PALEONTOLOGY

THE STRANGEST BIRD

Recent fossil discoveries reveal the surprising evolutionary history of penguins

By R. Ewan Fordyce and Daniel T. Ksepka

NOVEMBER IN ANTARCTICA, AND THE ICE is on the wane. Soon the emperors will go fishing. They'll spend the austral summer gliding through the frigid Southern Ocean, diving to depths of more than 1,500 feet in search of fish, squid and krill to gorge on before making the long trek inland for the winter to breed. When the time comes to haul out, they will launch themselves out of the water back onto the ice. That brief moment between sea and ice is the only time these penguins experience what most birds take for granted: being airborne.

Indeed, emperors and other penguins are bizarre birds. Like all birds, they possess feathers, wings and beaks and lay eggs. But penguins also exhibit a suite of characteristics that readily distinguishes them from their feathered friends. Their wings have evolved into flippers for swimming; their trademark tuxedo camouflages them from predators above and below; their dense

IN BRIEF

Penguins are weird birds in that they cannot fly and are instead proficient swimmers and divers.

Evolutionary biologists have long wondered how penguins evolved their peculiar traits and how some of their kind conquered the bitterly cold Antarctic.

Recent fossil discoveries have enabled researchers to piece together the penguins' evolutionary past, revealing that some of the traits that fortify them against the cold evolved under warm conditions.

Although penguins have triumphed over 60 million years of climate change, current warming conditions may outpace their ability to adapt.

R. Ewan Fordyce is a vertebrate paleontologist at the University of Otago in New Zealand. His fieldwork and research center on the fossil marine vertebrates of New Zealand, including penguins and whales.

Daniel T. Ksepka is a vertebrate paleontologist at North Carolina State University. One of his main research interests is reconstructing the evolution of penguins from their flying ancestors.

bones provide ballast for diving; their short, thick legs steer their body underwater and help give them that endearing (and energetically efficient) waddle on land. Thanks to these traits and others, penguins are masters of the marine realm, and many of their kind—the emperors among them—have managed to conquer one of the most extreme environments on the planet.

Paleontologists have long wondered whence these peculiar birds originated and how they spread across the Southern Hemisphere. Fossil discoveries made over the past decade have helped reconstruct the penguin's evolutionary march. It turns out that many of their signature features arose under far balmier conditions than the brutally cold settings that people tend to imagine when they think of penguins. Yet that history does not improve the odds that penguins will survive in the face of future warming. The new findings make clear that the biology and geographic distribution of these birds reflect a complex interplay of continental drift, shifting climate and natural selection over tens of millions of years—underscoring the vulnerability of today's penguins to the effects of rapid climate change.

ANCIENT ORIGIN

SCIENTISTS HAVE KNOWN about fossil penguins for more than 150 years, but the remains they recovered early on were mere scraps that held little information about the birds they came from. The very first penguin fossil to be identified was a single bone collected from New Zealand limestone by an unknown Maori. The fossil ended up with English anatomist Thomas Henry Huxley. Huxley identified the scrap as the anklebone of an extinct penguin larger than an emperor, which at three feet tall and 90 pounds is the largest of today's penguin species. He dubbed the fossil penguin *Palaeeudyptes antarcticus,* meaning "ancient good diver of the South." In the decades that followed, more remains of giant penguins came to light in New Zealand and beyond. But like the anklebone Huxley diagnosed, they were all fragmentary and hard to interpret. Scientists were left puzzling over how these giants lived, why they went extinct and where they fit in the bigger picture of penguin evolution.

The fossil record of penguins began to improve in the late 1970s, when one of us (Fordyce) came across a broken leg bone poking out of a sandstone cliff face near Waimate in southern New Zealand. Carefully chipping away at the surrounding rock, Fordyce found more bones of a large penguin that lived 27 million years ago. That partial skeleton provided new insight into the body plan of ancient penguins, but it was still too advanced to reveal their origins. It was not until the 1980s and 1990s that fossils fitting that bill came to light, when several specimens revealing the earliest known stages of penguin evolution turned up in the Waipara area of New Zealand. These remains, which date to between 62 million and 58 million years ago, show that early penguins superficially resembled cormorants, with their long, narrow beak and flexible wings. Yet on closer inspection, they were developing classic penguin traits. For example, their upper wing bones were flat and wide like those of modern penguins, their anklebone was short and broad, and their bones overall were denser than those of flying birds.

