanic temperatures possibly played for the dispersal of the first penguins. Added to this is the *Crossvallia* record in Antarctica and New Zealand, which further strengthened the links between these two large areas during the first million years of the group's evolution. *Crossvallia unienwillia* was a large penguin species, with a single record in the Paleocene of Seymour Island (Antarctica); due to the incompleteness of its skeleton, it has been repeatedly omitted from phylogenetic analyses. Its presence, however, indicates the presence of Sphenisciformes in Antarctica since the Paleocene [46,47]. *Crossvallia waiparensis* is the second species of *Crossvallia* that has been described for the Paleocene of New Zealand (Figure 3).

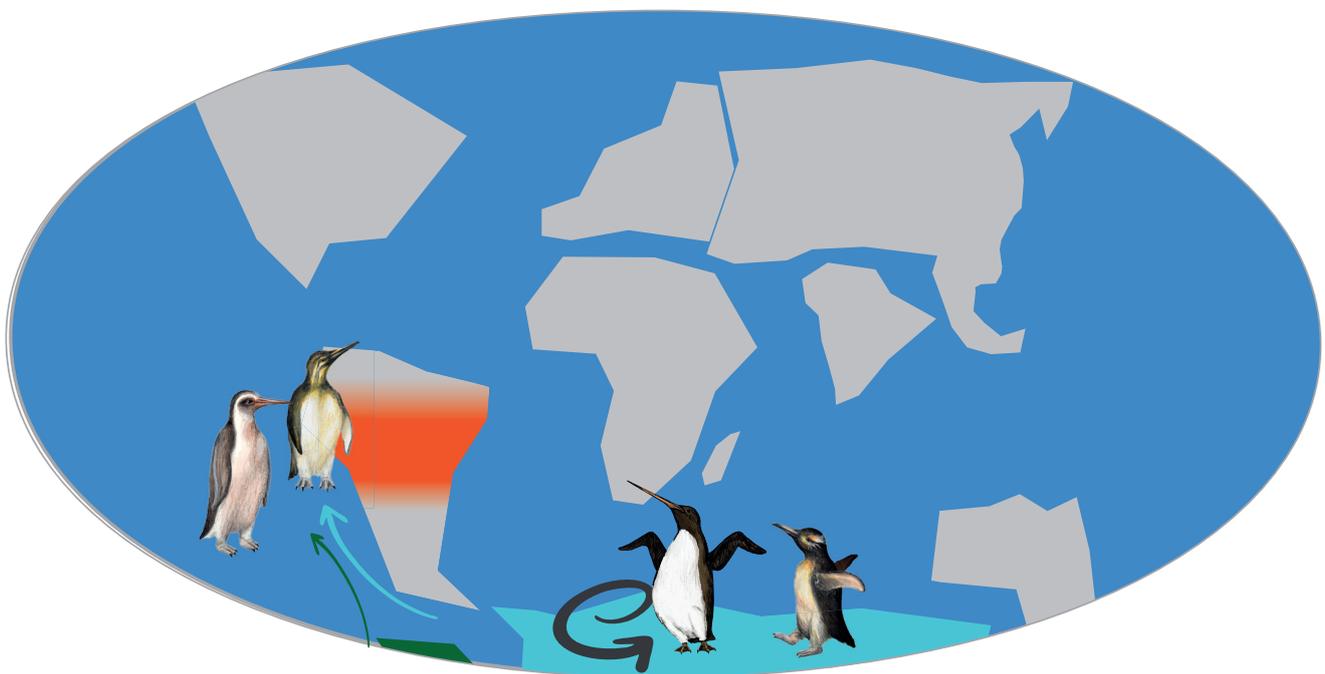


**Figure 3.** Middle-Late Paleocene biogeographical events: origin of Sphenisciformes in New Zealand (*Kupoupou stilwelli* in the image) and early dispersion to Antarctica, evidenced by the presence of *Crossvallia* (in the image).

