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Review

Penguin past: The current state of knowledge

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Abstract: Penguins (Aves: Sphenisciformes) hold much interest for many people, including (but not limited to) scientists. According to results of molecular studies, penguin history began in the Cretaceous, but the oldest bones assigned to these birds are Paleocene in age. The first fossil representative of Sphenisciformes formally described was *Palaeeudyptes antarcticus*, and this event took place 150 years ago. Since that time, several dozens of species have been erected, though not all of them have stood a test of time. The 21st century entered new dynamics into the paleontology of penguins, and (importantly) it concerned both the new material, and new theories. This paper summarizes what we currently know about extinct penguins and indirectly suggests the most promising areas for further research.

Key words: Southern Hemisphere, Aves, Sphenisciformes, evolution, fossil record.

Introduction

Penguins are highly specialized seabirds and simply intriguing creatures. They seem to have no special fear of humans despite the exploitation on a massive scale up to the beginning of the 20th century (del Hoyo *et al.* 1992). Obviously, some groups of indigenous inhabitants of southern continents have known penguins for millennia (*e.g.* Simeone and Navarro 2002). The first Europeans to see them, almost certainly the African Penguins, *Spheniscus demersus* (Linnaeus, 1758), and leave notes on this event were members of the voyage of Vasco da Gama in 1497/98 (del Hoyo *et al.* 1992). The word "penguin", however, started to be used to name those birds much later. The most agreed-upon explanation is that it was transferred from the now-extinct Great Auk *Pinguinus impennis* (Linnaeus, 1758), a flightless bird from the northern Atlantic, which the extant penguins resemble (Simpson 1976a).

Penguins are, and most probably always have been, confined to the Southern Hemisphere[1]. They breed as far north as the Equator and as far south as Antarctica, but only a few species of these birds are actually native to the Antarctic continent, and only a single species is equatorial. At present, there are 16–19[2] species of penguins (the exact number still being debated), and they are divided into six clearly defined genera (Davis and Renner 2003). Penguins form a sole family (Spheniscidae) within the order Sphenisciformes[3] (formerly called Impennes), and the monophyly of the Sphenisciformes appears to be beyond the question (Bertelli and Giannini 2005; Baker *et al*. 2006; Ksepka *et al.* 2006).

Penguins vary considerably in both body mass and standing height, ranging from 1.1 kg/40 cm for the Little Penguin, *Eudyptula minor* (Forster, 1781) to over 30 kg/115 cm for the Emperor Penguin, *Aptenodytes forsteri* Gray, 1844 (Williams 1995). Nevertheless, they share a very similar body form and structure. The most conspicuous penguin feature is flightlessness, although there is consensus that penguins had flying ancestors. To be precise, sphenisciforms are devoid of the ability of aerial flight while being the excellent wing-propelled divers (they are capable of "underwater flight"). Thus the most obvious adaptations of penguins are for underwater locomotion (wings as paddles, osteosclerotic bone structure and much more). They feed on crustaceans (mainly krill), fish and squids, and according to some authors, *e.g.* Davis and Renner (2003), penguin diversity as well as most aspects of their biology can be explained by the distance they travel for food.

Although penguins are biologically fascinating and ecologically important, the evolutionary processes that shaped them happened in the past. The first penguin fossil, an incomplete tarsometatarsus (Fig. 1), was collected by an unnamed Maori in the limestone of Kakanui (South Island, New Zealand) in about 1859, and brought (still partly in matrix) to Mr. Walter Mantell. Mr. Mantell gave it to his friend, Thomas Henry Huxley, who formally described the specimen erecting the first species of fossil penguin, *Palaeeudyptes antarcticus* Huxley, 1859. This bone is housed at the Natural History Museum in London (catalogue number A.1048). Several dozens of fossil penguin species have been described since that time (Ameghino 1905; Wiman 1905a, b; Marples 1952, 1953; Simpson 1971a, b, 1972a; Myrcha *et al.* 1990, 2002; and this is just a shortened list of "classic"

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[1] A number of individuals out of those breeding on the equatorial Galapagos Islands constitute the only exception to that "rule" (*e.g.* Davis and Renner 2003).

[2] 17 species according to del Hoyo *et al.* (1992) and Williams (1995), and this is the most widely accepted version.

[3] Following the phylogenetic approach, the Linnean family name Spheniscidae was applied by Clarke *at al*. (2003) to the clade comprised of the most recent common ancestor of all extant penguins and all of its descendants. Moreover, they (Clarke *et al.* 2003) coined the name Pansphenisciformes to label all taxa more closely related to present-day penguins than any other extant avian taxa, Sphenisciformes being reserved for all parts of this lineage with a loss of flight homologous with that of modern penguins.

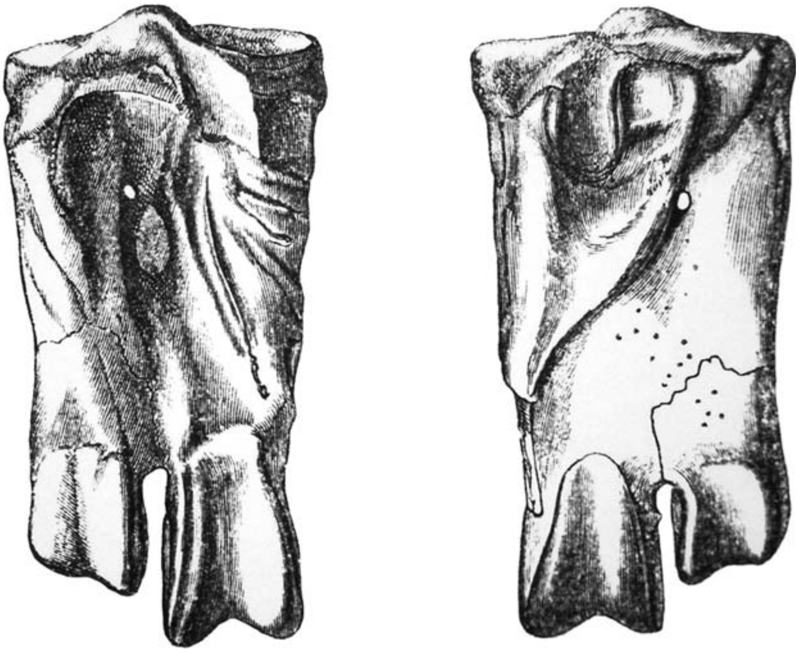

Fig. 1. The holotype tarsometatarsus of *Palaeeudyptes antarcticus* – dorsal (left) and plantar views. The bone is *ca* 62 mm long. From Huxley 1859.

works). Contributions reviewing fossil penguins and having a supraregional scope are rare; those by Simpson (1946, 1975, 1976a), Brodkorb (1963) and Fordyce and Jones (1990) have become the most influential ones.

The intent of this paper is to review fossil penguins according to the current state of knowledge in the 150th anniversary of Huxley's (1859) pioneering work. Unlike the above-mentioned approaches, I decided to follow "the arrow of geologic time" rather than present the local faunas of extinct sphenisciforms one after another.

