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**The Dissertation Committee for Nina Elise Triche certifies that this is the approved  
version of the following dissertation:**

**Systematics, Biogeography, and Evolutionary History of Fossil and  
Extant Penguins (Aves: Sphenisciformes)**

**Committee:**

---

Timothy B. Rowe, Supervisor

---

Christopher J. Bell

---

Julia A. Clarke

---

Ernest L. Lundelius, Jr.

---

James T. Sprinkle

**Systematics, Biogeography, and Evolutionary History of Fossil and  
Extant Penguins (Aves: Sphenisciformes)**

**by**

**Nina Elise Triche, B.S.; B.A.; M.S. Geo. Sci.**

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## **Dedication**

To my mother, without whom I would probably not know a penguin from a pear tree.

“It’s amazing, the human capacity to not notice things that you’re not interested in”

—Bram Gunther, Deputy Director of Forestry and Horticulture, New York City

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## PREFACE

The following dissertation covers the evolutionary history of penguins: their systematics, taxonomy, biogeography, and history of radiations and extinctions. Although written as a dissertation, I intend to immediately submit each chapter as a separate publication, which affects the organization of the work as a whole. Because each chapter will stand alone as a separate work, there is considerable overlap between the introductions for each chapter. Additionally, some figures and appendices, although slightly different, may present the same information from chapter to chapter. Work performed in any chapter that is cited in another appears as (Triche, Chp. X). For example, conclusions from Chapter 3, such as figured systematic hypotheses, are discussed parenthetically as (Triche, Chp. 3) in Chapter 1.

The first chapter presented here is a survey of penguins in time and space, with an evolutionary overview of penguin history. Much of this chapter is excerpted for inclusion within the introductions to the remaining chapters. The second chapter describes the osteology of fossil and living penguins from the evolutionary perspective gained in Chapter 3. This third chapter comprises a phylogenetic analysis of penguin taxa and therefore uses the data presented in Chapter 2 as material but also provides the evolutionary context for interpreting the anatomy described in the second chapter. Finally, Chapter 4 is an analysis of the biogeographic and evolutionary history of penguins based on the hypothesis of phylogenetic relationships presented in Chapter 3.

**Systematics, Biogeography, and Evolutionary History of Fossil and  
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Publication No. \_\_\_\_\_

Nina Elise Triche, Ph.D.

The University of Texas at Austin, 2007

Supervisor: Timothy B. Rowe

The excellent penguin fossil record is temporally long, among the oldest of modern birds, and contains fossils on every Gondwanan continent except India. However, most of fifty-nine named taxa are isolated skeletal elements, many of which are non-comparable. Fossil diversity is highest in New Zealand, with additional Antarctic and Patagonian faunas and fewer remains from Australia and South Africa. Phylogenetic hypotheses place penguins within Aves and Neornithes, but further relationships remain contentious. Recent work clarified living species' phylogeny, but none examined all fossil taxa.

I describe penguin skeletal anatomy using CT scans and museum specimens, providing the first such description for all living and extinct species in an explicitly phylogenetic framework. All elements are phylogenetically variable, intergeneric variation is large, and extinct taxa are more variable than extant. I recommend that future systematic works include all elements for extinct species diagnoses, osteology for living

species, and discussions of intraspecific variation. This description grounds my phylogenetic analysis, based on a 503-character matrix of osteological, myological, integumentary, and behavioral characters. This greatly expands previous datasets, and allows recovery of a highly resolved phylogeny, including monophyly of two extinct clades and the crown-group. Data partitions support different levels of relationship, whereas missing data and outgroup choice drastically affect recovered topology. Incorporating the maximum amount of data gives the highest resolution by recovering all relevant character states. I propose the first formal phylogenetic nomenclature for sphenisciforms, and define and diagnose previously used terms such as Panspheniscidae (total group), Sphenisciformes (known penguins), Spheniscidae (crown-group), Palaeudyptidae and Paraptenodytidae (two extinct clades). I coin Spheniscoidea (Spheniscidae + Paraptenodytidae) and Australodyptinae (*Aptenodytes* + *Pygoscelis*).

After calibration with geologic time, I calculate the completeness of the penguin record and determine confidence intervals to estimate a Cretaceous origin and an Eocene crown-clade origin. These dates and the derived phylogenetic placement of penguins suggest that numerous extant bird lineages may also have Cretaceous origins. I recover a New Zealand origin for penguins and a West Antarctic origin for the crown-group and extinct clades. Correlating penguins with tectonic and climatic data indicates an Eocene adaptive radiation, probably related to latest-stage Gondwanan breakup and associated global cooling.

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## Chapter 1: The Last Sixty-three Million Years of Penguins

“Le savant ne peut légitimement prétendre a une connaissance complète et profonde de sa science, s’il en ignore l’histoire.”

—George Sarton, 1913

### Abstract

A long documented history of discovery and description exists concerning the ecology, behavior, and physiology of penguins, while less research focuses on their evolutionary history and paleontological record. Recent years, however, produced numerous paleontological discoveries and a renewed interest in the evolution of penguins, indicating the need for an up-to-date review of work on penguin evolution, as presented here.

Penguins possess an excellent fossil record, including one of the oldest representatives of all modern birds, at 62.4my, and an unparalleled abundance and diversity within the Southern Hemisphere continents. Penguin fossils are known from every Gondwanan continent except India and from every area currently inhabited, including New Zealand, South America (Chile, Peru, and Argentina), South Africa, Australia, and the Antarctic Peninsula. Although most are isolated long bones, notably humeri and tarsometatarsi, every skeletal element is known and some collections include up to thousands of bones. However, such dense associations of penguin fossils come only from discrete localities and mainly from unassociated remains, hampering direct comparison of various species. Fifty-seven named taxa are currently recognized, among numerous unnamed and undescribed specimens. Most of this diversity, both extinct and Recent, is known from New Zealand, with further diverse faunas known from Seymour Island (Antarctica) and Patagonia. An additional proliferation of new discoveries occurred within the last five years, with new species described from Argentina, the Antarctic Peninsula, Chile, Peru, and New Zealand.

Phylogenetic hypotheses regarding penguins place them within the group Aves (birds) and the derived group Neornithes (modern or crown-birds), but their relationships with other seabirds remain contentious. Systematic work over the last five years clarified the relationships of living species, but the first hypotheses of relationships among extinct taxa appeared only in 2006, and a new hypothesis examining all diagnosable extinct taxa was only recently published. That allows, for the first time, numerous authors to propose further conclusions regarding penguin evolutionary history, as well as broader applications of the penguin record to analyses of avian (bird) evolution. New work on penguin biogeography suggests that the group originated either in New Zealand or in Antarctica and that their radiations and extinctions may be tied to the breakup of Gondwana and to repeated, Cenozoic, climate change. Recent research also includes the

potential Cretaceous origin and the possible repeated evolution of gigantism within these fascinating, flightless birds.

## **Introduction**

Penguins were discovered in the late sixteenth century and were studied in earnest since the early nineteenth century, with particular attention deservedly paid to their ecology and impressive cold-adapted physiology (e.g., Stonehouse, 1975; Emslie and McDaniel, 2002; Meyer-Rochow and Gall, 2003; Peck et al., 2006). They are renowned as Antarctic ‘underwater-flyers’ that possess unique adaptations to a frigid, aquatic lifestyle. Much penguin research focuses on the birds’ incredible ability to withstand temperatures well below freezing, even as chicks, to flourish on an extremely inhospitable continent, and to have lost the flight typical of other avians (birds) in order to become the most graceful and efficient of swimming avians (Simpson, 1946; Williams, 1995). Penguin anatomy is highly modified for swimming and diving, involving flattening of the arm bones, loss of skeletal pneumaticity, and numerous thermoregulatory modifications such as waterproof feathers (Marples, 1952; Williams, 1995). These adaptations result in a morphologically distinctive yet highly conservative group, which is probably why no author expressly tested penguin monophyly until recently (Bertelli and Giannini, 2005).

Phylogenetic analyses agree that penguins belong to the clade Aves, commonly known as birds, as well as to a number of more inclusive groups, namely Neornithes, Neognathae, and Neoaves (Cracraft and Clarke, 2001). Although penguins, or Sphenisciformes, are certainly neoavian, their exact relationships with other modern birds

remain contentious. The term Sphenisciformes (sphenisciforms) currently refers to all extant and extinct penguins and includes the extant group, Spheniscidae (or spheniscids; Clarke et al. 2003; Triche, Chapter 3). Penguins probably lie within a group of living seabirds, although authors disagree as to whether or not the group is monophyletic and which of the various seabirds is the sister taxon of Sphenisciformes (e.g., Sibley and Ahlquist, 1990; Mayr and Clarke, 2003; Livezey and Zusi, 2006, 2007). My hypothesis of the relationships of extinct and extant penguins, based on a recent cladistic analysis of penguin morphology, is diagrammed in Figure 1.1, while those of penguins and other neornithines are shown in Figure 1.2 (Mayr and Clarke, 2003). Although the phylogeny of extinct penguins was only recently examined (Slack et al., 2006; Walsh and Suarez, 2006; Bertelli et al., 2006; Ksepka and Bertelli, 2006), analysis of all diagnosable extinct and extant species has now resulted in a well-resolved cladogram (Triche, Chapter 3). The analysis supporting that phylogeny and resulting systematic revisions will be published in detail shortly.

The penguin fossil record is one of the longest of any known extant bird lineage and perhaps the longest within Neoaves (Vickers-Rich, 1976; Slack et al., 2006), as shown in Figure 1.3. The record extends back to the late Early Paleocene, approximately 62.4 mya (Slack et al., 2006), highlighting the importance of the penguins to broader analyses of avian evolutionary patterns (e.g., Dyke, 2001). Penguin fossils are known from every Gondwanan continent except India and, except for some Southern Ocean islands that are generally of Holocene, volcanic origin, every area they currently inhabit, including Patagonia, Tierra del Fuego, Peru, Chile, South Africa, Seymour Island in

Antarctica, New Zealand, and Australia (Simpson, 1971a, 1971c, 1972; Vickers-Rich, 1980; Olson, 1983; Fordyce, 1991a; Stucchi, 2002; Clarke et al., 2003; Emslie and Correa, 2003; Clarke et al., 2007). The known fossil penguin record begins in the Early Paleocene with two species of one genus from the South Island of New Zealand and one species from the Antarctic peninsula, and extends to numerous Holocene remains e.g., from Tasmania, the sub-Antarctic islands, and Chile (Tambussi et al., 2005; Slack et al., 2006). Penguins thus have one of the longest temporal ranges and earliest occurrences of any extant bird lineage and greatly surpass the records of all other Gondwanan birds (Vickers-Rich, 1976; Bochenski, 1985; Fordyce et al., 1986). Despite such an excellent record, dense associations of penguin fossils occur only locally and, although globally widespread, are known only from discrete localities (Fordyce and Jones, 1990).

Most penguin fossils are isolated long bones, notably humeri and tarsometatarsi, but every skeletal element is known, including a number of nearly complete skulls (Zusi, 1975; de Muizon, 1981). Most extinct species are named from single elements not comparable with other taxa. While reports freely exaggerate the size of gigantic Eocene species (e.g., Jenkins, 1974), penguins do in fact show great diversity in feeding adaptations (Zusi, 1975; Ksepka and Bertelli, in press), in latitudinal distribution throughout their history (Sibley and Monroe, 1990), and in size, ranging from 35 cm to over 1.5 m in standing height (Simpson, 1981; Jadwiszczak, 2001; Clarke et al., 2007). There is currently only one published hypothesis of the relationships of numerous extinct penguins (Ksepka et al., 2006), although more will be proposed shortly (Ando, pers. comm.; Triche, Chapter 3).

The skeletal anatomy of extant penguins was recently described (Triche, Chapter 2), filling a gap that had hindered the comparative value of extant species to understanding the diversity of extinct species. Previously, the most thorough descriptions of extant penguin osteology dated to the nineteenth century, with few modern contributions. The best of these older works is that of Pycraft (1898), while other detailed descriptions were provided by Reid (1835), Gervais and Alix (1877), Jullien (1882), Watson (1883), Filhol (1885), Menzbier (1887), Shufeldt (1901), and Waterston and Geddes (1909). These works approach anatomy in a non-Darwinian context and often using a weak comparative framework, but remain useful as starting points for anatomical exploration. A notable, newer, exception to the descriptive dearth is the work of von Stephan (1979, 1980), who described various structures within the penguin skeleton. A forthcoming functional analysis of penguin wing morphology promises to address penguin osteology (Ando, pers. comm.), and a comprehensive description recently examined extinct and extant penguin osteology (Triche, Chapter 2). The last is the only current work to describe all penguin osteology, in all extinct and living taxa, using an explicit phylogenetic framework for anatomical comparisons.

A number of authors described particular subsets of the penguin skeleton (Walker, 1867; Pycraft, 1907; Duerden, 1922; Saiff, 1974, 1976), while others discussed osteology in the context of myological, developmental, or functional analyses. These studies focus on the middle ear (Saiff, 1974; Anisimov, 1976), the distinctive ankle complex (Simpson, 1946; Marples, 1952), the mandible (Zusi, 1975), the appendicular musculature (Schreiveis, 1972), and the integument (Lowe, 1933), among other regions (Anthony and

Gain, 1912, 1913, and 1915; Prins, 1951; Crompton, 1953; Krasovskiiy, 1966; Stegman, 1970; Louw, 1992). Some publications on penguin fossil remains present osteological descriptions, although none of these includes more than a few species or a suite of fossils from one locality (Moreno and Mercerat, 1891; Ameghino, 1895; Lowe, 1933, 1939; Simpson, 1946, 1971a, 1971c, 1972; Marples, 1952, 1953; Myrcha et al., 2002; Clarke et al., 2003; Acosta Hospitaleche, 2004). Finally, a number of recent phylogenetic analyses of the Sphenisciformes scored penguin osteology in their character matrices, but did not actually describe that anatomy (O'Hara, 1989a, 1989b; Bertelli and Giannini, 2005; Bertelli et al., 2006; Walsh and Suarez, 2006). More inclusive cladistic analyses of Neornithes use similar data, again with no detailed anatomical description, and often code penguins only as a terminal taxon, do not code more than one penguin species, and do not all include the hypothetically most plesiomorphic penguin taxon (Cracraft, 1982; Livezey, 1989; Cracraft and Clarke, 2001; Kennedy and Page, 2002; Mayr and Clarke, 2003; Mayr 2005a). Additionally, no extinct penguin taxa were included in any such broader analyses.

Penguins are hypothesized to have originated somewhere in the Southern Hemisphere, although it is not clear when or where (Cracraft, 1973; Vickers-Rich, 1976; Bertelli and Giannini, 2005; Baker et al., 2006; Ksepka et al., 2006). Although they originated much earlier, penguins may have radiated extensively in response to the final breakup of Gondwana, concurrent with the opening of the South Tasman Sea and the Drake Passage, and with the initiation of the Circum-Antarctic Current that presently affects much of their distribution (Cracraft, 1973; Stevens, 1980). Analytical

biogeographic techniques have immeasurably advanced since earlier biogeographic analysis of penguins (Morrone and Crisci, 1995; but see Fordyce, 1990; Cracraft, 2000 for reviews) and now allow analytical testing of biogeographic hypotheses in a phylogenetic framework (Triche, Chapter 4). Until recently, biogeographic and other evolutionary hypotheses regarding penguins were largely speculative because of their lack of a comprehensive phylogeny (but see Bertelli and Giannini, 2005; Baker et al., 2006; Ksepka et al., 2006 for analyses based on phylogenies of extant taxa).

There was no review of research on extinct penguins in over fifteen years (Fordyce and Jones, 1990), and no such review ever documented in detail the history of discovery and research on all penguin fossils. Considering the length and quality of the penguin fossil record and the importance of these fossils to larger patterns such as the diversity gradient across the K/T boundary, the patterns of radiation of modern taxa such as crown Aves, and the higher relationships of that group, such a review is long overdue. A multitude of recent discoveries and publications (e.g., Slack et al., 2006; Bertelli et al., 2006; Walsh and Suarez, 2006; Ksepka and Bertelli, in press) makes an up-to-date review of penguin fossils particularly important.

### **First Discoveries**

The Honorable W. B. D. Mantell, postmaster of Wellington, New Zealand, acquired the first fossil penguin bone to be discovered in 1848 from a local Maori collector (Simpson, 1975a). The specimen, which T. H. Huxley subsequently studied in England, came from the Kakanui limestone of the Otago district. In 1859, Huxley named the first extinct penguin species *Palaeudyptes antarcticus*, in reference to its affinities to

an extant New Zealand genus, *Eudyptes*. Although the find consisted of only one bone, the element was a nearly complete, right tarsometatarsus, or ankle bone, which simplified its identification immensely. A nearly complete, second specimen of *P. antarcticus* emerged nearby in 1872, as reported by James Hector in that year, followed by two additional specimens from the same locality in 1873. The penguin fossil record now included nearly all the wing and leg elements of these birds. Hector used these finds to estimate the standing height of the extinct penguin to be 6-7 feet, which was a gross exaggeration for that species and initiated the enduring myth of giant extinct penguins (Hector, 1873).

The remaining years of the nineteenth century witnessed the discovery of numerous additional penguin fossils from New Zealand and Argentina. In 1891, Moreno and Mercerat catalogued their collection at La Plata, Argentina and named the new genus *Palaeospheniscus* and its three species as the first extinct penguins known from South America. The prolific paleontologist Florentino Ameghino later catalogued these fossils as part of his larger work on all extinct Patagonian birds (Ameghino, 1895). He also added a second family of penguins (Cladornidae) to the existing Spheniscidae using relatively minor characters of the tarsometatarsus. In total, Ameghino listed six extinct species in three genera, one of which was the newly coined *Paraptenodytes*. The tendency to split taxa, already present in the work of Ameghino, was particularly vigorous within extinct penguin systematics, resulting in a remarkable proliferation of species named from one element, from elements that do not overlap between taxa, from remains of only slightly different geologic or temporal provenance, and from elements of

only slightly different size. The family Cladornidae was later synonymized with the original, and currently sole group of penguins, Spheniscidae (Simpson, 1946). Much additional systematic revision affected penguin taxonomy, resulting in a greatly reduced number of species. Appendix 1.1 lists all currently known and valid, extinct penguins ordered by their geographic occurrence, along with the current location of referred specimens, history of publication, and museum acronyms.

The Swedish South Polar Expedition, led by Otto Nordenskjöld, was the first exploration of Seymour Island, a small landmass that lies off the East coast of the Antarctic Peninsula (Myrcha et al., 2002). Seymour Island, or the Isla Vicecomodoro Marambio in Argentinean literature, is the most important of all Antarctic fossil localities. Its Cretaceous and Tertiary deposits contain diverse and abundant remains of invertebrates, plants and, nearly unique among Antarctic deposits, a number of marine vertebrates. The Swedish vessel that discovered the island unfortunately sank, trapping the crew on Seymour island from 1901 to 1903, although every member survived the sojourn by subsisting on penguins. Although the expedition accomplished much scientific work in their three years on the island, not a single fossil was collected owing to the location of the shipwreck (Zinsmeister, 1988). During a subsequent expedition to the island, a member of the crew, J. Gunnar Anderson, made a large collection of fossil penguin bones, which is now housed at the Riksmuseet in Stockholm (Myrcha et al., 2002). The bones, as all penguin remains from Seymour Island, were unfortunately disarticulated and unassociated. Later study of the collection by Wiman (1905) resulted in six, new, monotypic genera based mainly on size groupings. Ameghino again

catalogued and systematically expanded the penguin remains from Seymour Island and Patagonia in 1905. He added six new species to the genus *Palaeospheniscus* and increased the number of known penguin genera to include *Perispheniscus*, *Argyrodyptes*, *Pseudospheniscus*, *Neculus*, *Metancylornis*, *Isotremornis*, *Arthrodytes*, and *Treleudytes*. Simpson later synonymized every one of these genera into a number of previously named genera (Simpson, 1972).

Australia yielded its first extinct penguin early in the twentieth century (Finlayson, 1938), at which point penguin fossils were known from the Late Eocene through the Miocene of four Southern continents. In 1930, W. R. B. Oliver compiled the first handbook of New Zealand birds, which included extant and extinct penguins. The extinct species then known from New Zealand had reached a total of eight, owing to the addition of *Pachydyptes ponderosus*, *Platydyptes novaezealandiae*, *P. amiesi*, *Archaeospheniscus lowei*, *Archaeospheniscus lopdelli*, *Duntroonornis parvus*, and *Korora oliveri*.

One of the first authors to do more than simply catalogue extinct penguins and to address them in an evolutionary context was Percy Lowe (1933, 1939). Although Darwin's theory had been accepted for decades by the time of Lowe's work, most authors of penguin literature had continued to publish only catalogues and systematic work addressing species and genera while ignoring higher level, evolutionary hypotheses. Lowe's conception of penguin evolutionary history was notable for being the first to specifically address relationships within the group. He correctly pointed out that early work, in particular that of Wiman, lacked any extant comparative material. There, for the

first time, Lowe compared material from Seymour Island, New Zealand, and Australia, and from numerous, although not all, extant taxa. However, his conclusions contrasted strongly with those of other scientists because of his contention that penguins were an ancient, basal group of birds that had diverged from all other extant taxa as early as had the Paleognathae. In modern terms, this would place Sphenisciformes as a stem group on the lineage leading to Neornithes and outside the group comprising all modern birds. Lowe supported his hypothesis by laying particular emphasis on the ‘primitive’ characteristics of penguins, noting their lack of flight feathers, extensive modifications for flight loss and swimming adaptation, and relatively conservative skeleton. Most of these features are today considered derived reversals, especially the flattening of the wing bones and loss of skeletal pneumaticity (Davis and Renner, 2003; Ksepka et al., 2006; Triche, Chapter 3). These characters do not connote plesiomorphic flightlessness, but the secondary loss of flight by penguins well after the evolution of this behavior in modern birds.

The difference of opinion regarding penguins’ relationship to other birds is mainly a difference in perspective. For example, characteristics of the humerus that Lowe considered nearly identical in all penguins as compared to other birds are viewed by Simpson (1946) and later workers as noticeably different in extinct penguins versus extant species, although these authors agree with Lowe on the morphology and homology of the structures. Lowe correctly interpreted much variation in penguin skeletal anatomy, but considered it to be of less importance than did other authors. A glaring critique of Lowe’s conclusions appeared in 1934 by the anatomist William K. Gregory, refuting the

idea that penguins are primitive and claiming that most characters cited by Lowe are in fact reversals that evolved well after the avian lineage acquired flight. That opinion was been supported by all subsequent work, which considers Lowe's 'primitive' characters in the broader context of all anatomy, not a few, specifically chosen characters. In light of recent discoveries of feathered dinosaurs and well-supported phylogenies of basal avian taxa, it is improbable that penguins lie within any clade other than Neoaves (e.g., Zhou and Zhang, 2002; Mayr and Clarke, 2003).

It was at this point in the history of research on extinct penguins that G. G. Simpson, the greatest authority on the subject, started to publish. His first work is still the most thorough overview of the occurrence of extinct penguin remains and the systematics of these extinct species, and remains the only primary source to address taxa from all known continents and time periods (Simpson, 1946). The work includes a fairly detailed description of *Paraptenodytes antarcticus*, based on a nearly complete specimen Simpson had collected in Patagonia in 1933. The specimen, housed at the American Museum in New York, is well-preserved and includes the first described fossil skull of a penguin, as well as most of its postcranial elements. It was recently redescribed and interpreted in a cladistic framework, as detailed below (Bertelli et al., 2006). Simpson also reviewed the Tertiary occurrence of all known extinct penguins, analyzed the comparative osteology of Miocene species, although a few skeletal elements remained unknown at the time, and proposed the first new taxonomy since that of Wiman (1905). That involved grouping all penguins into five subfamilies, including Spheniscinae (the extant group), Paraptenodytinae, Palaeospheniscinae, Palaeodyptinae, and Anthropornithinae. Finally,

Simpson speculated on the origins and biogeography of penguins. Following that publication, all work on penguins concentrated solely on single fossil discoveries or on the species or faunas present in one geographic area or country.

### **Further Discoveries**

#### **South America**

Until recently, all extinct penguins known from South America were Argentinean, specifically Patagonian (Simpson, 1972). Additionally, all were from the Early Miocene to possibly Late Oligocene Patagonia Formation, mostly from Chubut and Santa Cruz Provinces. The Argentinean record currently contains ten species, most of which are housed in Argentinean and Polish museums.

In 1972, Simpson reviewed the Argentinean material in what remains the most current discussion of extinct, Patagonian penguins (Simpson, 1972a). He included a number of collections and older literature by Ameghino, as well as the collection made by an American Museum of Natural History (AMNH) expedition to Chubut that Simpson led in 1933. Also included were specimens from the Museo de La Plata (MDLP), the Museo de Ciencias Naturales (MACN) in Buenos Aires, and a collection that Ameghino sold to the Natural History Museum (NHM) in London in 1896. Simpson's resulting taxonomy accepted nine species as valid, many of which were again diagnosed solely using size (Simpson, 1972a). That publication also extensively synonymized the species erected by Ameghino in 1905. Finally, Simpson opined that the Patagonian fauna, although lower in total diversity than that of New Zealand, is in fact the taxonomically richest locality because all nine species are from the same horizon. Species known from

Argentina are entirely restricted to that area, with no specific or generic overlap with New Zealand, Antarctica, or even other areas of South America, although a possible *Palaeospheniscus* species may exist in Peru and Chile (Acosta Hospitaleche and Canto, 2005; Acosta Hospitaleche and Stucchi, 2005). Considering that the highest diversity of penguins in a comparable geographic and temporal range is today only eight (in New Zealand and its sub-Antarctic islands), Patagonia did indeed contain a diverse fauna. New Zealand in the Oligocene, however, was home to a more diverse assemblage of thirteen extinct species, although these probably lived during a greater period of time. In 1980, Tonni reviewed the Cenozoic birds of Argentina, but added no species to Simpson's review. Simpson himself named another species, however, in 1981: *Microdytes tonni*, later renamed *Eretiscus tonii* (Olson, 1986), which is the smallest penguin known, extinct or living.

Collections also were made recently in Peru, from the Pisco Formation of the south-central coastal area. The formation is Late Miocene to Early Pliocene in age and contains at least three extinct penguin species (de Muizon, 1981; Stucchi, 2002; Stucchi et al., 2003). Importantly, these include a number of complete skeletons with nearly complete skulls (de Muizon, 1981). More recent work, including the Tierra del Fuego penguin and recent Chilean material, is discussed below.

### **Antarctica**

Although no Antarctic localities that produce penguin fossils are known other than Seymour Island, the last century witnessed a dramatic increase in remains from the island, in terms of taxon diversity, quantity of specimens, and known age range. The

geology of Seymour Island is thoroughly described in a multi-author volume containing chapters on geologic history, stratigraphy, and paleontology (Feldmann and Woodburne, 1988). Nearly all discoveries come from a single formation, the La Meseta Formation, of Middle to Late Eocene age (49.5-34.2 mya). These include fifteen accepted penguin species, two of which are conspecific with Australian fossils, and one genus of which is also known from New Zealand. Skull and mandible fragments are present, but most remains are disarticulated postcranial fragments. Four of the accepted species are larger than any extant penguin, and a number of bill morphologies that are presumably correlated with different feeding ecologies, are represented (Jadwiszczak, 2000, 2003). The great diversity of penguin taxa known from Seymour Island is probably an artifact of the abundant preservation of the locality, not a true reflection of high diversity on Seymour Island alone.

Following the original Swedish expedition, a number of countries made collections on Seymour Island, including the United Kingdom, Argentina, the United States, and a joint Argentinean-Polish expedition. Marples (1953) and Simpson (19721a) both used the collection resulting from the Falkland Islands' Dependencies (Great Britain) Survey of 1946. The Argentinean collecting expedition, which ran from 1973-5 under the direction of the GEOANTAR and MDLP, the current repository for collected penguin fossils, resulted in no new data except for a possible corroboration of the problematic genus *Ichtyornis* and one, as yet undescribed, articulated specimen (Cione et al., 1976; Simpson, 1981). Nothing anatomical was published from the US penguin collections, although they were made over a quarter century ago by a joint team from

Northern Illinois University and the Institute of Polar Studies at Ohio State University, and were used for climatic work and in taxonomic studies of other organisms (Elliot et al., 1975; Zinsmeister, 1982; Case, 1992).

Wiman originally divided the penguins of Seymour Island into six species in six monotypic genera, but Simpson reduced the genera by two (Simpson, 1946), instituting a taxonomy that lasted for nearly 50 years. Brian J. Marples, a zoology professor at the University of Otago in Dunedin, New Zealand, who published more papers on extinct penguins than anyone except Simpson (Fordyce, 2001), also reviewed the extinct penguins of New Zealand (1952) and of Seymour Island (1953). The latter review also utilized the British and earlier Swedish collections. Marples validated four of Wiman's six species and added a new genus, after which Simpson expanded that assessment to include at least six species, with two others of possible validity (Simpson, 1971a).

