



A history of shifting fortunes for African penguins

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Africa is home today to only a single breeding species of penguin, *Spheniscus demersus* (black-footed penguin), which is endangered with extinction. *Spheniscus demersus* has been the only breeding species of penguin to share African coastlines with humans over the last 400 000 years. Interestingly, African penguin diversity was substantially higher before the evolution of archaic humans. The fossil record indicates that a diverse assemblage of penguin species inhabited the southern African coasts for much of the Neogene. Previous excavations have identified four distinct species in Early Pliocene coastal marine deposits. Here we extend this pattern of high diversity and report the oldest record of penguins from Africa. Seventeen penguin specimens were identified from the Saldanha Steel locality, revealing the presence of at least four distinct species in South Africa during the Miocene. The largest of these species reached the size of the extant *Aptenodytes patagonicus* (king penguin), whereas the smallest was approximately the size of the smallest extant penguin *Eudyptula minor* (little blue penguin). Recovery of Miocene penguin remains is in accordance with earlier predictions of multiple pre-Pliocene colonizations of Africa and supports a higher level of ecological diversity amongst African penguins in the past.

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INTRODUCTION

Penguins have colonized every continent and numerous islands in the Southern Hemisphere. Many of the 17 extant species have wide geographical distributions that range along continental margins or across seaways. Most penguin colonies are situated well away from human settlement and are of little concern for conservation biology. Unfortunately, some penguins have smaller geographical ranges and are endemic to human-settled areas, and these species are vulnerable to, or endangered with, extinction.

The black-footed penguin, *Spheniscus demersus* (Linnaeus, 1758), in southern Africa was classified as endangered in 2010 (Birdlife International, 2012). Black-footed penguins depend heavily on sardines and anchovies in the Benguela upwelling system, and steady population declines have been linked to competition with Cape fur seals (*Arctocephalus pusillus*) and humans (Crawford *et al.*, 2007). Black-footed penguins have a long history of sharing coastal ecosystems with humans, but competition for marine resources is comparatively recent (Cruz-Uribe *et al.*, 2003; Klein *et al.*, 2004). The fossil record for African penguins offers a deep time perspective, revealing dramatic shifts in diversity before the appearance of archaic humans. Here we expand the early history of penguins in Africa and summarize the diversity of African penguins preceding the modern day decline.

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MIDDLE TO LATE MIOCENE (16.0 TO 11.6 MYA)

Africa has long been considered the final major landmass reached by penguins. The oldest known penguin fossils are from the Palaeocene of New Zealand (Slack *et al.*, 2006) and Eocene records are known from Antarctica, South America, and Australia (reviewed in Ksepka & Ando, 2011; stratigraphical nomenclature follows International Commission on Stratigraphy, 2012). However, the oldest record from Africa reported so far is a single Miocene bone briefly mentioned in a review of the Pliocene Western Cape avifauna (Olson, 1983). The apparent late arrival of penguins may be at least in part an artefact of gaps in the fossil record of Africa's tectonically passive southern continental margin, which preserves very few Early Neogene sediments (Gallagher *et al.*, 1999; Roberts *et al.*, 2007). Alternatively, penguins may only have arrived when new dispersal vectors such as the Antarctic Circumpolar Current and the South Atlantic Current became established (Ksepka & Thomas, 2012).

We recently surveyed Neogene fossils from the Western Cape and confirmed that a diverse group of penguins was present in South Africa during the Middle to Late Miocene (Figs 1, 2). The penguin

fossils described in this contribution were recovered from Saldanha Steel (Fig 1), and were collected from a conglomerate at the base of a 12 m excavation, which correlates to the Konings Vlei Gravel (Appendix). The age of the Konings Vlei Gravel was originally given as 7–9 Mya on the basis of vertebrate fossils (Roberts, 2006b). More recently, its estimated age was shifted to coincide with a period of moderately high sea level, and is now constrained between 10 and 12 Mya (evidence from Haq, Hardenbol & Vail, 1987, as cited by Roberts *et al.*, 2011). Hence, the penguin fossils described in the present study are most precisely considered as late Middle Miocene or early Late Miocene (10–12 Mya) in age.

INSTITUTIONAL ABBREVIATIONS

USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; SAM, South African Museum, Cape Town, South Africa.

SYSTEMATIC PALAEOONTOLOGY

SPHENISCIFORMES SHARPE, 1891

Specimens described here can be unquestionably attributed to penguins based on the osteosclerotic