The recent description of numerous taxa for the Paleocene of New Zealand indicates favorable conditions for the establishment and flourishing of the group. Although only two species of the genus *Waimanu* have been included (Figure 2), the New Zealand Paleocene sphenicofauna also includes other species such as *Kupoupou stilwelli*, *Crossvallia waiparensis*, *Sequiwaimanu rosieae*, and *Kumimanu biceae* (Figures 1 and 2). Although the Antarctic record is scarce during the Paleocene, this is probably due to a taphonomic bias rather than to regional environmental conditions, since the changes in the depositional environment of

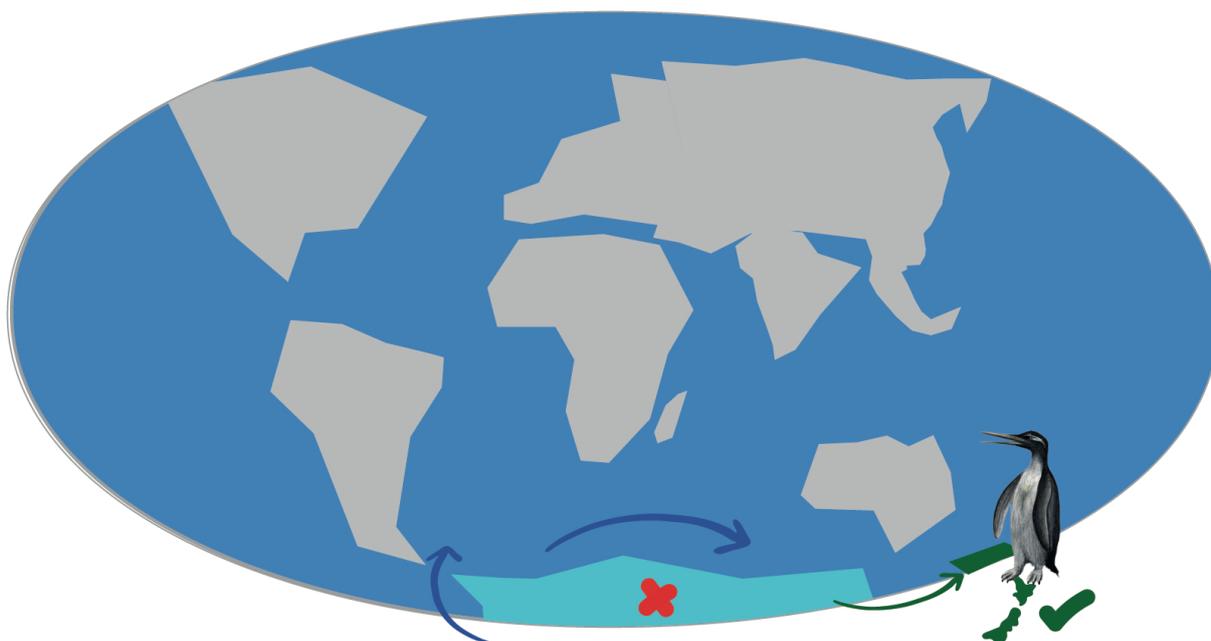
the James Ross Basin during the Eocene caused a more abundant and diverse penguin record [114].

During the middle Eocene, several lineages diversified in Antarctica, including forms of a wide spectrum of sizes, including some giant penguins such as *Anthropornis grandis* that reached 1.7 m high, and other tiny penguins such as *Aproskoditos microtero* that were only 0.35 m high. This shows great diversity, also evidenced in the number of species included in other genera, such as *Delphinornis*, *Tonniornis*, *Palaeudyptes*, and others (see Table 1). This broad diversity is probably associated with niche partitioning processes powered by the development of different bill morphologies and specializations in a wide range of trophic possibilities [115,116]. Among these taxa are the forms that reached the southern and central South American coasts, allowing the establishment of the *Perudyptes devriesi* lineages on the Peruvian coasts. The record of taxa typically Antarctic in southern South America during the middle Eocene [29,30] supports this hypothesis (Figure 4).



**Figure 4.** Main Eocene biogeographical events: the diversification of diverse Sphenisciformes lineages in Antarctica (i.e., *Palaeudyptes* and *Delphinornis* in the image) and early dispersal and colonization towards South America, evidenced by the presence of *Perudyptes* and *Incayacu* (in the image) and *Icadyptes*.