The Argentinean-Polish expedition that ran from 1985 until 1994 produced by far the most abundant fossil penguin material and resulted in a number of Polish papers on the taxonomy and ecology of new species. The Polish collection alone contains over one thousand bones, which are currently deposited at the Institute of Biology at the University of Białystok (formerly Warsaw University) in Poland (Millener, 1988). The presence of such an impressive number of bones almost certainly indicates that the marine Seymour Island beds lay offshore from a rookery (Myrcha et al., 2002). Work based on that collection originally appeared as a short abstract listing the presence of at least seven genera and fourteen species (Millener, 1988). The presence of shared species also

suggested that the Seymour Island fossils were part of a larger fauna including Australia and New Zealand taxa, but excluding those from South America (Millener, 1988).

A group of Polish biologists undertook the remainder of the work on the Polish collection. In 1990, they named a new species of *Palaeudyptes* and mentioned some unassignable upper jaw fragments suggestive of a new, piscivorous, species (Myrcha et al., 1990). Jadwiszczak speculated on the ecology and early evolution of these Antarctic penguins and calculated their body sizes, including standing height and weight, from long-bone extrapolations (Jadwiszczak, 2000, 2001, 2003). Myrcha again reported on the Argentinean-Polish collection in a detailed, taxonomic revision of all Seymour Island species that diagnosed all Seymour Island taxa and updated the nomenclature associated with penguin tarsometatarsal morphology (Myrcha et al., 2002). However, the work used only the morphology of 126 unassociated tarsometatarsi and contained no phylogeny, only a taxonomic revision based mainly on size categories and minor, and probably intraspecifically variable, differences in morphology (Triche, Chapter 2). The problem is probably unavoidable owing to the nature of the Seymour Island fauna, but it remains highly problematic to perform meaningful phylogenetic comparisons on piles of disassociated, single elements whose stratigraphic relation to each other is often not discernable.

There are a few locations along the Antarctic coast, the Antarctic Peninsula, and the Antarctic and sub-Antarctic islands that produced Late Pleistocene and Holocene remains of penguins resulting from long-term rookery occupation. All such remains belong to extant species, including *Aptenodytes patagonicus*, *Eudyptes? chrysolophus*, *E.*

*pachyrhynchus*, *Eudyptula minor*, *Megadyptes antipodes*, *Pygoscelis adeliae* and *P. antarctica* (Grant-Mackie and Simpson 1973; McEvey and Vestjens, 1974; Scarlett, 1983; Bochenski, 1986; Baroni and Orombelli, 1994; Emslie and McDaniel, 2002; Emslie et al., 2007; Triche, pers. obs.). The oldest of these date to 45,000YBP, and their presence usually correlates with times of warmer climatic regimes (Emslie et al., 2007).

### **South Africa**

Although one extant species of penguin, the Jackass, does inhabit South Africa today, extinct penguins were not discovered there until 1971 and remain systematically problematic (Simpson, 1971b). The first extinct penguin, *Spheniscus predemersus*, is known from fairly complete skeletons, and is similar to the Recent species, *S. demersus*. Three penguin fossil localities are known from South Africa, including Duinefontein, Ysterplaat, and Langebaanweg, all of which lie along the coast northwest of Cape Town (Hendey, 1975; Olson, 1985). All three are Early Pliocene (5 mya), marine deposits from a colder, sub-Antarctic climate (Olson, 1983). All primary work on South African penguins is by Olson and Simpson. In 1975, Simpson removed *S. predemersus* to a new genus, *Inguza*, and subsequently named three additional species, including *Dege hendeyi*, *Nucleornis insolitus*, and *Palaeospheniscus huxleyorum* (Simpson, 1975b, 1979a, 1979b). The most recent mention of South African penguins, in 1985, listed over 70 diagnostic penguin bones and accepted all four species proposed by Simpson, but placed all genera in quotation marks to indicate the probability that they are congeneric (Olson 1985).

## **Australia**

The first extinct Australian penguin to be discovered was the Late Eocene *Palaeudyptes antarcticus*, which had long been known from later, Oligocene deposits in New Zealand (Finlayson, 1938). The species was soon joined by three more bones ranging to the Early Miocene, but no second, diagnosable species was described for twenty years (Glaessner, 1955; Simpson, 1957). Subsequent publication included two new Miocene genera (Simpson, 1959, 1965), a new species named after Simpson (Jenkins, 1974), and a Seymour Island species, *Anthropornis nordenskjoldi*, from the Australian Late Eocene (Jenkins, 1985). Although no recent work examines the Australian extinct penguins, their fossil record does appear in larger reviews (e.g., Vickers-Rich, 1992).

The island of Tasmania also produced penguin remains, all of which are Holocene in age. A new species, *Tasidyptes hunteri*, from an 800-year old cave deposit, may be the first penguin species to have gone extinct within modern times, although the specific status of the taxon is questionable (van Tets and O'Connor, 1983). Macquarie Island, a sub-Antarctic island owned by Australia, also produces Holocene fossils, all assignable to the extant *Eudyptes schlegeli* or *Aptenodytes patagonicus*, from 6100 year old deposits (McEvey and Vestjens, 1974).

## **New Zealand**

New Zealand has the highest diversity of penguins, at sixteen species, the oldest remains, from the late Early Paleocene, and the greatest geographic and geologic range, with records from both islands that extend from the Paleocene to the Holocene (Fordyce

and Jones, 1990; Slack et al., 2006). Penguin fossils are more common on the South Island, especially in the Otago region, and are known from offshore islands only as Holocene remains of extant species (Millener, 1991).

Marples completed the first major work to focus on the New Zealand penguin fossils (Marples, 1952). In it, he revised Simpson's (1946) evolutionary taxonomy, fusing the Anthropornithinae into the Palaeedyptinae on the basis of similar humeri and coraco-sternal articulations. Marples also reviewed new material discovered since Simpson's work, including the first fossil penguin pelvis, furcula, and patella. He named four new genera and six new species, including members of *Platydyptes*, *Archaeospheniscus*, *Duntroonornis*, and *Korora*, which greatly extended the known range of New Zealand penguins. Marples also suggested that these new species formed an evolutionary lineage that was much more primitive than the spheniscine-like Argentinian material. He did not, however, speculate as to their origins. In 1962, Marples further condensed Simpson's subfamilies, joining the remaining three into a 'Patagonian species group' that he did not formally name. Marples' final publication on the subject came one year later (Marples and Fleming, 1963), with the description of a femur from Motutara Point on the North Island of New Zealand. That mid-Oligocene bone represented the first penguin found outside the South Island and, although unnamed, may be related to *Archaeospheniscus* (Marples and Fleming, 1963).

Simpson also worked extensively on the New Zealand fauna, revising the ages of the fossils and publishing a detailed revision of the pre-Pliocene material (Simpson, 1970, 1971c). He included a review of all fossiliferous sites and a revision of the then-current

taxonomy. He accepted most of Marples' specific identifications (Marples, 1952, 1960) and named the new species *Platydyptes marplei* after him, but abandoned his own earlier, subfamilial classification because he did "not believe that our present knowledge of extinct penguins is adequate basis for a subfamily classification that would be of evolutionary significance or otherwise useful." (Simpson, 1971c, pp. 366). The monograph was Simpson's largest work on New Zealand penguins (Simpson, 1971c), although he later added to it with some new, Late Pliocene, fossils from North Canterbury, on the South Island (Simpson, 1972). These included a new genus named after Marples (*Marplesornis*) and two new species belonging to modern genera (*Pygoscelis tyreei* and *Aptenodytes ridgeni*), that suggested that cooler climates, more similar to those of modern-day New Zealand, had allowed these Antarctic genera to disperse further to the north. Another North Island discovery appeared in 1973, known only as the 'Glen Murray' specimen, and dates from the warmer Oligocene (Grant Mackie and Simpson, 1973)

Further work on New Zealand penguins in the last century consisted almost exclusively of reviews, although a few primary studies appeared recently. The New Zealand and Australian chapters of *The Fossil Vertebrate Record of Australasia* (Fordyce, 1982) and its successor, *Vertebrate Palaeontology of Australasia* (Fordyce, 1991a, 1991b; Millener, 1991) both cover the fossil record of penguins, as does a chapter from the book *Penguin Biology* (Fordyce and Jones, 1990), which was the last review of extinct penguins worldwide. The emphasis on review papers is not from a lack of new material, however, as such evidence appeared in abundance throughout the 1980's

(Fordyce, Jones, and Field, 1986; Fordyce and Jones, 1987; Fordyce and Jones, 1988; Fordyce and Jones, 1990). The mid-Pliocene species *Tereingaornis moisleyi*, found in 1982 on the North Island, is fairly complete, and may be closely related to the extant *Spheniscus*. Additional remains of that species were discovered in 1987 and in 1988, resulting in four currently known specimens (Scarlett, 1983; McKee, 1987; McKee, 1988).

### **Recent Finds**

In recent years, there was a great increase in the number and diversity of known penguin fossils from all southern continents and from many previously unsampled horizons. Research includes descriptions of the two oldest penguins currently known, an exponentially expansion of the South American record outside of Argentina and a doubling of the amount of available cranial material.

#### **South America**

Penguin fossils were known from Peru since the early 1980s, but there were recently much more extensive discoveries there, many of which remain unpublished (Walsh, pers. comm.). Two new extinct species of the extant genus *Spheniscus* were recently named (Stucchi, 2002; Stucchi et al., 2003). Both come from the Pisco Formation, although one is dated as Late Miocene and the other as Late Miocene to Early Pliocene. The specimens, all of which are housed in Lima, Peru, include portions of a rostrum and skull and specimens larger than any extant *Spheniscus* species. The presence of *Palaeospheniscus*, previously known only from Argentina, was reported from some very limited material that is not yet described (Acosta Hospitaleche and Stucchi, 2005).

The oldest known specimen of *Spheniscus* will shortly be described (Göhlich, in review). All these species lie within a monophyletic *Spheniscus* clade (Triche, Chapter 3). Finally, two new species from the Middle Eocene of the Department of Ica, *Perudyptes devriesi* and *Icadyptes salasi*, represent both the oldest and the largest low-latitude penguins currently known (Clarke et al., 2007).

The first extinct penguin described from Chile, *Spheniscus chilensis*, was named in 2003 from the Late Pliocene (Emslie and Guerra Correa, 2003). Collected in 1983 from the Península de Mejillones, and housed in Antofagasto, the species is known from nearly every skeletal element, although most remains are unassociated. Morphologically, it is similar in size and proportion to *S. humboldti* and *S. magellanicus* that both occur on the coast of Chile today, although the extinct species is slightly smaller, with a reportedly distinctive humerus. A new Chilean locality with abundant penguin remains was also found on the northwest coast of Chile (Walsh and Hume, 2001), although only one of the species present there, *Pygoscelis grandis*, is named and described (Walsh and Suarez, 2006). The discovery of a giant, northerly *Pygoscelis* is notable in that it extends the geographic range of the currently sub-Antarctic genus to northern South America, about 27°S latitude, and nearly doubles the known body size of penguins within the clade (Walsh and Suarez, 2006). The locality, the Late Miocene to Late Pliocene Bahia Inglesa Formation, lies about 500 km south of the *S. chilensis* site, and also contains remains of the Peruvian penguins *S. megaramphus* and *S. urbinai*. There are also reports of another potential *Palaeospheniscus* species from the Bahia Inglesa, known from six new skull fragments (Acosta Hospitaleche and Canto, 2005)

The oldest penguin yet known from South America is only the second vertebrate fossil known from the Paleogene of Tierra del Fuego (Clarke et al., 2003). It is Eocene in age (42 mya), and retains only the pelvic girdle and limb bones. Although the Tierra del Fuego taxon almost certainly represents a new species, the specimen remains unnamed owing to its non-comparability with the elements generally known in other extinct penguin taxa (Clarke, pers. comm.). Also, the new nomenclature introduced in that paper remains unformalized because of the lack of a phylogeny including extinct species that would stabilize the definition of various names and because the paper predated the formal adoption of a code governing phylogenetic nomenclature. Clarke et al. (2003) coined but left unformalized several terms, including ‘Pansphenisciformes’, the penguin stem-group, or all taxa more closely related to crown-penguins than to other avians; ‘Sphenisciformes’, or all panspheniscids that have lost aerial flight in a fashion homologous to crown-penguins; and ‘Spheniscidae’, or crown-penguins. These terms will be explicitly defined elsewhere (Triche, Chapter 3), but are here used in the sense of Clarke et al. (2003). That work also suggested that the Tierra del Fuego species represents a basal sphenisciform and that crown-group penguins thus did not evolve until at least the Eocene, in agreement with previous work on early Paleogene specimens (Simpson, 1946; Clarke et al., 2003). As noted there, the presence of that sphenisciform taxon in the Eocene could only constrain the timing of the crown-group split when combined with a phylogenetic hypothesis, however, and would only affect the timing of that event if the Tierra del Fuego species is found to be closely related to the crown-group (Clarke et al., 2003).

Other recent work on the Argentinean record is by Acosta Hospitaleche and addresses Patagonian species. She reported two new, undescribed, paraptendyline specimens from the upper Miocene Puerto Madryn Formation, which constitute the first identifiable penguins from that locality (Acosta Hospitaleche, 2003). In subsequent publications, results from Acosta Hospitaleche's dissertation described the anatomy of three Argentine fossils in the context of a larger description and morphometric analysis of penguins (Acosta Hospitaleche, 2004; Acosta Hospitaleche and Gasparini, 2007). That work resurrected the subfamily taxa abandoned by Simpson, their author, including the Argentinean Paraptendyline, Palaeospheniscinae, and Spheniscinae, and resulted in a new Linnean taxonomy for these Argentinian species, but attempted no cladistic analysis (Acosta Hospitaleche, 2004). More recently, she also revised the systematic diagnosis for the genus *Arthrodyptes* (Acosta Hospitaleche, 2005) and named a new species, *Madrynornis mirandus* from the early Late Miocene of Chubut, Patagonia (Acosta Hospitaleche et al., 2007).

### **Antarctica**

In 2005, a paper reported the discovery of the oldest penguin then known, from the Late Paleocene of Seymour Island, about 55 mya (Tambussi et al., 2005). The specimen comprises a partial humerus with associated femur and tibiotarsus that, at the time, was 15 million years older than the next oldest described species. However, an unnamed Late Paleocene penguin from New Zealand was reported in an abstract nearly two decades earlier (Fordyce, Jones, and Field, 1986). Tambussi et al. (2005) named the Seymour Island find *Crossvallia*, after the formation in which it was preserved, and

provisionally identified it as an anthropornithid, suggesting an independent evolution of large body size in penguins. They concluded that that acquisition occurred twice in highly divergent environments, both in the warm Paleocene and in the much cooler Late Eocene. Alternatively, however, large penguins may have evolved in the Paleocene and remained large-bodied through the Eocene (Triche, Chapter 4). Lack of diagnostic penguin remains in intervening horizons constitutes only negative evidence, but at least does indicate no presence of smaller penguins evolving between *Crossvallia* and later large taxa. The results of recent phylogenetic work (Ksepka et al., 2006) also disagree with the suggestion of large size evolving multiple times, on the basis of a new cladogram topology. The analysis included some taxa suggested by Tambussi et al. (2005) to be closely related to *Crossvallia* (e.g., *Anthropornis*), but not *Crossvallia* itself, suggesting less confidence about any evolutionary conclusions regarding the unanalyzed taxon. Published description of the bird includes only some of its morphology, and figures illustrate only some of the known elements, indicating the need for further descriptive work on that taxon.

Using the earlier Polish work on fossil tarsometatarsi as a starting point (Myrcha et al., 2002), a recent study revised the taxonomy of all Seymour Island species in the Polish collections (Jadwiszczak, 2006a). Although all elements of the skeleton were included, resulting in the addition of 694 bones not previously reviewed, the methodology used is the same as used previously, that is, species definitions and diagnoses rely mainly on size classes, in the absence of a phylogenetic framework. The majority of the new elements are also assigned to previously accepted taxa based solely

on these size classes, even though the holotypes thus lack any elements other than the tarsometatarsus. That methodology may be unavoidable when revising a completely disassociated collection, but may also negatively impact subsequent research by erecting a potentially nonsensical taxonomy. For example, it is probable that many non-tarsometatarsal elements will be incorrectly referred to taxa based on tarsometatarsi, while new species will remain unrecognized if taxa are named only from the tarsometatarsi (as discussed below). The new revision also presents by far the most detailed measurements yet made on a penguin fauna, including numerous measurements for all skeletal elements, and reports the first occurrence of the neurocranium, pygostyle, furcula, os coxae, and ungual phalanx from Seymour Island.

Additional work was also recently completed on the Argentinean collection from Seymour Island, which now contains over 2,000 bones. It mainly involved the report of a range extension of two New Zealand taxa, *Palaeudyptes antarcticus*, and *Archaeospheniscus lopdelli*, into Antarctica, and the erection of two new species based on humeral remains: *Tonniornis mesetaensis* and *T. minimum* (Tambussi et al., 2006). That work must face the same limitations as all other studies of Seymour Island penguins i.e., the humeri are isolated and thus incomparable with numerous other taxa known from the island, but they do represent new humeral morphologies and are important enough to be named. As was subsequently shown, the size range of the two new species is well within that of taxa known from tarsometatarsi from the same horizon, suggesting potential issues regarding whether they should be synonymized with pre-existing Seymour Island species (Jadwiszczak, 2006b). The fact that the remains pertain to

penguins of equivalent same, however, does not mean that they pertain to the same species. Although Jadwiszczak was surely correct that new taxa should not be named using anything other than tarsometatarsi when working on the Seymour Island collections, Tambussi et al. were equally correct in that humeral morphology is just as systematically valuable as that of the tarsometatarsus and possibly less intraspecifically variable (Triche, pers. obsv.; Tennyson, pers. comm.). Intraspecific variability in penguin osteology is problematic in that it certainly exists but is generally not quantified, even in extant taxa.

Jadwiszczak's solution of organizing the Seymour Island remains into size classes and referring non-tarsometatarsal elements to previously named species is only somewhat more effective than naming new species from entirely new elements. The only way to attempt to explain the diversity of Seymour Island fossils, however, would be to place them in a phylogenetic context, as is now done (Triche, Chapter 3), and then to perform taxonomic revisions. Such methodology will be particularly helpful for the new species of *Tonniornis*, which was classified as Spheniscidae *incertae sedis* because of an inability to fit it into any of Simpson's original, sub-specific categories (Tambussi et al., 2006). When analyzed and placed in a phylogeny, however, the bird could be classified to a much more inclusive level than just Spheniscidae. For Seymour Island taxa, non-overlap among elements will prevent referral of certain specimens to pre-existing species and potentially cause taxonomic splitting, but will also insure that no specimen will be referred to a taxon to which it does not belong.

Finally, some new work on a partial braincase and other skull fragments from the Eocene La Meseta Formation resulted in the description of a new, although unnamed, species and new insights into the feeding behavior of extinct penguins based on lower jaw morphology (Ksepka and Bertelli, in press). Additional discoveries, of an upper jaw tip, numerous portions of humeri, and other fragments also extended the temporal range of Seymour Island penguins into the Early Eocene and suggested that not all giant penguins possessed elongate beaks (Jadwiszczak, 2006b).

### **New Zealand**

In 1986, an abstract appeared that reported the ‘Waipara’ bird, which purportedly represented the oldest penguin then known (Fordyce, Jones, and Field, 1986). It consisted of a humerus, coracoid, furcula, and ulna from the Early Eocene or Late Paleocene, but was not named or described in any detail. Two subsequent publications mentioned the find, but with no additional information (Fordyce and Jones, 1987, 1988). In their latest review of extinct penguins, Fordyce and Jones mentioned the additional presence of the interorbital region, mandibles, scapula, radius, synsacrum, vertebrae, and ribs (Fordyce and Jones, 1990). Their review listed five other new species then known from the Late Eocene-earliest Miocene of New Zealand, none of which were discussed since. Recently, additional Paleocene penguin remains were reported, but are not yet described (Jones and Manneringi, 1997).

These and additional authors recently formally named the ‘Waipara’ bird as two species: *Wimanu manneringi* and *W. tuatahi* (Slack et al., 2006). The former is based on only one specimen, recovered from the late Early Paleocene (62.4 mya) of the Waipara

Greensand of North Canterbury, in the South Island, whereas three specimens of *W. tuatahi* from the same provenance are early Late Paleocene in age (Slack et al., 2006). These ages suggest that modern birds originated much earlier and that modern seabirds, including penguins, are also older in origin than the Paleocene. Divergence dating based on DNA sequence data concurs, that modern birds, or Neornithes, originated at least 90-100 mya, in the Late Cretaceous, and that modern seabirds diverged from other shorebirds by 74 mya, in the Campanian (Slack et al., 2006). In addition to the great importance of the age of *Wimanu*, the oldest penguin is also morphologically unique. The genus contains numerous synapomorphies that undoubtedly place it within Sphenisciformes, but also a number of plesiomorphic characters subsequently lost in other known penguins. These include an elongated humerus, a square scapular blade, opisthocoelous thoracic vertebrae, and an elongated tarsometatarsus with shallow intermetatarsal grooves and a distinct medial hypotarsal crest, among others (Slack et al., 2006). The published description of *Wimanu* was short, but a detailed description of the genus will appear shortly (Ando, pers. comm.). *Wimanu* is the most basal sphenisciform and the earliest stem-penguin in all cladistic analyses in which it is included (Slack et al., 2006; Ksepka et al., 2006; Triche, Chapter 3).

## **Macroevolution**

### **Phylogenetic Hypotheses**

Phylogenetic hypotheses regarding living penguins only recently appeared, and those including fossils remain preliminary. Most older studies concerning penguins ignore phylogeny in favor of strict morphological description (e.g., Coues, 1872; Gervais

and Alix, 1877; Jullien, 1882), or reach contradictory systematic conclusions (e.g., Gregory, 1934; Lowe 1933, 1939; Simpson, 1946). Even systematic works through the remainder of the twentieth century often only mention phylogenetic analysis, although much basic data was collected. These include taxonomic revisions lacking a phylogenetic framework (Kinsky and Falla, 1976; Myrcha et al., 2002, 2006), extensive literature reviews (Fordyce, 1990; Fordyce and Jones, 1990), and proposals of potential systematic characters (Verheyen, 1958; Zusi, 1975). In the past three years, however, a number of cladistic analyses of extant penguins appeared (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Baker et al., 2006), some addressing their placement within Aves (Mayr and Clarke, 2003; Mayr 2004, 2005), and a smaller number regarding extinct species (Slack et al., 2006; Bertelli et al., 2006; Walsh and Suarez, 2006; Ksepka et al., 2006; Triche, Chapter 3).

**Placement of Sphenisciformes.** There is still no consensus regarding the placement of penguins within Aves, although most analyses propose an extant clade of shorebirds as their sister taxon. Authors today agree that penguins lie within Neoaves, but disagree as to where, and may leave penguins out of large avian phylogenetic analyses altogether (e.g., Mindell et al., 1997). Proposed penguin sister-taxa, based on both molecular and morphological analyses, include part or all of the tubenoses (albatrosses and petrels, or Procellariiformes; Simpson, 1946; Sibley and Ahlquist, 1990; Cooper & Penny, 1997), tubenoses followed by loons (Gaviidae; Van Tuinen et al., 2001; Livezey and Zusi, 2001, 2006, 2007), loons alone (Olson, 1985b), loons plus grebes (Podicipedidae; Cracraft, 1982, 1988; Sibley and Ahlquist, 1990; Mayr and Clarke,

2003), loons plus grebes plus flamingos (Phoenicopteridae; Mayr, 2004), loons followed by grebes (Ho et al., 1976), a paraphyletic Procellariiformes (McKittrick, 1991), and an unresolved position within a polytomy of penguins, loons, tubenoses, storks, and other aquatic and semi-aquatic neoavians (Ericson et al., 2006). Phylogenies proposed for the placement of penguins within Neoaves are diagrammed in Figure 1.4.

Two of the most divergent sister group suggestions are extant Ciconiidae (storks; Slack et al., 2003) and extinct Plotopteridae, a group of flightless seabirds known from the Tertiary of the North Pacific (Mayr, 2005a). The former relies on a maximum likelihood analysis of an entire mitochondrial genome, but includes no other seabird taxa, only members of Paleognathae, Galloanseres, and four Neoavians almost certainly unrelated to penguins (Slack et al., 2003). That study did not examine penguin relationships specifically, only avian phylogeny in general, but the exclusion of all previously hypothesized relatives of penguins does call the sister-taxon statement into question. Further work on that dataset places penguins in the midst of a clade of assorted seabirds, in no close relation at all to storks (Slack et al., 2006).

The latter study (Mayr, 2005a) examined a large number of extant and extinct bird clades with morphological data, but supported the Plotopteridae-Spheniscidae clade with only three synapomorphies among a large number of convergent and plesiomorphic characters. In addition, some character coding used a putative plotopterid specimen that may actually be a frigatebird, as no other analysis examined the phylogenetic placement of that specimen. The remainder of the plotopterid coding used only a few incomplete figures (e.g., Olson and Hasegawa, 1979), which illustrate only portions of the relevant

anatomy and probably do not present sufficient detail for use in character coding (Triche, pers. obs.). The analysis also failed to include any extinct penguins and one of the six extant genera, resulting in almost certain exclusion of any basal penguin character states that might or might not indicate true relationships with pterosaurs. For example, the stem-penguin *Wimanu* exhibits remarkable plesiomorphic similarities with procellariiforms, indicating that any resemblance between penguins and pterosaurs is strictly convergent (Slack et al., 2006; Triche, Chapter 3).

The variety of conclusions about the placement of penguins within Neoaves probably results from morphological and molecular convergence. Shorebirds invariably cluster together in analyses using either data type, but it remains uncertain whether or not such clustering reflects actual relationship (Livezey and Zusi, 2001, 2006, 2007). In particular, analyses generally agree that the morphology of Pterosaurs and penguins is convergent, coinciding with the fact that Pterosaur remains exist only in the Northern Pacific and those of penguins only in the Southern hemisphere (Olson and Hasegawa, 1979). Because Aves contains so many species, analyses of the group vastly under-sample most higher taxa, use one species of penguin at most, and often exclude many other possibly relevant seabirds. Recent consensus, however, tends to place Sphenisciformes within a large seabird/shorebird clade, the recently taxonomically expanded Ciconiiformes, and suggest that convergence may not be as misleading as previously thought (Mayr and Clarke, 2003; Ericson et al., 2006; Livezey and Zusi, 2006, 2007; van Tets et al., 2006). Furthermore, the majority of analyses that include Procellariiformes and Gaviidae support a sister-taxon relationships of these taxa with

penguins. Further work should attempt to integrate taxa and data from all available studies to examine seabird phylogeny in a more global analysis.

**Extant Species.** Authors only recently examined the phylogeny of extant penguins using cladistics, and these relationships remain somewhat problematic. In fact, researchers still recognize anywhere from sixteen to eighteen extant species depending on whether the Royal and Fairy penguins are considered as species or subspecies (e.g., Williams, 1995; Davis and Renner, 2003; Bertelli and Giannini, 2005; Ksepka et al., 2006), and continue to debate the various numbers of subspecies of other *Eudyptes* and *Eudyptula* species (e.g., Kinsky and Falla, 1976). Ignoring the exact number of species, various authors proposed phylogenies of the six extant genera that incorporate every possible relationship between them (Figure 1.5).

The first phylogeny proposed for penguin species was an evolutionary hypothesis based on overall similarity and never actually diagrammed as such (Simpson, 1946). That was basically the only such work for forty years, until the advent of cladistic methods. The first cladistic analysis of the interrelationships of penguins was an unpublished Ph.D. dissertation that used sixteen morphological characters and all extant species (O'Hara, 1989). Publications from that year also included a morphometric study of all extant penguins, resulting in a phenetic hypothesis of relationship (Livezey, 1989). A few years later, an allozyme analysis examined three extant species in the genus *Spheniscus* (Grant et al., 1994), while a behavioral phylogeny of four extant species grouped penguins with petrels (Paterson et al., 1995). More recently, a supertree analysis of all current procellariiform phylogenies included ten extant penguins in its dataset (Kennedy and

Page, 2002). In that analysis, penguins did form a monophyletic outgroup to all Procellariiformes, but some unexpected relationships resulted within the Spheniscidae, including complete lack of resolution in the strict consensus tree and presence of two non-monophyletic genera in the more-resolved Adams consensus tree. Although loss of resolution is inherent to strict consensus methods, these results also are artifactual because the original source trees used to construct the supertree contained numerous non-overlapping taxa. The problem, which is widespread in supertree analysis, results in a proliferation of artifactual polytomies and reduces the utility of the method for reconstructing species-level relationships (Gatesy et al., 2004). The preceding studies all support different relationships among penguin genera or contain so few taxa as to be non-comparable. They also tend to undersample the penguin clade, resulting in lack of resolution and highly divergent topologies.