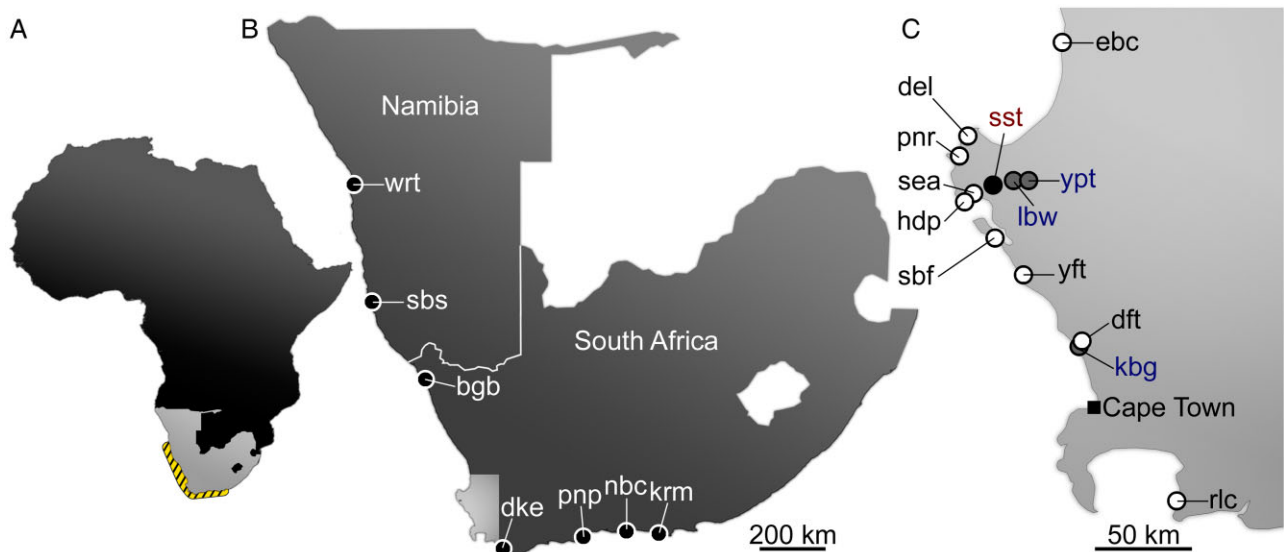


Figure 1. Fossil and modern penguin localities in Africa. A, black-footed penguin (*Spheniscus demersus*) breeding range along the southern coast of Africa (hatched region) (after Crawford *et al.*, 2007). B, Pleistocene and Holocene localities in Namibia and South Africa that have produced black-footed penguin bones. Note that the ancestral and modern ranges are congruent. C, Neogene and Quaternary localities in the Western Cape of South Africa that have produced penguin bones (Miocene, black circle; Pliocene, grey circle, Pleistocene/Holocene, white circle). Abbreviations: bgb, Boegoeberg; del, Duiker Eiland midden; dft, Duinefontein; dke, Die Kelders cave; ebc, Elands Bay cave; hdp, Hoedjiespunt; kbg, Koeberg; krm, Klasies River Mouth; lbw, Langebaanweg 'E' Quarry; nbc, Nelson Bay cave; pnp, Pinnacle Point; pnr, Paternoster midden; rlc, Rooiels cave; sbf, Stofbergsfontein midden; sbs, Steenbras Bay; sea, Sea Harvest; sst, Saldanha Steel; wrt, Wortel, Walvis Bay; yft, Ysterfontein; ypt, Ysterplaats. Locality information from references in text.