After analyzing these protopenguin fossils, Fordyce, Tatsuro Ando, then his graduate student at the University of Otago in New Zealand, and Craig Jones of GNS Science assigned them to two species of a new genus, *Waimanu,* meaning "water bird" in the Maori language. In life, the larger species, *Waimanu manneringi,* approached the size of the emperor penguin at about three feet tall, whereas *Waimanu tuatahi* probably stood roughly two and a half feet tall, a bit bigger than the modern day yellow-eyed penguin. Neither seems likely to have been able to fly in the air—both excelled instead at propelling themselves through the water.

Waimanu penguins are the oldest and most archaic penguins known. They are also some of the oldest representatives of any modern bird lineage. These penguins lived shortly after the catastrophic event that ended the Cretaceous period 65 million years ago and that doomed the dinosaurs and many other creatures. Some experts have suggested that the event eliminated almost all birds, with perhaps just a handful of lineages surviving. Such a scenario would imply that the penguin lineage and other modern bird lineages evolved rapidly from a single ancestral stock in the few million years following the mass extinction. Based on the available evidence from fossils and DNA analyses of modern birds, we think a more plausible explanation is that many modern bird lineages—including the penguin line—originated before that epic disaster struck and somehow managed to hang on when their dinosaur brethren could not.

That the earliest penguins have turned up in New Zealand is probably no coincidence. Many penguins today live around the country's coasts. Until humans arrived, less than 1,000 years ago, the islands there formed a temperate seabird paradise on the margins of the South Pacific and Southern oceans. The region was free of terrestrial predatory mammals and afforded space for breeding colonies, with abundant food in the surrounding seas.

Geologic evidence suggests that the area would have been equally conducive to the seabird way of life at the end of the Cretaceous, when penguins presumably got their start—albeit for somewhat different reasons. New Zealand today is the largest exposed area of a submerged mini continent known as Zealandia that broke off from the ancient supercontinent of Gondwana perhaps 85 million years ago. Thus liberated, Zealandia drifted northeast into the Pacific, carrying plants and animals, including dinosaurs, to its resting spot about halfway between the South Pole and tropics. As Zealandia drifted, it cooled and sank. Shallow seas flooded the land, and a broad continental shelf formed around its perimeter. Despite its isolation from other landmasses, Zealandia did not emerge from the end-Cretaceous extinction unscathed. Many of its marine and terrestrial organisms perished in that die-off. Yet what was bad for those creatures was good for penguins. With marine reptiles such as mosasaurs and plesiosaurs out of the picture, early penguins could swim the waters around Zealandia free of competition or predation.

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BREAKTHROUGH ADAPTATION

HAVING GOTTEN THEIR sea legs in Zealandia, penguins soon expanded their domain dramatically, dispersing across thousands of miles and into new climate zones. Fossils of *Perudyptes devriesi* from Peru show that penguins arrived close to the equator about 42 million years ago, settling in one of the hottest places on earth during one of the hottest times in the planet's history. Back then, the temperature in Peru was 86 degrees Fahrenheit or so, and average global sea temperature was 10.8 to 14.4 degrees F higher than it is today. Giant penguins such as *Anthropornis nordenskjoeldi* waddled onshore at Seymour Island in Antarctica around the same time. By 37 million years ago the birds had spread to almost every major landmass in the Southern Hemisphere.

Yet why, after restricting themselves to Zealandia for millions of years, did penguins suddenly start spreading across the Southern Hemisphere around 50 million years ago? Recently one of us (Ksepka) discovered an important clue to this mystery: a long-overlooked feature on the surface of fossil flipper bones. The humerus bears a series of grooves that are easy to miss among the markings associated with tendons and muscles. Ksepka first noticed the grooves in 2006 while studying the flippers of frozen penguins in the basement of the American Museum of Natural History in New York City in an attempt to figure out the relations between the markings on fossil bones and the soft anatomy of the flipper. At the same time, fellow penguin researcher Daniel Thomas was conducting similar investigations at the University of Otago with an eye toward figuring out how the penguins' ability to regulate their body temperature evolved.

As stewards of modern avian diversity, we can learn conservation lessons from the fossil record of penguins.

In comparing notes, Ksepka and Thomas realized that those grooves form at the spot where a cluster of arteries and veins presses against the humerus. These blood vessels make up a countercurrent heat exchanger called the humeral arterial plexus, which allows penguins to limit heat loss through the flippers and to maintain their core body temperature in cold water. In live penguins, hot blood leaving the heart gets cooled by the plexus before reaching the flipper tip, and cold blood returning from the flipper gets warmed before approaching the heart.