During the late Eocene and probably the early Oligocene, the Antarctic species would have completely disappeared. A highlighted diversification of the New Zealand lineages is evidenced at this time. Some colonizations in South America, such as those of *Icadyptes salasi* and *Inkayaku paracacensis*, are verified during the Eocene of Peru, and would be closely linked with the penguin fauna of New Zealand. According to our results, the three lineages (together with *Perudyptes devriesi*) would have independently colonized the subtropical Pacific coasts of South America during the late Eocene. These colonizations could be related with migrations produced by oceanic currents established from New Zealand to South America during the Eocene after the EEOC, with the opening of the Tasman Strait and the Drake Passage. The currents suffered notable alterations at the latitudinal level, ending in the establishment of the circum-Antarctic current, the main influencing factor in progressive Antarctic freezing during the Oligocene [117–119] (Figure 5).



**Figure 5.** Main Oligocene biogeographical events: the extinction of Sphenisciformes due to Antarctica cooling; New Zealand as a refuge and center of diversification, evidenced by the presence of many genera and species, such as the *Kairuku* (in the image).

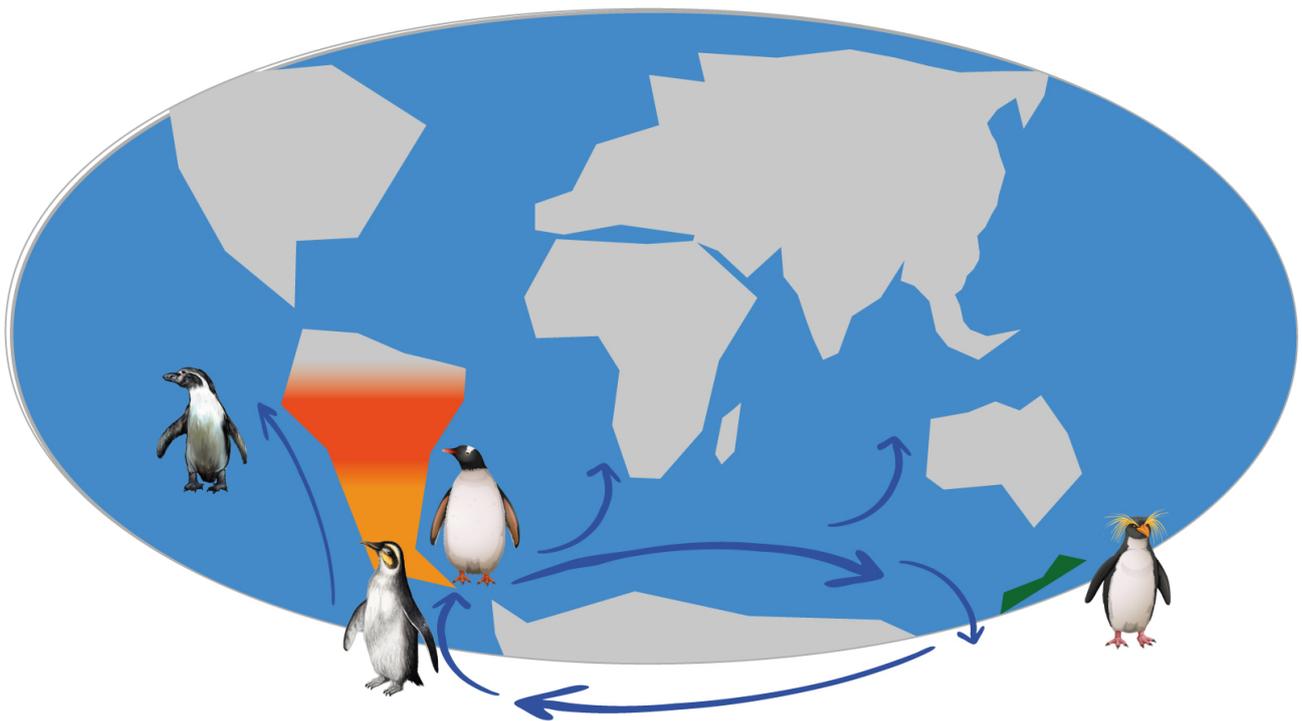
In this sense, we proposed that New Zealand could have played an important role as a refuge during the Oligocene for penguins that faced the climatic changes that transformed the Antarctic continent and the marine current regimes [117–120]. This idea is aligned with the presence of the Kaiika lineage, a taxa endemic to New Zealand [48], and the diversity of the genus *Kairuku* with three species recorded for the New Zealand Oligocene [60]. Likewise, *Palaeudyptes*, of presumably Antarctic origin, would have been present in New Zealand, as evidenced, for example, by *Palaeudyptes marplei* [42]. Therefore, the fossil findings suggest that after the extinction of almost all of the Antarctic forms, *Palaeudyptes* could have been one of the few lineages that would have colonized and persisted in New Zealand (Figure 5).