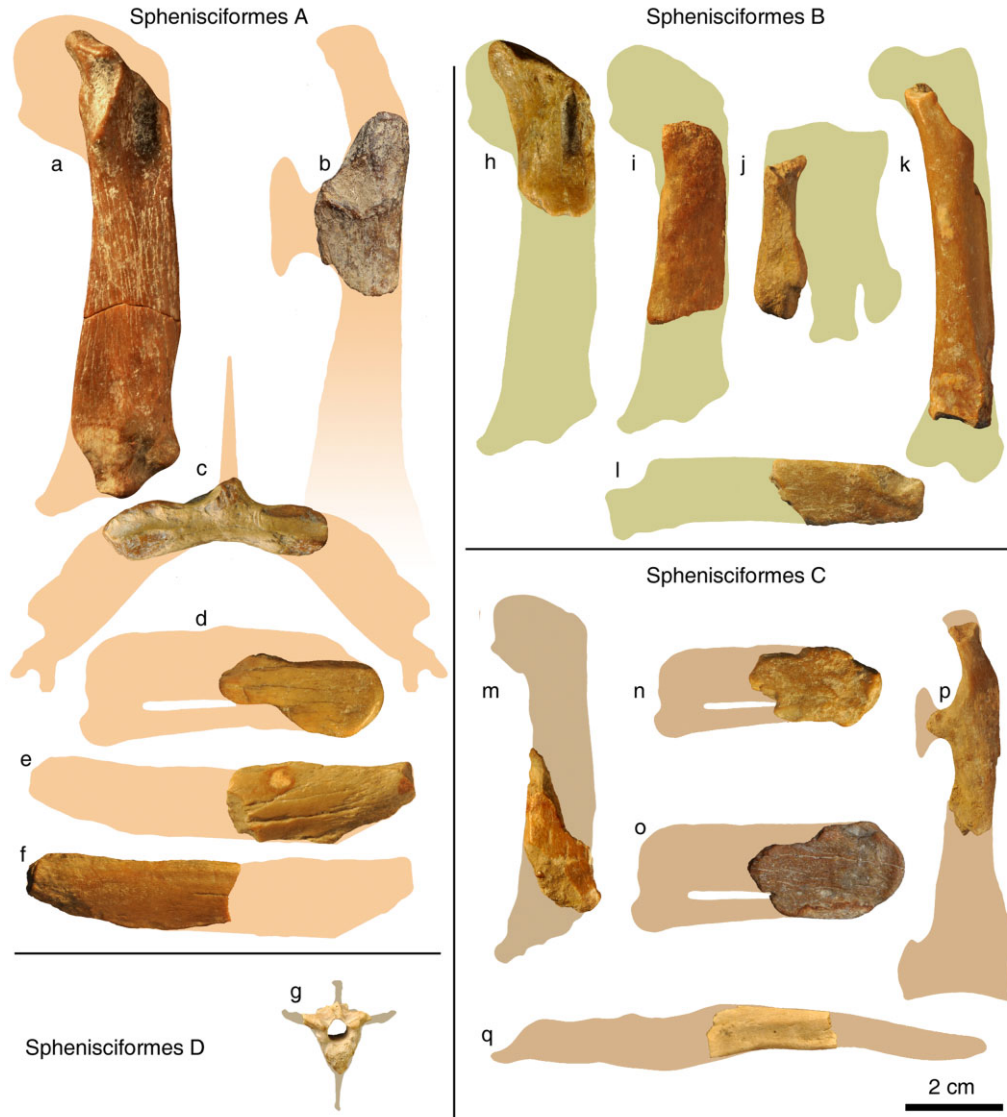


Figure 2. Four penguin taxa identified from the Saldanha Steel locality. *Sphenisciformes A* is the largest of the four taxa and is represented by fragments from a left humerus (SAM-PQSS000223-1, a, cranial), an omal portion of a left coracoid (SAM-PQSS000214-1, b, dorsal), a sternum fragment (SAM-PQSS000223-7, c, cranial), the proximal end of a right carpometacarpus (SAM-PQSS000211-1, d, caudal), the proximal end of a right ulna (SAM-PQSS000217-2, e, caudal), and the distal end of a right ulna (SAM-PQSS000217-3, f, caudal). *Sphenisciformes D* is the smallest penguin taxon identified from Saldanha Steel and is represented by a posterior thoracic vertebra (SAM-PQSS000223-6, g, cranial). *Sphenisciformes B* is the second largest of the four taxa and is represented by two left humeri (SAM-PQSS000220, h, cranial; SAM-PQSS000223-3, i, cranial), metatarsal IV from a right tarsometatarsus (SAM-PQSS000222-1, j, dorsal), the shaft of a right femur (SAM-PQSS000222-2, k, ventral), and a proximal end of a left radius (SAM-PQSS000223-4, l, caudal). *Sphenisciformes C* is the third largest of the four taxa and is represented by fragments from a humerus (SAM-PQSS000217-1, m, cranial), two carpometacarpi (SAM-PQSS000211-2, n, caudal; SAM-PQSS000223-5, o, caudal), a left coracoid (SAM-PQSS000214-2, p, dorsal), and a portion of the right mandibular ramus (SAM-PQSS000213, q, buccal). Silhouettes are based on modern taxa.

bone structure, pronounced flattening of the wing elements, and discrete features of individual elements (detailed below). All bones appear to pertain to adult individuals based on bone texture and complete fusion of complex elements (e.g. carpometacarpus). No discrete features supporting assignment to previously described Neogene taxa (e.g. *Palaeospheniscus*) were observed, so we opted to avoid either assigning elements to known species or naming new species.

SPHENISCIFORMES SPECIES A (FIG. 2)

Referred specimens: Sternum fragment (SAM-PQSS000223-7), omal portion of coracoid (SAM-PQSS000214-1), humerus (SAM-PQSS000220), proximal (SAM-PQSS000217-2) and distal (SAM-PQSS000217-3) end of ulna (possible one element), proximal end of carpometacarpus (SAM-PQSS000211-1).

Description: These specimens belong to a large penguin close in size to the extant *Aptenodytes patagonicus* (king penguin) (Fig. 3). The partial sternum includes the medial parts of the left and right sulci, the base of the carina, and base of the labrum internum. Most interestingly, the smooth bone of the cranial surface at the midline suggests that the sternum may have lacked a spina externa. The base of the spina externa typically extends across the cranial face of the sternum at the midline in extant penguins (Bertelli & Giannini, 2005) and is also present in the few fossil taxa in which this delicate region is intact (e.g. *Platydyptes* and *Marplesornis*; Marples, 1952; Marples, 1960). Uniquely amongst penguins, the spina externa is completely absent in *Aptenodytes* (Bertelli & Giannini, 2005). This would seem to support phylogenetic affinities with *Aptenodytes* for the fossil. However, because the base of the spina externa is restricted to the ventral margin of

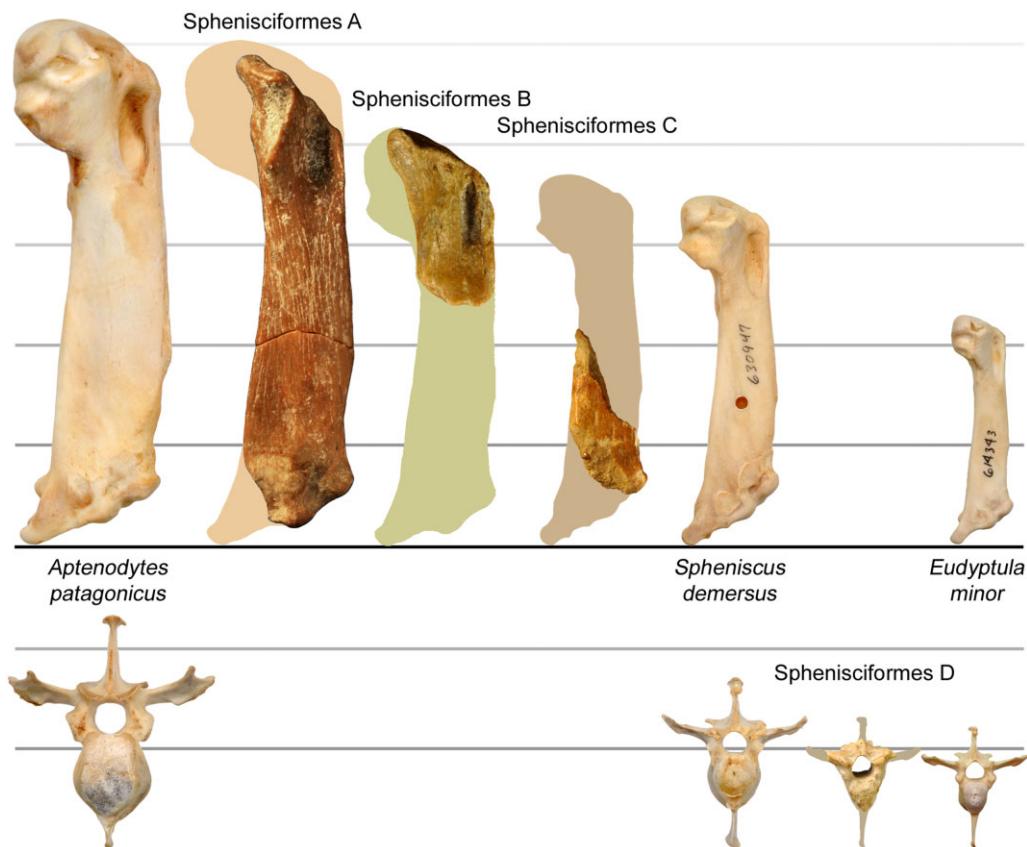


Figure 3. Miocene penguins from the Saldanha Steel locality spanned almost the complete size range of modern penguins. Humeri from Sphenisciformes A, B, and C are intermediate in size between king and black-footed penguins, and are larger than the humerus of a little blue penguin (*Aptenodytes patagonicus* USNM533568, *Spheniscus demersus* USNM630947, and *Eudyptula minor* USNM614343, respectively). Sphenisciformes D is represented by a posterior thoracic vertebra, which is comparable in size to the last posterior thoracic vertebra of little blue penguins. Grid lines are spaced every 2 cm.

the sternum in some specimens of *Pygoscelis* and *Eudyptes* (D. T. Ksepka, pers. observ.), we cannot conclusively determine whether the spina externa was completely absent or merely restricted in extent in the fossil specimen.