The first cladistic analysis of all extant species used breeding characters and the unique integumentary structure of penguins (Giannini and Bertelli, 2004). Those authors subsequently integrated their dataset into a combined morphological and molecular analysis, using mitochondrial DNA 12S and cytochrome b sequences, which resulted in a similar topology (Bertelli and Giannini, 2005). When analyzed separately, however, the morphological and molecular data partitions are strongly divergent and suggest that the number of molecular characters is swamping the included morphology or that there is insufficient breadth to one of these data sets. The latter study was the first to explicitly test the monophyly of Spheniscidae, which it strongly supported, and the first to combine molecules and morphology, including osteological and integumentary characters (Bertelli

and Giannini, 2005). No modern phylogenetic study has yet tested the monophyly of a penguin genus or any higher group. Although most analyses do recover penguin genera as monophyletic groups, many also do not include all species of each genus.

Finally, a molecular analysis of all eighteen proposed species used numerous genes, including RAG-1, mDNA-12S, rDNA-16S, COI, and cyt B, in support of a new phylogeny including divergence time estimates (Baker et al., 2006). The resulting topology is identical to that of the previous combined analysis, although it differs in most respects from the result recovered using morphology alone (Bertelli and Giannini, 2005). Work on relationships among extinct penguins generally agrees with the morphological signal (Walsh and Suarez, 2006; Bertelli et al., 2006; Ksepka et al., 2006) and with that in other morphological analyses (Simpson 1946; O'Hara, 1989), although extant genera appear to be less closely related to each other because of their close relationships with various extinct taxa (Triche, Chapter 3). Current consensus on extant penguin relationships thus seems to support the sister taxon relationships between a crested penguin clade (*Eudyptes* and *Megadyptes*) and a *Spheniscus-Eudyptula* clade, with conflicting results regarding the Antarctic genera *Aptenodytes* and *Pygoscelis*. More research, however, is required to explain the conflicting morphological and molecular signals present within penguins.

**Fossil Species.** Various authors dealt with the phylogeny of extinct penguin species almost since their original discovery. Published cladistic analyses, however, only addressed extinct penguins in the context of the phylogeny of extant species. Generally, hypotheses of phylogeny among extinct penguins were informal and consisted of short

appraisals of the degree of similarity between various faunas or species. Simpson, for example, proposed an evolutionary phylogeny of extinct species that included a number of separate, and highly specialized, extinct lineages, none of which was ancestral to modern species (Simpson, 1946). The modern group had therefore evolved from some as-yet undiscovered penguin ancestor (Simpson, 1946, 1971c, 1972). Within extinct penguin lineages, he found *Palaeudyptes* to be most similar to a *Pachydyptes-Platydyptes* group, all of which are more distantly related to *Anthropornis* of Seymour Island. These anthropornithine and palaeudyptine groups were thus distinct from the palaeospheniscine species of Patagonia. The paleospheniscines included the New Zealand genera *Dunroonornis* and *Korora*, although that is the only similarity Simpson noted between the faunas of the two continents (1971c). The only penguins he thought might be related to extant Spheniscidae, although not closely, are the extinct palaeospheniscines, a view shared by Marples (Simpson, 1946). All these hypotheses of relationship are recovered in the current phylogeny (Figure 1.1; Triche, Chapter 3). Thus, although Simpson's work well pre-dated cladistic analyses, his conclusions are mainly upheld by recent analyses. It is a testament to the seminal nature of his research on penguins that macroevolutionary conclusions reached over 60 years ago, using much less material and older methods, retain their validity.

Marples, in all his classifications, noted the probable phylogenetic similarity between species from Australia, New Zealand, and Seymour Island, which group was not at all similar to the separate lineage evolving in Argentina, nor to the derived group of extant species (Marples, 1953). That hypothesis was only formalized as a subfamilial

taxonomy, never a phylogenetic tree. He also agreed with Simpson that the Australasian group was not ancestral to modern species, but differed in linking the Argentinean group much more closely with the extant clade, despite the presence of a few morphological differences (1952). Marples' conclusions also differed from Simpson's when he separated the palaeudyptine penguins from the Argentinean *Parapterodytes* (1971c), a hypothesis now also corroborated (Figure 1.1; Triche, Chapter 3). The only other examination of phylogeny including extinct species until recently was that of Zusi, who performed a functional analysis of penguin skull structure. He used extant species and the few extinct species then known from cranial remains (*Parapterodytes antarctica* and *Palaeospheniscus novaezealandiae*) and found support for a monophyletic crown clade, but none for the placement of either taxon (Zusi, 1975).

The first cladistic analysis (Slack et al., 2006) to include an extinct penguin integrated the oldest known genus, *Wimanu*, into a previous analysis of Aves (Mayr and Clarke, 2003). The only other extinct penguins included in the new matrix were *Wimanu*, *Platydyptes*, and '*Palaeudyptes*', because the analysis was used specifically to examine the possible position of the new taxon as a stem-penguin (Slack et al., 2006). Results show *Wimanu* to be the unambiguous sister taxon to other sphenisciforms, and Panspheniscidae to be nested within a clade also containing Gaviidae, Podicipedidae, and Procellariiformes. Although the analysis was narrow in scope, including only three of the large number of extinct penguin species, that publication is noteworthy because it is the first cladistic treatment of an extinct penguin.

A second cladistic analysis examining the position of a single extinct taxon resulted in the conclusion that *Parapterodytes antarcticus* is the sister taxon to a monophyletic Spheniscidae (Bertelli et al., 2006). Data utilized in that work were identical to the authors' previous character matrix examining extant penguin phylogeny (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005), with the addition of one character that was somewhat adapted. The analysis examined only the one of three species included in *Parapterodytes* owing to the authors' focus on description of the cranial anatomy of a particularly well-preserved specimen of *P. antarcticus* and to their suspicions that the genus is not monophyletic. The sister-taxon status of *P. antarcticus* was highly supported, both by relative support values, a large number of synapomorphies shared with Spheniscidae, and the relatively complete scoring of the extinct taxon. However, addition of more extinct taxa greatly modifies the topology of the penguin stem-group (Triche, Chapter 3). Although *P. antarcticus* is unquestionably the outgroup to Spheniscidae when examined alone, globally it is much more closely related to other, extinct taxa (Triche, Chapter 3).

The third cladistic study of extinct penguins again examined the relationships of a single taxon, the new species *Pygoscelis grandis*, and again did not specifically address the relationships of living or extinct penguins (Walsh and Suarez, 2006). That study focused on post-cranial characters and did not include all living penguin species or any additional extinct taxa. The topology of the resulting cladogram is identical to that of O'Hara (1989) and to the morphological tree of Bertelli and Giannini (2005), although it does not include the genus *Megadyptes*, which forms the only incongruence between

these other two cladograms. The new species lies within a monophyletic *Pygoscelis* clade, but support for the node is low (bootstrap value of 58%), suggesting that the clade may be unsupported or that its potentially recent evolution may have resulted in low levels of divergence.

Another recently discovered species, *Madrynornis*, provided the impetus for cladistic analysis of a number of Argentinian species, including this new discovery as well as *Palaeospheniscus biloculata*, *Parapterodytes antarcticus*, *Spheniscus megaramphus*, and *S. urbinai* (Acosta Hospitaleche et al., 2007). This analysis suggests that *Parapterodytes* lies outside all other examined species, that *Palaeospheniscus* may be the sister taxon of the extant *Aptenodytes*, and that a monophyletic *Spheniscus* includes both extinct and extant species. The new species *Madrynornis* lies unambiguously as the sister-taxon to *Eudyptes*, a position that is highly supported by the fact that the species is 97.6% completely scored in their matrix (Acosta Hospitaleche et al., 2007).

Finally, there is an unpublished phylogenetic hypothesis based on a mainly morphometric analysis of three South American taxa (*Parapterodytes antarctica*, *Palaeospheniscus (Chubutodyptes) biloculata*, and a new, unnamed genus, MEF-PV 100), as well as fourteen extant species. That work placed *P. biloculata* as the sister taxon to the extant *Aptenodytes*, and the other two extinct taxa as subsequent outgroups to crown penguins (Acosta Hospitaleche, 2004). That topology basically agrees with the phylogeny adopted here, although my analysis does not show *P. biloculata* to be as deeply nested within the crown-clade (Triche, Chapter 3).

The first cladistic analysis to include numerous extinct penguin taxa examined 32 extinct and 18 extant taxa using tarsometatarsal morphology (Triche, 2005). It resulted in a highly resolved, if somewhat weakly supported, phylogeny. After the removal of six particularly incomplete taxa, the topology included a monophyletic crown-clade, five monophyletic extant genera, and resolution of one extinct clade of Antarctic and one of New Zealand species. Of the extant general, only *Spheniscus* proved to be paraphyletic.

The latest study added to the abundance of cladistic penguin work appearing in 2006 was the second analysis of multiple species of extinct penguins, and the first to be published (Ksepka et al., 2006). The matrix used was nearly identical to that of previous analyses examining extant species (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Bertelli et al., 2006), with the addition of only 26 novel characters to account for anatomical variation observed in extinct taxa. Analyzed species included nine taxa examined directly and an additional nine taxa coded from the literature, for a total of 18 out of the 59 currently named extinct species. The resulting cladogram recovered a mostly pectinate arrangement of extinct taxa leading up to a monophyletic crown-clade. Bremer support values suggest low support for most nodes, but the consensus tree is fairly well resolved. This dataset subsequently served to analyze the phylogenetic relationships of the two giant Peruvian species recently discovered (Clarke et al., 2007). This analysis suggests that the older of the two, *Perudyptes*, evolved early in penguin evolution, while the younger species, *Icadyptes*, lies within a paraphyletic assemblage of large-bodied, Eocene penguins.

The first proposed phylogeny of all diagnostic extinct and extant penguin species was recently completed (Triche, Chapter 3; Figure 1.1). That analysis used 503 osteological, myological, integumentary, and behavioral characters, many of which were newly proposed, to examine relationships among 51 extinct and 18 extant taxa. Although a subsequent publication will present details of the analysis and conclusions resulting from that phylogeny (Triche, Chapter 3), it is worth mentioning a few major points about the relationships of extinct species that are now known. For clarity, Figure 1.1 simplifies penguin phylogeny to only the relationships of well-known penguin genera, including the extant species, *Palaeudyptes* sp., and *Wimanu*. The crown-clade, Spheniscidae, forms a well-supported monophyletic group nested deep within Sphenisciformes. That group includes a few extinct taxa, nearly all of which are members of extant, monophyletic, genera, and none of which are known from before the Pliocene. Additionally, all extant genera are monophyletic, although some extinct taxa (e.g., the Pliocene, South African species) do not group with *Spheniscus* as expected, probably because of missing data. A number of extinct genera, on the contrary, are para- or even polyphyletic, indicating the need for more detailed analysis of the relationships of these taxa. These include *Platydyptes*, *Pachydyptes*, *Archaeospheniscus*, and especially the ‘*Palaeudyptes*’ group.

The closest outgroups of crown-penguins are members of the South American, ‘palaeospheniscid’ penguins, which corroborates the hypothesis of Simpson and Marples that extant penguins are most closely related to palaeospheniscids. The sister taxon of these species is a large monophyletic group of extinct species from New Zealand and Seymour Island, Palaeudyptidae. Within this clade, the Paleocene specimen from

Seymour Island, *Crossvallia*, is most closely related to the unnamed Tierra del Fuego species. These taxa evolved from the earliest branch of the large, basal clade, which accords well with the first appearance of the species in the fossil record. A small, extinct clade of Seymour Island penguins that includes most of the species named from tarsometatarsal morphology forms the basal group of penguins. The Argentinian *Paraptenodytes* is highly nested within that clade, in accordance with Simpson's hypothesis that the genus was less closely related to other Argentinian species (Simpson, 1946). Finally, *Wimanu* constitutes the basal-most member of Panspheniscidae, or all penguins, which is consistent with its status as the only extinct penguin showing truly plesiomorphic morphology. The topology predicts that new discoveries should include additional, flightless, stem-penguins from the Paleocene or even earlier.

### **Biogeographic Hypotheses**

A number of biogeographic observations and hypotheses exist to explain the current and historical distribution of penguins. Although the lack of a phylogeny currently handicaps such analyses, much speculation also exists concerning the underlying cause of the geographic pattern. These birds have probably always been restricted to the Southern Hemisphere, as they are today, although there is no accepted cause for such a limitation (Cracraft, 1973). Various hypotheses for the phenomenon include the presence of an equatorial climate barrier to penguin expansion, caused either by ambient temperature or lack of cold sea currents, the presence of numerous, terrestrial, Northern Hemisphere predators absent from the south, the lack of suitable, predator-free, offshore islands in the north, and the historical artifact that penguin species just arrived at

the equator and have not had sufficient time to disperse further (Simpson, 1946; Cracraft, 1973; Baker et al., 2006). The equatorial barrier hypothesis may be the most useful for further exploration, because there are certainly numerous aquatic predators in the Southern Hemisphere and because penguins are at least 63 million years old and thus certainly have had sufficient time to disperse past the equator. Penguins currently range north to central Africa and the equatorial Galapagos Islands, and include three species of *Spheniscus* that breed in the tropics (Davis and Darby, 1990). All such northerly penguins, however, rely on and are distributed in conjunction with cold-water, nutrient-rich systems such as the Humboldt Current off the western coast of South America. Such dependence may be the reason that penguins never managed to cross the equator, as all cold-water currents also fail to do so. At the other extreme, one of the smallest extant penguins, the 37cm Adelie (*Pygoscelis adeliae*), lives and breeds solely in Antarctica. Why the only other extant Antarctic species is the Emperor (*Aptenodytes forsteri*), which is the largest living penguin species at over a meter in standing height, also remains unexplained (Stonehouse, 1969).

Authors assign geographic areas occupied by penguins to a number of well-defined biogeographic provinces, which serve as the basic units of biogeographic analysis (Figures 1.6 and 1.7). These Southern Hemisphere provinces include the South Polar Province, the Magellanic Province or the west coast of South America, which is directly linked to the cold Humboldt Current, the Cookian and Antipodean Provinces of New Zealand, the combined Australian/Tasmanian Province, and the South African Province (Zinsmeister, 1979; Kennett, 1980). Most biogeographers divide the Southern Ocean into

a number of separate provinces to accommodate the sub-Antarctic and Antarctic islands that range from offshore New Zealand to offshore South America. These include the Kerguelan, Bouvet, South Georgian, and Macquarie Provinces, which can probably be combined as the Southern Ocean Province for the purpose of avian distributions (Chown et al., 1998). As the distribution of penguins within these areas highlights, and contrary to popular opinion, penguins are currently mostly associated with the temperate zone, not the polar regions (Figure 1.7; Simpson, 1975a; Baker et al., 2006).

Penguin biogeographic history is intimately linked to climate change. Extinct penguins lie entirely within the range and biogeographic provinces of extant species, although some differences exist. For example, ranges are currently reduced in some extant genera, as evidenced by the Late Pliocene presence of *Aptenodytes* and *Pygoscelis* as far north as New Zealand and Chile. Range reduction is probably related to the cooler temperatures inferred for that time in comparison with the present, which may have forced penguins further to the north as temperatures cooled (Simpson, 1975a; Walsh and Suarez, 2006). It is a fact long noted that extinct penguins often inhabited warmer environments than currently (e.g., Lowe, 1933). The discovery of the Paleocene Seymour Island penguin highlights that conclusion because the reconstructed Antarctic Paleocene environment included temperate to tropical forests (Feldman and Woodburne, 1988). Combined with the fact that Antarctic penguin remains are much more abundant in the Middle to Late Eocene than in earlier strata, it seems that penguins originated in a warm climate in the Cretaceous or Paleocene and then radiated extensively as climate cooled in the Late Eocene (Myrcha et al., 2002; Tambussi et al., 2005).

Because the climates of New Zealand and Seymour Island were probably similar in the Late Eocene and Oligocene, Simpson hypothesized that geographic separation and resultant genetic isolation probably caused the specific differences between the Seymour Island and New Zealand species (1971c). Differences between these and the Patagonian fauna, however, could result from the climatic differences inherent in the differing ages of the deposits (Simpson, 1971c). Because Patagonian forms are not closely related to the New Zealand/Seymour Island species, a climatic and temporal separation matches well with phylogeny (Triche, Chapters 3, 4).

It may also be that penguins always preferred a temperate climate and only dispersed from Antarctica when it was extensively glaciated in the Oligocene (Baker et al., 2006; Triche, Chapter 4). Some phylogenetic hypotheses accord with the scenario because all more northerly taxa (Spheniscidae, palaeospheniscids) lie within a single, more derived clade (Triche, Chapter 3). However, the discovery of very low-latitude penguins that are at least 42 million years in age show that penguins had certainly invaded the tropics by this time and suggest that a different explanation must be sought for why penguins dispersed from their probable southerly area of origin (Clarke et al., 2007).

There is a correlation between major climatic and ecologic events occurring throughout the history of penguins. For example, the K/T extinction of marine reptiles coincides with the radiation of penguins and marine mammals, and the Oligocene climatic 'optimum' with an increased abundance, although not increased diversity, of penguins (Fordyce and Jones, 1990). The decrease in abundance, size, and degree of

specialization of extinct species in the Miocene may be related either to concomitant climatic cooling or to competition with or predation by the newly radiating pinnipeds and cetaceans (Stonehouse, 1969; Simpson, 1975a; Fordyce and Jones, 1990). Half of all penguin diversity was extinct by that time, including the entire Palaeodyptidae (Triche, Chapter 3). Taxon pulses resulting from periodically adverse climatic conditions could explain the rapid, early expansion of penguins on Seymour Island (Jadwiszczak, 2003). Similar work examining the effects of climate on extant and Holocene penguins from Antarctica produced conflicting results. Most known Holocene rookeries seem to be abandoned in colder intervals, the Little Ice Age for example, probably owing to lack of sufficient food or unfavorable extent of sea-ice (Emslie, 1995; Emslie and McDaniel, 2002; Emslie et al., 2007). However, recent work shows that extant Adelie penguins expand their distributions as a result of decreasing temperatures and increased ice area, while extant chinstrap populations expand with increasing temperature and are adversely affected when temperatures fall (Trivelpiece et al., 1990; Fraser et al., 1992; Ritchie et al., 2004). Such changing distributions result because Adelie penguins breed on continental shelves, while chinstrap penguins prefer floating sea ice, and suggest that correlation of penguin extinctions with climate change may not be straightforward. Taken together, previous work points to the difficulty inherent in inferring causation or even basic patterns of penguin evolution, especially when lacking precise data regarding paleoclimate, ice presence and abundance, and ocean productivity.

As an alternative to or, more appropriately, in conjunction with climatic effects, many authors also noted the pervasive influence of Gondwanan breakup on Southern

Hemisphere organisms (e.g., Cracraft, 1973; Fordyce and Jones, 1990, Sanmartin and Ronquist, 2004). In view of the Gondwanan distribution and the timing of origin of penguins, which occurred just after initiation of the final separation of Gondwanan continents in the Late Cretaceous and the emergence between these continents of the large, shallow seas that penguins favor (Cracraft, 1973; Lawver and Gahagan, 2003), it is clear that tectonic events must have affected penguin biogeography. A forthcoming cladistic biogeographic analysis will take into account both vicariance and dispersal, including climatic and tectonic effects, in a more quantitative analysis of the biogeography of extinct penguins (Triche, Chapter 4). Some such work, which involves mapping biogeographic distributions onto phylogenetic trees, already exists (e.g., Bertelli and Giannini, 2005; Triche, 2004). These analyses suggest that the ancestral area of penguins lay either in the Australia-New Zealand-Antarctic Peninsula area (Bertelli and Giannini, 2005), the ‘core of Gondwanan’, presumably Antarctica (Baker et al., 2006), Australia-New Zealand (Ksepka et al., 2006), or New Zealand (Triche, Chapter 4.). Such broad geographic hypotheses probably result from the lack of fossil constraints on the input trees (Triche, 2004), although the long length of time considered may also affect the ancestral area reconstruction. Authors also infer a major, early, vicariant split between the Antarctic genera and the remaining species, followed by numerous, subsequent speciations and dispersal events (Bertelli and Giannini, 2005). However, their suggestion that the extant genera *Eudyptula* and *Spheniscus* diverged via a Pacific vicariance event would, at least if based on tectonic events, constrain the divergence to the Cretaceous, an extraordinarily old date for the divergence of extant species.

## **Other Patterns**

Lack of a phylogeny hampers hypotheses of other macroevolutionary events within penguin history, although authors note many patterns and potential processes. Numerous authors, for example, remarked on the lack of an obvious extinct ancestor of modern species. Simpson cited the observed dissimilarity between extant species and his two main lineages of extinct taxa as evidence that the ancestor of the crown-group remained undiscovered (1975a). Additionally, he implied that these extinct lineages had already undergone great specialization and that the extant group was less specialized and more plesiomorphic than extinct species. From a modern perspective, it is now clear that the crown-clade is most closely related to a known extinct group, the palaeospheniscids of South America (Triche, Chapter 3), although many extinct lineages were highly specialized, as Simpson suggested. Mapping the current phylogeny onto the geologic time scale indicates a large temporal gap between the sister taxa Paraptenodytidae and Spheniscidae, suggesting that we still lack taxa intermediate between the crown-group and most older species. The proximal outgroups of Spheniscidae, however, include a number of palaeospheniscids, which may therefore resemble most closely the ancestral crown-penguin. Recent molecular work that dates the crown-group to the Eocene of Seymour Island (e.g., Baker et al., 2006) prompted speculation that the ancestral crown-penguin probably either consisted of or was very similar to a species of *Delphinornis* (Jadwiszczak, 2006b). Such reconstructions are constrained, however, by the lack of any Antarctic penguin remains except from Seymour Island, which suggests that much of the penguin record in Antarctica may be missing. Although Baker et al. included no extinct

species in their analysis, their results do agree with other estimates of divergence timing (Triche, Chapter 4) on an Eocene divergence for the crown group. That estimate, however, is heavily dependent on the phylogenetic placement of a number of mostly incomplete Late Miocene fossils from South America (e.g., *Chubutodyptes*, *Eretiscus*) and may represent an overestimate of the age of crown -penguins. The best current estimate, therefore, is that crown-penguins probably originated near Seymour Island, but not necessarily when delphinornids were living. Phylogenetically, the closest relatives of Spheniscidae are South America palaeospheniscids, which together are related to Seymour Island delphinornids. The ancestral penguin may, therefore, be reconstructed using hypothesized synapomorphies of palaeospheniscids + Spheniscidae.

The origin of penguins is not only controversial in terms of their putative sister taxon, but also when discussing the method by which they lost flight in favor of wing-propelled diving. With the notable, and highly divergent opinion of Lowe (1933, 1939), who maintained that penguins had evolved directly from a non-volant ancestor before the origin of all other modern birds, all authors assert that penguins evolved from flying birds and subsequently lost the ability. Simpson held that the transition was necessarily abrupt owing to the impossibility of flying, swimming, and attaining large body size at the same time, and that it probably therefore occurred in a small, procellariiform ancestor similar to a diving petrel (1946, 1975a). Probably, the ancestral penguin never lost the ability to ‘fly’, but merely co-opted that function to underwater ‘flight’ and eventually evolved flippers (Simpson, 1946). A forthcoming functional analysis of penguin wing morphology may shed light on the transition (Ando, pers. comm.).

Accompanying the question of how the ancestral penguin evolved is the problem of when the transition occurred. The debate over the origin of modern Neornithes is currently intense, with much molecular and some fossil and biogeographic evidence pointing to a Cretaceous origin and initial radiation of modern birds and the survival of some (Hope, 2002; Dyke and van Tuinen, 2004; Ericson et al., 2006; van Tuinen et al., 2006) or even numerous (Cooper and Penny, 1997; Cracraft, 2000) modern lineages across the K/T boundary. Alternatively, a literal reading of the fossil record supports a much later Tertiary radiation of modern birds with few or perhaps only one modern lineage or 'ancestral stock' surviving the K/T extinction (e.g., Feduccia, 2005). Although nearly all evidence therefore agrees on a Cretaceous origin for Neornithes, with paleontological data generally suggesting a somewhat later date than most molecular data, disagreement remains concerning whether numerous or only a few lineages crossed the K/T boundary. Part of the problem is that only one Cretaceous taxon, *Vegavis*, is known that may be unambiguously diagnosed within Neornithes (Clarke et al., 2005). Other potential Cretaceous neornithines are currently either undiagnosable to any higher taxon or are taxonomically disputed (Hope, 2002).

The conflict is in some ways more apparent than real, however, because different authors use different definitions of Neornithes, either stem- or crown-clade based (Brochu and Norell, 2001; van Tuinen et al., 2006). The stem-clade Neornithes may well date to the Cretaceous and that period may contain numerous stem-lineages indicative of the modern bird radiation (e.g., stem-penguins), but most crown-group neornithines (e.g., crown-penguins) probably evolved only later, in the Tertiary (Mayr, 2005b; James,

2005). Neornithes probably therefore originated and split into numerous lineages in the Cretaceous, but its extant members only radiated extensively in the Tertiary, which is a logical compromise between the opposing sides of the debate. It does, however, remain debatable exactly how many lineages crossed the K-T boundary, with various molecular and paleontological data supporting both positions (e.g., Cooper and Penny, 1997 vs. Ericson et al., 2006).

The fossil record of penguins pertains to the debate because it dates the divergence time of penguins from other modern birds and may potentially include a Cretaceous representative, as stem-taxa older than the Early Paleocene *Wimanu* remain to be found. If penguins are Cretaceous or even earliest Paleocene in age, their phylogenetic placement within the derived Neoaves would tie the divergence date of Neoaves to at least the Late Cretaceous (Slack et al., 2006; Triche, 2006, Chapter 4), as is now done for Neornithes (Clarke et al., 2005).

Molecular clock estimates from modern taxa already place the origin of Sphenisciformes in the Late Cretaceous (71 mya) and the origin of the crown-group as early as the Late Eocene (40 mya; Baker, 2006). Alternatively, it may be the clade containing all shore- and seabirds that dates to the Late Cretaceous, implying that penguins and other included groups originated after the Cretaceous-Tertiary extinction (van Tuinen et al., 2006). That post-Cretaceous date (van Tuinen et al., 2006) appeared before data about the Paleocene penguin *Wimanu* were available, however, and therefore probably underestimates the age of that clade (Triche, 2006, Chapter 4). Additional hypotheses suggested that numerous extant aquatic lineages, including penguins, are

much younger than most other neornithines, possibly owing to slower genetic rates or differential extinction pressures in aquatic environments (van Tuinen et al., 2006). However, these dates refer to the appearance of crown-groups, not stem-groups, and ignore the fact that functionally modern, swimming penguins were already present at least by the Eocene (Simpson, 1971c). The discrepancy is that the main diversification and radiation of penguins did not occur concurrent with the origination of the crown-group, but much earlier.

New work using divergence dates from DNA sequence data and numerous fossil calibrations suggests that a large Neoavian clade of sea- and shorebirds in fact postdates the Cretaceous extinction (Ericson et al., 2006). However, that study also appeared too recently to incorporate the Early Paleocene age of *Wimanu* (and uses only a date of 55-65 mya, or the duration of the Paleocene), probably also underestimates the age of the clade Neornithes, and thereby potentially underestimates the date of origin of penguins as well (Brown et al., 2006; Triche, pers. obs.). The numerous problems associated with assuming a molecular clock and the large margins of error reported with these dates also require that they be regarded with caution (e.g., Brochu et al., 2004; van Tuinen and Hedges, 2004; Ho et al., 2005; Peterson, 2006; Pulquerio and Nichols, 2007). Factoring in the age of the oldest current extinct taxon, *Wimanu*, suggests that Neornithes originated at least 90-100 mya, in the Late Cretaceous, and that modern seabirds, including penguins, diverged from other shorebirds by 74 mya, in the Campanian (Slack et al., 2006). These dates are also supported by confidence intervals applied to fossil

dates (Triche, 2006). If various sources of data derived from penguins are correct, the Cretaceous origin of at least that one lineage of extant neoavians is supported.

Simpson, among others, hypothesized that penguins are an example of Bergmann's Rule, or the correlation between larger species and higher latitudes (Simpson, 1946, 1975a; Blackburn et al., 1999). That pattern holds for numerous extant and extinct species, although there are some notable exceptions. The causes of Bergmann's Rule remain unknown, although there are a number of potential ecological and phylogenetic mechanisms (Blackburn et al., 1999). Crown-penguins are highly vagile animals and disperse immense distances in the course of their yearly breeding cycle. They also have extremely narrow ranges of temperature tolerance and hence generally disperse longitudinally, not latitudinally (Kooyman, 2002), which perhaps explains the phenomenon of smaller species at lower, hotter latitudes. Although Bergmann's Rule originally applied to interspecific comparisons, a subsidiary intraspecific pattern is now termed James' Rule (Blackburn et al., 1999). That 'rule' is not as well investigated in penguins, with the only test, that of *Pygoscelis papua*, showing no corroboration (Stonehouse, 1967).

The size of extinct species raises perhaps the most public interest in extinct penguins, especially because some authors previously exaggerated some species to a standing height of as much as seven feet (Simpson, 1971c). The Patagonian species were nearly uniformly smaller than the clade of New Zealand and Seymour Island taxa, Palaeudyptidae, with only two of the nine Patagonian species reconstructed as being larger than the smallest of the Seymour Island representatives (Simpson, 1975a).