The identity of the grooves on the fossil flipper bones shed some surprising light on the origin of penguin thermoregulation. One of the most amazing aspects of modern penguin biology is the birds' ability to tolerate extreme cold. One would logically assume that the plexus evolved as an adaptation to frigid environments. But fossils suggest otherwise. Penguins such as the modest-sized *Delphinornis* from Antarctica show that this feature evolved at least 49 million years ago. The early *Waimanu* penguins from Zealandia show no hint of the trait at 58 million years ago, however. The plexus therefore must have evolved in the intervening time, when the earth was far warmer than it is today. Back then, Antarctica lacked permanent ice sheets and instead offered a temperate forested environment; Zealandia was even toastier.

What use did early penguins have for a heat-conserving plexus in this greenhouse world? Although sea-surface temperatures were high, early penguins probably foraged in cool upwelling regions, which are rich in nutrients and thus support a bounty of prey, including fish and squid. The plentiful food available in these waters comes with a risk, however. Because heat is lost more quickly in water than air, a warm-blooded animal—such as a human diver—can go into hypothermia even in warm seas if the water is below core body temperature. Warm-blooded penguins risked suffering the same fate in those cool upwellings—even with their insulating layers of fat and waterproofing feathers. Reducing heat loss through the flipper would have helped them conserve body heat on long foraging swims in chilly waters.

The humeral plexus may have also allowed penguins to survive the long open-water journeys by which they initially dispersed from Zealandia to other continents. We make that conjecture because the first waves of fossil penguins that show up outside Zealandia all appear to have the feature. Only much later would modern penguins co-opt this mechanism to invade the sea ice shelves that formed when the planet cooled.

VARIATIONS ON A THEME

AS PENGUINS SPREAD throughout the southern oceans, they underwent a remarkable radiation, evolving a huge diversity of forms. For one, New Zealand's *Pachydyptes ponderosus* ("stout diver") was a true giant, known only from a handful of thick bones dating to around 35 million years ago. Paleontologists have estimated the mass of this penguin at upward of 150 pounds. Imagine the splash from such a bird plunging into the water from a rocky perch! At the other end of the spectrum, 21-million-year-old *Eretiscus tonnii* ("tiny rower") from Argentina stood a mere one and a half feet tall. Perhaps like the living little blue penguin from New Zealand, members of this species came onshore in rafts composed of dozens of birds—a behavior that may reduce predation risk.

Some penguins carried extra-deadly weaponry. About 36 million years ago *Icadyptes* ("Ica's diver," named for a region of Peru) *salasi* patrolled prehistoric seaways equipped with a hyperelongated, reinforced beak mounted on a neck wrapped in strong muscles, ready to impale a passing fish or squid. Other penguins sported strange cloaks. Ksepka vividly recalls a night in Lima, when Julia Clarke of the University of Texas at Austin cleared away the rock concealing a beautifully preserved specimen of *Inkayacu paracasensis* ("water king") and exposed its 36-million-year-old feathers and skin—a once-in-a-lifetime find. Microscopic details later revealed evidence for reddish brown and gray pigments, indicating a striking departure from the traditional black-and-white tuxedo patterns of modern penguins.

Not only did ancient penguins evolve diverse forms, they evolved many of them. Scientists have named more than 50 fossil species in addition to the 19 extant species, and in numerous areas we have solid evidence that multiple penguin species lived together in the past. On Seymour Island, for instance, as many as 10 species occur in the same fossil beds. This overlap is fascinating because it suggests these species were able to carve out enough unique ecological niches from the same physical space to coexist. (By comparison, among modern penguins no more than five species share the same breeding ground.)

Ancient penguins succeeded in cohabiting, in part, by having a larger range of sizes than modern penguins display, which brings us back to those enigmatic giants from New Zealand. Working with Ando and Jones, we recently completed an in-depth study of some 27-million-year-old specimens, including the partial skeleton Fordyce found in the 1970s. Although they resemble Huxley's *Palaeeudyptes,* the fossils constitute a new genus, which we named *Kairuku*—Maori for "the diver that returns with food." The preservation of all the key bones in the skeleton allowed us to reconstruct the body size and proportions. Standing an estimated four feet, four inches tall and tipping the scales at 135 pounds or more, *Kairuku* penguins would have dwarfed today's emperors.