A humerus is preserved in two articulating pieces and lacks only the head and distal trochlear ridges. This element is slightly shorter than the smallest wild-captured *A. patagonicus* humeri for which measurements were available ($N=6$). Bifurcation of the fossa tricipitalis is indicated by an intact ridge. As in other penguins, the m. pectoralis fossa is deep and oblong, and the insertion for m. supracoracoideus is a proximodistally elongated scar. The shaft shows only slight sigmoid curvature, widens distally, and shows a distally placed preaxial angle. Morphologies of the distal end closely resemble those seen in crown clade penguins, including the orientation of the condylus dorsalis and condylus ventralis, the flattening of the condylus ventralis (which may be slightly exaggerated by wear), and the lack of a prominent shelf adjacent to the condylus ventralis (Marples, 1952; Ksepka, Bertelli & Giannini, 2006).

A few other specimens are grouped under species A based on large size. A fragment of a coracoid preserving the cotyla scapularis exhibits the flattened morphology of crown clade penguins rather than the deep concave morphology of stem taxa such as *Parapterodytes*, *Kairuku*, and *Icadyptes*. A proximal and a distal fragment of an ulna recovered from the same area may represent a single bone based on non-overlap, colour, and wear pattern, although unfortunately there is no clear contact between them. They indicate a slightly bowed shape and would yield a length of ~80.5 mm (slightly below the range of variation in extant *A. patagonicus*) if they do indeed represent the same individual. A heavily worn fragment of a carpometacarpus is also of the appropriate size to be assigned to this taxon but preserves no informative features.

Comments: Species A is near the upper size range of living penguins and far larger than the extant *S. demersus*. *Nucleornis insolitus*, the largest of the Pliocene penguin species known from Langebaanweg, is the only other fossil penguin reported from Africa that approaches *Aptenodytes* in stature. Although it is known with certainty only from the tarsometatarsus, the size of that bone as well as tentatively referred material suggests that *N. insolitus* and species A were close in size. Based on morphology, it is plausible that remains assigned to species A represent either a member of the *N. insolitus* lineage or a member of the *Aptenodytes* lineage. Apomorphies of the tarsometatarsus would resolve this issue, but unfortunately this element has not been recovered. Although *A. patagonicus* does not breed in South Africa today, the

species has been recorded as a rare vagrant to the region (Ross & Cockroft, 1985). Notably, the fossil species *Aptenodytes ridgeni* occurred in New Zealand during the Pliocene (Simpson, 1972). Confirmation of another member of the *Aptenodytes* lineage in the Miocene of South Africa would reinforce existing evidence for a historically broad distribution for the genus.

SPHENISCIFORMES SPECIES B (FIG. 2)

Referred specimens: Proximal end and shaft of left humeri (SAM-PQSS000220, SAM-PQSS000223-3), distal end of radius (SAM-PQSS000223-4), shaft of femur (SAM-PQSS000222-2), fourth metatarsal (SAM-PQSS000222-1).

Description: These specimens belong to a penguin that is ~20% smaller than species A, but substantially larger than species C. Based on available elements it was probably equivalent in size to the extant *Megadyptes antipodes* (yellow-eyed penguin). The two partial humeri clearly belong to a penguin based on the intact base of the large pneumatic tricipital fossa, deep m. pectoralis insertion, and osteosclerotic bone structure. The more complete humerus exhibits the derived trend of distally expanding shaft width that is also seen in species A. A distal end of a radius is also assigned to species B based on size, but preserves no noteworthy morphologies. A femur shaft assigned to this taxon is notably broad and shows a moderate degree of medial bowing. In most penguins, the shaft is straight, although pronounced bowing occurs in *Eudyptula minor*, some species of *Pygoscelis* and *Eudyptes*, and the fossil taxon '*Pygoscelis*' *grandis* (Walsh & Suárez, 2006). A fragment of a tarsometatarsus representing the detached fourth metatarsal preserves evidence of a very deep sulcus longitudinalis dorsalis lateralis, within which a foramen vasculare proximale laterale appears to have been present.

Comments: Elements from species B are rather poorly preserved. Although not very informative from a phylogenetic perspective, these specimens are important because they support the presence of an additional penguin taxon at the Saldahna Steel locality.

SPHENISCIFORMES SPECIES C (FIG. 2)

Referred specimens: Mandible fragment (SAM-PQSS000213), omal portion of coracoid (SAM-PQSS000214-2), fragment of distal humerus (SAM-PQSS000217-1), two proximal ends of carpometacarpus (SAM-PQSS000211-2 and SAM-PQSS000223-5)

Description: These specimens belong to a moderate-sized penguin, close in size to the extant *S. demersus* (Fig. 3). A partial mandible represents the portion of the ramus at which bifurcation of the dentary begins. Based on the intact portion, it is likely that the mandible was relatively straight and narrow, as in extant *Spheniscus*. Several extant penguins (e.g. some species of *Eudyptes* and *Pygoscelis*) exhibit a pronounced deepening near the midpoint of the mandible that is hypothesized to help accommodate a larger tongue (Zusi, 1975). A fragment of the coracoid from near the omal end, a fragment of a distal humerus preserving the radial condyle, and two fragments each representing the proximal end of a carpo-metacarpus are also assigned to this species based on size.

Comments: These elements potentially belong to a lineage leading to one of the smaller Pliocene penguin species known from Langebaanweg, which include *Inguza predemersus*, '*Paleospheniscus*' *huxleyorum*, and *Dege hendeyi*. They are grouped together for description because of size, although because the elements were isolated it is not possible to definitively rule out the presence of multiple species of overlapping size range as occurs at 'E' Quarry, Langebaanweg.