Presumably, that difference in size correlates to a difference in ecology, although the cause is speculative. The large, Seymour Island specimens also preserve the greatest range of body sizes. Wiman originally divided these remains into six size classes (1905), a grouping corroborated by long bone measurements (Case, 1992). Case also found that most of the Seymour Island localities and geologic units contain all six body size classes (Case, 1992). If one divides extant species of Antarctic or sub-Antarctic penguins into similar ranges as these classes, only three size groups and four species occur on average at a given locality, as compared with six and six in the Eocene of Seymour Island. That suggests that Seymour Island contained a high diversity of penguins, both in species number and in ecologic range (Case, 1992). Body size extrapolations do show that these extinct species were large, nearly twice the size of the largest living species, the Emperor Penguin (Jadwiszczak, 2001). The commonly preserved Seymour Island femur, tibiotarsus, and tarsometatarsus give estimates of 82kg and 166cm standing height for the largest known penguin, *Anthropornis nordenskjoeldi*. Intermediate forms such as *Palaeudyptes klekowskii* and *Marambiornis exilis* may have been 56 kg and 147 cm and 30 kg and 112 cm respectively, whereas the smallest species, *Delphinornis gracilis*, may have measured only 8 kg and 81 cm in standing height (Jadwiszczak, 2001).

Finally, recent authors asserted that the evolution of large body size occurred many times in the early history of penguins (Ksepka et al., 2006), although their analysis excluded one species suggested to also have attained great size (Tambussi et al., 2005), *Crossvallia unienwillia*, and numerous smaller, equally old species. I suggest that the acquisition of great size occurred only once, within the Palaeudyptidae (Triche, Chapter

3). The unique evolution of great size is supported by other recent phylogenetic work (Clarke et al., 2007), although these authors propose this acquisition in a paraphyletic group of penguins, after which giant size was lost. Interestingly, they also report giant penguin from very low-latitude localities, contradicting the presence of Bergman's Rule in penguins and the intuitive hypothesis that giant penguins should not inhabit tropical climates in times (Middle Eocene) of fairly warm global temperatures (Clarke et al., 2007). The authors' suggestion that a late Eocene period of increased oceanic productivity may be the driver of increased body size in Peruvian penguins should be investigated, but may have occurred much too late to have caused the evolution of early Middle Eocene penguins.

Authors often assume that the ecology of extinct penguins was similar to that of modern species. All of the sites from which fossils are known are deep-water marine deposits except the shallow marine Langebaanweg of South Africa, but all sites also lie near shore, suggesting that the birds died near their coastal rookeries. Examples include the Patagonia beds of Argentina and the La Meseta Formation of Seymour Island (Simpson, 1975a; Myrcha et al., 2002). The most common method of studying penguin ecology is to reconstruct their probable feeding behavior from their bill shape, although such work is obviously handicapped by the scarcity of fossil beaks (Zusi, 1975; Ksepka and Bertelli, in press). The two distinct bill morphologies of extant penguins are directly tied to their preferred prey. These are exemplified by the long, gracile, pointed beaks of *Aptenodytes*, and the short, vertically expanded, anteriorly squared rostra of *Spheniscus*. The former is used to spear fish, while the latter is used to catch krill and squid (Davis

and Darby, 1990). Both bill types are also seen in extinct species, among other morphotypes unknown in the modern fauna, and suggest the presence of similar feeding habits. None appear to be correlated with phylogeny, at least above the generic level (Triche, Chapter 3). Feeding mode may also correlate with the extent of adductor muscle development, which is indicated by the separation and size of the temporal fossae on the skull roof. Recent analysis suggests that these data indicate that Eocene and other ancient penguins possessed more powerful beak musculature than extant taxa (Ksepka et al., 2006).

## **Conclusions**

Extinct penguins were known for over 150 years and range through every Southern Hemisphere continent, from the Paleocene to the Recent. These remains are proliferate in places such as Seymour Island, and temporally wide ranging in others, particularly New Zealand. Compared with other extant birds, their excellent preservation potential and wide ranging distribution make penguins especially important for analyses of origination and extinction patterns, of broader evolutionary patterns within Aves, and of historical Gondwanan biogeography.

Particularly exciting recent work on penguins drastically expanded both their geographic and geologic ranges, and greatly increased their known taxonomic diversity and phylogenetic history. Although phylogenetic and accompanying hypotheses regarding extinct species are still in their infancy, much progress is made regarding crown-group phylogeny, biogeography, and divergence dating, and a promising start to reconstructing the phylogeny of extinct species exists. Remaining work includes detailed

descriptions of many newer discoveries such as the Paleocene species, additional undescribed specimens from Peru, and numerous fairly complete remains from New Zealand; further phylogenetic analysis of all extinct species; and taxonomic revisions of Sphenisciformes as a whole, an endeavor never attempted in a single publication. Additionally, much penguin evolution remains unexplained, such as their how and when they evolved from other birds; the scenario by which penguins evolved their derived morphology; and their broader biogeographic history, radiations and extinctions, and paleoecological events, including their potentially recurring gigantism. Finally, is it possible to determine if penguins originated in the Cretaceous, as a number of publications suggested (Triche, 2006; Baker et al., 2006; Slack et al., 2006)? Some of these questions, including those regarding systematic and cladistic biogeographic analyses, will be addressed shortly (Triche, Chapters 3, 4), but continued research and discovery of new specimens is required to answer others.

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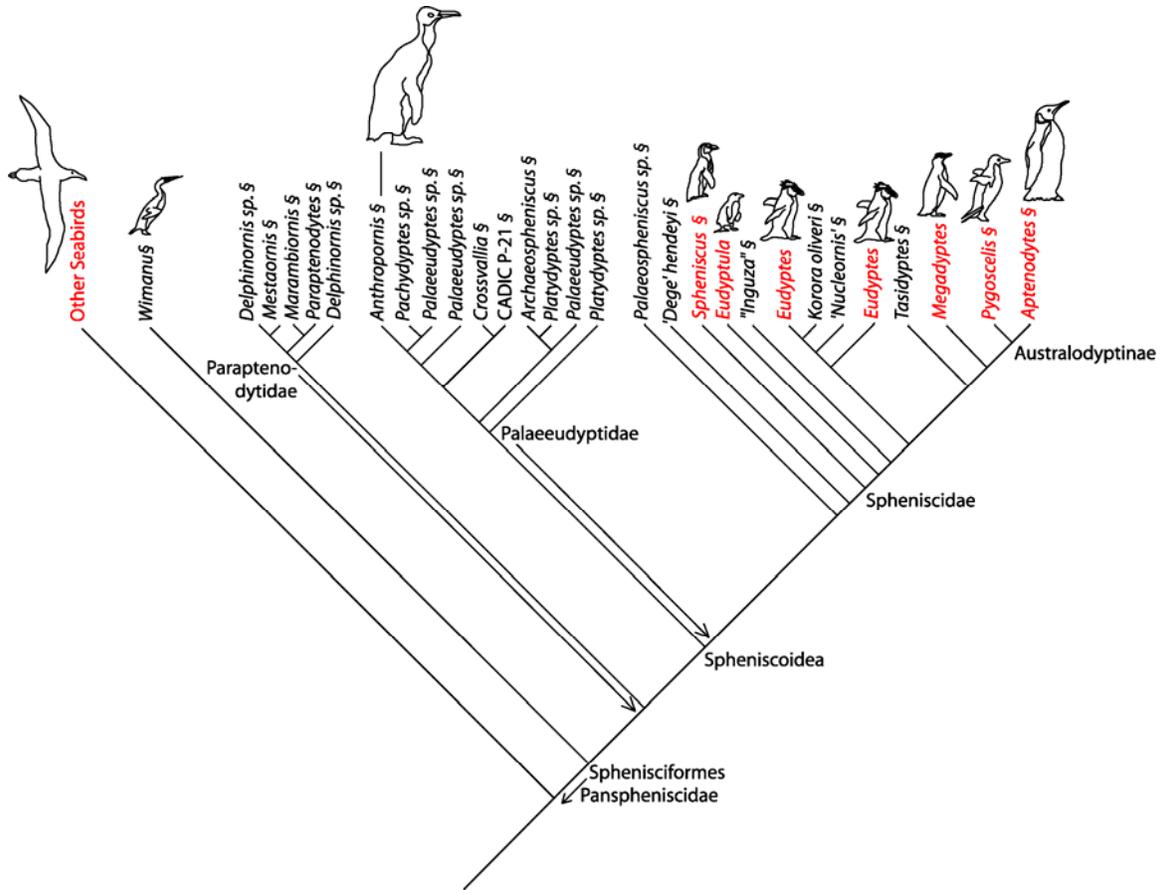
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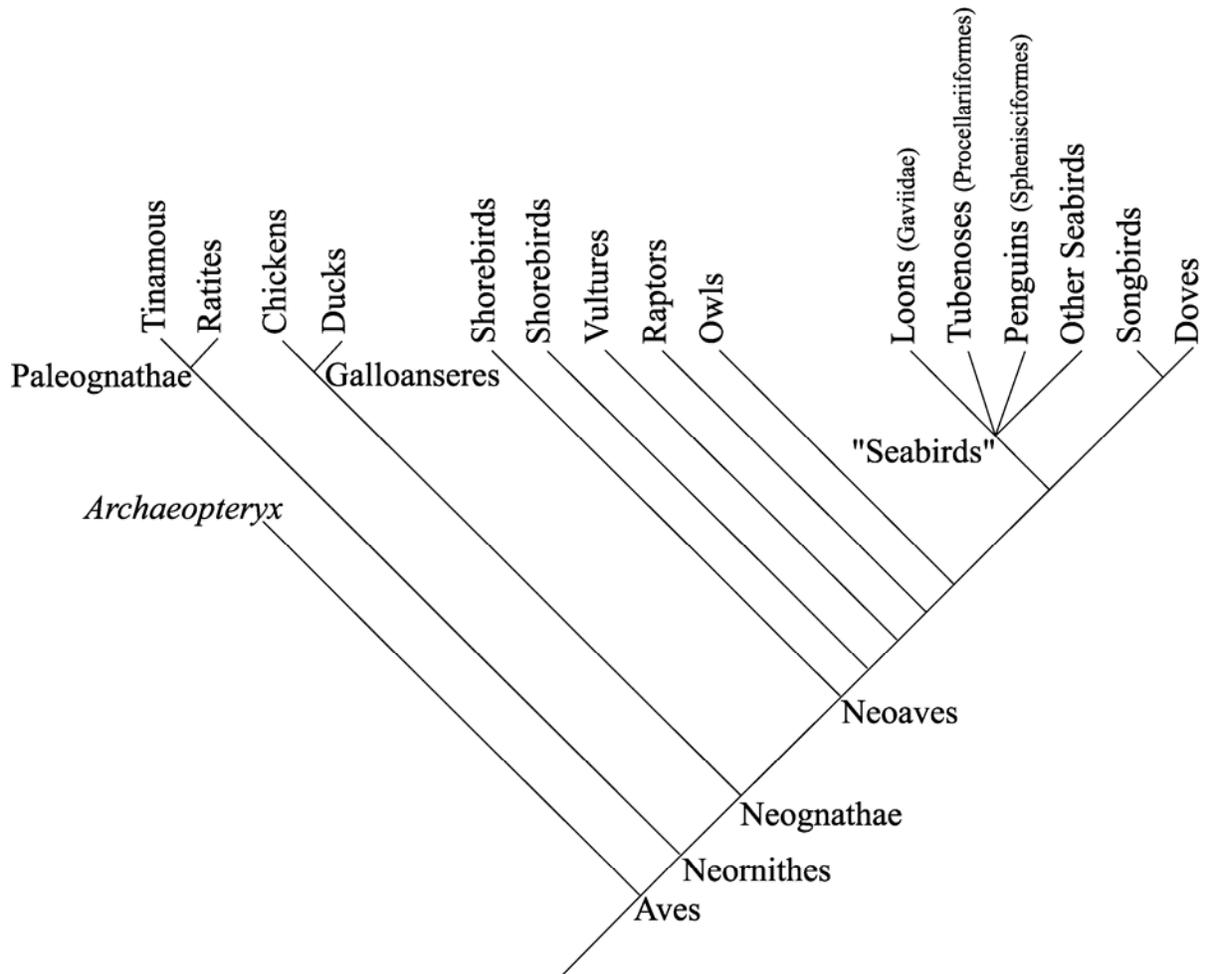
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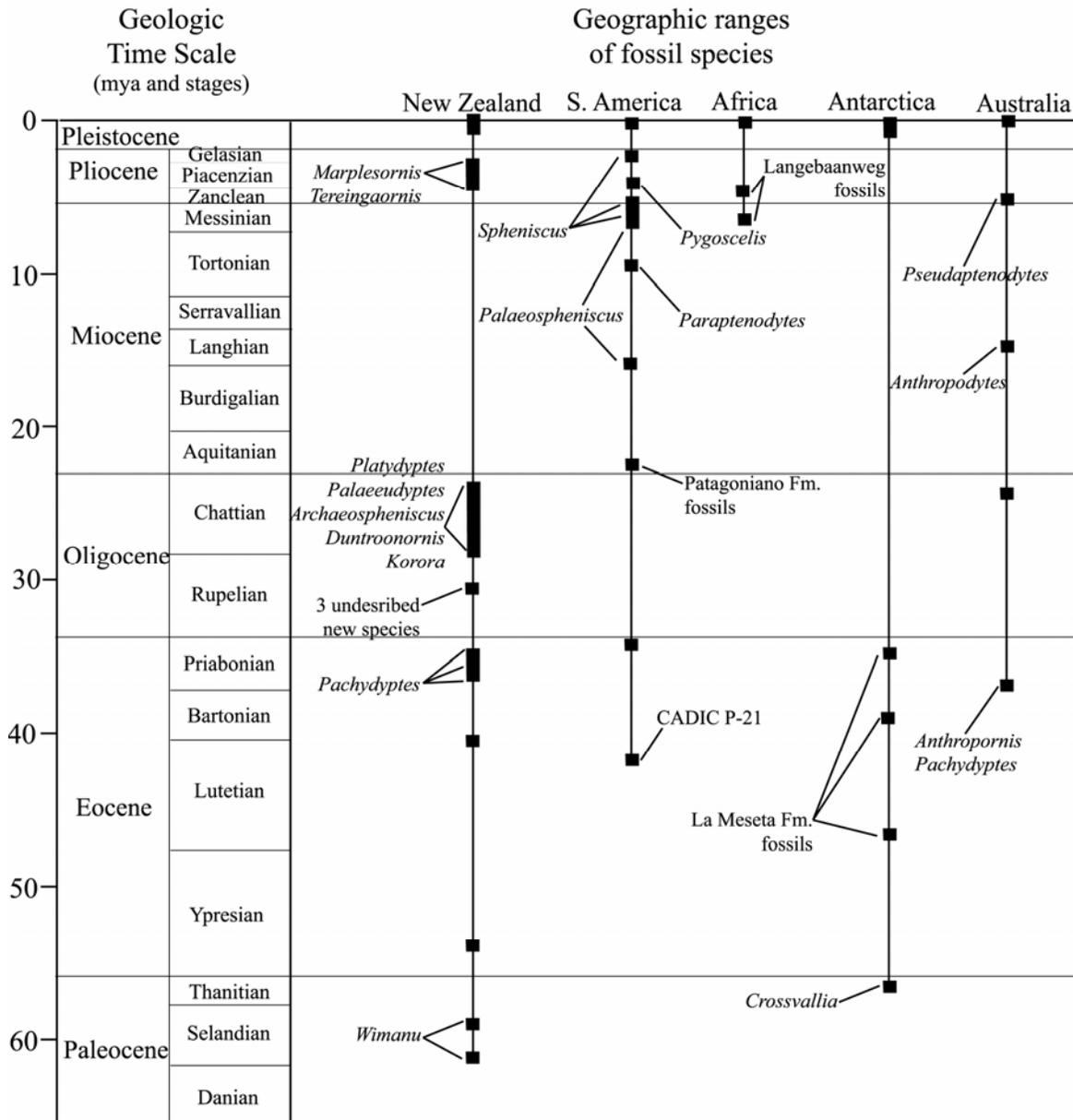
**Figure 1.1. Relationships of Major Clades of Extinct and Extant Penguins.** Simplified from a cladogram depicting the relationships of all penguin species (Triche, Chapter 3). Extinct taxa are indicated by §, extant taxa are in red. Arrows indicate stem-based names, all other names are node-based.



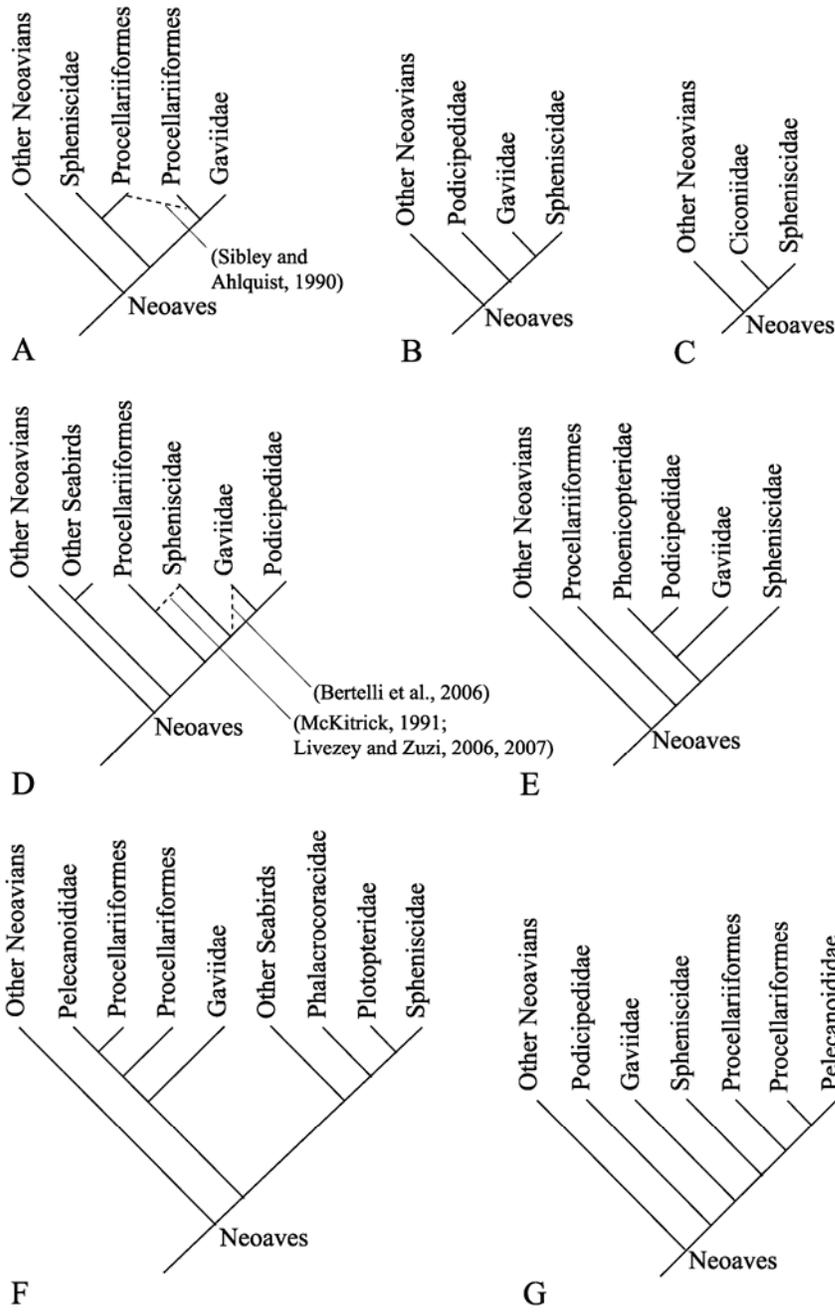
**Figure 1.2. Generalized Relationship of Sphenisciformes to Other, Selected Avians.**  
 After Mayr and Clarke, 2003.



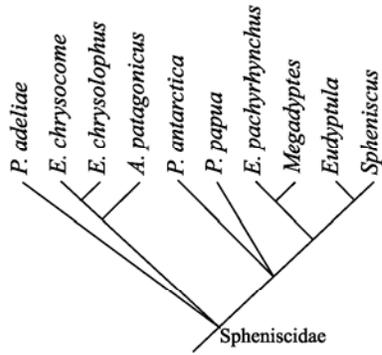
**Figure 1.3. Temporal Distribution of Extant and Extinct Penguin Species.** Blocks representing occurrences of penguin remains are plotted against the Cenozoic time scale (after Gradstein et al., 2004). Ages are determined in millions of years or to stage. Unlabelled blocks denote unnamed or unpublished occurrences and extant species. Inspired by Fordyce and Jones, 1990 (Figure 18.2).



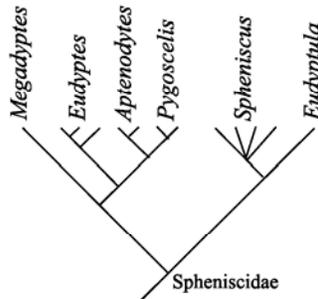
**Figure 1.4. Proposed Relationships between Spheniscidae and Other Neoavians.** A. Topology of Simpson, 1946; Sibley and Ahlquist, 1990; Cooper & Penny, 1997. B. Topology of Ho et al., 1976; Olson, 1985b. C. Topology of Slack et al., 2003. D. Topology of Cracraft, 1982, 1988; Sibley and Ahlquist, 1990; McKittrick, 1991; Mayr and Clarke, 2003; Bertelli et al., 2006; Livezey and Zusi, 2006, 2007. E. Topology of Mayr, 2004. F. Topology of Mayr, 2005a. G. Topology of Van Tuinen et al., 2001; Livezey and Zusi, 2001.



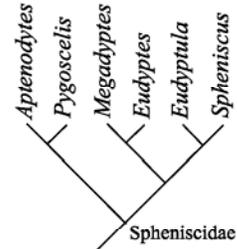
**Figure 1.5. Proposed Phylogenies of Extant Penguin Species.** See text for discussion of data used for each reconstruction.



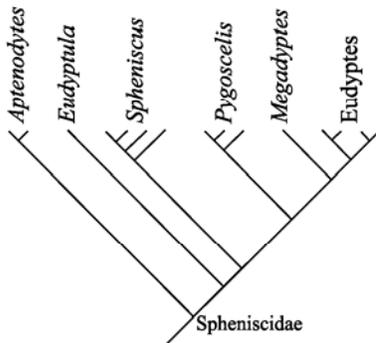
A Kennedy and Page 2002, Adams consensus tree



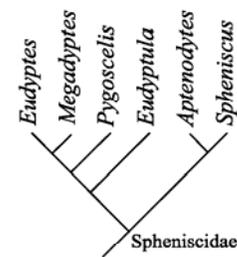
B O'Hara 1989



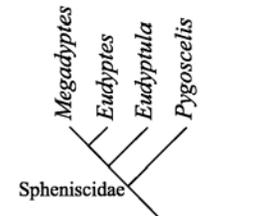
C Simpson 1946



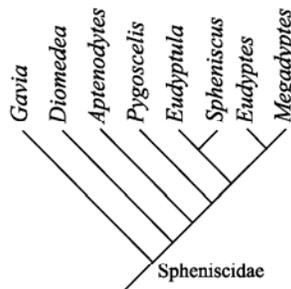
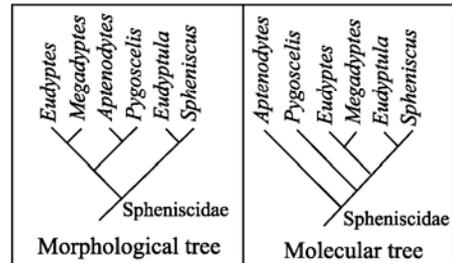
D Livezey 1989



