Penguin heat-retention structures evolved in a greenhouse Earth

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Penguins (Sphenisciformes) inhabit some of the most extreme environments on Earth. The 60+ Myr fossil record of penguins spans an interval that witnessed dramatic shifts in Cenozoic ocean temperatures and currents, indicating a long interplay between penguin evolution and environmental change. Perhaps the most celebrated example is the successful Late Cenozoic invasion of glacial environments by crown clade penguins. A major adaptation that allows penguins to forage in cold water is the humeral arterial plexus, a vascular counter-current heat exchanger (CCHE) that limits heat loss through the flipper. Fossil evidence reveals that the humeral plexus arose at least 49 Ma during a ‘Greenhouse Earth’ interval. The evolution of the CCHE is therefore unrelated to global cooling or development of polar ice sheets, but probably represents an adaptation to foraging in subsurface waters at temperate latitudes. As global climate cooled, the CCHE was key to invasion of thermally more demanding environments associated with Antarctic ice sheets.

Keywords: counter-current; fossil; penguin; thermoregulation

1. INTRODUCTION

Penguins have departed dramatically in body form and ecology from closely related flighted birds through adaptations to life as obligate marine divers. Foraging exposes penguins to water well below core body temperature and presents a constant threat of hypothermia, a risk avoided in part by managing the flow of heat along the wing. Blood is supplied to the wings of birds through a single major vessel that traverses the humerus as the brachial artery in most living birds [1], including Procellariiformes, the sister group to penguins [2,3]. By contrast, the brachial artery of penguins splits into three to five major vessels that traverse the humerus before anastomosing to two arteries at the humerus–radius joint [4–6]. Each humeral artery is associated with two or more veins to form a counter-current heat exchanger (CCHE), the humeral arterial plexus. Blood is supplied to the wing at core body temperature (38.5 °C) [7], and outgoing arterial blood heats the cooler incoming venous blood at the plexus; heat is thus conserved and returned to the body core instead of travelling further out along the wing to become lost to cold water [4,8]. The efficacy of the humeral plexus as a CCHE mechanism has been demonstrated by up to 30 °C internal temperature differences measured between the shoulders and wingtips of penguins [7,8].

Heat retention is integral to penguin-foraging strategy, and the humeral plexus CCHE is one of the few soft tissue structures related to heat retention that has an osteological correlate. We sought the first appearance of the humeral plexus by exploring the distribution of this osteological correlate in fossil stem penguins, to determine when penguins first developed a tolerance for extended cold water exposure.

2. MATERIAL AND METHODS

Dissections were performed on carcasses of wild specimens of the sooty shearwater (Puffinus griseus, n = 1), erect-crested penguin (Eudyptes sclateri, n = 1), little penguin (Eudyptula minor, n = 3) and yellow-eyed penguin (Megadyptes antipodes, n = 3) provided by the department of conservation, New Zealand and specimens of the king penguin (Aptenodytes patagonicus, n = 1), rockhopper penguin (Eudyptes chrysocome, n = 1), Adélie penguin (Pygoscelis adeliae, n = 2) and Humboldt penguin (Spheniscus humboldti, n = 1) that died in captivity, donated by SeaWorld (see electronic supplementary material, figure S1). Dissections revealed that the humeral plexus lies within one or more grooves, here collectively termed the humeral arterial sulcus, which are incised into the cranial surface of the humerus (figure 1). Humeral arterial sulci were considered to be present in fossil penguin humeri when three specific consistent characteristics in the plexus-bearing humeri of extant penguins could be identified in the fossil: (i) presence of a ridge bordering the most proximal edge of the sulcus, delimiting it from the smooth diaphyseal surface (sulci may also variably feature several ridges delimiting individual channels); (ii) orientation of the sulcus so that the proximal-most extent (origination) and its associated border lies towards the posterior edge of the humerus, whereas the distal-most extent of the sulcus (termination) lies within the brachial depression and/or against the radial condyle; and (iii) width of the sulcus is broad enough to contain a humeral plexus.

Presence/absence of the humeral arterial sulcus was coded as a binary character and traced with MESQUITE [9] using the most inclusive phylogeny of Sphenisciformes available [10]. Ancestral character state reconstructions were explored under both parsimony and maximum likelihood (ML) models with multiple branch length reconstruction strategies as implemented in MESQUITE (electronic supplementary material, figures S2–S5).

3. RESULTS

We have identified the humeral plexus in all extant penguin genera by dissection. This, combined with published data [4,5,11], supports the presence of humeral plexi in all extant penguin species and the most recent common ancestor of the extant Spheniscidae (figure 2). In extant penguins and outgroups, the humeral arterial sulcus is a two-way osteological correlate [12] for the humeral plexus: the presence or absence of the bony sulcus correlated directly with the presence or absence of the vascular plexus.

