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The Sunken Laboratory: Ancient Penguins and the Lost World of Zealandia

Biology * Evolution * DNA

1. Introduction: The Archipelagic Laboratory of Zealandia

Separated from Gondwana approximately 80 million years ago, the submerged continent of Zealandia (Te Riu-a-M ui) has functioned for 60 million years as both an evolutionary cradle and refugium for Southern Hemisphere marine avifauna.[1][2] While Paleocene giants such as Kumimanu fordycei (~154 kg) demonstrated early in Sphenisciformes evolution that the penguin body plan could support immense bulk, paleontologists long assumed that giant penguins vanished during the Paleogene as marine mammals radiated.[3]

In September 2025, a landmark study in the Journal of Paleontology by Alan Tennyson, Felix Marx, Daniel Ksepka, and Daniel Thomas overturned this timeline by describing a colossal Pliocene skull (cataloged as NMNZ S.048857) assigned to the crown genus Aptenodytes -- the lineage of living King (A. patagonicus) and Emperor (A. forsteri) penguins.[4][5] Whereas modern Aptenodytes species are cold-adapted specialists restricted to polar sea ice and the Antarctic Convergence, their giant Pliocene relative inhabited the warm, subtropical shelf waters of New Zealand just 3 million years ago, sharing a rich coastal ecosystem with ancestral monk seals and procellariiform seabirds.[4]

2. Geological Context: The Tangahoe Formation and the Mid-Piacenzian Warm Period

Discovered in 2015 by collector John Buchanan-Brown inside a carbonate mudstone concretion on Ohawe Beach, South Taranaki, NMNZ S.048857 derives from the Tangahoe Formation.[4][6] Constrained via magnetostratigraphy, index mollusks (Phialopecten triphooki), and oxygen isotope stages to the Waipipian Stage between 3.36 and 3.06 million years ago (Ma), these mid-shelf (50-150 m depth) siltstones preserve a critical window for climate science: the Mid-Piacenzian Warm Period (mPWP).[6]

During the mPWP, atmospheric CO2 levels hovered near 400 ppm, global mean temperatures stood 2-3 deg C above pre-industrial baselines, and eustatic sea levels were 10-25 meters higher than today.[4] Crucially, local sea surface temperatures (SSTs) in the Tasman Sea around Taranaki reached 14-20 deg C -- roughly 10-20 deg C warmer than the polar waters inhabited by modern Aptenodytes -- demonstrating that crown great penguins once thrived in subtropical greenhouse seas.[4]

3. Cranial Morphology and Taxonomic Diagnosis of NMNZ S.048857

Although missing the mandible and posterior braincase fragments, the cranium and rostrum of NMNZ S.048857 preserve diagnostic synapomorphies of Aptenodytes: widely separated temporal fossae on the skull roof, supraorbital salt gland fossae lacking raised lateral borders (distinguishing it from Eudyptes, Megadyptes, and

Pygoscelis), and an elongated rostrum comprising ~60% of total skull length.[4]

Morphometric comparisons show the skull is approximately 35% larger than that of an adult Emperor Penguin (A. forsteri, which reaches 1.3 m and 45 kg), indicating a body mass exceeding 50 kg.[4] Furthermore, unlike the hooked, decurved premaxillary tips used by living King and Emperor penguins to grasp soft-bodied squid, the Tangahoe specimen possesses a robust, wide internarial bar and a straight, unhooked beak tip, pointing to a specialized pursuit-diving niche targeting large subtropical shelf fishes via spear-like strikes or ram-feeding.[4]

| Morphological / Ecological Trait | | Aptenodytes sp. (Tangahoe Fossil) | | Aptenodytes forsteri (Emperor) | | Aptenodytes patagonicus (King) |

| Cranial Dimensions | | ~35% larger than Emperor | | Modern reference standard (22-45 kg) | | Smaller and more slender than Emperor |

| Rostrum Proportion | | ~60% of total skull length | | ~50% of total skull length | | ~60% of total skull length |

| Premaxillary Beak Tip | | Unhooked (straight), robust | | Decurved (hooked) | | Decurved (hooked) |

| Temporal Fossae | | Widely separated at midline | | Widely separated at midline | | Widely separated at midline |

| Thermal Niche (SST) | | Subtropical (14-20 deg C) | | Polar (<0 deg C) | | Sub-Antarctic (3-8 deg C) |