Origins of penguins

It has been obvious for some time that penguins arose from volant birds (Bannasch 1986; Raikow *et al.* 1988). Nowadays, other proposals (*e.g.* Lowe 1933, 1939) are solely of historical interest. The earliest fossils assigned to Sphenisciformes (discussed in the next section) provide a lower estimate of 61–62 Ma (Early Paleocene, *i.e.* close to the K/T boundary) for the divergence between penguins and other Neornithes (Slack *et al.* 2006). Slack *et al.* (2006) argue that the great disparity between penguins and their sister taxa suggests that the process that gave rise to sphenisciforms was the Late Creataceous neornithine radiation. They (Slack *et al.* 2006) predicted this process began at 90–100 Ma (supported by mitochondrial DNA analyses using fossil calibrations). Estimates of divergence time obtained by Baker *et al.* (2006) via molecular dating (nuclear DNA, mitochondrial DNA and both sets combined) suggest that penguins originated about 71 Ma (95% CI 62.4–77.3 Ma). All these results are in line with Simpson's (1975)[4] belief that "the time must have been in the Cretaceous".

At present, it is not possible to locate one particular center for the origin of penguins. The temptation to automatically point towards the region the oldest bones come from can be misleading as the fossil record from the Paleocene epoch is scarce (Fordyce and Jones 1990; Tambussi *et al.* 2005; Slack *et al.* 2006), and the Paleocene and Eocene penguins are known from localities on opposite sides of Antarctica (Simpson 1971a, b; Jenkins 1974, 1985; Myrcha *et al.* 2002; Clarke *et al.* 2003, 2007; Tambussi *et al.* 2005, 2006; Jadwiszczak 2006a; Slack *et al.* 2006; and references cited therein). At least two genera were circumpolar in their distribution by the end of the Eocene epoch (Simpson 1971a, b; Jenkins 1985; Myrcha *et al.* 1990, 2002; Jadwiszczak 2006a; Tambussi *et al.* 2006). Furthermore, three Eocene species of penguins from the Antarctic Peninsula were placed by Ksepka *et al.* (2006) near the base of the cladogram immediately above two species from the Paleocene of New Zealand, Paleocene Antarctic fossils were not included in their analysis (see also Jadwiszczak 2006b). One cannot also forget that southern continents were closer to each other during that time period.

The closest extant relatives of penguins appear to be among the Ciconiidae, Fregatidae, Gaviiformes, Podicipediformes or Procellariiformes as suggested by many independent analyses based on morphological, behavioral and molecular data (taxa arranged in alphabetical order; Simpson 1946, 1975; Ho *et al.* 1976; Marples 1962; Cracraft 1981, 1982, 1985, 1988; Olson 1985; O'Hara 1989; Sibley and Ahlquist 1990; van Tuinen *et al.* 2001; Mayr and Clarke 2003; Baker *et al.* 2006; Ksepka *et al.* 2006; Slack *et al.* 2006; Watanabe *et al*. 2006; Clarke *et al.* 2007; Livezey and Zusi 2007; and others). Loons and tubenoses seem to be the most frequently chosen outgrups in phylogenetic analyses of Sphenisciformes. Recently, Mayr (2005) proposed the Northern Hemisphere Plotopteridae as a sister taxon of penguins. These flightless wing-propelled diving birds are known from the Late Eocene–Early Miocene time period, and exhibit similar wing morphology to penguins (Mayr 2005, and references cited therein). Furthermore, they share some derived characters with "pelecaniform" Suloidea (Sulidae, Phalacrocoracidae and Anhingidae). Hence it is not surprising that the cladistic analysis by Mayr (2005) resulted in the clade Plotopteridae + Spheniscidae being a sister taxon of the Suloidea.

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[4] George Gaylord Simpson (1902–1984) was the most influential and prolific student of fossil penguins.

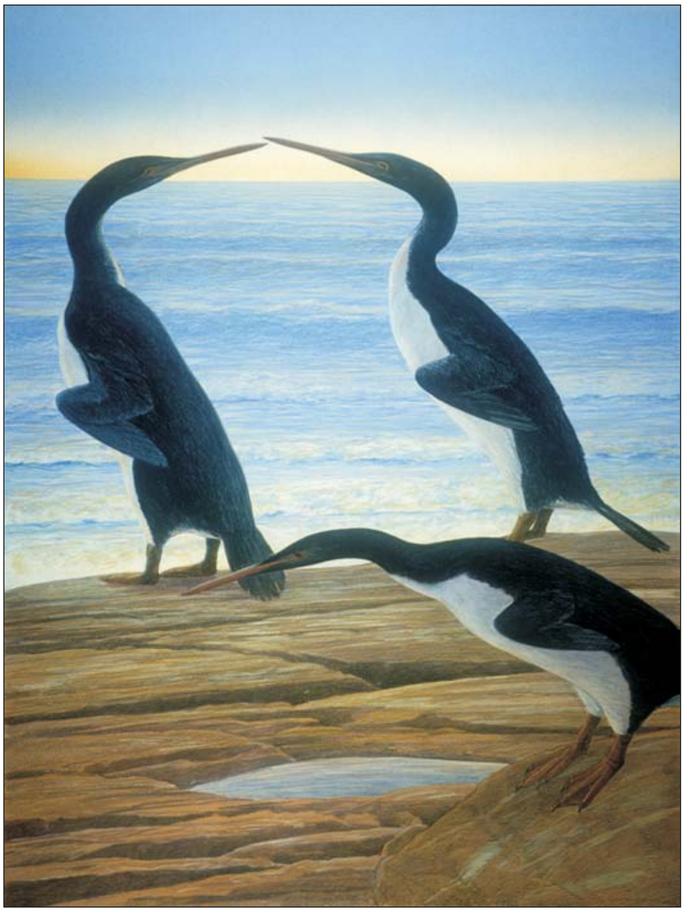

Fig. 2. Three individuals of *Waimanu tuatahi* on a New Zealand beach in Paleocene times. Reconstruction © Geology Museum, University of Otago; artist Chris Gaskin. Used with permisson.

The fossil record

Paleocene. — The oldest known penguin fossils come from the early Paleogene of New Zealand (the Waipara Greensand, North Canterbury; Fordyce and Jones 1990; Jones and Mannering 1997; Slack *et al.* 2006). Four associated (though partial) skeletons represent two congeneric species, that cladistically belong in the stem-Sphenisciformes (Slack *et al.* 2006; see also Clarke *et al.* 2003). These are *Waimanu manneringi* Jones, Ando *et* Fordyce, 2006 (holotype only) and *Waimanu tuatahi* Ando, Jones *et* Fordyce, 2006 (or the Waipara bird of Fordyce and Jones [1990]; Fig. 2), from the late Early Paleocene (60.5–61.6 Ma) and the early Late Paleocene (58–60 Ma)[5], respectively (Slack *et al.* 2006). They were rel-

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[5] Or just the Late Paleocene in the case of some specimens.

atively large penguins (*ca* 80–100 cm tall; Slack *et al.* 2006) with long narrow bills (not an unusual feature in early penguins) as well as relatively long wings and tarsometatarsi (as compared to geologically younger sphenisciforms), somewhat loon-like in appearance (Fig. 2, Slack *et al.* 2006: fig. 1C). Fordyce and Jones (1990) took note of other Paleocene remains, a fragment of coracoid, scapula and a tiny fragment of the humeral head (C. Jones, personal communication, 2003), which had belonged to another wing-propelled diver, possibly penguin. The coracoid resembles that of *Waimanu*, but is larger. They were recovered from the Moeraki Formation (north of Dunedin, New Zealand), and came from slightly younger sediments than *Waimanu* (Fordyce and Jones 1990; C. Jones, personal communication, 2003).