We identified the humeral arterial sulcus in 19 fossil species. Humeral sulci were absent in the most basal
and oldest penguin taxon *Waimanu* (two sufficiently well-preserved humeri; approx. 62 Ma) [13]. Humeral sulci were present in humeri attributed to the small Seymour Island penguins *Delphinornis*, *Marambiornis* and *Mesetaornis* [10,14–16]. All sufficiently undamaged humeri from *La Meseta* Formation (approx. 49 Ma) of Seymour Island that we examined (including *Palaeudyptes* and *Anthropornis*) preserve a well-developed sulcus [14,17]. All stratigraphically younger and phylogenetically more crownward taxa for which the humerus is sufficiently preserved possess a humeral sulcus (figure 2), except that no evidence of a sulcus was discernable in one stem penguin, *Perudyptes devriesi* (approx. 42 Ma, Peru). Although some modern juvenile *Spheniscus* penguins lack sulci, the holotype specimen of *P. devriesi* appears to represent an adult [10], so we coded this taxon as absent for the sulcus character. The absence of a sulcus in *P. devriesi* is optimized as a secondary loss under all ancestral state reconstruction models. Alternatively, the absence in *Perudyptes* may be an artefact, given the imperfect preservation of the single known specimen. Regardless, the origin of the sulcus by 49 Ma is supported whether the sulcus is considered absent, present or unknown in *Perudyptes*. Further, we note that the origin of the sulcus deep in the penguin stem lineage at greater than 49 Ma is supported regardless of whether the sulcus is considered present or unknown in *Delphinornis*, *Marambiornis* and *Mesetaornis* because the sulcus occurs in the contemporaneous taxa *Anthropornis* and *Palaeudyptes*.

### 4. DISCUSSION

Phylogenetic and stratigraphic data indicate that the plexus originated prior to 49 Ma, but after the loss of aerial flight in penguins, and are consistent with a single origin of this structure. Because no Cretaceous penguin fossils are known and the flightless Palaeogene *Waimanu* (approx. 62 Ma) lacks a humeral sulcus, it is likely that the humeral CCHE evolved during the Late Palaeocene or Early Eocene. After the Cretaceous–Tertiary mass extinction event, climates warmed later in the Palaeocene epoch (approx. 55 Ma) and peaked early in the Eocene epoch (approx. 49 Ma) [18]. Geochemical signals (oxygen isotopes, Mg/Ca ratios, alkenones) [19,20] suggest that Early Eocene sea-surface habitats were warmer than 25°C at both the equator (proto-Peru) and 55’S (Zealandia or proto-New Zealand), and approximately 15°C at 63’S (proto-Seymour Island) during the Early Eocene. The humeral plexus evolved during a time of marked warmth, indicating that its evolution was unrelated to the expansion of polar ice sheets and invasion of glacial environments by penguins.

The lack of significant Early Cenozoic cooling events [19] rules out a cool-climate driver for the evolution of the CCHE. Rather, the CCHE appears to have evolved in concert with dramatic skeletal modifications in Early Palaeogene stem penguins—changes that promoted neutral buoyancy and drag reduction, and thus improved long-distance swimming and deep-diving. Of note are the rapid evolution of large body size, osteosclerotic (densely thickened) limb bones related to buoyancy regulation and a hydrofoil wing with a compressed (fusiform) cross section, a semi-rigid elbow, and a relatively high surface area to volume ratio [13–15,21]. Indeed, the humeral arterial sulcus enables the blood vessels of the plexus to be drawn flush with the surface of the bone to preserve the hydrofoil profile of the wing.

We propose that the CCHE evolved to offset the energetic costs associated with increased foraging duration. Although oceans surrounding Early Cenozoic penguin localities were tropical/subtropical at the surface [19], subsurface temperatures were still significantly cooler than penguin body temperature of about 38°C [7]. More importantly, longer feeding excursions far from the shoreline present greater thermoregulatory challenges, requiring a heterothermic solution. Basal penguins, which lacked the heat-conserving benefits of the humeral plexus CCHE, may have favoured or even been restricted to inshore foraging. Interestingly, basal penguins lacking evidence of a humeral plexus (*Waimanu* spp.) have been recovered only in the Palaeocene of New Zealand. Following the evolution of the humeral plexus, more-crownward penguin taxa spread rapidly to localities around the Gondwanan rim and later dispersed across wide swaths of open ocean [14,15,21,22]. We suggest that the evolution of the CCHE preceded, and probably played a major role, in Eocene phylogenetic radiations and dispersal events within Sphenisciformes, leading to trans-oceanic invasion of high latitudes. Millions of years later, the humeral plexus was one key to the successful invasion of icy Antarctic environments.

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Figure 2. Optimization of the presence of the humeral arterial sulcus onto the strict consensus cladogram of Sphenisciformes from Ksepka & Clarke [10]. Taxon name colours indicate whether the humeral arterial sulcus was observed to be present (red), absent (blue) or uncodeable owing to lack of an adequately preserved humerus (grey). Pie charts represent ancestral state reconstructions: the dark outer edge represents the reconstruction under parsimony (blue, sulcus absent and red, sulcus present) and the lighter interior portion indicates reconstructions under ML using the Markov k-state one symmetrical model (blue, sulcus absent; red, sulcus present and grey, equivocal owing to missing data) with branch lengths based on the time-calibrated cladogram from Ksepka & Clarke [10]. See electronic supplementary material for further details and alternate branch length reconstruction schemes.