4. Trophic Structure of the Tangahoe Marine Community

Far from an isolated anomaly, the Tangahoe Aptenodytes anchored a finely partitioned Pliocene marine vertebrate guild preserved across the South Taranaki beds.[6] Alongside the giant penguin swam Eomonachus belegaerensis ("Dawn Monk Seal"), a 2.5-meter phocid whose discovery established a Southern Hemisphere origin for Monachinae seals and proved that pinniped coexistence did not preclude penguin gigantism.[7][8]

Concurrently, two smaller crown penguins partitioned coastal and pelagic foraging zones: Eudyptula wilsonae (~1 kg), an ancestral little penguin hunting nearshore shoaling fish, and Eudyptes atatu (~4 kg), a dawn crested penguin whose slender piscivorous bill indicates that the heavy krill-crushing rostra of modern Eudyptes evolved only later during Pleistocene Southern Ocean cooling.[6][2] Overhead, giant petrels (Macronectes tinae), diving shearwaters (Ardenna buchananbrowni), deep-billed petrels (Procellaria altirostris), and giant pseudo-toothed pelagornithids completed this high-productivity subtropical food web.[8][9][10][11]

| Trophic Guild | | Taxon | | Estimated Mass | | Ecological Role in Tangahoe Biota |

| Apex Aquatic Predator | | Carcharodon sp. (Great White Shark) | | >1,000 kg | | Predator of pinnipeds and large diving birds |

| Apex Aerial Predator | | Hieraaetus moorei / Circus teauteensis | | 3-15 kg | | Late Plio-Pleistocene terrestrial/coastal raptors |

| Large Meso-Predator | | Aptenodytes sp. indet. (NMNZ S.048857) | | >50 kg | |

Deep-diving offshore piscivore |

| Large Meso-Predator | | Eomonachus belegaerensis (Dawn Monk Seal) | | ~200 kg | | Shelf piscivore and cephalopod hunter |

| Medium/Small Penguins | | Eudyptes atatu & Eudyptula wilsonae | | 1-4 kg | | Pelagic and nearshore small-fish specialists |

| Aerial Pelagic Guild | | Macronectes tinae & Pelagornis sp. | | 4-30 kg | | Coastal carrion/chick scavenger and surface glider |

5. The Turnover Hypothesis: Top-Down Raptor Predation vs. Climate

If Aptenodytes tolerated 20 deg C subtropical waters, why did the lineage vanish from Zealandia and retreat to the Antarctic ice? Rather than invoking climate change, Tennyson et al. advance a biotic Turnover Hypothesis rooted in nesting behavior and top-down predation.[4][5]

Unlike burrowing Eudyptula or forest- and crevice-nesting Eudyptes and Megadyptes, Aptenodytes penguins are obligate surface foot-brooders, incubating a single egg atop their feet inside an abdominal brood pouch for weeks on open beaches or ice.[4] Prior to 2.5 Ma, mammal-free Zealandia lacked terrestrial predators capable of threatening a 50-kg brooding adult. Between 2.4 and 2.2 Ma, however, dispersal from Australia gave rise to Forbes' Harrier (Circus teauteensis) and the 15-kg Haast's Eagle (Hieraaetus moorei), an apex raptor capable of killing 200-kg moa.[4]

Encumbered by foot-brooding on exposed beaches, giant Aptenodytes colonies became defenseless targets for aerial raptors, whereas cryptic burrow- and canopy-nesting penguins survived.[4] This selective filter demonstrates that the fundamental thermal niche of Aptenodytes spans warm subtropical waters, while its modern realized niche in polar Antarctica reflects a predator-free glacial refuge -- reinforcing Zealandia's dual role in shaping global biodiversity.[2][4]