The third and last named species of Paleocene penguins reported so far is *Crossvallia unienwillia* Tambussi, Reguero, Marenssi *et* Santillana, 2005. Unfortunately, its record consists solely of three incomplete bones (humerus, femur and tibiotarsus) recovered from the upper part of the Cross Valley Formation of Seymour Island, Antarctic Peninsula (Late Paleocene, 55–56 Ma; Tambussi *et al.* 2005). Tambussi *et al.* (2005) estimated the "total size" of the bird to be between 127.5 and 142.5 cm (*i.e.* it had been clearly larger than the largest modern penguins). It is important to mention that the climate in the northern Antarctic Peninsula was warm and wet during most of the Late Paleocene time period (*e.g.* Dingle *et al.* 1998), so *C. unienwillia* inhabited a totally different environment in terms of thermal (needless to say, not only thermal) conditions than their extant Antarctic relatives. For the paleogeographic map showing localities of known Paleocene penguins, see Fig. 3.

Eocene. — The fossil record of Eocene penguins is much more abundant compared to that of the previous epoch. The earliest bones come from the two lowermost units of the La Meseta Formation[6] of Seymour Island, Antarctic Peninsula (Myrcha *et al.* 2002; Jadwiszczak 2006b), and are Early Eocene in age (Marenssi 2006; see also Porębski 1995, 2000). Interestingly, some of them are very similar to their counterparts assigned to large-bodied species so far known from the Middle and Late Eocene strata of the formation (Jadwiszczak 2006b).

The vast majority of Antarctic penguin fossils (thousands of specimens[7]) were discovered within the upper part of the La Meseta Formation thus are Late Eocene in age (Myrcha *et al.* 1990, 2002; Jadwiszczak 2006a). No articulated skeletons are known (but see Tambussi *et al.* 2006: p.146), and almost all specimens are single bones. Tarsometatarsi appear to be the most useful bones for taxonomic identifica-

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[6] English "the" and Spanish "la" mean the same (they are definite articles), however, in the case of this formation, they are used together so widely (also by me) that I decided not to change this form here.

[7] Collections of fossil penguins from the La Meseta Formation are scattered throughout the world (*e.g.* Jadwiszczak 2006a), but the largest sets are housed at the Museo de La Plata (La Plata, Argentina) and the Institute of Biology, University of Białystok (Białystok, Poland). They are probably also the largest collections of extinct sphenisciforms ever.

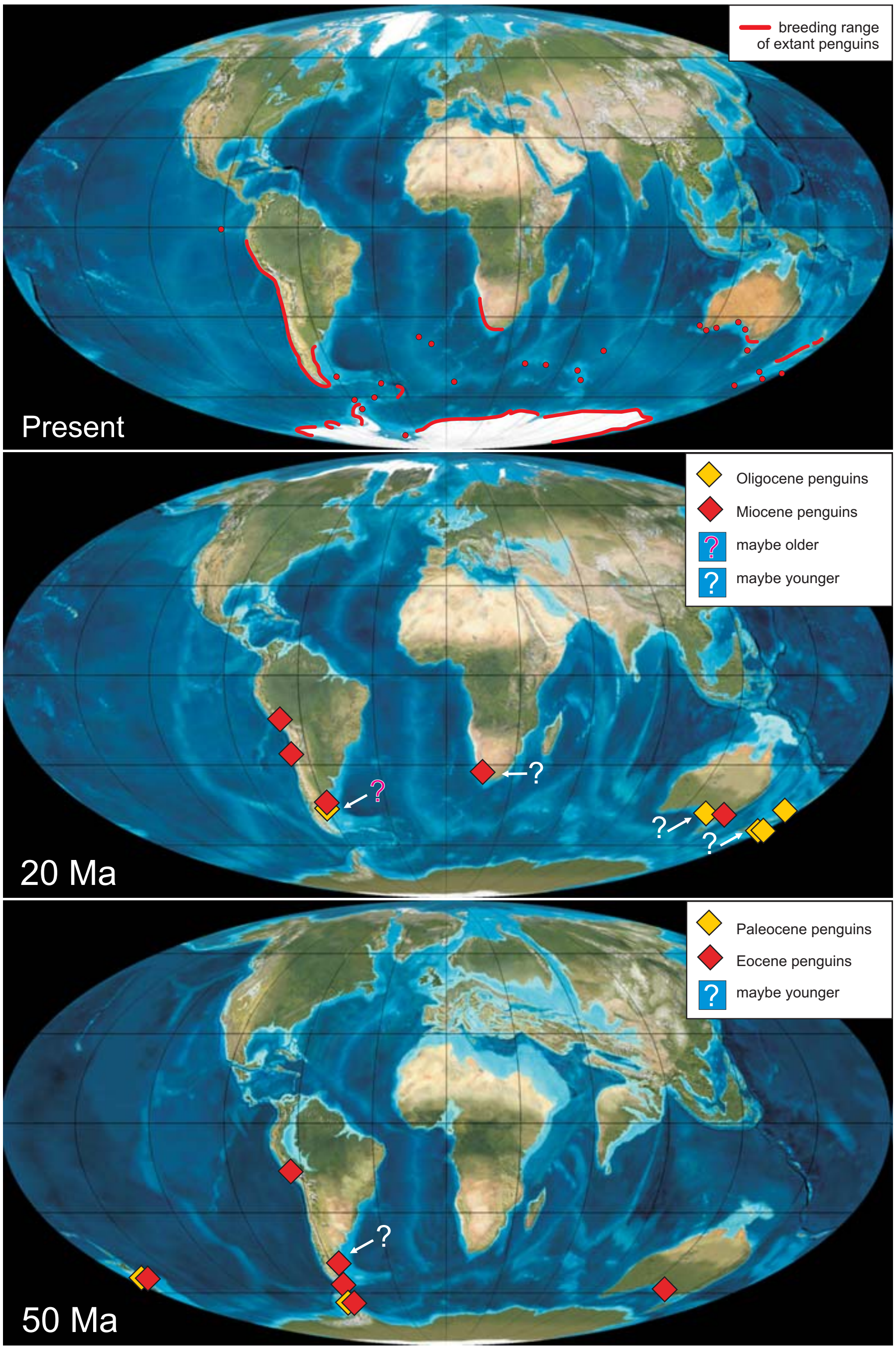

Fig. 3. Distribution of present-day penguins and localities of known fossil penguins from the Paleocene–Miocene time period. A single marker may represent more than one locality. The maps are Mollewide projections created by R.C. Blakey (http://jan.ucc.nau.edu/~rcb7/mollglobe.html). Used with permission.