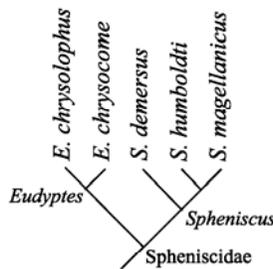
E Giannini and Bertelli 2004



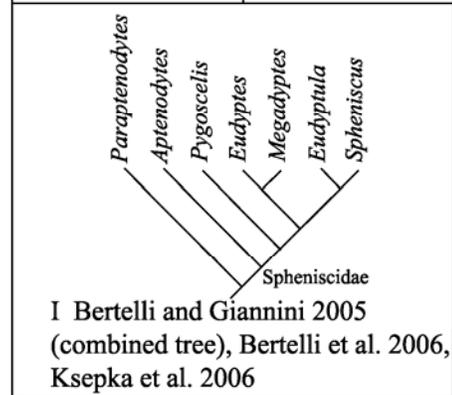
F Paterson et al. 1995



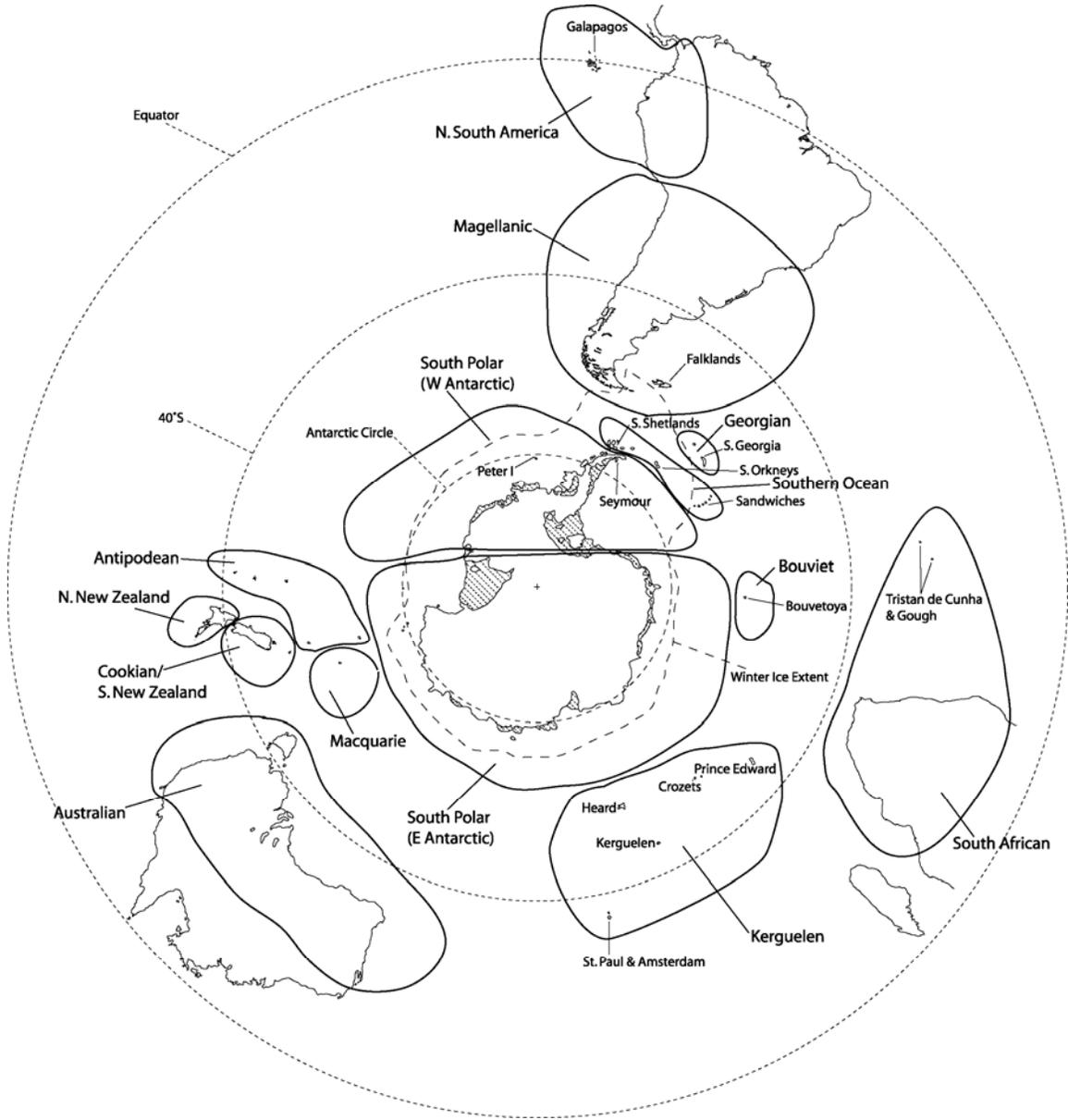
G Baker et al. 2006



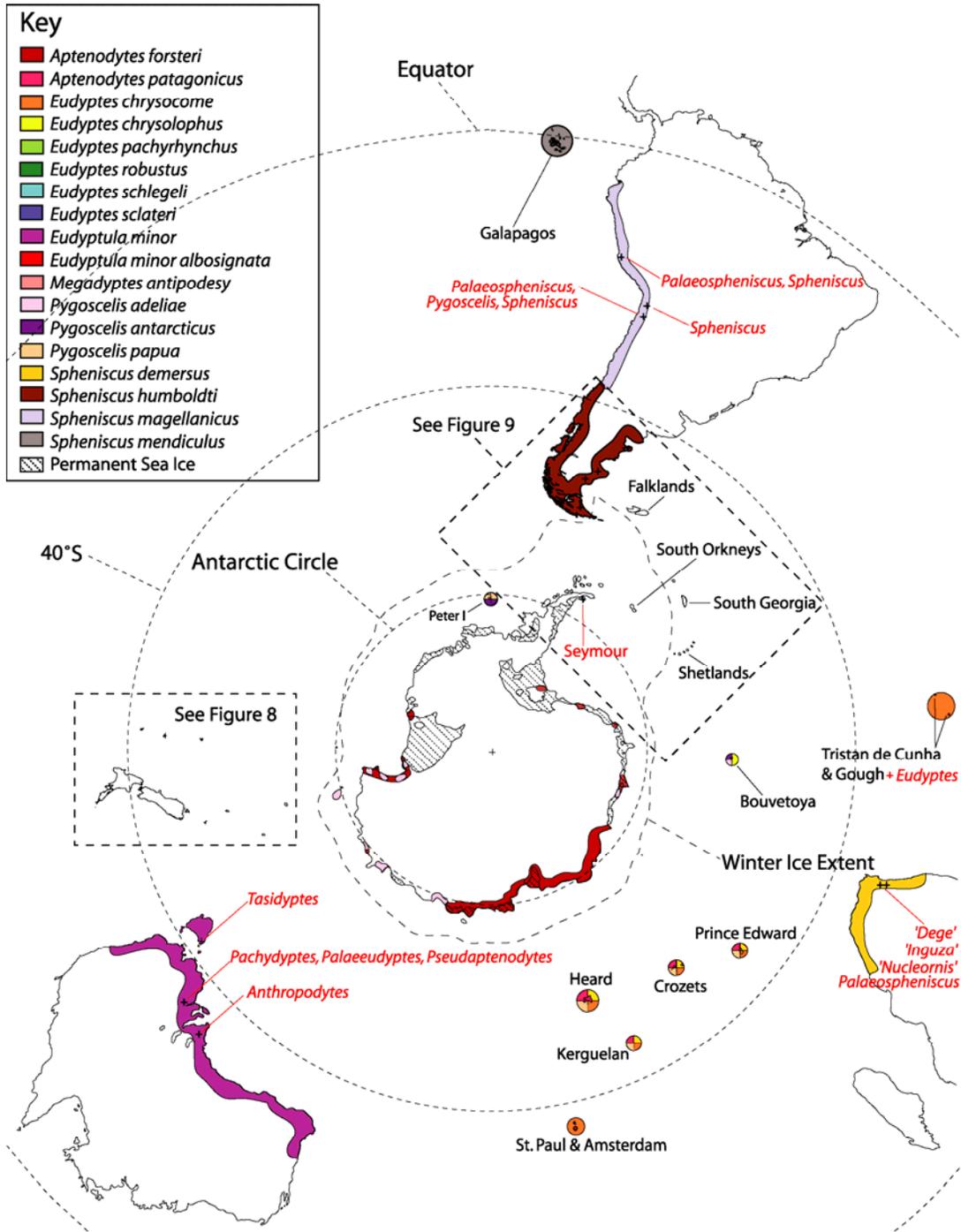
H Grant et al. 1994



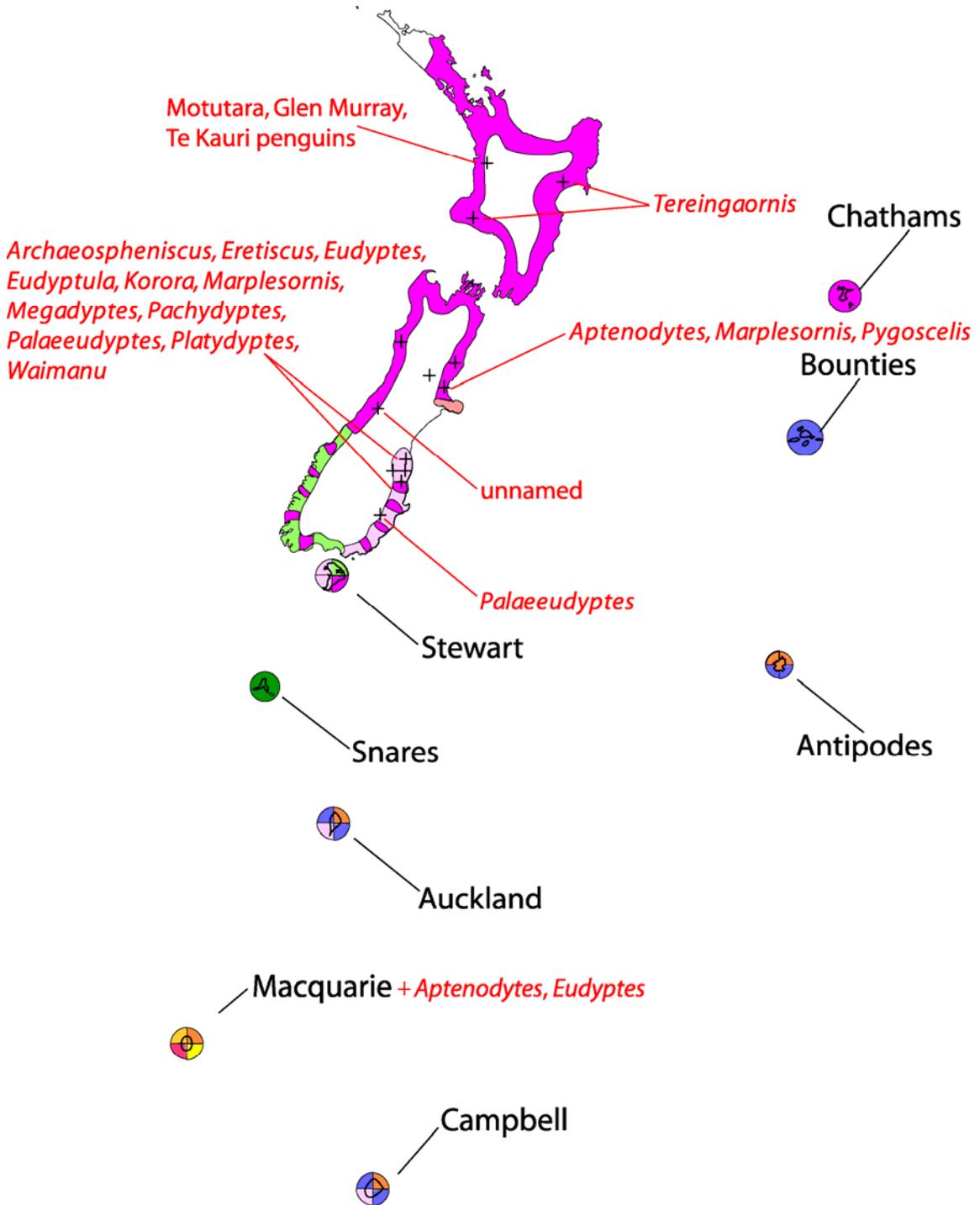
**Figure 1.6. Southern Hemisphere Biogeographic Provinces** (Zinsmeister, 1979; Kennett, 1980; Chown et al., 1988). Boundaries are approximate only.



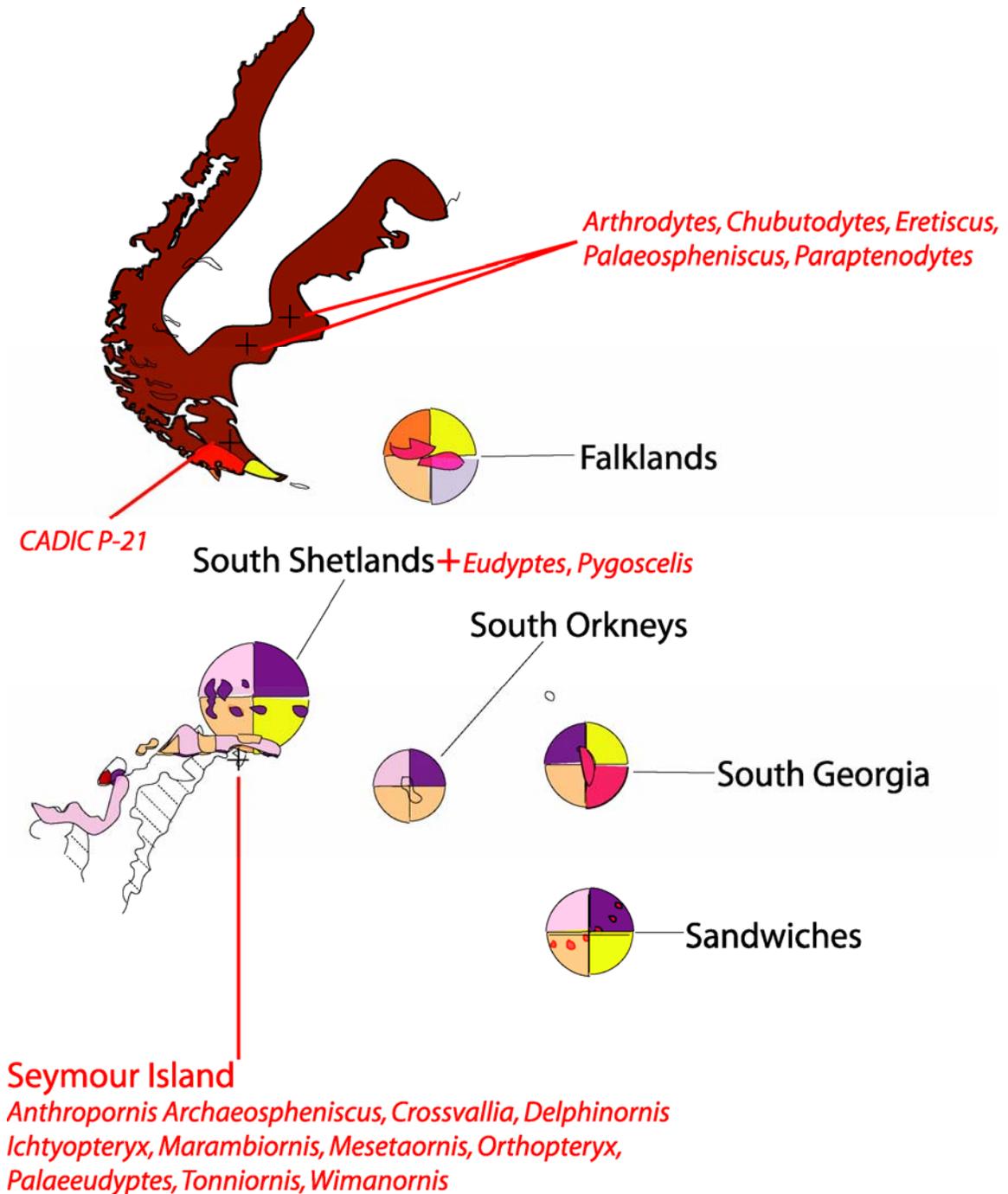
**Figure 1.7. Worldwide Geographic Distribution of Extant and Extinct Penguin Species.** Fossil localities are marked with a black X and a list of genera present in red text. Breeding ranges of extant species are circled in color (Wilson, 1983; Harrison, 1985). Overlapping distributions are indicated with pie diagrams (islands) and banded colors (continents).



**Figure 1.8. Geographic Distribution of Penguin Species in New Zealand.** Continued from inset in Figure 7. Key and symbols as in Figure 7.



**Figure 1.9. Geographic Distribution of Penguin Species in South America.** Continued from inset in Figure 7. Key and symbols as in Figure 7.



## **Chapter 2: Descriptive Skeletal Anatomy of Extinct and Extant Penguins (Aves: Sphenisciformes)**

### **Abstract**

Penguins belong to the group Aves (birds), as well as modern birds (Neornithes), but their relationships with other modern avians (birds) remain contentious. Recent phylogenetic analyses of penguins clarified the relationships between living species, but no hypothesis examines all extinct taxa, despite the presence of an excellent fossil record. Fossil remains extend to the late Early Paleocene, 61.6 mya, highlighting the importance of penguins to broader analyses of avian evolution. The penguin fossil record also includes 57 named taxa known from every Gondwanan continent. Although most of these remains are isolated long bones, notably humeri and tarsometatarsi, every skeletal element is at least represented in the total record. Penguin anatomy was described for nearly 200 years, including work on much of the fossil record and on much of the extant diversity, but no previous description examines all living and extinct species or examines osteology in the context of an explicit phylogenetic framework.

I here describe penguin skeletal anatomy using, for the first time, Computed Tomography (CT) scans of extant penguin skulls that allow 3-D, digital rendering of the internal anatomy of these birds (available online at [www.digimorph.org](http://www.digimorph.org)). I incorporate these scans with direct observation of every extant and most extinct species to result in a complete description of the osteology of Sphenisciformes. This anatomical description serves as the basis for a subsequent phylogenetic analysis of extinct and living penguins that will be published shortly.

Description of the penguin skeleton shows that phylogenetically informative variation is present in all skeletal elements, not just more commonly examined bones such as the humerus and tarsometatarsus. Implications for future penguin research include the recommendation that all known elements be included in diagnoses of extinct species, that the highly variable osteology be included in those of living species, and that the extensive intraspecific variation observed in living species also be considered in future systematic works. Additionally, I show that interspecific variation in penguins is much lower than that between genera, which are osteologically distinct, and that extinct taxa are much more variable than extant species.

### **Introduction**

Penguins are known worldwide as being among the oddest of all avians (birds). These semi-aquatic, wing-propelled divers are renowned for their unique adaptations to a

frigid, aquatic environment. Even considering their extreme difference from other birds, however, authors still often underestimate the surprising widespread distribution, adaptable nature, and variability of penguins. The anatomy of penguins is highly modified for swimming, and involves extreme arm bone flattening, loss of skeletal pneumaticity, and numerous thermoregulatory modifications (Marples, 1952; Williams, 1995). These variations result in a morphologically distinctive yet conservative group, which is probably why no one questioned penguin monophyly until recently. Penguins, or Sphenisciformes (sphenisciforms), were probably always restricted to the Southern Hemisphere as they are today, although only speculation exists as to the reason for that limitation (Cracraft, 1973). Extant penguins, or Spheniscidae (spheniscids) currently range north to the equator, at the Galapagos, and central Africa (e.g., *Spheniscus demersus*), and include four species that breed in the tropics. At the other extreme, one of the smallest extant penguins, *Pygoscelis adeliae*, lives and breeds solely on Antarctic ice sheets. The only other extant Antarctic species (*Aptenodytes forsteri*) is also the largest, a coexistence that remains unexplained (Stonehouse, 1969). The penguin fossil record is diverse and probably the longest of any known extant bird lineage (Vickers-Rich, 1976; Slack et al., 2006), extending back to at least 61.6 mya. It also included forms of diverse size (35 cm to over 1.5 m standing height) that endured great temperature ranges, as do some species today (e.g., the South African Jackass Penguin), on every Gondwanan continent excluding India (Fordyce and Jones, 1990).

Penguins were discovered in the late sixteenth century and studied in earnest since the early nineteenth century, with particular attention deservedly paid to their ecology

and impressive cold-adapted physiology (e.g., Stonehouse, 1975; Emslie and McDaniel, 2002; Meyer-Rochow and Gall, 2003; Peck et al., 2006). The skeletal anatomy of penguins, however, remains incompletely described. All detailed descriptions of their osteology date back to the nineteenth century, and few modern studies specifically addressed any aspect of penguin morphology. For example, the current best osteological description of a penguin is that of Pycraft (1898), while other thorough, early descriptions were provided by Reid (1835), Gervais and Alix (1877), Jullien (1882), Watson (1883), Filhol (1885), Menzbier (1887), Shufeldt (1901), and Waterston and Geddes (1909). These works are often outdated, and many approach anatomy in a non-Darwinian context, but remain extremely useful as starting points for anatomical exploration. Most also ignore or do not address in detail the interspecific or even intergeneric variation within penguins. A notable recent exception to that descriptive dearth is the work of von Stephan (1979, 1980), who described penguin osteology in German. Lastly, a forthcoming functional analysis of penguin morphology also addresses penguin osteology (Ando, pers. comm.).

A number of authors described either particular structures of the penguin skeleton (Pycraft, 1907; Duerden, 1922; Walker, 1867; Saiff, 1974, 1976) or discussed osteology in the context of myological, developmental, or functional analyses. Structural descriptions include the middle ear (Anisimov, 1976; Saiff, 1974), the mandible (Zusi, 1975), the wing (Stegman, 1970; Louw, 1992), the distinctive ankle complex (Marples, 1952; Simpson, 1946), portions of the cranial musculature (Prins, 1951), the appendicular musculature (Schreiveis, 1972), and the integument (Lowe, 1933). Studies of

development in penguins include the skull (Krasovskiiy, 1966), the chondrocranium (Crompton, 1953), and the wing and hindlimb (Anthony and Gain, 1912, 1913). Publications on penguin fossil remains also occasionally yielded osteological descriptions, although none of those includes more than a few species or a suite of fossils from one geographic region (Ameghino, 1895; Moreno and Mercerat, 1891; Lowe, 1933, 1939; Simpson, 1946, 1971a, 1971b, 1972; Marples, 1952, 1953; Myrcha et al., 2002; Clarke et al., 2003; Acosta Hospitaleche, 2004; Bertelli et al., 2006; Clarke et al., 2007). Finally, recent phylogenetic analyses of penguins utilized penguin osteology in their character coding, but without specifically describing that anatomy (O'Hara, 1989a, 1989b; Bertelli and Giannini, 2005; Bertelli et al., 2006; Ksepka and Bertelli, 2006). A few cladistic analyses of larger taxa also coded penguins, again with no description, but only as Spheniscidae or Sphenisciformes, excluding potential variation or plesiomorphic states within penguins (Cracraft, 1982; Livezey, 1989; Kennedy and Page, 2002; Mayr and Clarke, 2003; Mayr, 2005; Livezey and Zusi, 2006, 2007). A recent description of the skull of the extinct *Parapterodytes antarcticus* provides the most detailed osteological description thus far (Bertelli et al., 2006). Although that species is included in the following discussion, I do not describe the species in detail, and readers are referred to (Bertelli et al., 2006) for further information on that taxon.

Here, I present the first modern, comprehensive, description of penguin osteology, using computed tomography (CT) data from the skulls of five extant penguin species and four outgroups, as well as examination of osteological specimens of all extant and most extinct species. CT data were applied once before to a penguin, albeit using a whole head

(Osa et al., 1993), but are used for the first time here as a tool for describing osteology in penguins. In addition to traditional description, CT scans also allow for the discovery of previously undocumented, internal, skull anatomy. Future phylogenetic analyses of penguins will also require a thorough description of the osteology of all penguin species in an explicitly phylogenetic context, which is performed here for the first time.

## **Material and Methods**

### **Taxa Examined**

**Ingroup.** Current taxonomies still recognize anywhere from sixteen to eighteen extant species depending on whether the Royal (*Eudyptes chrysolophus schlegeli*) or Fairy penguins (*Eudyptula minor albosignata*) achieve full species status (Giannini and Bertelli, 2004; Davis and Renner, 2003; Williams, 1995). Debate also surrounds the various numbers of subspecies of penguins, for example within the *Eudyptula minor* complex (Kinsky and Falla, 1976). The diversity of extinct species is especially confusing and may include 44 to 60 species (Fordyce and Jones, 1990). These disparities owe more to a lack of detailed study than to actual disagreement, however, because much of the diversity of extinct species arises from taxonomic inflation of poorly studied specimens and most disagreement on species status results from an inability to study widely separated collections. Currently, relationships among extant species are well tested but those among extinct taxa are less well examined or remain ignored. Analyses of phylogenetic relationships among extant taxa include an unpublished, morphological analysis (O'Hara, 1989), one phylogeny of three extant species using molecular allozyme data (Grant et al., 1994), one behavioral phylogenetic analysis using data from four extant

species (Paterson et al., 1995), and one older morphometric study (Livezey, 1989). Additionally, a more recent, comprehensive analysis yielded a phylogenetic hypothesis based on breeding characters and the unique feather structure of penguins (Giannini and Bertelli, 2004), and a subsequent analysis combined morphological (integument and osteology) and molecular datasets (Bertelli and Giannini, 2005). More recent, systematic analyses that include fossil remains, however, either address only taxonomy, not phylogeny (Myrcha et al., 2002; Jadwiszczak, 2006), simply review previous work (Fordyce, 1991; Fordyce and Jones, 1990), or include only one extinct taxon (Slack et al., 2006; Bertelli et al., 2006; Walsh and Suarez, 2006). All of these strongly support the monophyly of penguins, although no study specifically tested the monophyly of any penguin genus or higher taxon. A few recent analyses also examined numerous extinct taxa as well as extant penguins (Triche, 2005, Chapter 3; Ksepka et al., 2006; Clarke et al., 2007; Ando, pers. comm.). Figure 2.1 shows the phylogenetic hypothesis used here to interpret the completed morphological description. My analysis recovered the oldest extinct penguin (*Wimanu*) as the most basal stem-penguin, two large, extinct clades of Seymour Island and New Zealand extinct taxa, a monophyletic crown-group (Spheniscidae), and a number of younger, extinct taxa that lie outside the crown group in a pectinate arrangement (Triche, Chapter 3). The term ‘penguin’ is used here in synonymy with Panspheniscidae, or the total-group of penguins, while Spheniscidae refers to the crown-group.

Appendix 2.2 lists the extant, extinct, and outgroup specimens examined for osteological information. I examined all eighteen extant penguin species, both accepted

and putative. Fossil specimens utilized include all currently diagnostic extinct species except *Icadyptes*, *Madrynornis*, *Perudyptes*, and *Tonniornis*, all of which were described after completion of this study. I include 51 named species from all known geographic and geologic distributions, including the north and south islands of New Zealand, South Africa, Argentina, Chile, Peru, and Seymour Island, which lies off the Antarctic Peninsula. I also examined numerous other specimens of named species, unnamed species, and species of dubious validity. Although nearly all extinct penguin species are fairly conservative in that their morphology is noticeably similar to extant species, I also included the one recently discovered penguin genus (*Wimanu*) that does show distinctly plesiomorphic morphology (Slack et al., 2006).

**Outgroups.** Comparison to appropriate penguin outgroups is problematic because penguins currently have four proposed sister-taxa within Neoaves, and are occasionally left out of avian phylogenetic analyses altogether (Mindell et al., 1997). All proposed penguin sister-taxa are shorebird clades. These include part or all of Procellariiformes or tubenoses (albatrosses and petrels; Simpson, 1946; Sibley and Ahlquist, 1990; Cooper & Penny, 1997), Procellariiformes then Gaviidae (loons; Van Tuinen et al., 2001; Livezey and Zusi, 2001, 2006, 2007), Gaviidae (Olson, 1985), Gaviidae plus Podicipedidae (grebes; Cracraft, 1988; Sibley and Ahlquist, 1990; Mayr and Clarke, 2003), Gaviidae then Podicipedidae (Ho et al., 1976), a paraphyletic Procellariiformes (McKittrick, 1991), or the extinct group Plotopteridae (Mayr, 2005). The disagreement may stem from morphological or molecular convergence because shorebirds invariably cluster together, but it is uncertain whether it reflects actual relationship (Livezey and Zusi, 2001, 2006,

2007). Because Aves contains so many species, analyses of the entire group vastly under-sample most taxa involved, using one species of penguin at most, and often excluding a number of shorebirds. Extinct taxa did not alleviate the problem because they are thought to be extremely similar to extant species morphologically and thus provide no link to other bird groups, whereas the only penguin specimen that supposedly shows more plesiomorphic morphology (*Wimanu*) remains incompletely described (Fordyce et al., 1986; Slack et al., 2006; Ando, pers. comm.). To accommodate the lack of outgroup resolution, I examined all extant, proposed outgroups in order to resolve apomorphic character states.

### **Nomenclature and Description**

Nomenclature for osteological description follows that of Baumel and Witmer (1993), with anatomical terms anglicized for convenience. Terminology specific to penguins, especially regarding bones such as the humerus and tarsometatarsus, follows that of Simpson (1946), Marples (1952), and Myrcha et al. (1990). Any terms not found explicitly in these sources are my own and are indicated as such at first use. The presence and location of completely fused skull elements that are thus indeterminate in adults are inferred from a penguin ontogenetic series (Crompton, 1953). Extant genera were assumed to be monophyletic, an assumption that most analyses uphold (Giannini and Bertelli, 2004; Walsh and Suarez, 2006; Bertelli et al., 2006; Ksepka et al., 2006), but that was only recently formally tested (Triche, Chapter 3). Accordingly, much of the description refers to generic taxa, implying the same morphology for all included species. All measurements were made with vernier calipers to the nearest millimeter.

The text describes the general osteological condition found in extant penguins. Observed inter- and intraspecific variation, derived character states, and variation seen in extinct species are all described subsequently. The large number of penguin species precludes describing in detail the condition found in every taxon, however. The order of description moves from the axial to appendicular skeleton and from front to back within these sections. It also follows the major regions of the skull, including the fenestrae, rostrum, orbital series, otic series, palate, braincase, and mandible. This description is intended as the basis for a complementary phylogenetic analysis of penguin species. Such a work is beyond the scope of this paper, but will be published shortly (Triche, Chapter 3).. The text incorporates published and unpublished character data throughout, noting parenthetically the provenance of each character.

### **CT Scanning Parameters and Image Processing**

My descriptions are based in part on high-resolution X-ray computed tomographic (HRCT) images of five penguin skulls. HRCT is a non-destructive technique used here to acquire digital serial sections, or slices, of a skull. This provides detailed information about cranial osteology and allows visualization of the internal structure of an object such as a skull without incurring physical damage. The technique is extremely useful in the case of rare or delicate specimens (e.g., Maisey, 2001), and can be used to digitally remove skulls from whole heads, single elements from braincases, or internal passages from bones. HRCT employs grayscale values to indicate differential attenuation of X-rays caused by density and elemental contrast of materials in the scanned object, for example, bone, muscle and skin (Rowe et al., 1997). Unlike standard X-radiographs,

HRCT data can resolve the three-dimensional relationships of materials in the scanned object by rendering a stack of a continuous series of slices through the specimen (Rowe et al., 1997). Such renderings can be made in any plane, so that all surfaces of an object are visible, while various structures such as skeletal elements can be digitally isolated (Ketcham and Carlson, 2001).

Each specimen was scanned at The University of Texas High-Resolution X-ray CT facility (UTCT) according to the procedure described here. Appendix 2.1 lists values for scanning parameters for each of the five scans. The original, coronal slices were digitally resliced in the horizontal and sagittal plane using a calculation of the interslice spacing in pixels, each of which represents a slice spacing of 0.087 mm. Slices in the coronal stack progress from the anterior end of the skull to the posterior, horizontal slices proceed from the dorsal surface to the ventral, and sagittal slices move from the right side to the left. The coronal slices were rendered in Vox-Blast™ to provide three-dimensional visualizations of the skull. Rotating and cut-away movies of both the original slices and the three-dimensional visualizations were then animated in QuickTime Pro.

## **Results: Description**

### **General Comments**

The penguin skull is typical of seabird taxa, being triangular and elongate in dorsal view, and robust compared with other avians (Fig. 2.2; Cracraft, 1982). It ranges from around 8-20 cm in length, although the skulls of some extinct species may have been twice that length (Jadwiszczak, 2001). The penguin skull is tall posteriorly, although it may be flattened dorsoventrally (as in *Eudyptula*, *Megadyptes*, and some *Eudyptes*).

The rostrum is generally long and gracile, with a laterally expanded tip, but is short and anteriorly triangular in *Eudyptes*, *Megadyptes*, and *Spheniscus* (Fig. 2.3). The anterior width of the skull as measured between the lacrimals is generally narrow, less than half the width between the postorbital processes, but is wider proportionately in *Spheniscus*, where it is at least half the posterior width. Images of the six CT scans are figured first (Figures 2.5-2.9), followed by those of the outgroups (Figure 2.10). The penguin skeleton lacks pneumaticity entirely. It is also generally short, squat, and streamlined. The appendicular girdles are greatly hypertrophied and solid, as is the postcranial skeleton in general. The limbs are shortened and the pectoral limb is greatly flattened, while the manus is reduced and immovably fused and the pes is greatly shortened in length.

### **Skull**

**Fenestrae.** *Orbit.* This opening is large in penguins, and lies anteroventral to the braincase and posterodorsal to the beak (Figure 2.2). Its dorsal border forms an enlarged ridge, which is completed in *Megadyptes*, *Pygoscelis*, and some *Eudyptes*. The frontal and parietal border the opening dorsally, as does the lacrimal anterolaterally, the mesethmoid and orbital septum medially, the ectethmoid anteromedially, the palatine and pterygoid ventrally, and the braincase posteriorly. The opening is nearly circular, but is slightly elongated posteroventrally. It contains no more than 13 scleral ossicles, which overlap with each other to form the scleral ring (Mayr, 2005).

*Antorbital Fenestra.* This medium-sized, triangular opening is anteriorly pointed in all penguins and elongated in *Aptenodytes*, some *Eudyptes*, and *Pygoscelis* (Figure 2.5b). It extends anterior to the nares, although it just reaches them in *Spheniscus*.