SPHENISCIFORMES SPECIES D (FIG. 2)

Referred specimen: Posterior thoracic vertebra (SAM-PQSS000223-6).

Description: This vertebra represents a very small penguin. Based on comparisons to extant penguins, it probably represents the third to last thoracic vertebra. It is much smaller than the same element in *S. demersus* and is approximately the size seen in *Eudyptula minor* (the smallest extant penguin species; Fig. 3). The vertebra is identified as belonging to a penguin based on the opisthocoelous corpus, large and cranially positioned fovea costalis, and proportionally large neural canal. Phalacrocoracidae and AnHINGIDAE also possess opisthocoelous caudal thoracic vertebrae and occur in the Neogene of South Africa (Olson, 1983). Phalacrocoracidae and AnHINGIDAE vertebrae are easily distinguishable from the Saldahna Steel specimen because the corresponding thoracic vertebra bears a much smaller fovea costalis on each side and is pierced by a small foramen near the caudal margin of the neural arch, which is absent in penguins. Additionally, the fovea costalis is situated caudal to the level of the cranial zygapophysis in Phalacrocoracidae and AnHINGIDAE, whereas it is located directly ventral to the cranial zygapophysis in penguins.

Comments: This single element indicates the presence of a very small penguin in the Saldahna Steel fauna. Although the size overlaps with that of *Eudyptula minor*, there are no discrete morphological features preserved that would support a close phylogenetic relationship with that taxon, or alternatively rule one out. Although represented only by a single bone, this small taxon was not necessarily rare because taphonomic biases appear to favour preservation of larger, more robust elements at Saldahna Steel. Only a few volant bird bones were identified in the collections, and large, worn fragments of bones from mammals are common. Penguins are likely to be over-represented relative to other birds because of their dense osteosclerotic bone structure, and large species are likely to be over-represented as a result of their greater ability to withstand wear.

PLIOCENE (5.3 TO 2.6 MYA)

Most of our knowledge of Africa's fossil penguins comes from large collections of isolated specimens recovered from the prolific Early Pliocene Langebaanweg 'E' Quarry, which has yielded thousands of specimens of birds (Rich, 1980; Olson, 1983; Haarhoff, 1988; Stidham, 2006; Manegold, 2010a, b; Manegold & Louchart, 2012) along with fossils from many other marine and terrestrial taxa (e.g. Hendey, 1973; Hendey, 1981; Hendey, 1982; Van Dijk, 2003; Botha & Gaudin, 2007; Avery & Klein, 2011). Additional specimens are known from the contemporary Koeberg (originally identified as Duinefontein) and Ysterplaats localities (Simpson, 1973; Simpson, 1979a; Olson, 1985) (Fig. 1). These fossils form the basis for four species of penguins: *I. predemerus*, *N. insolitus*, '*P.*' *huxleyorum*, and *D. hendeyi* (Simpson, 1973; Simpson, 1975; Simpson, 1979a; b; Olson, 1983; Olson, 1985). All of these species died out prior to the Middle Pleistocene.

PLEISTOCENE TO RECENT (THE LAST 2.6 MILLION YEARS)

Spheniscus demersus first appears in the fossil record between 270 000 and 400 000 years ago (Klein *et al.*, 1999; Cruz-Uribe *et al.*, 2003). Middle Pleistocene black-footed penguins are reported from three localities in the Western Cape of South Africa: Duinefontein (270–400 Kya), Hoedjiespunt (200–300 Kya), and Pinnacle Point (164 Kya) (Klein *et al.*, 1999; Stynder *et al.*, 2001; Cruz-Uribe *et al.*, 2003; Marean *et al.*, 2010; Avery & Klein, 2011; Fig. 1). Hyenas or other small carnivores probably transported scavenged penguin remains to Duinefontein (Duinefontein 2 and Duinefontein North) and Hoedjiespunt (Stynder *et al.*,

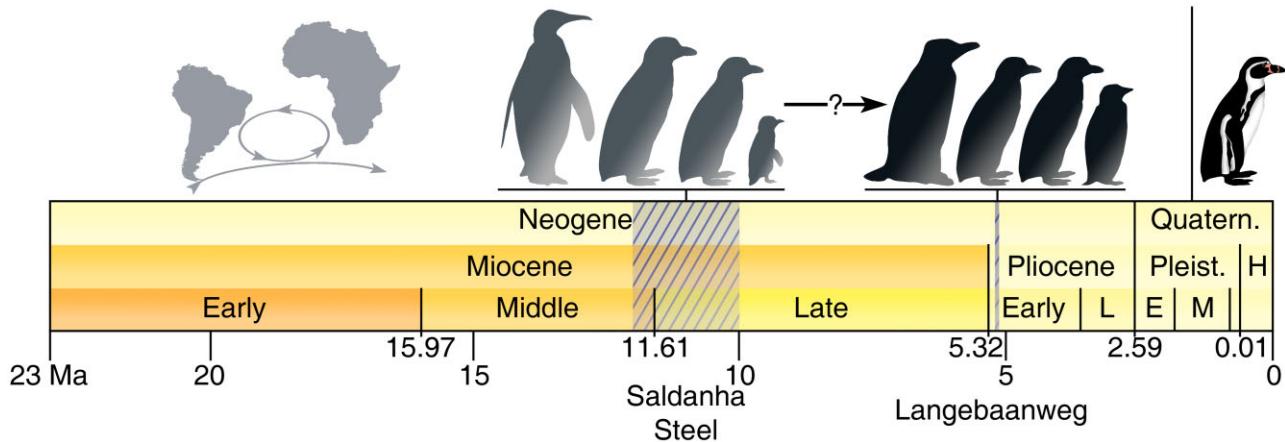


Figure 4. A history of shifting fortunes for African penguins. Oceanic currents have provided a dispersal mechanism for penguins since at least the beginning of the Neogene (Ksepka & Thomas, 2012). The earliest record for African penguins is a diverse assemblage from Saldanha Steel (12–10 Mya). The four Saldanha Steel penguin taxa span almost the complete range of body sizes seen in living species. African penguins were still diverse in the Early Pliocene (5.15 Mya; Roberts *et al.*, 2011), with four distinct species recovered from Langebaanweg and nearby localities, although the relationships between the Miocene and Pliocene penguins is uncertain. All four Langebaanweg penguins became extinct before the Middle Pleistocene, when records for the black-footed penguin (*Spheniscus demersus*) begin. Chronostratigraphical data from the International Commission on Stratigraphy (2012). Silhouettes are scaled to approximate body size based on comparisons to bones of extant taxa. Abbreviations: E, Early; H, Holocene; L, Late; M, Middle; Pleist., Pleistocene; Quatern., Quaternary.