tion of isolated remains of fossil penguins (*e.g.* Walsh *et al.* 2007), and most of the named species from Seymour Island (and many other localities) are based on this element (Wiman 1905a, b; Marples 1953; Simpson 1971a; Myrcha *et al.* 1990, 2002; Jadwiszczak 2006a). These are: *Anthropornis grandis* (Wiman, 1905), *A. nordenskjoeldi* Wiman, 1905, *Archaeospheniscus wimani* (Marples, 1953), *Delphinornis arctowskii* Myrcha, Jadwiszczak, Tambussi *et al*., 2002, *D. gracilis* Myrcha, Jadwiszczak, Tambussi *et al*., 2002, *D. larseni* Wiman, 1905, *Ichtyopteryx gracilis* Wiman, 1905, *Marambiornis exilis* Myrcha, Jadwiszczak, Tambussi *et al*., 2002, *Mesetaornis polaris* Myrcha, Jadwiszczak, Tambussi *et al*., 2002, *Palaeeudyptes gunnari* (Wiman, 1905) and *P. klekowskii* Myrcha, Tatur *et* del Valle, 1990[8] (Fig. 4). *I. gracilis* is based on such a fragmentary specimen that was described by Simpson (1971a) as being “essentially indeterminate at present” (see also Myrcha *et al.* 2002 and Jadwiszczak 2006a). Recently, I reviewed several hundred bones other than tarsometatarsi suggesting ten species (without *I. gracilis*) sorted into six genera as a minimum reliable estimate of the Eocene Antarctic penguin diversity (Jadwiszczak 2006a). On the other hand, Millener (1988) suggested the existence of up to seven genera and some fourteen species of penguins from Seymour Island. Last year, I described an intriguing (though incomplete) tarsometatarsus of a small penguin that, in my opinion, represented an undescribed genus and species of Sphenisciformes (Jadwiszczak 2008). However, because of the fragmentary nature of the material, I did not decide to erect a new taxon. This finding and suggestions expressed in Myrcha *et al.* 2002 and Jadwiszczak 2006a are decidely in line with Millener’s (1988) conviction.

Unfortunately, not only tarsometatarsi were used as holotypes of fossil species from the La Meseta Formation. The oldest such a case is more than a hundred years old (Wiman 1905a, b). *Orthopteryx gigas* Wiman, 1905 had been based exclusively on a large partial synsacrum and Simpson (1971a) described this taxon as “essentially indeterminate”. I agree with him, most probably the bone belonged to *A. nordenskjoeldi*. Another work that introduced taxon based solely on the non-metatarsal features is that of Simpson (1971a). *Wimanornis seymourensis* Simpson, 1971, the species of large-bodied penguins, is represented by two humeri, and (in my opinion) is most likely not a distinct taxon (Jadwiszczak 2006a). Recently, Tambussi *et al.* (2006) erected two new species (and a new genus) of penguins, *Tonniornis mesetaensis* Tambussi, Acosta Hospitaleche, Reguero *et* Marenssi, 2006 and *T. minimum* Tambussi, Acosta Hospitaleche, Reguero *et* Marenssi, 2006, based on humeri. I (Jadwiszczak 2006b) criticized their (Tambussi *et al.* 2006) decission not only because of the choice of skeletal elements (humeri are generally characteristic bones, however, their assignment to small-bodied species is problematic, see Jadwiszczak 2006a),

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[8] *Palaeeudyptes* (genus known also from other regions and epochs) was paraphyletic in results from Ksepka *et al.* 2006 and Clarke *et al.* 2007.

Fig. 4. A 1.6 m long *Palaeeudyptes klekowskii* hunting a fish (the Late Eocene of Antarctic Peninsula). Artist Dorota Cyranowska. This reproduction was originally prepared for the *National Geographic Polska* (NG Polska 8, 2007). Used with permission.

but also formal inaccuracies. Moreover, they (Tambussi *et al.* 2006) assigned a number of bones to two species so far known exclusively from the Oligocene of New Zealand. Again, I had to raise my objections (Jadwiszczak 2006b). To my mind, there is too weak a basis for considering the Oligocene New Zealand taxa part of the Eocene Seymour Island assemblage (for details see Jadwiszczak 2006b).

Individuals from six species belonging to four genera most probably were not larger than Emperor Penguins, the heaviest and tallest modern sphenisciforms (Jadwiszczak 2001). Interestingly, most of them (*D. arctowskii*, *D. gracilis*, *M. exilis*, *M. polaris* and the enigmatic tarsometatarsus mentioned earlier) are known solely from the youngest unit of the La Meseta Formation, *i.e.* Telm7 (Myrcha *et al.* 2002; Jadwiszczak 2006a). Another group consists of the so-called giant penguins (this term was criticized by Simpson [1976a]), at least some of them had long and dagger-like bills (Olson 1985; Myrcha *et al.* 2002; Jadwiszczak 2003; see also Jadwiszczak 2006a: p. 40 and fig 18a; Jadwiszczak 2006b: p. 194 and fig. 4a). Its largest representatives, birds assigned to *A. nordenskjoeldi*, could weigh more than 80 kg, their body lengths exceeded (considerably in some cases) 165 cm (Jadwiszczak 2001; see also Livezey 1989).

Most, if not all, of the La Meseta penguins may have co-existed in the West Antarctic during the Late Eocene epoch, just prior to the final break-up of Gondwana and the rapid expansion of continental ice sheets near the Eocene/Oligocene boundary (Simpson 1975; Case 1996; Jadwiszczak 2006a; Tambussi *et al.* 2006; and references cited therein). I proposed the adaptive radiation under periodically unfavourable trophic conditions as an explanation for the abundance of the Eocene Antarctic penguins (Jadwiszczak 2003). According to Myrcha *et al.* (2002), a number of factors, including environmental (abiotic components) and ecosystem changes, were responsible for the accelerated evolution of penguins during the Eocene. In fact, through the considerable part of this epoch the Antarctic Peninsula followed the global trend of climate deterioration (documented to be somewhat step-like with several reversals in the Antarctic) and accompanying evolution of biota (Gaździcki *et al.* 1992; Dingle *et al.* 1998; Zachos *et al.* 2001; Myrcha *et al.* 2002; Birkenmajer *et al.* 2005; Francis *et al.* 2008). The change was really radical: from a warm greenhouse world (the Late Paleocene/Early Eocene thermal maximum, "PETM") to the glacial Antarctic icehouse (Gaździcki *et al.* 1992; Dingle *et al.* 1998; Birkenmajer *et al.* 2005; Francis *et al.* 2008).

According to Baker *et al.* (2006; multiple gene evidence) the common ancestry of extant penguins dates back to *ca* 40 Ma, *i.e.* the Eocene epoch, when *Aptenodytes* diverged as the basal lineage. What is more important here is that they (Baker *et al.* 2006) additionally suggested an Antarctic origin of extant taxa. By contrast, there is no fossil evidence for the extant penguin radiation in the Eocene (Myrcha *et al*. 2002; Jadwiszczak 2006a; Clarke *et al.* 2007), and the oldest bones assigned to an extant genus are from the Miocene epoch, from outside the Antarctic (*e.g.* Göhlich 2007).

The fossil record of Eocene penguins is not restricted to the Antarctic, however. Traveling northwards, we can encounter several South American localities. The first American fossil penguin from that epoch comes from the Leticia Formation at Punta Torcida, Tierra del Fuego, Argentina (Clarke *et al.* 2003). It is represented by parts of an associated pelvic girdle and limb (nearly complete tibiotarsus, fibula and two incomplete femora). This relatively large sphenisciform (slightly smaller than the Emperor Penguin) is late Middle Eocene in age (Clarke *et al.* 2003). One cannot exclude the possibility that in future the Punta Torcida bird will be assigned to a taxon known from the La Meseta Formation. Moreover, there are two other Argentine fossil penguins, *Arthrodytes andrewsi* (Amegino, 1901) and *Paraptenodytes robustus* (Ameghino, 1885)[9] that may be Late Eocene in age. Their remains (humerus, coracoid and scapula, and tarsometatarsi, humeri and femora, respectively) are known from the San Julián Formation (Late Eocene–

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[9] A number of bones assigned to this species have been also reported from the Bahía Inglesa Formation (Late Miocene/Early Pliocene, Chile; Acosta Hospitaleche *et al.* 2002). In my opinion, this assignment should be verified.