### 3.2. Neogene History of Penguins

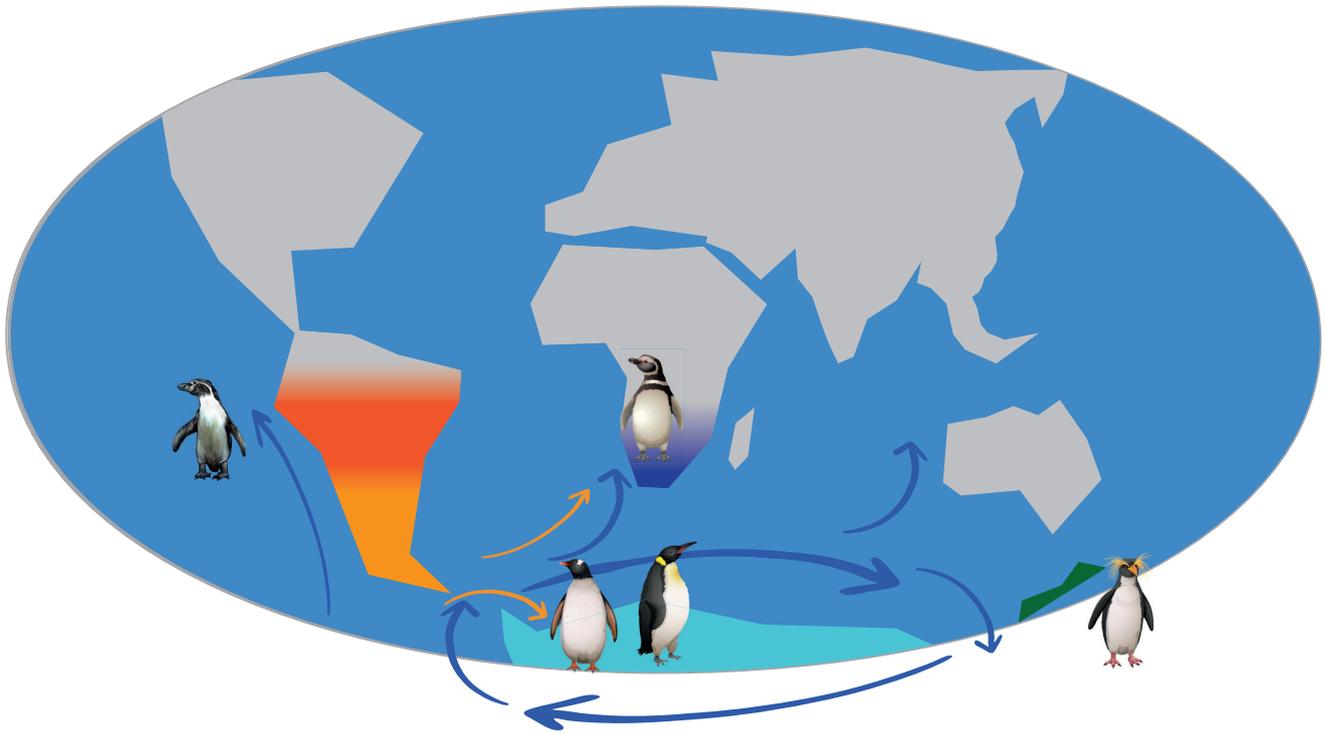
According to our results, the taxa recorded in Patagonia (Argentina), would have had a New Zealand origin. Presumably, the establishment of the Antarctic circumpolar current would have allowed the dispersion of the lineages from New Zealand to southern South America, possibly given the similar environmental conditions in both places that might have been decisive for aspects related to the feeding and breeding areas. In this way, from the colonization of southern South America at the beginning of the Miocene, several lineages would have developed. First, *Paraptenodytes* (including *P. robustus* and *P. antarcticus*), and later, *Eretiscus tonni* and *Palaeospheniscus* (with a high diversity constituted by *P. bergi*, *P. patagonicus*, and *P. biloculata*), established a wide presence in southern South America, as evidenced by the fossil record of Patagonia Argentina [61,64,70,71], and reached the coasts of Chile and Peru by the middle Miocene [81,121].