Dorsally, the nasal forms the border of the antorbital fenestra, while the lacrimal flanks the opening medially and rounds its margin posteriorly. Ventrally, the maxilla forms its border anterolaterally, the palatine does so medially, and the jugal does so posterolaterally.

*Naris.* The large, holorhinal nostrils open externally in all penguins (Figure 2.5a). It is only medium-sized in most *Spheniscus* and some *Eudyptes*. The naris extends throughout nearly the entire length of the rostrum and terminates posterior to the anterior margin of the antorbital fenestra in all species except *Spheniscus*. The naris is flat dorsally and expands laterally as it extends posteriorly. It is also holorhinal i.e., with a rounded posterior border ending anterior to the nasal process of the premaxilla (Garrod, 1873; Cracraft, 1982).

*Choana.* The internal naris lies in the posterior half of the skull and is open ventrally, separated medially from its pair by the vomer (Fig. 2.5c, g). The choana is bordered laterally by the palatine, anteriorly by the maxillopalatine process of the maxilla and posteriorly by the lacrimal. The choana is a small, oval, shallow opening that constitutes a “curved, smooth plate, slightly differentiated from [the] main palatine” (Bertelli and Giannini, 2005, pp. 227) in basal penguins and a “ridged [surface] separated from [the] palatine by [a] low keel” (Bertelli and Giannini, 2005, pp. 227) in more derived taxa (*Spheniscus*, *Eudyptula*, and some *Megadyptes*; Mayr, 2005).

*Foramen Magnum.* This opening is large, lying dorsal to the occipital condyle of the basioccipital, ventral to the supraoccipital, and medial to the exoccipitals (e.g., Figure 2.5f). The opening is broader than tall in the outgroups and most extinct

species, and equally as tall as is broad in most extant penguins. In *Aptenodytes patagonicus*, *Megadyptes*, and *Paraptenodytes antarcticus*, the opening is taller than it is broad, while *Eudyptes* shares the original condition (e.g., Figures 2.7f vs. 2.11). The exoccipitals indent the foramen slightly laterally, although this condition may be absent (*Eudyptes chrysolophus*) or enlarged (Gaviidae, Podicipedidae). The foramen opens the skull posteriorly at a slight ventral angle.

**Rostrum. Premaxilla.** Each premaxilla is prong-shaped, extending posteriorly from an anterior, fused, point both dorsal to and ventral to the external naris (e.g., Figure 2.5a). Its dorsal, longer section extends to the nasals posteriorly, inserting narrowly between them as the nasal process. The state is a short process in some *Eudyptes* and a short, wide one in *Spheniscus*. The process is free from the nasals, although it may be fused with them proximally in some *Spheniscus* and some *Eudyptes*, and fused proximally as well as along its entire length in remaining *Spheniscus* and all *Eudyptula*. The ventral, shorter section of the premaxilla extends to the maxilla posteriorly, ventral to the nasal. The bone is sutured with its pair in penguins, but fused in *Eudyptes chrysolophus*, *Pygoscelis*, and *Spheniscus*. The premaxilla is usually long and slender, with a downwardly deflected tip (except in *Eudyptula robustus*), and a marked groove running distally from the nostril nearly to the end of the bone (except in *Pygoscelis*). The tomial ridge in birds is the cutting edge of the rhamphotheca, or the horny covering of the beak. The ridge and its bony correlate are present in all penguins and lie at the same level as the basitemporal plate, except in Australodyptinae (*Aptenodytes* and *Pygoscelis*), where they lie dorsal to the plate.

*Maxilla.* This bone lies ventral to the nasal, posterior to the premaxilla, dorsal to the palatine, and anterior to the jugal. It flanks the choana laterally and the antorbital fenestra medially, and floors the posterior section of the nasal passage posteriorly (e.g., Figure 2.5a). The bone and its maxillopalatine process are much reduced in all penguins. The horizontal maxilla is diagonally tilted, with its lateral edge lying ventral to its medial one. Laterally, it forms the anteriormost portion of the jugal arch, where it surrounds the jugal bone. The bone fuses dorsolaterally with the nasal and ventromedially with the palatine in two diagonal scarf joints that sandwich the maxilla horizontally in between. The anterior edge of the bone is completely fused in the premaxillary contact. In ventral view, the long, slender, posteriorly-rounded, maxillopalatine process extends posteriorly from the posterior margin of the maxilla, anterior to the choana. It usually forms the majority of the maxilla and contacts only the palatine ventrally, except in *Spheniscus humboldti* and *Spheniscus demersus*. The paired processes are separate in ventral view, both from each other and from the rest of the bone, with the vomer inserted freely between them.

*Nasal.* The nasals fuse posterior on the midline to form a posterior plate (e.g., Figure 2.5b). Each bone extends anteriorly from this plate as a prong that comprises both the dorsal and the ventral margins of the posterior section of the naris (e.g., Figure 2.5a). The dorsal process of the nasal is shorter and thinner, and flanks each premaxilla laterally, while its ventral process, which is much longer and somewhat thicker, extends ventrally to overlies the lower premaxilla halfway through the length of the naris. The body of the nasal forms a diamond shape, the posterior section of which is the frontal

process. That process is triangular, posteriorly pointed, and elongated in *Aptenodytes*, *Eudyptes*, and some *Spheniscus*. It inserts medially into the frontal, to which it is fused in all species except *Aptenodytes forsteri* and *Eudyptes chrysolophus*, in both of which this character state is lost. The nasal is thin and angles ventrally at about 45° as it progresses anteriorly. Its dorsal process flattens upon reaching the nasal process of the premaxilla, while its ventral process continues to descend at the same angle. At the naso-frontal contact, the two bones meet to form a transverse indentation of varying depth and width. In Sphenisciformes, the depression forms a strong hinge between the skull and rostrum. This hinge is enlarged in *Aptenodytes* and *Eudyptula* and lost in some *Eudyptes*.

*Lacrima*. Each lacrimal lies ventral to the nasal, posterior to the antorbital fenestra, dorsal to the maxilla and jugal, and lateral to the frontal (e.g., Figure 2.5a, c). Each bone lies lateral and ventral to the nasal, although *Spheniscus* and some *Eudyptes* have no lateral extension. The bone is covered by the frontal in dorsal view in penguins, but is visible dorsally in *Spheniscus* and extensively visible in *Eudyptes chrysolophus* and *Eudyptes schlegeli*. The lacrimal forms a vertical bar and a dorsal, anteriorly depressed, plate that follows the sloping nasal. The ventral edge also slopes, but dorsally as it curves along the jugal bar. Both the posterior and anterior surfaces of the vertical bar are concave owing to extended dorsal and ventral edges and to the curved posterior wall of the antorbital fenestra, respectively. Both the dorsal and ventral surfaces are expanded in width and length. The orbital process is reduced nearly to nonexistence, while a unique anteroventral process contains the lacrimal foramen. This square process extends ventromedially from the anterodorsal corner of the bone. The short lacrimal-jugal contact

forms a flattened ‘boot’ ventrally (Lowe, 1933). The lacrimal foramen is generally large, although small in *Aptenodytes* and *Megadyptes*. It lies posterior to the choana and anterior to the body of the bone and is thus visible laterally.

*Ectethmoid.* The ectethmoids lie widely separated from the lacrimal, posterior to the antorbital fenestra (e.g., Figure 2.5a). Each is a flat, transverse plate, oriented slightly anteriorly on its lateral edge. Its dorsal edge is entirely fused to the frontal, and its medial edge with the interorbital septum, but the bone is free ventrally and laterally. This ventrolateral section is greatly emarginated in penguins, but unemarginated in *Aptenodytes* and *Eudyptula*.

*Mesethmoid.* This single, midline bone fuses laterally with the ectethmoid, anteriorly with the nasal, dorsally with the frontal and the parietal, posteriorly with the laterosphenoid, and ventrally with the palate and the parasphenoid rostrum (e.g., Figure 2.5a). It is restricted to and forms the entire orbital septum, which is fully ossified, although it is larger in *Pygoscelis* and *Spheniscus*. The bone is thin and excavated to greater or lesser extent by the orbitocranial foramen, which is enlarged in *Aptenodytes*. Although such foramina are not seen in *Paraptenodytes antarcticus* (Bertelli et al., 2006), this absence may arise from the incomplete preservation of the bone.

**Orbital Series.** *Frontal.* The paired frontals fuse on the midline in all adult penguins. Each element also sutures with the nasal anteriorly and fuses with the parietal posteriorly, the mesethmoid and laterosphenoid anteroventrally, and the braincase posteroventrally (e.g., Figure 2.5b). The bone is approximately rectangular, narrowed anteriorly as the interorbital section, and extended anterior to this as paired nasal

processes. The thin, elongate nasal process extends anterolaterally and somewhat ventrally lateral to the frontal process of the nasal, to just contact the lacrimal. The interorbital portion is wide in penguins, but extremely narrowed in the clade (*Eudyptes* + *Megadyptes* + *Pygoscelis* + *Aptenodytes*) and in *Aptenodytes*. The posterior section of the bone is nearly flat and usually extends laterally as the postfrontal process. It does not extend in *Eudyptula*, *Spheniscus*, some *Eudyptes*, and *Paraptenodytes antarcticus*, but simply curves gently into the parietal. This process extends ventrally from the posterolateral edge of the bone. It is generally thick and perfectly vertical, but thin in *Eudyptula*, some *Spheniscus*, *Eudyptes chrysocome*, and *Paraptenodytes antarcticus*, and angled posteriorly in *Spheniscus* and *Pygoscelis*. Laterally, the frontal contains the large, supraorbital salt gland fossa, which curves diagonally along the orbital border. The fossa is a wide, sloping, bumpy indentation that holds the enlarged salt gland in life (Giannini and Bertelli, 2004). A wide shelf lies along the rim of the fossa in both the clade (*Eudyptes* + *Megadyptes* + *Pygoscelis* + *Aptenodytes*) and in *Spheniscus*.

*Parietal.* The penguin parietals fuse on the midline to form one element in adults, and each is also completely fused with the frontal anteriorly and the supraoccipital posteriorly. The frontoparietal contact is thus not distinguishable in adult penguins (e.g., Figure 2.5b). Its shape is a transverse rectangle that lies posterior to the postfrontal process. It terminates posteriorly at the exoccipital wings, and contains no parietal fontanel.

*Jugal.* Each jugal extends from the maxilla to the quadrate and borders the orbit ventrally (e.g., Figure 2.5a). Anterodorsally, the lacrimal overlies the jugal, which

inserts deeply into the quadrate condyle posteriorly and into the maxilla anteriorly. The bone is extremely thin and nearly circular in cross-section. The jugal is straight in penguin outgroups and in *Wimanu*, ventrally curved in its midlength in remaining penguins, and contains strong, ventral bowing in the clade (*Eudyptes* + *Megadyptes* + *Pygoscelis* + *Aptenodytes*). Finally, the bar has a sigmoid shape in *Pygoscelis*.

*Quadratojugal*. This ossification forms the posterior section of each jugal bar and is completely fused anteriorly with the jugal in the adult (e.g., Figure 2.5a). The point of fusion can be seen in *Aptenodytes* as a slight lateral depression. The bone is strongly curved in most species.

**Otic Series.** *Quadrate*. The quadrate in penguins is broad and stout as compared with that of other birds (Walker, 1867; e.g., Figure 2.5a). It forms orbital and otic processes, and lies laterally within the skull. Each quadrate contacts the quadratojugal posterolaterally, the squamosal dorsally, the pterygoid ventromedially, and the mandible posteroventrally. The deep, quadratojugal cup surrounds the quadratojugal, although somewhat more shallowly in *Paraptenodytes antarcticus* and *Pygoscelis*. The quadrate neck, dorsal to the main body of the bone, is long and slender in penguins, as compared with all outgroups. The quadrate head is shallowly grooved, dividing it into two capitula. The groove is weaker in *Paraptenodytes antarcticus* (Bertelli et al., 2006). The otic process extends dorsally from the neck to insert into the otic recess dorsally. It contains a secondary, anterolateral process for attachment of the *m. adductor mandibulae externus, pars profunda*, a small process that forms a tubercle in all penguins except *Wimanu*, and a distinct ridge in *Eudyptula* and Australodyptinae. The mandibular process of the

quadrate rests in the articular surface of the mandible. This process consists of the lateral, medial, pterygoid, and caudal condyles, the last of which is lost in *Pygoscelis* and some *Eudyptes*. The mandibular articulation generally lies directly ventral to the otic recess, but lies anteriorly in *Aptenodytes*, *Eudyptula*, and *Eudyptes schlegeli*, owing to an anteroventral angling of the quadrate. It is possible that this variable angle arises owing to differential drying of a kinetic skull, but the articulation does appear solid. In most species, the lateral condyle lies in the same transverse plane as the medial condyle, while in *Aptenodytes* and some *Eudyptes* it lies anterior to the medial one. The pterygoid condyle extends anterolaterally from the anterior edge of the mandibular process to contact the pterygoid in a posteriorly concave articulation. It is generally only slightly extended from the body, but greatly extended as a tubercle in *Aptenodytes* and reduced to confluence with the mandibular process in *Eudyptula*.

The orbital process of the quadrate extends anteromedially from the anterior surface of the quadrate neck, from which it is distinctly separated by a sharp ridge (Figure 2.5e). The process is anteriorly triangular, long, and short vertically, and may be greatly extended (in *Paraptenodytes antarcticus* and *Pygoscelis*), or heightened (in *Aptenodytes* and *Megadyptes*). The dorsal edge of the orbital process is sharp and dorsally concave, and extends dorsally at about a 45° angle. The distal end of the process is generally expanded into a vertical hook, although it is merely pointed in *Spheniscus humboldti*, *Spheniscus magellanicus*, and *Paraptenodytes antarcticus*, and truncated in *Pygoscelis* and some *Eudyptes*. The lateral surface of the process, as well as that of the bone, is

usually sharply excavated, as is the medial surface of the process (except in *Pygoscelis* and *Spheniscus*).

*Squamosal.* The squamosal lies on the posterolateral surface of the braincase, contacts the quadrates ventrally, forms the nuchal crests and temporal fossa, and contains the otic recess (e.g., Figures 2.5a, e). Each also contacts the supraoccipital posteriorly, the laterosphenoid anteriorly, the parietal dorsally, and the prootic medially. The thin, deep, nuchal crest extends from the dorsal surface of the skull posteroventrally to the paroccipital process. The crest is excavated posteriorly, separating it from the cerebellar dome of the supraoccipital. The temporal fossa, which excavates the skull anterior to the nuchal crest, is expanded in all penguins, but is extensively excavated dorsally in *Spheniscus* and in the stem-penguin *Wimanu*, nearly reaching the midline in dorsal view. Laterally, the fossa forms a shallow, horizontal platform (Cracraft, 1982), which is deepened in all extant species and reduced in Australodyptinae. In the extinct taxon *Paraptenodytes antarcticus*, the fossa is deepened and wide antero-posteriorly; it is much narrower in extant species. Posteriorly, the horizontal platform contains the lateral foramen for the *rami occipitalis arteriae ophthalmicae externae*. The foramen is reduced or vestigial in most species, but is an enlarged opening in Australodyptinae. The otic recess underlies the horizontal platform, just medial to the quadrate articulation, and is also greatly enlarged (Mayr, 2005). The recess is distinctly visible laterally, anterior to the quadrate, in *Aptenodytes forsteri*, whereas it lies barely anterior to the articular facet of the quadrate in all other species except some *Spheniscus*. A greatly enlarged lateral tympanic wall borders the recess anteriorly, separating it from the laterosphenoid bone.

Anterior to the temporal fossa, the reduced temporal crest is small and barely discernable, although it is more distinct in older species such as *Paraptenodytes antarcticus*. It extends anterolaterally from the nuchal crest into the postorbital process.

The quadrate contact lies within the otic recess, where the squamosal envelops the otic process of the quadrate dorsally and dorsolaterally (Figure 2.5a, e). The quadrate thus projects dorsally into the horizontal floor of the temporal fossa, which curves slightly ventrally to enclose the quadrate laterally. The otic process of the quadrate is completely hidden in lateral view by this extension. The supraoccipital completely fuses with the quadrate posteriorly. The nuchal crest lies dorsolateral to and curves gently into the cerebellar dome of the supraoccipital in a ventromedially concave curve. This quadrate-supraoccipital contact continues anterodorsally via the parietal, which is also completely fused with the squamosal. Anteriorly, the laterosphenoid also fuses with the squamosal, as it curves posterolaterally into the temporal fossa, just ventral to the postorbital process. Posterior to the otic recess, the medial wall of the squamosal flanks the lateral wall of the prootic, deep to the lateral wall of the braincase. This contact is invisible externally and only viewable with CT data (e.g., Figure 2.11).

*Columella.* Each columella extends horizontally through the otic recess from a medial footplate, which rests in the fenestra ovalis of the prootic. The columella is small, but extends just to or slightly beyond the lateral edge of the otic recess.

**Palate.** *Vomer.* The vomers lies anterior to the palatine, medial to the maxillopalatine, and ventral to the nasal passage, although it contacts only the palatine (Figure 2.5g). Each lies directly ventral to the nasal, in the anterior portion of the skull. It

is laterally compressed into a thin, vertical plate, which inserts slightly posteriorly into the body of the palatine and sutures with its pair along the midline of the skull. The majority of the bone is free from all contact, however, because only the posteriormost section inserts into the palatine. The vomer is short vertically and forms the medial dividing wall of the choanae.

*Palatine.* The palatines lie midway through the length of the skull, extending from the pterygoids posteriorly to the premaxillae anteriorly (e.g., Figures 2.5g). Each flattened bone is composed of a narrow, anterior, maxillary process and a wide, posterior plate. The maxillary process is tubular and horizontal, while the posterior plate is flat posteriorly but dorsally humped anteriorly. The anterior portion of the palatine plate is horizontal in most species, but its anterior edge angles dorsally in *Eudypetes*. The maxillary process extends far anteriorly and is widely separated from its pair. The posterior plate is rectangular in ventral view, with a posterior extension that lies only along the midline of the skull. The anterolateral edge of the maxillary process of the palatine fuses with the maxilla anteriorly, and sutures with the posterior end of the maxillopalatine process of the maxilla posteriorly. The palatine sutures medially with the vomer, which lies medial to and extends ventral to the anterior portion of the palatine plate. Posterior to this, the palatine sutures to its pair, then barely inserts into the pterygoid articulation posteromedially. The bone also underlies the interorbital septum and the parasphenoid rostrum perpendicularly. The palatine surrounds the ventral choana, which lies medial to the palatine, posterior to the maxillopalatine process and anterior to

the palatine plate. As described for the maxilla, the palatine surrounds the choana posteriorly to form a curved, smooth plate or a ridged border in various penguin species.

*Pterygoid.* The pterygoids lie posterior to the palatine and anterior to the quadrate, contacting the parasphenoid rostrum anteromedially (e.g., Figures 2.8e). Each comprises a thin, flat, horizontal plate that angles upwards anteriorly. The bone is nearly horizontal, although it is upturned anteriorly in *Eudyptes*. The bone is shorter and more triangular in penguins than in any outgroup. It is more sharply triangular in *Eudyptes* than in other genera, in which the pterygoid has rounded corners. The corners of the triangular bone lie medially, anterolaterally, and posterolaterally, this last being most extended, as a vertical rod that contacts the quadrate posterolaterally. The pterygoid is also more anteriorly elongated than triangular, however, in *Paraptenodytes antarcticus*. Dorsally, the element bears a crest along its midline that extends posterolaterally along the length of the rod, although this structure is lost in *Eudyptes* and apomorphically condensed into a distinct tubercle in *Paraptenodytes antarcticus* (Bertelli et al., 2006). The pterygoid in *Paraptenodytes antarcticus* also bears an enlarged, ventromedial flange, which is autapomorphic for the species. The pterygoid articulates with the palatine on its medial corner, where the latter inserts into a shallow, medially hooked, pterygoid cup. Except for this, the entire anterior margin of the bone is free. The pterygoid also forms a posterolateral process that bears a dorsally concave articular surface for articulation with the quadrate.

**Braincase.** The braincase lies posterior to the orbit, to which it is approximately equal in size (e.g., Figure 2.5a). It consists of the basioccipital, basisphenoid, fused

parasphenoid rostrum, laterosphenoid, supraoccipital, exoccipital, and prootic. The braincase is known completely only from extant species and the extinct species *Paraptenodytes antarcticus* (Simpson, 1946), *Marplesornis novaezealandiae* (Simpson, 1972), *Spheniscus megaramphus* (Stucchi et al., 2003), *Spheniscus urbinai* (Stucchi, 2002), and a number of unfigured and undescribed Chilean and Argentinian species (Acosta Hospitaleche and Canto, 2005; Walsh, pers. comm.).

*Basioccipital.* This single, midline bone lies ventrally within the braincase, posterior to the palate and interorbital septum, medial to the squamosal, and ventral to the exoccipital (e.g., Figures 2.5b). It forms the flat, horizontal, basitemporal plate in ventral view, which lies dorsal to the level of the occipital condyle. Ventrally, it forms a large, flat basitemporal plate that fuses anteriorly with the basisphenoid and its parasphenoid rostrum. This basitemporal plate is hexagonal in most species, and anteriorly triangular in some *Spheniscus* and in Procellariiformes. In ventral view, the plate is centrally depressed, owing to paired anterolateral bony walls and the ventrally deflected occipital condyle. These bony ridges lie on the anterior edges of the plate and meet anteriorly. The bone contains the robust, paired, basal tubercles posterolaterally, which project directly ventrally from the plate just anterolateral to the occipital condyle. The condyle, which forms ventrally of the basioccipital and laterally of the exoccipitals, forms the posterior nadir of the basitemporal plate and is excavated anteriorly by the subcondylar fossa. This fossa deeply excavates the ventral surface of the plate. It is deepened in *Aptenodytes* and in *Paraptenodytes antarcticus* (Bertelli et al., 2006).

Anteriorly, the basioccipital overlies the pterygoid slightly along the lateral margins of the parasphenoid rostrum (Figures 2.5b). The bone is also fused with the exoccipitals posterodorsally, with the laterosphenoids anterodorsally, and with the prootics mediodorsally. These contacts are all completely fused and invisible in the adult. Anteriorly, the eustachian tubes of the middle ear exit the skull through the basioccipital (e.g., Figure 2.5e). They are mostly bony in penguins, forming a distinctly visible bony tube that opens just lateral to the base of the parasphenoid rostrum. Within penguin, this tube extends to the anterior end of the basiptyergoid plate, but terminates at its posterior end in *Aptenodytes* and *Eudyptula*. Internally, the eustachian tubes extend transversely posteriorly before opening into the middle ear.

*Basisphenoid.* The single, median basisphenoid floors the anterior portion of the braincase (Figure 2.5b). It is completely fused posteriorly and indistinguishable from the basioccipital in the adult penguin. The basisphenoid also fuses with the parasphenoid anteriorly.

*Parasphenoid.* The midline parasphenoid rostrum extends far anteriorly from the ventral section of the braincase (Figure 2.5b). It is narrow laterally, short vertically, and fused with the interorbital septum anteriorly and dorsally and with the basisphenoid posteriorly. In *Pygoscelis* and *Spheniscus*, the rostrum is a weak, ventral, longitudinal groove.

*Laterosphenoid.* The laterosphenoids form the anterolateral wall of the braincase, posterior to and on either side of the interorbital septum (Figure 2.5a). Each forms an anteriorly convex, posteriorly curved, diagonal plate whose dorsal edge is

inclined anteriorly. Each fuses with the frontals dorsally, the mesethmoid anteriorly, the prootics posterolaterally, and the basioccipital ventrally. The orbitocranial fonticuli perforate the bone anteriorly, connecting the orbit with the cranial cavity. They are variable both inter- and intraspecifically. For example, in *Aptenodytes*, one large fonticule lies at the posterodorsal corner of the orbit, and one to three smaller ones lie anterodorsal to that. The same configuration is found in *Eudyptes*, *Eudyptula*, and *Megadyptes*, but all fonticuli are relatively smaller and the smaller grouping may be absent in *Eudyptes*. The frontal contact lies dorsally, where the nearly vertical laterosphenoid intersects the nearly horizontal frontal perpendicularly. Posterior and somewhat ventral to this, the laterosphenoid meets the prootic in a tall, vertically fused, suture. Anteriorly, the mesethmoid contact is also perpendicular, as the interorbital septum inserts longitudinally between the two transverse laterosphenoids. Finally, the basisphenoid slightly underlies the laterosphenoids posteroventrally. This contact forms as the laterosphenoid bone flattens gently into the horizontal basisphenoid. The origin of the *m. pseudotemporalis superficialis* lies in the midpoint of the orbital surface of the bone. This origin is particularly well marked in *Paraptenodytes antarcticus*, dividing the surface into equal sized ventral and dorsal sections (Bertelli et al., 2006).

The laterosphenoid also contains the openings for cranial nerves (CN) II, III, IV, V, and VI (e.g., Figures 2.5a). The optic incision for CN II and the ophthalmic nerve (Va) foramen lie anteriorly within the bone, just posteroventral to the orbitocranial foramen. Neither foramen closes fully, but only notches the anterior margin of the bone slightly. The oculomotor nerve (CN III) foramen lies posteroventral to those for CN II and CN Va,

and is larger than both of these, although still small. The minute trochlear nerve (CN IV) foramen is nearly confluent with that for CN III, to which it lies lateral and just slightly dorsal. Both foramina lie in a slight depression on the anteroventral surface of the bone, and both open internally into the vertically triangular hypophyseal fossa, which excavates the anteroventral corners of the paired laterosphenoids. The foramina lie close together, but are further separated in *Megadyptes*, *Pygoscelis*, and some *Eudyptes*. The maxillomandibular nerve (Vb, c), foramen which serves for passage of both the maxillary and mandibular branches of the fifth cranial nerve in birds, is large. It lies at the laterosphenoid-prootic contact, in the posteroventral corner of the laterosphenoid, just ventral to the horizontal squamosal platform and just anterior to the otic recess. This oval opening extends from the endocranial space for a short distance transversely through the laterosphenoid/prootic wall.

*Supraoccipital.* The single, midline supraoccipital forms the posterodorsal wall of the braincase, is excavated by the external occipital veins, and forms the posterior nuchal crest, the cerebellar dome, and the dorsal margin of the foramen magnum (Figure 2.5c). The bone lies vertically, posteroventral to the parietal and posterior to and separating the exoccipitals and, anterior to this, the prootics. In posterior view, the nuchal crest forms the lateral extremities of the supraoccipital. The crest is dorsally semi-circular in Australodyptinae; square in *Eudyptes*, *Eudyptula*, and *Megadyptes*; and dorsally triangular in *Paraptenodytes antarcticus* and *Spheniscus* (Bertelli et al., 2006). The supraoccipital overlies the endocranial space and forms the greatly expanded cerebellar dome. This lies dorsal to the foramen magnum and the paroccipital process of the

exoccipital, and bulges posteriorly from its dorsal connection with the nuchal crest. The dome is vertical, but slightly posteriorly tilted on its ventral end. This slight angle is accentuated by a distinct, posteroventral hook that is visible in lateral view, just dorsal to the foramen magnum (Figures 2.5a). This hook is absent in three penguin clades (in the clade *Eudyptula* + *Megadyptes*, within *Spheniscus*, and within *Eudyptes*). Deep grooves for the exit of the external occipital veins lie just ventrolateral to the cerebellar dome, lateral and just dorsal to the foramen magnum. They are shallowed in *Megadyptes* and *Pygoscelis papua*. The grooves extend posteroventrally and are enclosed by bone for half their anterior length. A styliform process is absent in all penguins (Mayr, 2005).

*Exoccipital.* The exoccipitals lie lateral and ventral to the supraoccipitals, dorsal to the basioccipital, and posterior to the prootic (Figure 2.5f). Each forms the posterior portion of the braincase and the paroccipital processes and contains foramina for the exit of cranial nerves IX and X and the carotid canal. Each bone is a vertical rectangle in posterior view, extending from the nuchal crest dorsally to a point just ventral to the occipital condyle. The exoccipital is completely fused with the supraoccipital dorsally and dorsomedially, and with the basioccipital ventrally. It fuses completely with the lateral opisthotic early in ontogeny, and the two are indistinguishable in the adult penguin. The exoccipital projects ventrally on each side to form the paroccipital process (e.g., Figure 2.5f). This process is enlarged, as in Procellariiformes, when compared with the smaller process of Gaviidae and Podicipedidae. The paroccipital process angles diagonally in posterior view, although a vertical condition exists in Australodyptinae and *Eudyptes*). The paroccipital process also extends posteriorly and

may be flattened posteriorly to curve onto the lateral surface of the skull, as in *Eudyptula*. Additionally, an autapomorphic condition in *Parapterodytes antarcticus* involves posterior tilting of the paroccipital process such that its lateral edge extends posteriorly, exposing a flat anteromedial surface not visible in extant species. The process is also bifid in *Parapterodytes antarcticus*, divided into ventral and dorsolateral extensions (Bertelli et al., 2006).