Early Oligocene; Acosta Hospitaleche 2005; Acosta Hospitaleche and Tambussi 2008).

Recently, two Eocene penguins have been discovered in Peru (Clarke *et al.* 2007). One new species, *Perudyptes devriesi* Clarke, Ksepka, Stucchi *et al.*, 2007, is based on several elements including head bones, humeri and the incomplete tarsometatarsus, and was approximately the size of the King Penguin (*Aptenodytes patagonicus* Miller, 1778). It comes from the basal Paracas Formation, Department of Ica (Middle Eocene). Another new species, *Icadyptes salasi* Clarke, Ksepka, Stucchi *et al.*, 2007 from the Late Eocene strata of the Otuma Formation (Department of Ica), was a real giant (above 1.5 m standing height) as indicated by its partially preserved skeleton (*e.g.* hind limbs are missing; Clarke *et al.* 2007; Ksepka *et al.* 2008). Both species from Peru had straight, elongate bills. According to Clarke *et al.* (2007), two equatorial ingressions by Paleogene penguins are supported: dispersal from the Antarctic (by the Middle Eocene) and a second from New Zealand (by the Late Eocene). Moreover, unlike Tambussi *et al.* (2005), they (Clarke *et al.* 2007) suggest a single origin of extremely large size in the penguin lineage. Additional material indicates the presence of undescribed penguin taxa in the Otuma Formation (Acosta Hospitaleche and Stucchi 2005; Clarke *et al.* 2007).

The oldest post-Paleocene and formally described penguins from New Zealand are of Late Eocene age (Marples 1952; Simpson 1975; Fordyce and Jones 1990; Cooper 2004). These are *Pachydyptes ponderosus* Oliver, 1930 (Runangan; Oamaru, South Island) and *Palaeeudyptes marplesi* Brodkorb, 1963 (Kaiatan or Runangan; Burnside, South Island). Both were "giant" penguins[10], the former being larger, similar in size to *Anthropornis* (Simpson 1975; Jenkins 1985; Livezey 1989). Additional fossils were described as *Palaeeudyptes* sp. indet. (not *marplesi*) or just *Palaeeudyptes* sp. (Simpson 1971b, 1975; see note in the "Eocene" section regarding doubtful monophyly of this genus).

The Late Eocene penguin bones come also from southern Australia. They were assigned to *Palaeeudyptes* sp. (specimens from Christies' Beach, near Adelaide; Simpson 1975, and references cited therein) and *Anthropornis nordenskjoeldi* (several bones including a characteristic partial coracoid and fragments of humeri from the Blanche Point Marls near Adelaide; Jenkins 1974, 1985). Although the tarsometatarsi of the supposed Australian representatives of the latter species are missing, I am ready to admit that most likely birds from these genera (but see note in the "Eocene" section regarding doubtful monophyly of *Palaeeudyptes*) had circumpolar distribution during the Eocene epoch. For the paleogeographic map showing localities of known Eocene penguins, see Fig. 3.

Oligocene. — Sphenisciform remains from this epoch were collected in New Zealand and Australia. South American fossils may be represented by two species

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[10] Based on partial skeletons, tarsometatarsal features known only for *P. marplesi*.

from the San Julián Formation mentioned in the previous section. Although some authors (Fordyce and Jones 1990; Clarke *et al*. 2003; and references cited therein) do not preclude a Late Oligocene age for some other penguin-bearing strata from Argentina, Acosta Hospitaleche and Tambussi (2008) in their recent work use solely Early Miocene age for them.

The fossil record from New Zealand is relatively dense (Simpson 1971b; Fordyce and Jones 1990; Ando 2004). The most famous Oligocene penguin is surely *Palaeeudyptes antarcticus* Huxley, 1859, a large bird known from an incomplete tarsometatarsus (found near Oamaru, South Island, probably Early Oligocene in age; see Simpson 1971b and note in the "Eocene" section regarding doubtful monophyly of this genus). There are also other remains assigned to the genus *Palaeeudyptes*, but their relationships with *P. antarcticus* are uncertain (Simpson 1971b).

Another taxon from this epoch is *Archaeospheniscus* represented by two species of large penguins (larger than *A. wimani* from the Eocene of the Antarctic): *A. lowei* Marples, 1952 and *A. lopdelli* Marples, 1952. Both are based on partial skeletons (tarsometatarsi are known only for the latter species) recovered from the Kokoamu Greensand at Duntroon (South Island) and they are Late Oligocene (Duntroonian) in age. Recently, another partial skeleton from the Kokoamu Greensand was referred to this genus; preliminary identification had been made on the humerus (Riedel 2006). According to Riedel (2006) this specimen may be a new species. Another interesting fossil, an incomplete skeleton of a large sphenisciform from the Late Oligocene (Kokoamu Greensand, near the Waihao River), has morphology similar to that of Oligocene *Palaeeudyptes*, and its bill is elongate like in the Eocene "giant" forms (Fordyce and Jones 1990; see also Olson 1985; Myrcha *et al.* 1990; Jadwiszczak 2003). Although some bones are missing, the Waihao bird is one of the best preserved fossil penguins discovered so far (Fordyce and Jones 1990: fig. 18.6; Williams 1995: fig. 2.2).

Ando (2004) noted that among New Zealand fossil penguins, two forms from the latest Oligocene/earliest Miocene of South Canterbury (South Island), *i.e.* the Hakataramea bird[11] (a tiny sphenisciform; Fordyce and Jones 1990) and *Platydyptes* Marples, 1952[12] (middle- to large-bodied penguins; Marples 1952; Simpson 1971b; Fordyce and Jones 1990), contrast considerably with more "archaic" forms such as those belonging to *Palaeeudyptes*. They appear to represent important stages in the modernization of the penguin wing, and the former bird is hypothesized to be an ecological equivalent of the present-day Little Penguin (Ando 2004). The Hakataramea bird is not the only small-bodied penguin from New Zealand of about Late Oligocene age. *Duntroonornis parvus* Marples, 1952 and *Korora oliveri* Marples,

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[11] Thought by Cozzuol *et al.* (1991) to be conspecific with *Eretiscus tonni* (Simpson, 1981) from Patagonia (but see Acosta Hospitaleche *et al.* 2004).

[12] *P. novaezealandiae* (Oliver, 1930), *Platydyptes amiesi* Marples, 1952 and ?*Platydyptes marplesi* Simpson, 1971 (Simpson 1971b, 1975).

1952 from the Waitaki Valley region (South Island), both based on the tarsometatarsus, show (as do some La Meseta penguins) that not all Paleogene Sphensiciformes were “giants”. Furthermore, Grant Mackie and Simpson (1973) and Fordyce and Jones (1990) reported other remains of Oligocene penguins, possibly representing new taxa.