2001; Cruz-Uribe *et al.*, 2003), whereas Pinnacle Point was occupied by humans. Tool cut marks on penguin bones have not been reported, although Cruz-Uribe *et al.* (2003) observed that ‘... [s]mall-carnivore tooth marks are apparent on many of the bird bones, and some exhibit etch marks from digestion ...’. Human artefacts and penguin bones have been recovered from Middle Pleistocene sediments at Klasies River Mouth, a coastal cave in the Eastern Cape of South Africa during the Middle Pleistocene (125 Kya) (Deacon, 1995).

Black-footed penguins have also been reported from two Late Pleistocene hominin-bearing localities in the Western Cape: Ysterfontein (46–115 Kya) and Sea Harvest (> 40 Kya) (Grine & Klein, 1993; Klein *et al.*, 2004). Penguins reported from Late Pleistocene Boegoeberg (71 to 37 Kya) in the Northern Cape were probably transported by hyenas (Klein *et al.*, 1999; Fig. 1). Interestingly, Pleistocene hominid localities in South Africa that have ready access to the ocean tend to lack fish bones (Klein *et al.*, 2004), which suggests that black-footed penguins did not compete directly with humans for food resources.

Abundant fish remains in latest Pleistocene and Holocene fossil penguin localities represent the seminal stages of food competition between humans and penguins (Klein *et al.*, 2004). Black-footed penguins have been reported from Die Kelders, Elands Bay, and Rooiels caves, and the Paternoster, Stofbergfontein, and Duiker Eiland middens in the

Western Cape, as well as Nelson Bay Cave in the Eastern Cape, with specimen ages ranging from 13 to 0.45 Kya (Avery, 1981, 2011; Avery & Underhill, 1986). The species has also been reported from two late Holocene localities in Namibia (Avery, 1984, 1985; Fig. 1).

DISCUSSION

A recurring theme in regional studies of fossil penguins is that many well-sampled fossil localities support higher levels of diversity in the past than are seen in the same regions today (Myrcha *et al.*, 2002; Jadwiszczak, 2006; Ksepka & Clarke, 2010). A similar phenomenon has also been noted for some other marine tetrapod groups such as sirenians, which are represented by multispecies communities at many fossil localities but today show almost no range overlap between individual species (Domning, 2001; Velez-Juarbe, Domning & Pyenson, 2012). This general trend of greater past diversity in penguin communities is now documented in Africa for the latter half of the Neogene. The four Saldanha species establish a high level of diversity in the Miocene (Fig. 4). At this single locality, four species spanning nearly the entire size range of modern penguins co-existed (Fig. 3). Unfortunately, the anatomical preservation of the Saldanha assemblage is currently insufficient to resolve the relationships with the younger Pliocene penguins. It is quite possible some

or all of the Saldanha species are ancestral to the Langebaanweg species, although more material is needed to test their relationships.

When the four Early Pliocene penguin species from Langebaanweg and nearby localities were first described, stratigraphical relationships amongst the various sites were not well established and it was thought that some species were Miocene in age (Simpson, 1973). Thus, species diversity levels remained unclear until Langebaanweg, Ysterplaats, and Duinefontein were shown to be equivalent in age, identifying *I. predemersus*, *N. insolitus*, '*P. huxleyorum*', and *D. hendeyi* as contemporaneous during the Early Pliocene (Olson, 1983; Fig. 4). These four Pliocene species spanned a wide size range, from the diminutive *I. predemersus* (approximately 15% smaller than *S. demersus*) to the large *N. insolitus* (approximately the size of the extant *A. patagonicus*). Miocene and Pliocene penguin diversity in South Africa is reminiscent of the modern-day Falkland Islands, where five breeding species contribute to a diversity 'hot spot' for living penguins [king, gentoo, macaroni, magellanic, and western rockhopper (Stonehouse, 1967)]. Considered together, the Neogene South African and modern Falkland Island records indicate a long history of high sympatric penguin diversity in the South Atlantic.

Penguin diversity in Africa crashed between the Early Pliocene and the Pleistocene. A gap in the local record leaves the pattern and timing of this decline in diversity uncertain (Fig. 4). The youngest records of the four extinct Langebaanweg species are dated to 5.15 Mya, whereas the oldest verified record of *S. demersus* are dated to 270–400 Kya (Klein *et al.*, 1999; Cruz-Urbe *et al.*, 2003). Thus, it remains uncertain whether the extinctions of the four Pliocene species were sudden or gradual, and whether any of these fossil species overlapped with *S. demersus*.

Two possible drivers for the recent decrease in penguin diversity are changes in sea level and restructuring of marine communities around the Western Cape. The Saldanha Steel marine fauna is still poorly documented, but the penguin species were contemporaneous with a diverse assemblage of shark taxa (including *Carcharodon megalodon*), as well as undescribed seals (Pinnipedia: Phocidae) and cetaceans (Hendey, 1976; D. B. Thomas, pers. observ.). Five to seven Myr later, the four Langebaanweg species were contemporaneous with several now-extinct seabird species from groups that typically occur in sub-Antarctic waters such as prions and diving petrels (Olson, 1983), several sharks and cetaceans (undescribed specimens), as well as phocid seals (e.g. *Homiphoca capensis*) and *Arctocephalus* fur seals (Pinnipedia: Otariidae) (Avery & Klein, 2011). Marine faunal restructuring between the Pliocene

and middle Pleistocene involved the loss of phocid seals, many procellariiforms and four penguin species, the retention of *Arctocephalus*, and the arrival of *Spheniscus*. It is noteworthy that the final replacement of true seals by otariids appears to have occurred contemporaneously in South America (Valenzuela-Toro *et al.*, 2013). The paucity and limited taxonomic resolution of the late Cenozoic marine fauna limits study, although it should be noted that anecdotally, an increase in the Cape fur seal (*Arctocephalus pusillus*) population since the late 19th century has altered the carrying capacity of the Benguela upwelling ecosystem for *S. demersus* (Crawford *et al.*, 2007; elaborated below).