The Miocene was a crucial time for the establishment of the most modern faunas [36,71,122]. Our results suggest that from New Zealand to Southern South America, three biogeographical events that were probably related with the intensification of the Antarctic circumpolar current during the middle and late Miocene [89], deserve to be highlighted. This new scenario favors the selection of physiological and biochemical adaptations to face colder environmental regimes, an idea strongly supported by genomic studies [35,122]. Thus, our results are consistent with the biogeographical proposals from the crown group [35,38]; see also [123].

The first event corresponds to the diversification of *Spheniscus*, widely recorded during the Mio-Pliocene of Chile and Peru [36]. Here, an origin in the south of South America and a dispersion towards the north, which was probably influenced by the beginning of the establishment process of the Humboldt current during the middle Miocene (15–12 Ma) is proposed. The ecological preferences of the *Spheniscus* lineage are consistent with colder waters and a diet based on fish [116]; it could be possible that these traits were inherited from their ancestors. This is also supported by the fossil record of these areas and even by the fossil record of Antarctic [54]. By the middle Miocene, there is a vast record of penguins attributed to *Spheniscus*, mainly in Chile and Perú, represented by species such as *Spheniscus urbinai*, *S. megaramphus*, *S. muizoni*, and *S. chilensis*. The diversification of the modern lineages corresponding to *Spheniscus* would have been relatively recent. Respectively, *S. humboldti* and *S. demersus* might have colonized the central-northern Pacific coast of South America and the coasts of southern Africa from southern South America during the Pleistocene [77,124]. In addition, and recently, *S. humboldti* colonized the Galapagos archipelago, allowing the origin of *S. mendiculus* [122]. These processes were probably related to the expansion of the polar caps during the glaciations, reaching almost 40° South latitude, altering the structure of the marine currents and the latitudinal thermal gradient [125]. Thus, our results are consistent with previous proposals [77] of multiple colonization events in Africa for Sphenisciformes. This is supported by the presence of *Nucleornis insolitus*, *Dege hendeyi*, and *Inguza predemersus* in the fossil record, which colonized Africa independently at the end of the Miocene (Figures 6 and 7).



**Figure 6.** Main Miocene biogeographical events: the colonization of lineages from New Zealand to South America due to circum-Antarctic oceanic currents (i.e., *Parapterodytes* in the image); diversification and expansion of *Spheniscus* across South America.; origin and diversification of *Megadyptes-Eudyptes* clade from New Zealand; diversification of clade *Pygoscelis* in southern South America.



**Figure 7.** Main Plio-Pleistocene biogeographical events: *Spheniscus* dispersion towards South Africa; *Pygoscelis* and *Aptenodytes* lineages colonized Antarctica; *Eudyptes* lineage from New Zealand expanding across circum-Antarctic islands.

A second biogeographical event corresponds to the clade *Megadyptes-Eudyptes*, with a probable common ancestor in New Zealand. These results are consistent with previous analyses about the biogeographical history for this clade [38]. In addition, our findings suggest a strong generalist condition for these geographical occupations. The lineage would have developed wide dispersal capacities around Antarctica, reaching multiple continental islands close to the mainland masses, which would have generated advantages in terms of the absence of possible predators and competition for resources. However, the cooling processes that intensified during the Plio-Pleistocene led to the formation and growth of ice caps in the Antarctic Ocean. Therefore, these glacial and interglacial intervals would have generated isolation and subsequent speciation in some of these lineages [35]. On the other hand, the scenarios of allopatric speciation by isolation in islands for the *Eudyptes* lineage are discussed by some authors, such as Frugone et al. [126], who proposed a greater effect of the thermal zonation of the Antarctic polar front and the subtropical currents on the definition of species. Consequently, the strong dispersal capacity and a more generalist condition would not have allowed the necessary genetic isolation and subsequent speciation, as seems to be evidenced in *E. schlegeli* and *E. chrysolophus*. In this way, *Eudyptes* would be an example of a generalist lineage that, with its different species, migrated from New Zealand throughout the Southern Hemisphere, reaching southern South America, subantarctic islands, and Africa [35,126] (Figures 6 and 7).