In 2006, the children of the Hamilton Junior Naturalist Club discovered a partial fossil penguin skeleton near Kawhia, on the west coast of the North Island of New Zealand (see http://www.waikatomuseum.co.nz/page/pageid/2145833246). The Kawhia penguin, a large-sized sphenisciform, is thought to be either 40 million years old (*i.e.* Eocene in age; information after the online version of *The New Zealand Herald*, article by M. Erwin dated 19 February 2006), or (more likely) 10–15 millions years younger (*i.e.* Oligocene in age; according to N. Harcourt, curator of science at the Waikato Museum – an estimate based on the established age of rocks in the Te Kuiti Group which are widespread in the Kawhia area; see the web page cited above). The formal description of these remains is not available, however.

The Oligocene record of Australian fossil penguins is rather poor. Glaessner (1955) and Simpson (1957, 1975) reported two bones (humerus and femur) representing distinct but unidentified species from the Late Oligocene or Early Miocene of South Australia (Gambier limestone, near Mt Gambier)[13]. One of them could be larger than the Emperor Penguin; the second form was slightly below the mean size of the King Penguin (Simpson 1957). For the paleogeographic map showing localities of known Oligocene penguins, see Fig. 3.

Miocene. — The fossil record of South American penguins from this epoch is abundant (Simpson 1972a; Acosta Hospitaleche and Tambussi 2008; and references cited therein). Moreover, the oldest remains assigned to any extant penguin genus are of Miocene age (Göhlich 2007). Simpson (1972a), the author of the most-cited twentieth-century review of South American sphenisciforms, knew only the bones from Patagonia. Interestingly, his latest work on fossil penguins (Simpson 1981) was devoted to *Eretiscus tonni* (Simpson, 1981), a small penguin from that region and epoch[14]. However, many other bones have been found as well

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[13] Last year, I had an opportunity to visit the Swedish Museum of Natural History in Stockholm, home of the oldest collection of fossil penguins from the La Meseta Formation, Seymour Island, Antarctic Peninsula (*e.g.* Wiman 1905a, b). The museum has also a set of casts of Australian specimens from the Eocene and Oligocene epochs; however, of particular interest are labels that accompany these specimens. The Eocene humerus (see Simpson 1957) was described as the “holotype of *Pteronectes finlaysoni* n. gen. et n. sp. Jenkins”, and the Eocene tibiotarsus (Simpson 1957) as “cf. *Antropornis grandis*”. The age of the bones mentioned in this paragraph was reported as the Late Early Oligocene (probably also by Jenkins), and the humerus was described as “humerus in paratype series of *Pteronectes hectori* n. gen. et n. sp. Jenkins”. Interestingly, after running a query against several scientific databases available online (the Index to Organism Names or ION, Paleobiology Database and Google Scholar), the output field was blank.

[14] According to Simpson (1981), it was the smallest known penguin either fossil or extant.

Table 1

Changes introduced recently into the list of Patagonian fossil penguins.

Species after Simpson (1972a, 1981) and Olson (1986)	Species after Acosta Hospitaleche and Tambussi (2008)
Palaeospheniscus gracilis	synonym of *P. bergi*
Palaeospheniscus bergi	*Palaeospheniscus bergi*
Palaeospheniscus patagonicus	*Palaeospheniscus patagonicus*
Palaeospheniscus wimani	synonym of *P. biloculata*
Chubutodyptes biloculata	*Palaeospheniscus biloculata*
Paraptenodytes antarcticus	*Paraptenodytes antarcticus*
Paraptenodytes robustus	*Paraptenodytes robustus*
Paraptenodytes brodkorbi	synonym of *P. robustus*
Arthrodytes grandis	synonym of *P. robustus*
A. andrewsi as a synonym of *A. grandis*	*Arthrodytes andrewsi*
Eretiscus tonni	*Eretiscus tonni*
	Madrynornis mirandus

as numerous papers have been published since that time. The latest revision of South American fossil penguins is that by Acosta Hospitaleche and Tambussi (2008; Table 1). The Miocene species from extinct genera include (a "systematic proposal"[15]; Acosta Hospitaleche and Tambussi 2008, and references cited therein): *Eretiscus tonni* (Simpson,1981) (Gaiman Formation, Argentina; Early Miocene), *Palaeospheniscus bergi* Moreno *et* Mercerat, 1891 (Gaiman Formation, Argentina; Early Miocene), *Palaeospheniscus biloculata* (Simpson, 1970) (Gaiman Formation, Argentina; Early Miocene), *Palaeospheniscus patagonicus* Moreno *et* Mercerat, 1891 (Gaiman Formation, Argentina; Early Miocene), *Paraptenodytes antarcticus* (Moreno *et* Mercerat, 1891)[16] (Monte León Formation, Argentina, Early Miocene and Puerto Madryn Formation, Argentina, early Late Miocene) and *Madrynornis mirandus* Acosta Hospitaleche *et al.*, 2007 (Puerto Madryn Formation, Argentina; early Late Miocene). According to the compilation by Acosta Hospitaleche and Tambussi (2008; see also Göhlich 2007), the remains of *P. biloculata*, *P. antarcticus* and (mentioned in the "Eocene" section) *P. robustus* come also from the Late Miocene–Early Pliocene Bahía Inglesa Formation, Chile (but see Chávez 2007 and Acosta Hospitaleche and Canto 2007). Holotypes are almost exclusively single bones (mainly tarsometatarsi), although *M. mirandus* is based on a nearly complete and articulated skeleton (Acosta Hospitaleche *et al.* 2007).

Extant genera are represented by *Spheniscus muizoni* Göhlich, 2007 (Pisco Formation, Peru; latest Middle or earliest Late Miocene), the only representative

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[15] Some of its aspects appear to be controversial, however.

[16] See also Bertelli *et al.* 2006.

of this group that is entirely Miocene in age, *Spheniscus megaramphus* Stucchi, Urbina *et* Giraldo, 2003 (Pisco Formation, Peru; Late Miocene–Early Pliocene), *Spheniscus urbinai* Stucchi, 2002 (Pisco Formation, Peru; Late Miocene and Early Pliocene), *Pygoscelis calderensis* Acosta Hospitaleche, Chávez *et* Fritis, 2006 (Bahía Inglesa Formation, Chile; Middle Miocene–Middle Pliocene) and *Pygoscelis grandis* Walsh *et* Suárez, 2006 (Bahía Inglesa Formation, Chile; Late Miocene–?Early Pliocene[17]) (Stucchi 2002; Stucchi *et al.* 2003; Acosta Hospitaleche *et al.* 2006; Walsh and Suárez 2006; Göhlich 2007). Additionally, Walsh and Hume (2001) described some remains from the Bahía Inglesa Formation (Middle Miocene–Early Pliocene) as cf. *Spheniscus*.

The holotype of *S. muizoni* is partial postcranial skeleton (humeri and one tarsometatarsus among others), and suggests the bird was about the size of the African and Magellanic Penguins *Spheniscus magellanicus* (Forster, 1781). Its remains are most similar to those of *S. urbinai* (Göhlich 2007), though the latter was more impressive in terms of size (25% larger than modern representatives of *Spheniscus*; Stucchi 2002). *S. megaramphus* was slightly larger than *S. urbinai* (Stucchi *et al.* 2003); however, whereas the former is represented solely by cranial material, the latter is based on an almost complete skeleton[18]. *P. calderensis* is another penguin based exclusively on cranial material (three skulls). It was comparable in terms of body size to its present-day congenerics (Acosta Hospitaleche *et al.* 2006).