Abiotic influences on penguin diversity should also be considered. It has previously been hypothesized that sea level change may have led to the crash in penguin diversity between the Pliocene and the present (Ksepka & Thomas, 2012). Roberts *et al.* (2011) reconstructed the subaerial land surface in the area surrounding Langebaanweg during the Early Pliocene. Citing glacio-eustasy as the principal control, Roberts *et al.* (2011) considered sea levels in the Saldanha Bay region to have been up to 90 m higher during the Early Pliocene, drowning much of the land area exposed today and replacing it with a network of islands. The modern-day land surface in the Saldanha Bay region has an estimated area of 120 km² and approximately 200 km of coastline. In contrast, the 90 m highstand of the Early Pliocene (Roberts *et al.*, 2011:fig. 12b) reduced the land surface to 20 km² but increased the coastline to 270 km (Ksepka & Thomas, 2012: supplementary material). The diverse penguin fauna from the Middle to Late Miocene may have flourished across islands while local sea level was high (Roberts *et al.*, 2011). Penguin diversity was also high during the early Pliocene, but whether the Pliocene species are closely related to the Miocene species is not yet resolved. Previously, we proposed that a sea level fall during the Late Pliocene–Pleistocene may have eliminated island breeding areas and provided land bridges for predators (Ksepka & Thomas, 2012). A large drop in sea level also occurred in the Saldanha region during the latest Miocene, which raises the question of whether penguin diversity in Southern Africa may have experienced multiple cycles of rise and fall tied to sea level fluctuations. At present, assessing the relative importance of physical and biological drivers for the Late Cenozoic shifts of penguin diversity in southern Africa awaits better resolution of the fossil record.

The proximal driver for the decline in *S. demersus* populations is less ambiguous. The ancestors of *S. demersus* arrived from South America at least 400 000 years ago, to a strand habitat populated with archaic humans (Stynder *et al.*, 2001; Marean *et al.*, 2010).

Penguins were a minor part of the human diet compared to coastal molluscs and terrestrial vertebrates. Middle Pleistocene humans did not compete with penguins for marine resources, and evidence for coastal fishing is only found from the latest Pleistocene onward (Klein *et al.*, 2004). Later, however, large-scale commercial fisheries targeting penguin-prey items in the Benguela upwelling system (anchovy, *Engraulis encrasicolus*; sardine, *Sardinops sagax*) began in the mid-20th century (Crawford, Shannon & Pollock, 1987). Furthermore, reduced hunting pressure has in recent years buoyed the population of Cape fur seals (*Arctocephalus pusillus*), which also target anchovy and sardine (Crawford *et al.*, 2007). Competition for food resources has been cited as a major factor influencing the decline in black-footed penguin populations (Crawford *et al.*, 2007; Birdlife International, 2012).

Insight from the fossil record reveals that the history of penguins in Africa has not been static or simple. Penguins have a long history on the continent, and many lineages have dispersed to Africa and successfully foraged from the southern shorelines for millions of years (Ksepka & Thomas, 2012). Yet, Africa has proven to at times become untenable for individual penguin species, with at least four species being driven to extinction before the Middle Pleistocene. The black-footed penguin is the scion of the most recent dispersal to Africa, and with continued conservation efforts, it will hopefully avoid the fate of its forebears.

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APPENDIX

REGIONAL GEOLOGY

Vertebrate fossils from the West Coast region of Western Cape Province in South Africa have thus far been reported only from a thin package of Neogene and Quaternary strata overlying Neoproterozoic basement (Roberts *et al.*, 2011). Five sedimentary units are currently recognized between Saldanha Bay (33.04°S, 18.00°E) and the West Coast Fossil Park (32.96°S, 18.11°E): the Elandsfontyn Formation, Prospect Hill Formation, Varswater Formation, Lange-

baan Formation, and Springfontyn Formations (oldest to youngest, respectively). The Elandsfontyn Formation is mostly coarse to medium angular sand regularly interspersed with angular gravel. Peat is common as localized lenses and has produced abundant pollen grains, which provide biostratigraphical support for an approximately middle Miocene age (~16 to 12 Mya; Coetzee & Rogers, 1982; Roberts, 2006a). The Elandsfontyn Formation has been mapped over 20 km², whereas the Prospect Hill Formation has only been identified from the type section (33.00°S, 18.92°E). The Prospect Hill Formation is a calcareous fine to medium sand with periodic and heavily cemented horizons. Calcareous layers have produced ratite eggshell comparable to *Diamantornis wardi*, which has an age range of 10 to 12 Mya in neighbouring Namibia (Roberts & Brink, 2002; Stidham, 2008). The Prospect Hill Formation is likely to be a littoral equivalent of the more terrestrial Elandsfontyn Formation.