During the middle Miocene a third diversification process of the clade *Pygoscelis-Aptenodytes* is revealed in our results. The radiation center was probably from southern South America with lineages such as *Madrynornis* endemic to Patagonia, and a common ancestor of *Pygoscelis* and *Aptenodytes* with an outstanding skill of dispersion in the circum-Antarctic waters. These ocean currents became colder and colder since the intensification of the circum-Antarctic current 11 Ma ago, thanks to the development of biochemical and metabolic adaptations associated with thermoregulation, optimization of oxygen consumption and ATP production [35,122,126]. This would have allowed them to reach a circum-Antarctic distribution during the middle and late Miocene, as evidenced by the

presence of *Pygoscelis tyreei* and *Aptenodytes ridgeni* in New Zealand, as well as the presence of *P. grandis* and *P. calderensis* in southern South America. The southern parts of Argentina and New Zealand may have been linked during the late Middle Miocene as areas of constant exchange of species with other regions, powered by the latitudinal direction of marine currents [118]. Finally, together with the cooling and the Pleistocene glaciations, processes of population isolation occurred by the formation of polar caps and the consequent changes in the currents. Some patterns triggered by glacial-interglacial intervals modified the genetic flow between populations and promoted isolation scenarios and the subsequent speciation in the Antarctic lineages. Consequently, the adaptations previously developed along the crown group lineage evolution, which allowed the occupation of more extreme thermal niches in increasingly cold waters, would have been key exaptations in the colonization and subsequent biomic specialization in extreme tundra conditions. The modern species *Aptenodytes forsteri* and *Pygoscelis adeliae* are examples of that process (Figures 6 and 7).

#### 4. Conclusions

Despite using a different phylogenetic proposal, a flexible scenario for dispersal possibilities, and an alternative areas delimitation, our results are broadly consistent with previous findings about the main paleobiogeographical patterns during penguins' evolutionary history. Thus, our findings are broadly consistent with a New Zealand center of origin for Sphenisciformes during the late Cretaceous and early Paleogene, supporting the hypothesis generated by analyses proposed by diverse authors [28,38]. With respect to the Eocene, we found an outstanding diversification and dispersion of penguins geographically associated with Antarctica, due to the establishment of temperate conditions triggered by PETM and EECO. The Oligocene and early Miocene represented a turnover in the Spheniscofauna; the extinction of Antarctic lineages consolidated New Zealand and Southern South America as refuges associated with the latitudinal contraction of temperate biomes and warm marine currents. The outcomes suggest that crown group Sphenisciformes flourished during the Miocene and many adaptations from their ancestors would probably be established as exaptations to face increasingly cold environmental conditions during the Neogene. Thus, some lineages expanded their areas towards subtropical latitudes in South America and Africa, while other lineages (*Pygoscelis* and *Aptenodytes*) developed the colonization capacity for the hardest climatic environments, such as the tundra conditions in Antarctica during the Pleistocene glaciations. All these statements are, however, provisional, and subject to new findings and subsequent analyses. Although the penguin record is quite complete in comparison with those of other bird taxa, several deficiencies and important gaps are recognized during the time periods considered. We trust, however, that the efforts of numerous researchers currently working on these studies will at least partially reverse these findings.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14040255/s1>, Figure S1: Biogeographical results of BioGeoBEARS under DEC model; Figure S2: Biogeographical results of BioGeoBEARS under DEC + J model; Figure S3: Biogeographical results of BioGeoBEARS under DIVALIKE model; Figure S4: Biogeographical results of BioGeoBEARS under DIVALIKE + J model; Figure S5: Biogeographical results of BioGeoBEARS under BAYAREALIKE model; Figure S6: Biogeographical results of BioGeoBEARS under BAYAREALIKE + J model; Table S1: Results of model test with statistical support of BioGeoBEARS analyses for all models; Table S2: Complementary results of model test with statistical support of BioGeoBEARS analyses comparing all models according to +J parameter.

**Author Contributions:** Conceptualization, J.S.P., C.A.H.; methodology, J.S.P., C.A.H.; formal analysis, J.S.P., C.A.H.; investigation, J.S.P., C.A.H.; resources, J.S.P., C.A.H.; data curation, J.S.P., C.A.H.; writing—original draft preparation, J.S.P., C.A.H. writing—review and editing, J.S.P., C.A.H. All authors have read and agreed to the published version of the manuscript.

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