Fossil penguins from the Early Miocene of New Zealand may be represented by at least two forms from South Canterbury listed in the previous section – *Platydyptes* and the Hakataramea bird. Some other penguins listed there (*Archaeospheniscus*, *Duntroonornis* and *Korora*) also cannot be excluded. Moreover, supposed Pliocene species from North Canterbury (see next section) may be in fact Miocene in age (Fordyce and Jones 1990).

All known Australian species that are probably of Miocene age come from Victoria. These are: *Anthropodyptes gilli* Simpson, 1959, *Pseudaptenodytes macraei* Simpson, 1970 and ?*Pseudaptenodytes minor* Simpson, 1970 (Gill 1959, Simpson 1959, 1965, 1970, 1975), and their holotypes are humeri (Simpson 1959, 1965, 1970). The last two species may be Pliocene in age (Fordyce and Jones 1990). *A. gilli* was a large penguin (Simpson 1959), heavier than the extant Emperor Penguin (Livezey 1989) whereas *P. macraei* was close to the King Penguin in size (Simpson 1970). Also some penguin fossils from the Western Cape Province of South Africa (see next section) may be as old as Late Miocene (Rich 1980; Fordyce and Jones 1990; Matthews *et al.* 2007; but see Brooke 1993). For the paleogeographic map showing localities of known Miocene penguins, see Fig. 3.

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[17] Walsh and Suárez (2006) stated that *P. grandis* came from an ?Early Pliocene level of the formation, though the referred material (unlike the holotype and topotype) was Late Miocene in age.

[18] The holotype is Early Pliocene in age, some paratypes are older (Stucchi 2002).

Pliocene. — In South America, the record of fossil penguins from the Pliocene epoch consists of at least three species. *Spheniscus chilensis* Emslie *et* Guerra Correa, 2003 comes from the Caleta Herradura de Mejillones Formation (Late Pliocene), Chile. Its holotype is a complete humerus (paratypes are numerous) similar in size to that of the Magellanic Penguin (Emslie and Guerra Correa 2003). Another species, *Spheniscus urbinai* is known from the Late Miocene (see previous section), but its holotype (a nearly complete skeleton) and some referred specimens come from the Early Pliocene of the Pisco Formation, Peru (Stucchi 2002). *Pygoscelis grandis*, like *S. urbinai*, spans two epochs (see previous section). Its holotype is a partial associated skeleton suggesting the body size around that of the King Penguin (Walsh and Suárez 2006).

The Pliocene penguin fauna from New Zealand is represented by up to five species. Fossil remains of *Tereingaornis moisleyi* Scarlett, 1983 are known from North Island, the type locality being at Te Reinga (near Wairoa, Northern Hawke's Bay; Scarlett 1983; McKee 1987). This was a rather small penguin, as indicated by type humeri (tarsometatarsi are not known), possibly referable to the genus *Spheniscus* (Scarlett 1983). Fragmentary bones representing a second species of penguin, somewhat larger than *T. moisleyi*, were reported[19]. Other New Zealand penguins come from South Island. *Marplesornis novaezealandiae* (Marples, 1960) is based on an associated and articulated partial skeleton found near the mouth of the Motunau River (Marples 1960; Simpson 1972b). It was of medium size in comparison with modern penguins (Simpson 1972b; Livezey 1989). Penguins assigned to present-day genera (according to Ksepka *et al.* 2006 this cannot be reliably resolved at present), *Pygoscelis tyreei* Simpson, 1972 and *Aptenodytes ridgeni* Simpson, 1972, come from localities close to that of *M. novaezealandiae*. The first of them is similar in size and structure to the Gentoo Penguin, *Pygoscelis papua* (Forster, 1781), the second species resembles the Emperor Penguin but is slightly larger (Simpson 1972b; Livezey 1989). Both are represented by type specimens only (partial skeletons; Simpson 1972b). However, assignments of last three species to the Pliocene epoch are uncertain, and they may be Miocene, Pliocene or Pleistocene in age (McKee 1987; Fordyce and Jones 1990). Moreover, one or two Australian species may be as young as Pliocene (see previous section).

Simpson (1971c, 1973, 1976b, 1979a, b) described four species and genera from South Africa (south-western Cape Province, currently the Western Cape Province) considered being Pliocene in age. Olson (1983) suggested that they probably belong to a single genus, either *Spheniscus* or a taxon closely related to it. The last assignments known to me are those by Clancey *et al.* (1987; see also Brooke 1993) and they are as follows: *Spheniscus predemersus* Simpson, 1971 (*Spheniscus* in Simpson 1971c, *Inguza* in Simpson 1976b), *Spheniscus hux-

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[19] Society of Avian Paleontology and Evolution Information Letter 10 (1996).

leyorum (Simpson, 1973) (?*Palaeospheniscus* in Simpson 1973), *Spheniscus hendeyi* (Simpson, 1979) (*Dege* in Simpson 1979a) and *Spheniscus insolitus* (Simpson, 1979) (*Nucleornis* in Simpson 1979b). The type specimens of African species are single bones, either humeri or tarsometatarsi (Brooke 1993). Furthermore, some Late Pliocene vertebrate fossils from Cockburn Island (Antarctic Peninsula) may represent penguin bones (Jonkers 1998).

Pleistocene and Holocene. — The record of Pleistocene penguins comes from at least three regions. Late Pleistocene (pre-Glacial Maximum) remains from New Zealand are known *e.g.* from Cape Wanbrow (South Island), including an undescribed species of *Eudyptes* (Grant-Mackie and Scarlett 1973; but see Worthy and Grant-Mackie 2003: p. 446) as well as the Little Penguin, the Fiordland Penguin *Eudyptes pachyrhynchus* Gray, 1845 and the Yellow-eyed Penguin *Megadyptes antipodes* (Hombron *et* Jacquinot, 1841) (extant taxa; Worthy and Grant-Mackie 2003, and references cited therein). Interestingly, this site yielded the only fossil penguin eggs from outside Antarctica (attributed to the Little Penguin; Worthy and Grant-Mackie 2003; see also Emslie and Patterson 2007).

During the Late Pleistocene, Antarctica witnessed the repeated expansion and collapse of huge marine-based ice shelves as well as fluctuations in continental ice sheets. It seems likely that such conditions were not too limiting for the extant Emperor Penguin owing to its adaptation to the extreme cold and surrounding ice (even during their breeding season). Present-day Antarctic penguin species that nest in the ice-free zones close to the unfrozen sea, such as the Adélie Penguin, *Pygoscelis adeliae* (Hombron *et* Jacquinot, 1841), were obviously present in the region, but they were separated into refugia (Ritchie *et al.* 2004). Thus, although some bones assigned to extant species (from the genus *Pygoscelis*) are more than 40 thousand years old (Late Pleistocene; Emslie *et al.* 2007), it is not surprising that the majority of subfossil bones found so far are Holocene in age (Baroni and Orombelli 1994; Tatur *et al.* 1997; Ritchie *et al.* 2004; Emslie and Woehler 2005; Shepherd *et al.* 2005).