The supraoccipital contact lies dorsomedially, extending vertically along the margins of the cerebellar dome (Figure 2.5f). Anteriorly, the exoccipital contacts the squamosal in a transverse fusion that lies dorsal and posterior to the inner ear. Anteroventrally, the basioccipital-exoccipital contact lies transversely, ventral to the inner ear. The prootic contacts the exoccipital anteriorly and transversely. All contacts are completely fused, but perforated by various openings.

Three foramina, for the glossopharyngeal (CN IX) and vagus (CN X) nerves and the carotid canal, exit the bone within the parabasal fossa, a small depression that lies just lateral to the basal tubercle and medial to the posterior wall of the otic recess (e.g., Figure 2.5b). The carotid canal is by far the largest opening, and exits the bone posteriorly, ventrolateral to the other two foramina and just dorsal to the level of the basal tubercle. The foramen for CN IX is a tiny, lateroventral opening that lies midway between that for CN X and for the carotid canal. The vagus nerve foramen opens dorsal to the lateral edge of the basal tubercle, in a slightly larger opening than that for CN IX. Internally, all three foramina coalesce into one canal, which originates in the vagoglossopharyngeal ganglion fovea. This fovea lies posteroventrally within the braincase, just anterodorsal to the

occipital condyle and posterior to the ventral end of the otic pillar. It is convergently enlarged in both *Spheniscus* and *Pygoscelis*.

*Prootic.* The prootics lie nearly at the posteroventral corners of the skull, posteroventral to the laterosphenoids, ventral to the squamosals, dorsal to the basioccipitals, and anterior to the exoccipitals (e.g., Figure 2.5e). Each forms the otic region and contains the otic wall, maxillomandibular foramen (for CN Vb, c), facial foramen (for CN VII), pneumatic foramen, fenestra ovalis, and ethmoid foramen, as well as the openings for cranial nerves XI, and XII. Externally, the prootic is a slightly rounded plate that ventrally continues the curve of the laterosphenoid and dorsally curves upwards to indent the skull just below the temporal platform of the squamosal. Its ventral section, which is particularly enlarged in some *Spheniscus*, forms the enlarged otic wall. In medial internal view, as seen in CT slices, the prootic is not flat, but forms the vertical otic pillar, posteroventral to the endocranial space (e.g., Figure 2.5e). This pillar tilts laterally and posteriorly as it ascends upwards to fuse with the squamosal just medial to the otic recess. The pillar is thick and hollowed by numerous foramina, and curves more anteriorly in *Spheniscus*. All prootic contacts are fused, as described above.

The maxillomandibular foramen (for CN Vb, c) opens laterally within the prootic. The opening is wide in penguins, but narrow and posterolateral in *Eudyptula* and *Pygoscelis* (e.g., Figure 2.6a). It may be single or separated into two foramina by a short ridge, which may or may not contain a secondary foramen (Saiff, 1973). A pneumatic foramen lies posterior to the dorsal rim of the tympanic cavity, deep to the stapedia artery foramen in all species except *Eudyptes* and some *Spheniscus* (contra Saiff, 1973).

The foramen for the facial nerve (CN VII) is present convergently, being found only in *Aptenodytes* and all outgroups (Saiff, 1973; Bertelli and Giannini, 2005; Triche, Chapter 3), in which it exits the prootic posterior to the maxillomandibular foramen. The accessory (CN XI) and hypoglossal (CN XII) cranial nerves also lie within the prootic; the latter lies dorsomedial to the basal tubercle and lateral to the occipital condyle. There may be one, two, or three foramina for the exit of cranial nerve XII. The number of foramina is intraspecifically variable, although always double in *Aptenodytes*. The placement and size of foramina for CN XI and XII vary only slightly between penguin species, and the opening for CN XII marks the fusion between the prootic and exoccipital ossifications. Finally, the small fenestra ovalis, which serves to form the base of the columella, lies posterior to the maxillomandibular foramen and within the otic recess.

**Mandible.** The penguin lower jaw, or mandible, is generally slender and elongate (Figure 2.5d). The dentary, splenial, angular, and articular/prearticular compose the mandible, which contains the anterior and posterior mandibular foramina, the coronoid process, and the retroarticular process. Generally, each ramus is slender throughout. The jaw is markedly deepened at its midpoint, however, in *Eudyptes* and is deep throughout in the extinct Peruvian *Spheniscus*. The anterior mandibular fenestra is a robust, elongate opening that arose in the ancestor of the clade (Australodyptinae + *Eudyptes* + *Megadyptes*) and is much enlarged in *Aptenodytes*. It is formed anteriorly by the bifurcation of the dentary and posteriorly by the internal angular process of the angular (Figure 2.5a). In lateral view, it extends from the level of the antorbital fenestra just to the anterior section of the orbit. In species that possess an anterior fenestra, a shallow, medial

groove extends from it posteriorly, ventral to the medial mandibular fossa. The posterior mandibular fenestra lies anterior to the articular surface and posterior to the palatine. It is significantly smaller and rounder than the anterior fenestra, and is visible medially and laterally in all penguins. The posterior mandibular fenestra lies entirely within the angular and, in medial view, within the medial mandibular fossa, more anteriorly in penguins than in their outgroups. The mandibular fossa is oval, open dorsally, and fairly shallow, but deepened in *Aptenodytes*, *Megadyptes*, some *Spheniscus*, *Paraptenodytes antarcticus*, and *Wimanu*.

*Dentary.* The dentaries form the anteriormost portion of the mandible and suture to each other at their anterior tips (e.g., Figure 2.5d). Each also contacts the splenials anteromedially, the angulars posterolaterally, and the prearticulars posteromedially. The dentary is an elongate, flattened rod whose anterior section is straight, with a pointed tip. The tip is pointed in the outgroups, truncated in the clade (Australodyptinae + *Eudyptes* + *Megadyptes*), and strongly truncated and squared off in *Spheniscus* (e.g., Zusi, 1975). The anterior section of the bone is sigmoid in *Eudyptula*, *Pygoscelis*, and some *Spheniscus*. The dorsal edge of the dentary is generally straight in lateral view, except in *Eudyptes* and *Pygoscelis*, in which it arches dorsally (Figure 2.5a). The dorsal edge extends for more than half the length of the entire mandible, although it was shortened independently a number of times within Spheniscidae. Posteriorly, and unlike the condition in all outgroups, the dentary is bifurcate, forming a dorsal and a ventral posterior process. The angle between these processes is small, and the ventral process is usually short dorsoventrally and elongate anteroposteriorly. The process is,

however, tall vertically and abruptly tapered posterior to the anterior mandibular fenestra in *Eudyptes*, *Megadyptes*, *Pygoscelis*, and some *Spheniscus*, and shortened in *Eudyptes*, *Megadyptes*, and *Pygoscelis*.

The dentary meets with its pair at the strongly fused mandibular symphysis, which is vertical and short in all penguins. It contacts the splenial medially, along its posterior half. Only the ventral section of the dentary forms this contact, which is fused in *Spheniscus* and all outgroups. Posteroventrally, the angular inserts between the dentary and splenial for a short distance. The dentary here lies laterally only, and the angular vertically flanks both its dorsal and ventral processes. The dentary-surangular contact lies medial to that with the angular. It is short, involving only the tip of the surangular and the posterior tip of the dorsal process of the dentary.

*Splenial.* The dorsoventrally short, anteroposteriorly elongate splenial forms the medial margin of each mandible and contacts the dentary anteriorly, the angular posteriorly and laterally, and the surangular posterodorsally (e.g., Figure 2.5d). Each splenial forms a thin plate that lies ventral to the anterior mandibular fenestra. The dentary suture may be visible in the adult (*Aptenodytes*) or entirely obliterated (as in *Eudyptes* and *Spheniscus*). It lies anteriorly, along the ventral margin and medial surface of the splenial. Posteriorly, the medial surface then contacts the angular, while the overlying surangular contacts the posterior edge of the splenial. The surangular contact, which forms along the curved posterior margin of the splenial, is tall and vertical in penguins, but short and horizontal in *Aptenodytes*.

*Angular.* This bone forms the posterior half of each mandible, contains the retroarticular and coronoid processes, and merges anteriorly with the surangular (e.g., Figure 2.5a, d). It also contacts the articular posterodorsally, the splenial anteromedially, and the dentary anterolaterally. The bone is elongate, anteriorly vertical and thin, and posteriorly flattened into the retroarticular process. Anteromedially, the surangular extends to form the anterior margin of the medial mandibular fossa. It may be slender, as in *Aptenodytes* and *Eudyptula*, or dorsally thicker, as in remaining genera. Ventral to the surangular contact, the bone inserts lateral to the splenial and medial to the dentary to form the ventral margin of the mandible. Dorsal to the surangular, the angular forms the coronoid process, which is a small tubercle. The coronoid process may lie anterior to the posterior mandibular fenestra, or in a position on the anterior tip of the fenestra, as in *Aptenodytes* and *Eudyptula*, or posterior to the fenestra, as in *Eudyptes* and *Pygoscelis*. Posteriorly, the angular forms the retroarticular process, which extends posteriorly, ventral to the articular. It is elongate and thin transversely, but missing entirely in all outgroups. It is particularly elongate in *Eudyptula* and *Spheniscus*, and contains a dorsal, midline fossa in all species except *Eudyptula sp.* When compared with the articular surface, the process is equal in size in *Aptenodytes*, *Pygoscelis*, and *Paraptenodytes antarcticus* (Bertelli et al., 2006), narrower in *Eudyptes* and *Eudyptula*, and both longer and narrower in *Spheniscus*.

*Articular.* The articulars lie posteriorly within the mandible and form the articular surface that meets the quadrate (e.g., Figures 2.5b, g). It fuses indistinguishable with the prearticular. Each forms a medial and a lateral mandibular process and contacts

the angular ventrally. This contact is also completely fused in all species, and occurs as the bone flattens horizontally to meet the thin, vertical angular. The lateral articular border extends straight posteriorly in *Aptenodytes*, *Eudyptula*, and *Pygoscelis*, but is posteriorly inturned in the remaining genera. This angling causes the entire articular surface to turn diagonally in relation to the axis of the mandible. In lateral view, the bone is also ventrally excavated, ventral to the articular surface, except in *Eudyptula* and *Pygoscelis*. This excavation is deeper in *Paraptenodytes antarcticus* (Bertelli et al., 2006). The medial surface is also excavated, forming a small fossa in some species (*Aptenodytes*, *Eudyptula*, some *Eudyptes*, and *Pygoscelis antarcticus*). The articulatory surface is small in the outgroups, especially in comparison to their larger skulls, but is robust in penguins and small in *Pygoscelis*. It is gently indented and sub-triangular anteriorly, and lies between the medial mandibular process posteriorly and the lateral one anteriorly. The medial process contains an accessory midline fossa in all taxa except *Spheniscus* and some *Eudyptes*. The medial process is hooked only in penguins, weakly in most species and strongly in *Aptenodytes* and *Spheniscus*. The lateral mandibular process is hooked in Gaviidae, but never in penguins.

### **Axial Skeleton**

**Vertebrae.** The penguin axial column contains cervical, thoracic, sacral, and caudal vertebrae, including the pygostyle (Figure 2.12). No fused notarium is present because all thoracics are free. There may be 42 or 43 total elements, including fifteen cervicals, seven thoracics, twelve or thirteen fused sacrals, six to eight caudals, and the pygostyle. The vertebral column is robust and non-pneumatic. The opisthocoelous centra

project robustly anteriorly in all penguins except *Wimanu*, whose centra project much less. This condition is intermediate between all other penguins and their outgroups, wherein the centra project only slightly. Anteriorly, the cervical vertebrae are short and compact, and the third through sixth elements usually bear ventral processes. The atlas is typical of most birds, but does project distinct lateral processes. The hypoapophysis also projects ventrally from the atlas as a medium-sized, longitudinal ridge. The axis is typical in shape to that of other birds, but possesses more elongate dorsal and ventral processes. The carotid arches of all posterior cervicals form canals. In nearly all outgroups, the third cervical bears a bony bridge to connect the transverse and caudal articular processes, a feature that is absent in penguins (Mayr and Clarke, 2003; Mayr, 2005). There may be a stout anteroventral process on the ventral surface of either the sixth (*Aptenodytes*, *Eudyptula*, *Megadyptes*, *Spheniscus*, Procellariiformes, and Gaviidae) or the eighth (*Aptenodytes* and *Eudyptula*) cervical vertebra that is unique to these groups (Simpson, 1946; Bertelli and Giannini, 2005). The process is elongated vertically when present on the sixth cervical and elongated horizontally when present on the eighth. The posterior three to five cervicals bear laterally elongated transverse processes. In Australodyptinae, the transverse processes are also deflected dorsally on the twelfth and thirteenth cervicals (Bertelli and Giannini, 2005). The thoracics are longer vertically than horizontally, with elongated ventrolateral and spinosus processes, that latter of which are tall but thin. Posteriorly, the ventrolateral processes shorten and converge into the ventral process, at the fifth thoracic. The last thoracic is heterocoelous in all outgroups, is weakly

opisthocoelous condition in *Wimanu*, and is completely opisthocoelous in all other penguins (Mayr, 2005).

All sacrals are fused into the synsacrum, which is long and narrow in penguins, as compared with most other birds, but is extremely elongate in Gaviidae and Podicipedidae (Figure 2.13). It contains seventeen or eighteen fused vertebrae in these outgroups, twelve in most penguins, and thirteen in some *Aptenodytes*, some *Eudyptes*, and some *Spheniscus* (Mayr and Clarke, 2003). The fusion is complete and obliterates individual transverse processes dorsally, leaving only very small intertransversal foramina. The synsacrum is columnar in *Wimanu*, however, clearly exhibiting the outline of each component vertebra, and probably represents the ancestral condition for penguins (Slack et al., 2006). The anterior articulation surface is anteriorly convex in all penguins, but anteriorly concave in all outgroups (van Tets and O'Connor, 1983). A robust ventral projection extends from the first fused vertebra in *Eudyptula*, *Megadyptes*, some *Eudyptes*, *Wimanu*, Gaviidae, and Podicipedidae. Dorsally, the synsacrum is sigmoid in shape, being wide anteriorly, then narrowed, then widened again near the acetabulum, then narrowed posteriorly. In all penguins, the widest portion lies anterior to the acetabulum, while the widest portion lies posterior to the acetabulum in Procellariiformes and Podicipedidae and the bone never widens in Gaviidae. This bone owes its sigmoid shape to the lengthening and shortening of the transverse processes, which are longer in all penguins than in any outgroup (Cracraft, 1982). Posterior to the acetabulum, the ratio of length to width of the vertebrae is much smaller than in the outgroups (around 1:2 as opposed to 2:1). A keel is also present dorsally in all penguins and most outgroups. The

ventral surface is flat posteriorly, except in *Pygoscelis* and some *Spheniscus*, in which it is lightly grooved.

Including seven free caudals and the pygostyle, there are eight caudal vertebrae in all outgroups and most penguins (Figure 2.12c). In *Spheniscus* and some *Eudyptes*, however, there is an extra free element, for a total of nine caudals. A number of these bear haemal spines, including two in some *Spheniscus*, three in *Eudyptes*, *Eudyptula*, *Pygoscelis*, some *Spheniscus*, and Podicipedidae, and four in *Aptenodytes*, *Megadyptes*, Gaviidae, and Procellariiformes. These spines are bifurcate in all penguins, although never in the pygostyle, and single in Procellariiformes and Podicipedidae. They are also large in the outgroups and are enlarged in *Aptenodytes*, but reduced in other penguins. The pygostyle is perforate caudoventrally in penguins, as well as in Phalacrocoracidae and Procellariiformes.

**Ribs.** In penguins, ten vertebral ribs articulate with the thoracic vertebrae, while only nine do so in all outgroups. Additionally, seven or eight cervical ribs articulate with the cervical vertebrae (Figure 2.12b) and numerous free cervicothoracic ribs do not articulate with any vertebrae, but lie between the cervical and thoracic regions of the vertebral column. The elongated cervical ribs generally begin at the fourteenth cervical vertebra in penguins, except in *Eudyptes* and some *Eudyptula*, where they begin at the thirteenth, as in all outgroups. The ribs bear uncinatous process, which are wide and spatulate in all penguins, but narrow in all outgroups. These processes are also fused with the ribs in some outgroups, but never in penguins.

## **Appendicular Skeleton**

The appendicular skeleton is non-pneumatic and solid in all penguins, extant and extinct. However, the skeleton is particularly pachyostotic, with noticeably thicker walls in some species (*Parapterodytes*, some *Palaeudyptes*, the Tierra del Fuego species, and *Wimanu*; Simpson, 1946; Clarke et al., 2003; Slack et al., 2006).

**Pectoral Girdle.** The penguin pectoral girdle is pachyostotic, non-pneumatic, enlarged, and highly stiffened. It consists of the coracoids, scapulae, sternum, and furcula.

*Coracoid.* The coracoid in penguins is elongated and generally rod-like in comparison with that of other birds, contacting the sternum proximally, the scapula posterodistally, and the furcula anterodistally (Figure 2.14). It forms part of the glenoid fossa and contains the supracoracoid fenestra. The coracoid is vertical and angles anteriorly and laterally as it extends distally from the sternal contact. The bone is thinner and more elongate than the tubular element of penguin outgroups, and each is somewhat flattened anteroposteriorly. The coracoid shaft is robust in all penguins and curved in *Anthropornis*, some *Delphinornis*, *Pachydyptes*, some *Palaeudyptes*, and *Wimanornis*. The distal end, or acrocoracoid, is flared in all outgroups and in *Wimanu*, but its condition in all other penguins is straight and not flared. The acrocoracoid extends to form the anteromedially hooked head of the bone, which is noticeably more anterior in some *Palaeospheniscus* and absent in all outgroups. The head is flattened slightly dorsoventrally and squared off anteriorly. It is much thicker dorsoventrally in *Spheniscus*, *Palaeudyptes antarcticus*, *Parapterodytes antarcticus*, and *Wimanu*. In *Eudyptula*,

*Megadyptes*, *Spheniscus*, and some *Eudyptes*, the head forms a 90° angle with the bone, while it rests on a bent neck in remaining extant species and in *Palaeodyptes*, *Paraptenodytes antarcticus*, and all outgroups. Its lateral surface is flat in extant species, laterally concave in *Paraptenodytes*, some *Palaeodyptes*, and Gaviidae, and laterally convex in some species of *Palaeospheniscus*. The medial surface is also flat in most species, except *Pachydyptes*, some *Palaeodyptes*, *Paraptenodytes antarcticus*, and Procellariiformes, in which it is medially concave.

Proximally, the coracoid is wide in some *Palaeospheniscus*, *Wimanu*, and all outgroups, narrow in most other penguins (e.g. Figure 2.14), and intermediate in *Eudyptula* and *Anthropornis*. This extremity is dorsally concave and narrow at the sternal contact, although it is flat in all outgroups. These outgroups, as well as *Wimanu* and Podicipedidae, also possess an elongated lateral process extending from the proximal end, which is absent in all other penguins (Mayr, 2005). The penguin coracoid does, however, extend a dorsal process from the medial angle of the proximal end. This process is generally small, although it is enlarged in some *Pygoscelis* and some *Spheniscus*, and absent in *Aptenodytes* and *Megadyptes*. In some *Spheniscus*, the process extends far enough to form an elongate foramen. The procoracoid lies along the midlength of the bone proximodistally and may form a complete supracoracoid fenestra. This opening is a flat, vertical rectangle that extends from the anteromedial margin of the bone. Dorsally, the process is separated from the shaft of the bone by a vertical, anterior groove that the process curves around anteriorly, before extending slightly dorsally on its laterally corner, past the remainder of the process. The procoracoid is much larger in penguins

than in all outgroups, and is tall in all penguins except *Eudyptula*, *Pygoscelis*, and some *Spheniscus*. The supracoracoid fenestra is present in all penguins, although it forms only an elongate notch in Australodyptinae, *Eudyptula*, and a number of fragmentary extinct species, and is particularly enlarged in *Megadyptes* and some *Spheniscus*.

The scapular facet of the coracoid articulates with the coracoid tubercle of the scapula (Figure 2.14). This small, shallow, facet lies dorsolateral to the supracoracoid fenestra, on the posterior surface of the bone, and is enlarged in all outgroups. Lateral and dorsal to the facet, the humeral articulation, or glenoid facet, is much larger, although equal in depth to the scapular facet in all penguins. It is a vertical oval, lying on the posterolateral surface of the shaft of the bone, and extending from the level of the dorsal end of the procoracoid to just below the hooked acrocoracoid head. Dorsal to the sternal articulation, the sternocoracoidal impression excavates the posteriorly concave, proximal surface of the bone. This impression is deep in extant species and shallower in many extinct species, as well as Gaviidae and Podicipedidae, and contains extensive secondary sculpturing in penguins.

*Scapula.* The scapula in penguins is a thin, elongated, posteriorly expanded bone (Figure 2.14). It extends posteriorly from the coracoid and humeral articulations to flank the sternum dorsally. Posteriorly, the scapula forms a rounded paddle shape (Bertelli and Giannini, 2005 Mayr, 2005), although *Wimanu* retains a condition that is pointed and much thinner dorsoventrally. In *Aptenodytes*, *Megadyptes*, and some *Eudyptes*, the scapular head forms about a 45° angle of torsion with the posterior blade. The medial scapular surface is flat in most penguins, but hollowed for the

ribs (subscapular fossa present) in *Eudyptes schlegeli*, *Eudyptula*, *Pygoscelis adeliae*, some *Spheniscus*, Gaviidae, and Podicipedidae. This surface may also bear a distinct proximodorsal ridge, as in *Aptenodytes forsteri* and most *Eudyptes*, a shallow proximodorsal depression, as in *Eudyptes schlegeli*, *Pygoscelis*, some *Spheniscus*, and some gaviids, or neither structure. The posterior end of the scapula is truncated and nearly flat in most penguins, but is rounded in *Spheniscus* and some *Eudyptes*. This end may contain one small foramen, as in *Aptenodytes* and some *Eudyptes*.

Anteriorly, the coracoid and humeral articulations (sternocoracoidal process) are thicker than the rest of the bone, which is extremely thin, more so in *Eudyptula* and *Pygoscelis* (Figure 2.14). The proximal edge is flat and nearly vertical in extant species, medially concave in *Anthropornis* and *Paraptenodytes antarcticus*, and flat and nearly horizontal in all outgroups. The glenoid articulation of the scapula is larger than that for the coracoid in all penguins, and of equal size in the outgroups. The glenoid fossa formed by the coracoid, scapula, and furcula is large, except in Podicipedidae. The supra- and infraglenoid tubercles are lost in all penguins, as is the scapular spine (Louw, 1992). The acromion, which articulates with the furcula, is small and extends only to the coracoid articulation, much less far than in the outgroups Gaviidae and Procellariiformes (Mayr, 2005). This process is distinctly laterally hooked in most australodyptines and in some *Spheniscus*. The scapula articulates with the coracoid and furcula in a flat butt joint that rests evenly on the other bones.

*Furcula.* The two fused clavicles form the penguin furcula, which is U-shaped in anterior view (Figure 2.15). Each limb of this U ascends posterodorsally from

the ventral apophysis in an anteriorly convex curve, thickening throughout. The limbs are thin in transverse section, but thicker longitudinally, especially proximally. The ascending curve culminates dorsally at the coracoid articulation, where it flattens posteriorly into the scapular tuberosity. This projection is extended longitudinally to project posteriorly beyond the coracoid to the scapula. It articulates posteriorly with these two bones, but is free anteriorly. The furcular apophysis is present only in Australodyptinae, Procellariiformes, and Gaviidae, projecting proximally in *Aptenodytes* and posteriorly in remaining taxa. As opposed to all outgroups, the penguin furcula is flattened proximally, along the scapular tuberosity. This proximal projection is sharply pointed in all penguins except *Aptenodytes* and *Megadyptes*, in which it is rounded. The coracoid articulation is a thickened, bumpy projection whose lateral and dorsal surfaces abut the acrocoracoid process of the coracoid. The scapular articulation lies horizontally in *Eudyptula*, most *Spheniscus*, and some *Eudyptes*, but is angled in remaining taxa. The articular surface thus lies laterally in all outgroups and in some *Eudyptes*, and medially in *Pygoscelis*, *Megadyptes*, and *Eudyptes chrysocome*. The furcula does not contact the sternum in any penguin or outgroup.

*Sternum.* This midline element is enlarged and elongated in all penguins (Figure 2.15). The sternum is composed of a ventral, vertical carina and a dorsal, horizontal plate, which is curved dorsally and laterally compressed on each side to form a U shape in anterior view, a penguin synapomorphy. In all outgroups, this shape is much wider and not at all laterally compressed (Fordyce and Jones, 1990). Dorsally, the sternum is oblong, although shorter in all outgroups, and extends paired craniolateral

processes, paired lateral trabeculae, and a posterior median trabecula. The pointed sternal carina is dorsoventrally short in penguins, but may extend far anteriorly, as in *Aptenodytes* and *Megadyptes*. It exceeds the level of the coracoid sulcus in all penguins, but not in any outgroup. It is low in penguins, especially anteriorly, but high in Australodyptinae and all outgroups. The carina is also triangular, shortening posteriorly. The rostrum lies anteriorly, where the carina meets the dorsal plate, although rostral spines are absent in all species except *Eudyptula minor*. The furcular facet is also lost in all penguins. The horizontal, coracoid sulcus lies on the anterior margin of the dorsal plate, ventral to the craniolateral process. It forms a deep groove in all penguins and is always continuous with its pair at the midline, as opposed to the condition in most other birds, where the sulci overlap (Cracraft, 1982). The rostrum does separate the two coracoid sulci, but only slightly. The elongated craniolateral process, which extends on either side of the carina and coracoid sulci, has a laterally narrowed base and extends further than in any outgroup. It is rectangular, with a rounded anterolateral border, and extends slightly dorsally as it progresses. The process in penguins lies much more medially than in all outgroups, in which it is completely lateral to the coracoid sulcus. A foramen perforates the craniolateral process in *Spheniscus* only. The lateral trabecula extends from the posterolateral corner of the penguin sternum. This process is horizontal and generally thick transversely, although it may be thin, as in *Pygoscelis*, *Spheniscus*, and Gaviidae. Posteriorly, the lateral trabecula extends beyond the median trabecula, as in all outgroups except Gaviidae, and curves medially around the main bone to enclose a deep posterior notch, the lateral incision. There may be two such incisions contained in

Procellariiformes. The median trabecula in penguins may be either narrow, as in *Aptenodytes*, *Megadyptes*, and most *Eudyptes*, or wide, as in the remaining penguins and all outgroups, and may also be perforated, as in *Eudyptula*, *Eudyptes schlegeli*, and Gaviidae.

**Pectoral Limb.** The penguin pectoral limb consists of the humerus, radius, ulna, radiale, ulnare, carpometacarpus, and digits 1 (two phalanges) and 2 (one phalanx). The limb is extremely flattened and pachyostotic, and the allular digit is lost.

*Humerus.* Penguin humeri are among the two most commonly preserved fossil elements because of their stout, pachyostotic condition. They are generally short and thick, with highly derived distal ends (Marples, 1952; Figure 2.16). The humeral flattening results in a longitudinal orientation that is also somewhat oblique, with the posterior edge extended medially. The shaft of the bone thus contains an internal and an external surface, which do not correspond exactly with the anterior and posterior surfaces of the humerus in other birds. This results in the head of the humerus being offset medially from the shaft of the bone. The bone is slightly less flattened in some extinct species, but retains the distinct morphology of its distal end in all penguins except in *Wimanu sp.*, in which the distal end is not offset. The ratio of width to height for penguin humeri is about 1:4 in extant species and 1:3 in the extinct genus *Archaeospheniscus*. It is slightly more elongate in some more basal extinct taxa, such as *Palaeudyptes* and *Wimanornis*, and extremely elongate in *Wimanu* and in all outgroups. The head of the humerus is smaller than in the outgroups, but still robust, and smallest in *Archaeospheniscus*, *Palaeospheniscus*, *Paraptenodytes*, and *Platydyptes*. The head is also

distinctively shaped, being extended entirely posterior and somewhat medial to the shaft of the bone and squared off in extant species. It is bean-shaped in some extinct species of *Palaeodyptes* and in the genus *Wimanu*, and rounded, as in other birds, in *Parapterodactylus robustus*. It is sometimes somewhat flattened in the same dimension as the shaft, but only in *Anthropornis*, *Palaeodyptes*, and *Wimanornis*. Proximally, the head serves for attachment to the coracoid and scapula, and to form the glenoid fossa, into which the articular surface arches proximomedially. These articulations are smaller than those of penguin outgroups. The sulcus for the transverse ligament attaches to the medial, articular, surface of the head ventrally. This sulcus is shallow and short in the outgroups, but deepened in penguins. It is also short and round in *Spheniscus* and all extinct species (contra Mayr, 2005), and the condition of long and rectangular in remaining extant species. A second, separate pit lies in the posterior portion of the sulcus in *Platydyptes* and in Spheniscidae, although it is lost in a few extant species.