The Varswater Formation conformably overlies the Elandsfontyn Formation and is subdivided into four members. The lowermost Langeenheid Clayey Sand (Vc) member is fine sand and carbonaceous clay sharply overlain by the rounded and matrix-supported cobbles of the Konings Vlei Gravel (Vk) member. Very fine to medium sands of the Langeberg Quartz Sand (Vs) member unconformably overlie the Vk, and are in turn conformably overlain by quartz sand, phosphorite grains, and abundant vertebrate fossils of the Muishond Fontein Phosphatic Sand (Vm) member. Most penguin specimens described from South Africa are derived from the Vm member. Palaeomagnetic and sea level reconstruction data give an age of 5.15 Mya for the Vm (Roberts, 2006b; Roberts *et al.*, 2011). The Langebaan Formation is composed of calcareous cemented sand beds with abundant shell fragments that unconformably overlie the Varswater Formation. The Langebaan Formation contains invertebrate fossils (e.g. *Donax rogersi* and *Fissurella glareata*) from the Plio-Pleistocene transition (~2.6 Mya) and Acheulian artefacts with an age range of ~1.5 to 0.5 Mya (Roberts *et al.*, 2011). The Springfontyn Formation includes middle Pleistocene and Holocene unlithified, aeolian sands (dated with optically stimulated luminescence; Roberts *et al.*, 2011). The oldest reported black-footed penguin fossils were excavated approximately 90 km south of Saldanha Steel, from sediments that are consistent with the Springfontyn Formation (Klein *et al.*, 1999).

SALDANHA STEEL LOCALITY

Fossil material described in the current study was collected from the bottom of a 12-m-deep excavation for an industrial steel plant (Saldanha Steel: 32.98°S,

Figure A1. Facies correlations in the Western Cape of South Africa provide a Middle to Late Miocene age for penguin fossils. The stratigraphical sequence at the Saldanha Steel locality (reproduced from borehole data) is interpreted with reference to two sections approximately 9 km inland. Penguin fossils were excavated from a gravel facies within the Saldanha Steel sequence, which is laterally equivalent to the 12–10 Mya Konings Vlei Gravel member in the Varswater holostratotype. The Saldanha Steel borehole log was compiled by Jones and Wagener, Consulting Civil Engineers, Rivonia, South Africa (22 January 1996). Borehole S1 and the Varswater holostratotype sequences were reproduced with reference to Coetzee & Rogers (1982), Rogers (1982), and Roberts (2006a, b). The Saldanha Steel and Borehole S1 sections are presented with the same scale and sea level datum (asl, above sea level). The scale of the Varswater holostratotype is expanded relative to the other sections.

18.02°E). A 30.45 m bore hole through the site was logged prior to excavation (22 January 1996, Jones and Wagener, Consulting Civil Engineers, Rivonia, South Africa) (Fig. A1). Carbonaceous material is restricted to the lower 10.5 m of the section, which includes conformable silty-sand, sand, and sandy-gravel beds. Silty-peat transitions through black clay (0.95 m) into a thick lens of pale grey clay (4 m). Fine sand unconformably overlies the clay (1.05 m), and is in turn overlain by angular gravels with oyster shell fragments (gen. et sp. indet.) and the penguin fossils described in the current study (1.95 m). These gravels are in turn overlain by moderately cemented fine sandy-clay (3 m) and fine sands (9 m), which form a calcrete immediately below the surface (1.4 m). Penguin fossils from the Saldanha Steel excavation were briefly described in a 1997 report by Dr David Roberts, which was prepared for the Agency for Cultural Resources Management (unpubl. data).

COMPARATIVE STRATIGRAPHY

The Saldanha Steel stratigraphical section can be correlated with two well-studied sections approximately 9 km inland at the West Coast Fossil Park, (1) Borehole S1 and (2) the Varswater holostratotype (Fig. A1). Borehole S1 is a 102.6 m section through the Elandsfontyn, Varswater, and Langebaan formations, and the Varswater holostratotype is a 14 m section through the Varswater and Langebaan formations (Rogers, 1982; Roberts, 2006b). The base of the Varswater holostratotype is a clay-rich sand (Vc), overlain by rounded gravels (Vk), fine- to medium-grained, subangular sand (Vs) and medium to coarse sand with peletal phosphorite grains (Vm). A lateral equivalent to the Vc-Vk-Vl-Vm sequence in the Varswater holostratotype can be identified in the uppermost 70 m of Borehole S1. The Langeenheid Clayey Sand (Vc) is represented in Borehole S1 by clay and fine sand (1.8 m thick) that grades into very fine, fine, and medium sands (9.4 m thick). Unconformably

overlying the sand sequence is a 1.4-m-thick conglomerate, which transitions from a clast-supported unit to a matrix-supported unit, and eventually to a medium sand (cf. Vk). A 0.4-m-thick layer of fine sand represents the Langeberg Quarz Sand (Vs), and is overlain by fine to medium sand with peletal phosphorite nodules (8.6 m thick; cf. Vm).

Borehole S1 mostly sectioned Elandsfontyn Formation (45.5 to 102.6 m), which also contains useful sedimentary sequences for correlating with the Saldanha Steel site. Carbonaceous material in Borehole S1 is restricted to a clay-peat horizon that grades into a noncarbonaceous clay (8.8 m thick; Rogers, 1982). The peat and carbonaceous clay (Ec) horizon is conformably overlain by medium to coarse sand (Es) at the uppermost Elandsfontyn Formation (Roberts, 2006a), which is unconformably overlain by the lateral equivalent of the Langeenheid Clayey Sand (Vc) discussed above.

The stratigraphical sequence in Borehole S1 (Ec-Es-Vc-Vk-Vs-Vm) can be identified in the Saldanha Steel section. Carbonaceous material in the Saldanha Steel section occurs in clay horizons and conglomerates. An uppermost silty peat transitions to pale grey clay; we propose this to be the equivalent of the Ec horizon identified in Borehole S1 (Fig. A1). Conformable coarse sands of the Es horizon are not represented at Saldanha Steel. Instead, the Ec clay is unconformably overlain by sand (fine to coarse), which is overlain by a clast-supported conglomerate. We identify these horizons as lateral equivalents of the Langeenheid Clayey Sand and Konings Vlei Gravel members. Moderately cemented fine sandy-clay overlies the gravels, which is characteristic of both the Langeberg Quarz Sand and Muishond Fontein Phosphatic Sand members. The Neogene sequence between the Varswater holostratotype and the Saldanha Steel sections gently slopes towards the ocean, and is not interrupted by substantial faulting or folding (Roberts *et al.*, 2011).