We think the size of these ancient New Zealand penguins was an adaptation for swimming long distances, from rookeries on the low islands of Zealandia out to the edge of the continental shelf. Large body size would have also allowed for efficient diving into deep water to search for prey such as squid because larger birds can swim more rapidly, store more oxygen for long dives and conserve body heat more efficiently. Presumably the larger fossil penguins on Seymour Island were likewise able to swim farther and deeper to hunt, whereas the smaller species foraged closer to land.

AN UNCERTAIN FUTURE

AS STEWARDS of modern avian diversity, we can learn conservation lessons from the fossil record of penguins. Most of the penguin extinctions that have taken place over the past 60 million years occurred long before humans appeared. *Homo sapiens* is not completely innocent, however. At least one penguin species—a relative of the yellow-eyed penguin known as *Megadyptes waitaha*—appears to have gone extinct, at least in part, as a result of human hunting. Although penguins are almost never intentionally hunted today, they remain under threat from both local and global forces, including overfishing, oil spills and introduced predators. Yet perhaps more troubling than these forces in the long run is the threat posed by climate change.

Penguins have done a remarkable job of adapting to dramatic shifts in climate. They have thrived both in the steamy equatorial zones of the earth during a greenhouse phase and in the ice-bound wastelands of modern Antarctica. We might mistake the success of penguins over the past 60 million years of climatic shifts for resilience against anything global warming can throw at them. This mistake would be grave, though. When it comes to adapting to climate change, tempo is critical. Paleontologists have found evidence that many species moved their ranges gradually during major prehistoric climate shifts, such as those that accompanied advancing and retreating glaciers in the past few hundred thousand years of ice age interglacial cycles.

FINDINGS

A Panoply of Penguins

Fossil discoveries and analyses of DNA from modern-day penguins suggest that this distinctive group of birds got its start while dinosaurs still roamed the earth. The oldest known fossil penguins hail from what is now New Zealand and date to between 62 million and 58 million years ago. The catastrophic event that extinguished the dinosaurs and other terrestrial and marine predators allowed penguins to thrive in the balmy waters around the submerged mini continent of Zealandia. Then, around 50 million years ago, penguins suddenly started spreading across the Southern Hemisphere, probably thanks to a key evolutionary innovation: a countercurrent heat exchanger called the humeral arterial plexus that helped the birds maintain core body temperature in cool water. As penguins dispersed, they evolved a tremendous diversity of sizes and shapes—much more than modern penguins exhibit. The evolutionary tree at the bottom right shows the relations of a number of penguin species.