Pleistocene penguin bones from South Africa come from several sites, *e.g.* the Hoedjiespunt Peninsula (Saldanha Bay, Western Cape Province) and Boegoeberg (Northern Cape Province). They were assigned to the extant African Penguin, and were probably Late Pleistocene in age (Klein *et al.* 1999; Stynder *et al.* 2001).

At least three Holocene penguin extinctions have been reported so far. The first of the supposed lost species is *Tasidyptes hunteri* Van Tets *et* O'Connor, 1983 recovered from a 13th century midden on Hunter Island, Tasmania; a bird about the size of the Rockhopper Penguin, *Eudyptes chrysocome* (Forster, 1781) (Van Tets and O'Connor 1983; see also Harrison 1984). Fordyce and Jones (1990) called the material "debatably diagnostic". Another extinction event is thought to have occurred as recently as 500 years ago in southern New Zealand (Boessenkool *et al.* 2009). Genetic and morphological analyses revealed previously unrecognized sister species of the Yellow-Eyed Penguin (*Megadyptes antipodes*), namely *Megadyptes* *waitaha* Boessenkool *et al.*, 2009. Interestingly, Boessenkool *et al.* (2009) explained this event in terms of human predation and proposed it as a factor that had triggered the range expansion of *M. antipodes*. The Chatham Islands Penguin (most probably from the genus *Eudyptes*), the most recent of the supposed lost species, may have come extinct in the late 19th century as a bird kept captive at some time between 1867 and 1872 might refer to this taxon (Tennyson and Millener 1994).

Remarks on the origin and evolution of extant penguins

There are currently two competing scenarios explaining the origin and evolution of extant penguins. One of them, proposed by Baker *et al.* (2006), locates the common ancestry of modern Sphenisciformes (*i.e.* Spheniscidae *sensu* Clarke *et al.* 2003) in the Eocene of Antarctic. The suggested order and timing of divergence was as follows: *Aptenodytes* (Eocene), *Pygoscelis* (Eocene or Oligocene), the split between *Spheniscus–Eudyptula* and *Eudyptes–Megadyptes* (Oligocene). The split between *Spheniscus* and *Eudyptula* took place in the Oligocene or Miocene, and *Megadyptes* diverged from *Eudyptes* in the Miocene. *Aptenodytes* and *Pygoscelis* speciated in the Miocene, the latter maybe also in the Oligocene. Speciation events within *Eudyptes* took place within about the last eight million years and those within *Spheniscus* were even more recent. According to Baker *et al.* (2006), the observed diversity of penguin species is due to the northwards dispersal (caused by the major cooling events) and inevitable isolation that promoted allopatric speciation.

Ksepka *et al.* (2006, see also Clarke *et al.* 2007) disagree with this view. In their opinion, cooling provided speciation opportunities to colonize an extreme environment, and this probably happened recently. Clarke *et al.* (2007) suggested the Miocene epoch for the common ancestry of the present-day genera. Unlike Baker *et al.* (2006), they (Ksepka *et al.* 2006) emphasize the importance of Subantarctic regions for penguin evolution, and locate the common ancestry of all the extant genera in the Antarctic Peninsula, the Scotia Arc and New Zealand. Apart from biogeography and timing, the proposed (Ksepka *et al*. 2006; Clarke *et al.* 2007) pattern of divergence events within Spheniscidae (*sensu* Clarke *et al.* 2003) is like that in Baker *et al.* 2006 (Fig. 5).

Concluding remarks

Penguins are quite well represented in the fossil record of birds. Such a situation is partly due to a huge boost the paleontology of sphenisciforms got in the 21st century. This and a number of new molecular studies conducted on extant penguins enabled comprehensive phylogenetic analyses, but also raised new questions (*e.g.* doubtful monophyly of *Palaeeudyptes*; see Fig. 5). Definitely,

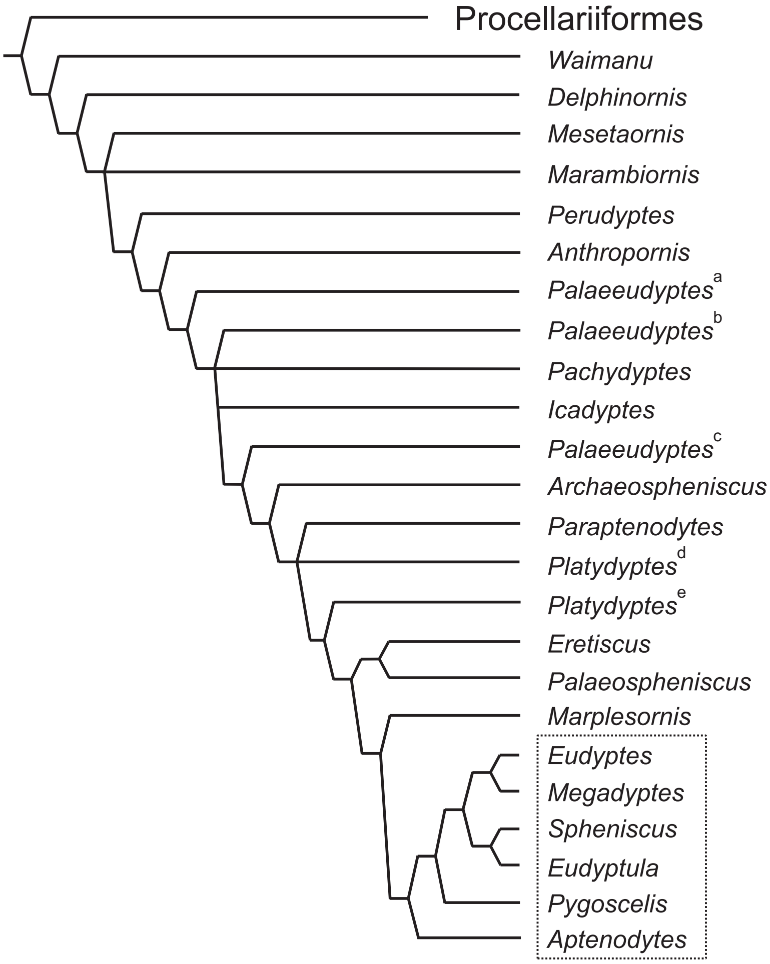

Fig. 5. Synthesis of penguin evolution (generic level). Based on data from Clarke *et al*. 2007. [a] *Palaeeudyptes klekowskii* and *P. gunnari* (Antarctic species); [b] *Palaeeudyptes* sp. (OM C.48:73-81; specimen from Burnside, Dunedin, New Zealand); [c] *Palaeeudyptes* sp. (OM C.47:25 and C.47:23; specimens from Duntroon, New Zealand); [d] *Platydyptes amiesi*; [e] *Platydyptes marplesi* and *P. novaezealandiae*. A dotted rectangle surrounds extant genera.

new fossils are still needed, particularly from the Late Cretaceous–Early Eocene and Miocene time periods, *i.e.* intervals most probably crucial for the evolution of Sphenisciformes. Additionally, the lack of precise dating of some important specimens, resulted from complex geology of some regions, makes the verification of important hypotheses impossible. Also spatially, the fossil record of penguins is far from being perfect. For example, it would be very interesting to study Paleogene Antarctic penguins from outside the James Ross Basin. Nevertheless, even the quick look at the list of the most recent references assures that the paleontology of Sphenisciformes is in its “golden epoch”.

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