6. Conclusion: Refugia, Predation Walls, and Conservation

The Tangahoe giant skull NMNZ S.048857 proves that crown-group penguin gigantism persisted into the late Pliocene and that great penguins are not physiologically obligated to polar ice.[4] Instead, their restriction to high-latitude refugia was driven by the Plio-Pleistocene arrival of giant aerial raptors -- a top-down "predation wall" mirrored in the modern era by introduced mammalian predators that continue to bar surface-brooding penguins from reclaiming New Zealand's mainland coasts.[4]

Updates... (Nov 20, 2026): Replaced ResearchGate, DeviantArt, Wikipedia, and timed-out news links with verified peer-reviewed paleontological DOIs (including Tennyson et al. 2025, Ksepka et al. 2023, Thomas et al. 2020/2023, Rule et al. 2020, and McKee 1985) and standardized 1:1 inline citation parity.

Works Cited

* Massey University (Aug 13, 2020). Newly-described fossils reveal an ancient origin for New Zealand penguins. https://www.massey.ac.nz/about/news/newly-described-fossils-reveal-an-ancient-origin-for-new-zealand-penguins/

* Thomas, D. B., Tennyson, A. J. D., Scofield, R. P., et al. (Aug 12, 2020). Ancient crested penguin constrains timing of recruitment into seabird hotspot. Proceedings of the Royal Society B, 287(1932), 20201497. https://doi.org/10.1098/rspb.2020.1497

* Ksepka, D. T., Field, D. J., Heath, T. A., et al. (Feb 8, 2023). Largest-known fossil penguin provides insight into the early evolution of spheniscifform body size and flipper anatomy. Journal of Paleontology, 97(2), 434-453. https://doi.org/10.1017/jpa.2022.88

* Tennyson, A. J. D., Marx, F. G., Ksepka, D. T., & Thomas, D. B. (Sep 2025). Emperor penguin's fossil relatives inhabited subtropical waters. Journal of Paleontology, 99(5), 1209-1217. https://doi.org/10.1017/jpa.2025.10162

* West Coast Penguin Trust (Sep 2025). Penguin fossils tell the penguin story, including some found on the West Coast. https://www.westcoastpenguintrust.org.nz/news/penguin-fossils-tell-the-penguin-story-including-some-found-on-the-west-coast/

* Thomas, D. B., Tennyson, A. J. D., Marx, F. G., & Ksepka, D. T. (Jun 2023). Pliocene fossils support a New Zealand origin for the smallest extant penguins. Journal of Paleontology, 97(3), 711-721. https://doi.org/10.1017/jpa.2023.30

* Rule, J. P., Adams, J. W., Marx, F. G., et al. (Nov 11, 2020). First monk seal from the Southern Hemisphere rewrites the evolutionary history of true seals. Proceedings of the Royal Society B, 287(1938), 20202318. https://doi.org/10.1098/rspb.2020.2318

* Tennyson, A. J. D., & Salvador, R. B. (2023). A New Giant Petrel (Macronectes, Aves: Procellariidae) from the Pliocene of Taranaki, New Zealand. Taxonomy, 3(1), 57-67. https://doi.org/10.3390/taxonomy3010006

* Tennyson, A. J. D., Salvador, R. B., Tomotani, B. M., & Marx, F. G. (2024). A New Diving Pliocene Ardenna Shearwater (Aves: Procellariidae) from New Zealand. Taxonomy, 4(2), 237-249. https://doi.org/10.3390/taxonomy4020012

* Tennyson, A. J. D., & Tomotani, B. M. (2021). A new fossil species of Procellaria (Aves: Procellariiformes) from the Pliocene of New Zealand. Pap is Avulsos de Zoologia, 61, e20216116. https://doi.org/10.11606/1807-0205/2021.61.16

* McKee, J. W. A. (1985). A pseudodontorn (Pelecaniformes: Pelagornithidae) from the middle Pliocene of Hawera, Taranaki, New Zealand. New Zealand Journal of Zoology, 12(2), 181-184. https://doi.org/10.1080/03014223.1985.10428278