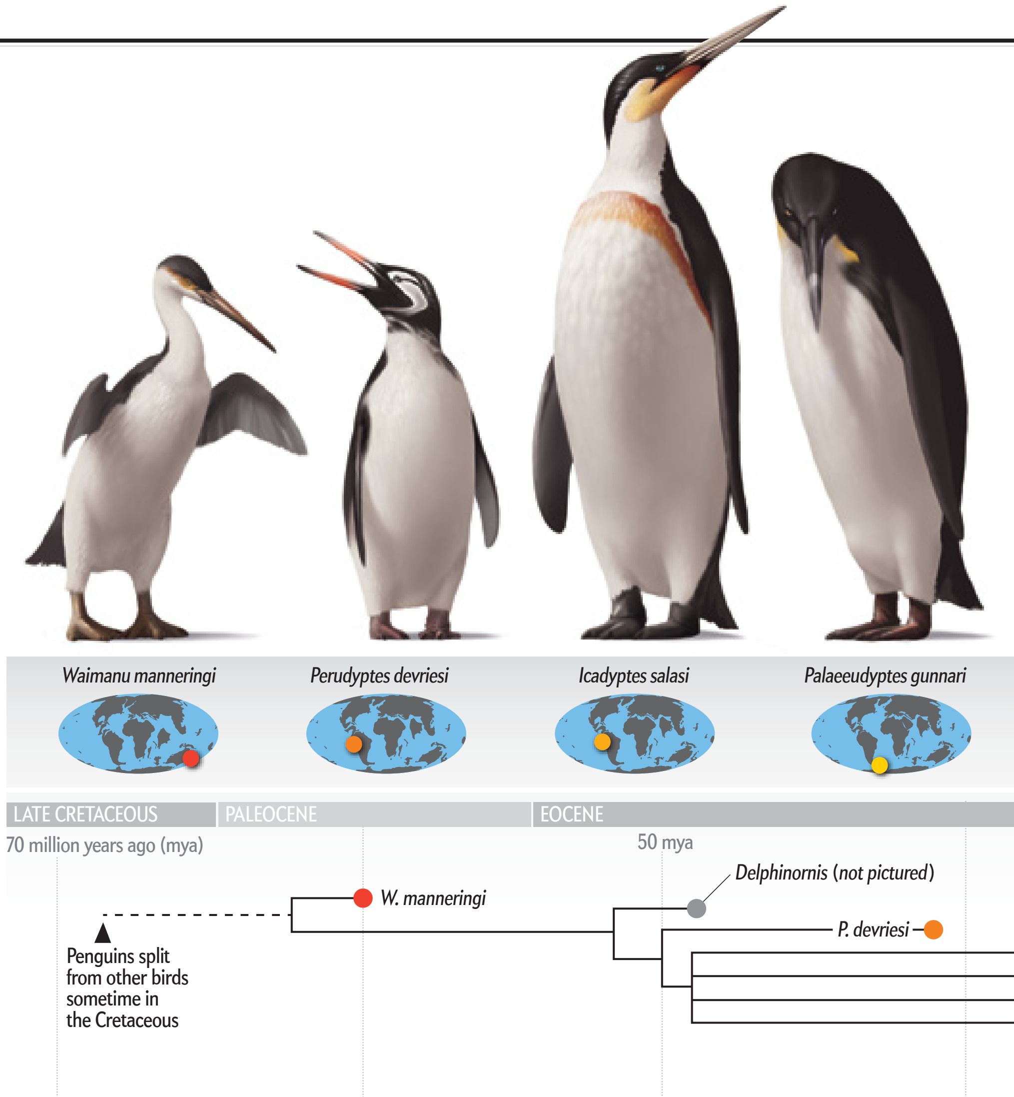

Illustration by Stephanie Abramowicz, Maps by XNR Productions

Some species respond very slowly, which is fine when climate is warming a few degrees over the course of a few million years. Yet if temperatures climb several degrees over the course of a few decades, as many models predict could happen, species may not have time to relocate to more suitable habitats. Or there may be no suitable habitats to which to move.

Consider the Galápagos penguin. This small bird generally flourishes in the equatorial sunshine but suffers severe population drops during strong El Niño years, when Pacific Ocean currents are disrupted and the cold, food-rich waters that usually envelop the islands are replaced with warmer, nutrient-depleted ones. Because these penguins do not stray far from their home islands, they will literally have nowhere to go if warming makes the Galápagos Islands unsuitably hot for raising chicks or catching food.

Emperor penguins, for their part, face a different challenge. These birds may never set foot on dry land throughout their lives, breeding as they do on thick sheets of sea ice. If ice sheets melt too soon in the year, breeding colonies may be destroyed. The penguins' allegiance to their colonies magnifies this danger: many individuals return to the same exact location to breed, year after year, so the seemingly simple solution of moving to a new patch of ice may not be viable, because their breeding behavior is so deeply ingrained.

As paleontologists, we are increasingly aware of the fragility of modern penguins. Penguins today are less diverse in their morphology and more restricted in their ecological roles, and fewer species of them exist today than was true millions of years ago. Although biologists think of them as quintessentially modern birds, in many ways living penguins are survivors of a great dynasty that has yielded some of the most interesting animals ever to have roamed land or sea. What a tragedy it would be if these extraordinary creatures perished on our watch. SA

MORE TO EXPLORE

Penguin Heat-Retention Structures Evolved in a Greenhouse Earth. Daniel B. Thomas, Daniel T. Ksepka and R. Ewan Fordyce in *Biology Letters*, Vol. 7, No. 3, pages 461–464; June 23, 2011.

New Fossil Penguins (Aves, Sphenisciformes) from the Oligocene of New Zealand Reveal the Skeletal Plan of Stem Penguins. Daniel T. Ksepka et al. in *Journal of Vertebrate Paleontology*, Vol. 32, No. 2, pages 235–254; March 2012.

March of the Fossil Penguins (blog): **http://fossilpenguins.wordpress.com**

SCIENTIFIC AMERICAN ONLINE
View a slide show of modern penguins at **ScientificAmerican.com/nov2012/penguins**