Ventral to the humeral articular surface, the bicipital crest lies proximovertrally on the bone (Figure 2.16a). This is not a large crest in penguins, as the tripital fossa is enlarged to hollow the entire head of the humerus and thus excavates the crest such that it forms only a narrow bordering ridge. This rim is not present on the tripital fossa of any outgroup. The bicipital crest just underlies the capital ligament groove, which separates the crest from the head of the humerus. The groove is enlarged and deepened in penguins, although it is shallower in *Eudyptula*, *Megadyptes*, *Spheniscus*, and *Archaeospheniscus*. Caudally, the groove is tapered in *Spheniscus*, *Pachydyptes*, *Palaeodyptes*, *Palaeospheniscus*, *Platydyptes*, and some *Wimanornis*, as

well as in Gaviidae and Podicipedidae. In all other penguins, the groove remains wide throughout. The tricipital fossa is a circular opening that is somewhat dorsoventrally flattened in *Eudyptes*, *Spheniscus*, and some *Palaeospheniscus* and squared off in *Paraptenodytes* and *Platydyptes*. The fossa lies on the caudal side of the shaft in all outgroups, but on the ventral side in penguins, owing to the odd humeral flattening. It is large and excavates nearly the entire humeral head in all taxa except *Paraptenodytes*, in which the fossa is medium in size only. It is much deeper than in any outgroup, but lost the pneumatic foramen. The opening is usually bipartite in penguins, although this condition is intraspecifically variable, with the opening remaining only partially divided in some *Eudyptula*, some *Megadyptes*, and some *Spheniscus* (Bertelli and Giannini, 2005). It is also single in *Wimanornis* and most *Palaeospheniscus*. The bony partition that divides the fossa in two is oriented nearly longitudinally in all extant species except the genus *Aptenodytes*, as well as in their closest relative, *Palaeospheniscus*. It is nearly transverse, however, in most other extinct species. In *Palaeospheniscus*, the ventral partition is smaller than the dorsal and is excavated into a distinct pit.

The humeral shaft is generally straight, although slightly sigmoid in *Anthropornis*, *Palaeoeudyptes*, *Platydyptes*, *Wimanu*, and some *Wimanornis* (Figure 2.16). Proximally, just anterior to the head of the bone, the deltoid crest extends slightly from the ventral surface. The crest is present in penguins, but greatly reduced (Mayr, 2005), and encloses the vertical fossa that serves as insertion point for the *pectoralis primus*. The fossa is deep, rectangular, and elongate in most penguins, as compared with the shallow groove of *Wimanu* and of all outgroups. The insertion for attachment of the *latissimus dorsi* lies

just ventral to the level of the deltoid crest, on the opposite side of the bone. This insertion is extremely small and shallow, although slightly larger in *Pachydyptes* and most *Palaeudyptes*. It is elongate in all outgroups and most extinct species, but rounded in some extant penguins (Australodyptinae and *Spheniscus*). Just dorsomedial to the *latissimus dorsi* insertion, that for the *supracoracoideus* forms an elongate impression that extends dorsomedially to the humeral head. The insertion is usually straight, but curved somewhat convexly anteriorly in *Aptenodytes*, 'Dege', *Platydyptes*, and some *Palaeudyptes* species. The insertions for the *supracoracoideus* and for the *latissimus dorsi* are far separated in outgroups and in *Palaeudyptes*, but lie close together in all other penguins. The former is separated by a small fossa in the crown-group and in *Palaeudyptes*, *Palaeospheniscus*, *Platydyptes*, and *Wimanu*. The fossa is enlarged in taxa such as *Aptenodytes*, *Megadyptes*, *Pachydyptes*, and *Wimanornis*. The fossa is generally closed distally, although it is open in *Spheniscus*, *Pachydyptes*, and *Wimanu*. In *Platydyptes*, the fossa extends to the *latissimus dorsi* insertion as a sharp ridge.

The humerus shaft narrows distally in penguin outgroups and retains this condition in *Wimanu* (Figure 2.16). The clade comprising all other penguins possesses a shaft that remains equally thick throughout, whereas the crown-group shows a shaft that widens distally. The shaft is often also offset distally to form the preaxial angle. This slight angle lies just distal to the midpoint, along the anterior margin. It is present only in penguins, and is found in all extant and most extinct species. The genera 'Dege', *Dunroonornis*, *Eretiscus*, 'Inguza', *Marplesornis*, and *Wimanu* all possess a nearly straight angle that measures about 170°. Proximal to the angle, the shaft extends nearly

ventrally, but turns more posteriorly distal to this angle. The preaxial angle varies greatly among species, being sharper and more abrupt in *Aptenodytes*, some *Spheniscus*, *Archaeospheniscus*, *Spheniscus*, *Palaeudyptes*, and some *Palaeospheniscus*, and rounded in remaining species. The preaxial angle is large in most species in which it is found, measuring, for example, about 140° in *Pygoscelis* and about 155° in *Aptenodytes* and *Eudyptes*.

Owing to the extreme flattening of the humerus, the radial and ulnar condyles that lie laterally and medially on the anterior surface of the bone in most avians are displaced in penguins to lie anteriorly and posteriorly on the anteroventral corner of the humerus (Figure 2.16a). The angle between these condyles and the shaft of the bone varies within penguins, being straight in all outgroups and in *Wimanu*, but about 120° in most living species, as well as in *Anthropornis*, *Palaeudyptes*, *Platydyptes*, and *Wimanornis*, and about 135° in *Spheniscus*, *Orthopteryx* and *Pachydyptes*. This corner is generally bumpy in outline, owing to the slight extension of the radial condyle, but may be greatly extended, as in *Orthopteryx*, *Palaeudyptes*, some *Palaeospheniscus*, and *Parapterodytes*. Although the radial condyle is generally the same width as the ulnar condyle, it is narrow in *Parapterodytes* and all outgroups, and wider in *Orthopteryx*. The rounded radius and ulnar condyles are equal in size in *Eudyptula* and most extinct species, but the ulnar condyle is larger in *Orthopteryx*, *Parapterodytes*, and *Wimanornis*, as well as in all other extant genera except *Eudyptes*, in which it is smaller. The extinct taxa *Palaeudyptes*, *Palaeospheniscus*, and *Platydyptes* also contain smaller ulnar condyles than radial ones. The opposite, posteroventral, corner is greatly extended

posteriorly and contains the displaced tendinal grooves (scapulotricipitalis and humerotricipitalis sulci). The medialmost of these two grooves is shallower but extended further posteriorly. The lateralmost groove is much deeper and bordered medially by a trochlea present only in penguins (O'Hara, 1989; Bertelli and Giannini, 2005). This trochlea extends posteriorly, as opposed to the other two, which extend posteroventrally and usually extends further than the posterior edge of the bone, except in *Anthropodytes*, *Archaeospheniscus*, *Eudyptula*, 'Inguza', *Platydyptes*, and *Spheniscus*. Dorsal to the ulnar condyle, the ectepicondylar attachments, which serve as the origination of the *m. ectepicondylo-ulnaris*, sculpt the external surface of the bone along its midline. They lie more dorsally in *Anthropornis*, *Pachydyptes*, and *Wimanornis*. The ectepicondylar process is absent in all penguins, as is the distal pneumatic fossa.

*Radius*. Penguin radii are flat, rectangular, and short, although the degree of flattening is less in *Anthropornis* and *Palaeedyptes* (Figure 2.17). Each bone is hooked proximally on its preaxial edge. This hook, which serves for attachment of the *m. brachialis internus*, is shorter and much less pronounced in *Eudyptula*. It is sharply concave in all genera except *Aptenodytes*, *Eudyptula*, and *Wimanu*, in which the hook is much flatter. The shaft and head of the bone are curved in all outgroups, a condition retained in *Wimanu*, whereas all other penguins possess a straight shaft with a head that extends straight proximally. A few extinct genera, such as *Palaeedyptes* and *Platydyptes*, have a head that is offset posteriorly from the shaft of the bone. The penguin radius has characteristically robust tendinal grooves, both those lying along the shaft of the bone and the distal, oblique grooves for the metacarpal extensors. Both these grooves

are shallowed in *Megadyptes*, whereas the distal oblique grooves are shallowed in *Pygoscelis* and *Spheniscus*. None of these grooves are discernable in penguin outgroups.

*Ulna.* The ulna of penguins is flat and elongate but short, with an extended, posteriorly pointed, triangular, postaxial wing (Figure 2.17). Each contacts the humerus proximally and the ulnare distally. The bone is always shorter than the humerus, as opposed to the equal length condition of all outgroups. As with the radius, the ulna is slightly less flattened in some extinct genera, such as *Anthropornis*, *Palaeodyptes*, and *Parapterodytes*. Proximally, the ulna in penguins is widened and flattened horizontally for articulation with the humerus, except in *Eudyptes*, *Anthropornis*, and *Palaeodyptes*, in which it is only widened. This articular surface is also hollowed concavely for the humerus in nearly all penguins, although it forms an undulating surface in *Aptenodytes* and *Palaeospheniscus*. The postaxial border is a smoothly curved triangle that extends to the humerus in some species, a condition shown in numerous taxa (e.g., *Aptenodytes*, *Pygoscelis*, *Spheniscus*, *Palaeospheniscus*, and *Parapterodytes*). A small foramen is often present on the proximomedial corner of the extended postaxial triangle, as in *Eudyptes*, *Eudyptula*, *Anthropornis*, and *Palaeospheniscus*.

*Radiale.* The radiale is a lateromedially wedge-shaped bone in penguins, whereas its shape has a more complicated outline in the outgroups (Figure 2.17). Viewed dorsoventrally, however, they form an hourglass, or semi-circular shape, which is rectangular in *Eudyptes*, in some *Spheniscus*, and in some extinct genera, including *Anthropornis*, *Palaeodyptes*. The bone is also fairly undulatory in *Aptenodytes* and Gaviidae and Podicipedidae, but smooth in all other species. A foramen exists in three

groups of spheniscids (*Eudyptula*, *Pygoscelis*, and some *Spheniscus*), but only forms an indentation in remaining species. Finally, the radial articulation is flattened in most penguins, but cup-shaped and concave in *Eudyptes*, most *Pygoscelis*, *Anthropornis*, and Gaviidae and Podicipedidae.

*Ulnare*. One of the most distinctive bones in the penguin skeleton, the ulnare is an extremely derived, flattened plate (Figure 2.17). It is triangular in shape, and inserts medially into the ulna-carpometacarpal articulation with its most obtuse point. Its ulnar articulation is thus displaced onto a large ventrocaudal process. The other two points of this triangle are greatly extended, lateroproximal and laterodistal to the ulna articulation. The proximal point is also extended into a distinct process in all penguins, although this is lost in *Eudyptula* and *Spheniscus*.

*Carpometacarpus*. The carpometacarpus contacts the radiale and ulnare proximally and digits two and three distally (Figure 2.18). It is flattened and completely fused at both ends, as in all outgroups. Proximally, the articular surface is semicircular and slightly widened dorsoventrally. The surface is flat in Procellariiformes and not widened in Gaviidae and Podicipedidae. The shaft of the bone is composed of three fused metacarpals, the first two of which are often completely fused and thus wider than the third. Three states are present involving the proximal fusion of metacarpal one with metacarpal two: metacarpal one may be completely fused, as in *Anthropornis*, *Paraptenodytes*, and *Wimanu*. The bone may also end abruptly, a condition found in the outgroups and in a clade of palaeodyptine extinct species. In Spheniscidae + *Palaeospheniscus*, however, a different condition arose: here, metacarpal one slants

distally into metacarpal two before terminating just proximal to the midpoint of the bone. In *Wimanu*, the metacarpal forms a distinct, proximal, process. In some species (*Aptenodytes patagonicus*, *Eudyptes chrysolophus*, *Eudyptes pachyrhynchus*, *Spheniscus mendiculus*, *Pachydyptes*, and *Palaeospheniscus*), the termination of metacarpal one forms a notch on the midsection of the preaxial edge, a condition that arose independently a number of times.

Although fused at its ends, the third metacarpal is free from metacarpal two through its midsection and forms a deep groove where it fuses distally with the second metacarpal (Figure 2.18). This groove is shallow in penguins, but deepened a number of times within penguins (e.g., in *Paraptenodytes*, *Aptenodytes*, some *Spheniscus*, and *Anthropornis*). The third metacarpal also generally extends further distally than the rest of the bone, except in a clade of palaeoedyptid penguins and in the outgroups, in which the three metacarpals extend equally far. Two facets indent the distal margin of the bone for articulation with the phalanges. The first of these, which covers the distal end of fused metacarpals one and two, is nearly flat in most penguins and outgroups, excepting *Eudyptula*, *Pygoscelis*, and *Paraptenodytes*, in which it is extremely proximally concave. These two distal facets are separated by a shallow groove, which is greatly deepened in *Aptenodytes* and *Spheniscus*.

*Manual Phalanges.* As in other avians, the penguin manus is highly fused (Figure 2.17b). Spheniscids have further reduced the manus, however, by losing digits four, five, and the alular completely and retaining only two phalanges of the second digit and one of the third. All penguin phalanges are highly flattened and short, whereas those

of all outgroups are tubular and long (Bertelli and Giannini, 2005). The first phalanx of the second digit is rectangular and straight, while the second is sub-triangular but elongate, and curves slightly posteriorly as it extends distally. The third digit is also sub-triangular, but much narrowed and more pointed distally. It bears a hooked, proximal process that curves dorsally along the posterior margin of the carpometacarpus (Bertelli and Giannini, 2005).

**Pelvic Girdle.** The fused ilium, ischium, and pubis, or os coxae, comprise the pelvic girdle of penguins (Figure 2.13). These constituents are completely fused to each other, but only sutured to the synsacrum medially, in the clade of all penguins excluding *Wimanu*. The synsacrum and os coxae are completely fused in this oldest penguin and in all outgroups (Pycraft, 1898; Lowe, 1933; Clarke et al., 2003).

*Os Coxae.* As compared with other avians, each os coxae is elongate anteroposteriorly and short dorsoventrally (Figure 2.13). Each contains the acetabulum, the ilioischadic foramen, and the ischiopubic fenestra. As opposed to the condition in Gaviidae and Podicipedidae, in which the bone is mediolaterally compressed with reduced dorsal illial crests (Mayr and Clarke, 2003), the penguin os coxae has anteriorly enlarged illial crests and a deeper postacetabular section. Its ventral keel is robust in all outgroups but extremely weak in all penguins. The ilium forms the dorsal margin of the bone, extending from nearly the anterior end of the synsacrum to the third caudal posteriorly. The preacetabular ilium is wide and paddle-shaped, with an expanded anterior end that is widely separated from its pair, as opposed to the condition in Procellariiformes. This paddle is notched anteriorly in all penguins and in

Procellariiformes, with two such notches in *Eudyptes*, *Megadyptes*, and some *Spheniscus*. When present, these notches are particularly deepened in most *Spheniscus* and *Eudyptes*. The ventral surface of the ilial blade is dorsally concave in *Eudyptes*, *Eudyptula*, and most *Spheniscus*, and the lateral edge is curved in *Eudyptula*, *Megadyptes*, some *Spheniscus*, some *Eudyptes*, and Procellariiformes (Clarke et al., 2003). Iliac fenestration is present in Podicipedidae and always absent in penguins.

Posterior to the ilioischadic fenestra, the ischium underlies the ilium. The ischium is deeper than the ilium, and meets the latter dorsally to form a U-shaped indentation in the posterior margin of the os coxae (Figure 2.13a). This fusion is only a slight notch in Gaviidae, and is sharper and V-shaped in some *Eudyptes* and Podicipedidae. Posteriorly, the ischium slightly exceeds the ilium in length in all penguins and in Podicipedidae, while it exceeds the latter greatly in other outgroups (Bertelli and Giannini, 2005). Finally, the pubis lies ventral to the other two pubic bones, extending posteriorly from the ventral margin of the acetabulum. It passes ventral to the obturator foramen, then forms the ventral margin of the ischiopubic fenestra. It is extremely thin, both dorsoventrally and transversely. Posteriorly, the pubis remains straight and of equal depth throughout, except in Australodyptinae and Gaviidae, in which it is decurved and slightly deepened. Excepting its anteriormost point, this bone never contacts the ischium. However, it does partake in the acetabulum in some outgroups (Gaviidae and Podicipedidae) and in *Spheniscus mendiculus* and *Eudyptes chrysolophus*.

The ilioischiadic fenestra is oval and medium-sized (Figure 2.13a). It lies in a nearly vertical plane, with its dorsal edge tilted slightly medially and its anterior margin curved laterally owing to the formation of the antitrochanter. This structure is fairly robust and lies at the posterodorsal corner of the acetabulum, just ventral to the dorsolateral ilial crest. The ilioischiadic fenestra underlies this crest, which occludes the fenestra dorsally in all penguin taxa except *Pygoscelis*, as well as in Gaviidae and Podicipedidae (Zusi, 1975). The acetabulum is perfectly circular and fairly small. It lies somewhat ventral to the level of the ilioischiadic fenestra, and just anterodorsal to the obturator foramen. The acetabulum is of equal size or smaller than the ilioischiadic fenestra in all penguins except in the clade (Australodyptinae + Eudyptes + Megadyptes), in which it is larger (Shufeldt, 1901; O'Hara, 1989; Bertelli and Giannini, 2005). The ischiopubic fenestra is a small slit that opens caudally in all penguins and some outgroups, although it is wide and closed caudally in Procellariiformes and Gaviidae (Bertelli and Giannini, 2005). The obturator foramen indents the ischium at its most anteroventral point and nearly reaches the acetabulum anteriorly.

**Pelvic Limb. Femur.** The femora of penguins are tubular and short (Figure 2.19). Each is typical of other avians, which all possess a reduced trochanter and enlarged head. The obturator and iliotrochanteric impressions are pronounced, as is the lateral condyle and tibiofibular crest. The femur is fairly thin, with a length to width ratio of less than 9:1, although this ratio is exceeded in some basal taxa, such as Procellariiformes and the extinct species *Anthropornis nordenskjoeldi* (Livezey, 1989; Mayr and Clarke, 2003). Compared with the tarsometatarsus, the femur of penguins is longer than that of all

outgroups, and Spheniscidae possesses particularly shorter tarsometatarsi, which are less than half the femoral length. The trochanter forms the most proximal portion of the bone in the outgroups and in *Wimanu*, but the clade including all remaining penguins possesses a condition where the trochanter and the head lay equally proximally. Spheniscidae, however, has the head most proximally (O'Hara, 1989). The femoral head is particularly large in pygoscelids, and it overlies a prominent, uniquely sphenisciform, rugosity. This structure is lost in some extinct species and in most *Eudyptes*. The impression of the capital ligament, found on the posterior margin of the dorsal surface of the head, is broad and deep in *Eudyptes* and *Pygoscelis* (Clarke et al., 2003; Walsh and Suarez, 2006), but is narrow and shallow in all other species and outgroups. In lateral view, the articular surface is indented dorsally to form a U shape in all penguins except *Wimanu*, in which the surface is flat. This U is further deepened to a V shape in a number of genera, including *Aptenodytes* and *Palaeospheniscus* (Clarke et al., 2003). Laterally, the obturator and iliotrochanteric impressions are enlarged into a flat, sculptured, rugosity that covers the entire proximal surface of the bone.

The shaft of the femur is straight in penguins, as in, for example, *Aptenodytes*, but sigmoid or bowed shape in *Eudyptes*, *Pygoscelis*, and *Archaeospheniscus* (Figure 2.19b). It usually meets the head perpendicularly, but this angle is greater than 90° in *Pygoscelis*, some *Eudyptes*, and all outgroups. The femoral neck is always short, and the width of the bone always increases as it extends distally. In extinct penguins, the trochanter may form a sharp crest, as in *Palaeudyptes*, some *Palaeospheniscus*, *Paraptenodytes*, and all outgroups, or a bumpy process, as in all extant species, *Anthropornis*, and some

*Palaeospheniscus*. Although it is reduced as compared with other avians, the trochanter does project slightly in all species, more so in *Aptenodytes*, some *Eudyptes*, and some *Palaeospheniscus*. This projection extends proximally in *Aptenodytes*, *Megadyptes*, *Anthropornis*, and *Palaeudyptes*, and anteriorly in remaining species and outgroups (Clarke et al., 2003). The medial supracondylar crest is also usually strongly projected medially, except in most *Eudyptes*, *Megadyptes*, *Spheniscus*, *Paraptenodytes*, and all outgroups, and its lateral pair is generally absent, except in *Eudyptes*, *Megadyptes*, *Palaeospheniscus*, *Paraptenodytes*, and Procellariiformes (Clarke et al., 2003).

The preaxioventral ridge, which lies just dorsal to the condyles on the anterior surface of the bone, is robust and enlarged in *Aptenodytes*, some *Eudyptes*, and some *Palaeudyptes* (Figure 2.19b). Medial to this ridge, the smooth patellar groove lies along the midline of the ventral femur and extends ventrally to separate the ventral femoral condyles. The groove is wide and shallow in all penguins except *Spheniscus*, in which it is slightly narrower and deeper. In *Wimanu*, the groove is deep and offset from the femoral shaft. The condyles both project ventrally, the lateral one more so. This condyle is vertically elongated, while the medial is horizontal and flattened posteriorly. They lie close together in the clade (*Spheniscidae* + *Palaeospheniscus*), but show a far separated condition in all other extinct species and all outgroups (Simpson, 1946). The lateral condyle contains two vertical, anteriorly curved processes: the lateral, fibular trochlea and the larger, medial, tibiofibular crest. In *Aptenodytes* and Procellariiformes, the fibular trochlea is enlarged to nearly equal the size of the tibiofibular crest. The two structures are separated by the fibular groove, which is enlarged in Sphenisciformes, and ends in a

proximal pit in many extinct species. Just dorsal to the condyles and ventral to the supracondylar crests, the popliteal fossa indents the bone along its midline. The fossa is deep and discrete in penguins, but shallower and less distinct in *Eudyptula*, *Megadyptes*, some *Eudyptes*, some *Palaeudyptes*, and some outgroups (Clarke et al., 2003).

*Patella*. The patella of penguins is distinctive, both in extant species and across extinct diversity (Figure 2.18c). It is greatly enlarged in comparison with all outgroups (Mayr, 2005), being about 2.7 cm in length and 2.4 cm in width in *Aptenodytes forsteri*. The bone is wedge-shaped and rounded in most species, but sharp and acutely wedge-shaped in *Eudyptes*. The patella is also perforated for passage of the tendon of the *m. ambiens* (O'Hara, 1989; Bertelli and Giannini, 2005; Mayr, 2005), although this foramen is lost in the outgroups and forms only a groove in Spheniscidae. In the clade (Australodyptinae + *Eudyptes* + *Megadyptes*), the groove is greatly deepened, a condition lost in *Pygoscelis*.

*Tibiotarsus*. The tibiotarsi of penguins are by far the longest of their limb bones (Figure 2.20). Each is robust, more so than in the outgroups, and contains the cnemial, patellar, and fibular crests, as well as the extensor sulcus and canal. The bone contacts the femur and patella proximally, the fibula laterally, and the tarsometatarsus distally. As in all birds, is composed developmentally of the fused tibia, tibiale and fibulare. The transverse cnemial crests lie at the proximal end of the anterior face of the tibiotarsus. They are unprojected, as compared with outgroups, and extend only to the femoral articulation in extant species, although extinct species show an intermediate, slightly projected morphology. The lateral crest is turned outward from the transverse,

and thickened distally. The horizontal, patellar crest connects the lateral and medial crests dorsally. It overhangs the proximal shaft of the tibiotarsus in all penguins and never in outgroups, although it is also less robust in penguins. These crests enclose a depression, the intercnemial sulcus, that is thus closed proximally and open distally. Posteriorly in penguins, the popliteal tuberosity extends proximally all the way to the articular surface, except in *Eudyptula*, *Megadyptes*, and *Pygoscelis* (Bertelli and Giannini, 2005). The fibular contact occurs at the fibular crest, which lies on the lateral edge of the tibiotarsus, just proximal to the midpoint of the bone. The crest is robust and extends laterally away from the bone. The two elements are separated by the distal interosseal foramen, which lies between the distal end of the fibula and its more proximal articulation. The foramen is small in all outgroups and larger in penguins.

At the distal end of the bone, the medial condyle extends distally past the lateral condyle, a condition that is lost in most *Spheniscus*, *Eudyptula*, and *Pygoscelis* (Figure 2.20a; contra Mayr, 2005). The medial condyle is also slightly deflected medially from the shaft of the bone, as compared with Procellariiformes and Podicipedidae (Clarke et al., 2003; Mayr, 2005). Its epicondyle extends medially past the condyle in *Aptenodytes*, some *Eudyptes*, *Anthropornis*, and *Paraptenodytes*. Just dorsal to the condyles, on the midline of the bone, lie the extensor sulcus and canal. The sulcus is a broad, lateral, groove except in *Spheniscus*, where it is apomorphically narrow and lies medially (Clarke et al., 2003). The sulcus extends distally, straight along the shaft of the bone, and is enclosed proximal to the condyles by the supratendinal bridge to form the extensor canal. The bridge is generally short, but much heightened in *Eudyptes* and *Pygoscelis*, as well as

Procellariiformes, and lies diagonally in *Wimanu*. The extensor canal foramina, which exit the extensor canal proximally and distally, are generally small openings, but is enlarged in a number of taxa, for example, in *Aptenodytes*, some *Eudyptes*, *Anthropornis*, *Palaeospheniscus*, and all outgroups (Emslie and Guerra Correa, 2003). The small, vertical sulcus for the *m. fibularis* lies on the dorsolateral corner of the lateral condyle and extends vertically proximally for a short distance. It is noticeably deepened and elongated in *Eudyptes*, *Eudyptula*, *Megadyptes*, and *Palaeospheniscus*, and lies medially in the two oldest extinct penguins, *Crossvallia* and *Wimanu*.

*Fibula*. The penguin fibula is robust as compared with other avians, especially Procellariiformes (Clarke et al., 2003; Figure 2.20). Each is thickened proximally and extends about three-quarters of the length of the tibiotarsus, where it tapers to a point. The shaft of the bone is sub-rectangular and often ridged longitudinally. The fibula is mediolaterally thick in most penguins and in Podicipedidae, but thin in *Spheniscus*, *Palaeoeudyptes*, the Tierra del Fuego species, most *Eudyptes*, and all other outgroups. This mediolateral width narrows significantly at the dorsal femoral articulation in most penguins and in Procellariiformes (Clarke et al., 2003). The articular surface contacts the large fibular trochlea of the femur as a dorsally concave, horizontal surface, which is flattened in *Wimanu* and in Procellariiformes. The fibula also contacts the tibiotarsus for nearly its entire length. This contact occurs at the dorsalmost tip of the fibula, where its medial surface sutures flatly to the tibiotarsus, as well as along the pronounced fibular crest and at the ventral tip of the fibula. The two bones here suture and sometimes fuse, an intraspecifically variable condition.

*Tarsometatarsus*. The penguin tarsometatarsus, or ankle bone, is the most distinctive element in its skeleton and also the most commonly preserved in the fossil record (Figure 2.21). In some larger species, it is extremely reduced and widened, nearly forming a square, while it is plesiomorphically more elongate and waisted medially in *Wimanu* and the outgroups. As in all birds, the bone comprises the three, fused metatarsals, as well as the single, fused distal tarsal, which forms the proximal portion of the tarsometatarsus, or the hypotarsus. The dorsal surface of the bone is thus composed of the hypotarsus proximally, the three fused metatarsals in the midsection, and the trochleae distally. Deep grooves separate the metatarsals and contain various vascular foramina of high variability, regarding their presence, location, and size. Proximally, the ventral, or plantar, surface contains the lateral and medial hypotarsal crests.

In penguins, the width of each tarsometatarsus is less than half its height (Figure 2.21). In Spheniscidae + *Palaeospheniscus*, the bone is widened to be equal to or greater than half of its height, although this condition is lost a number of times (e.g., in some palaeospheniscines). The bone is much greater than one quarter the length of the tibiotarsus in all outgroups, but only one quarter this length in penguins and less than one quarter in Australodyptinae and *Palaeospheniscus*. The actual length of the tarsometatarsus may be divided into four size classes: small, as in all living taxa except *Aptenodytes*; medium, as in *Aptenodytes* and most extinct species; large, as in a few extinct taxa; and extra large, as in all outgroups and the largest extinct species (*Anthropornis*, *Palaeodyptes klekowskii* and *Palaeodyptes marplesii*). The width of the ankle bone also varies within penguins and may be either thin or thick.

Proximally, the hypotarsus forms the flattened, rectangular, articular surface (Figure 2.21d). Compared with all outgroups, it is enlarged in penguins, extremely so in *Aptenodytes*, *Eudyptes*, *Anthropornis*, *Delphinornis*, and *Paraptenodytes*. The ligamental sulcus, which is reduced in *Archaeospheniscus*, cuts into the plantar edge of the hypotarsus, extending from the intercotylar area to the lateral edge of the bone. It just underlies the intercotylar eminence, which is expanded laterally in penguins (contra Bertelli and Giannini, 2005). This protuberance is generally wide and upraised, although not in some extinct species. Underlying the eminence, just dorsomedial to the ligamental sulcus, is the intercotylar area, or depression, which is reduced in penguins. The medial cotyle, which articulates with the tibiotarsus, is often deeply depressed, although some taxa have flat articulations (e.g., Australodyptinae, *Eudyptula*, and extinct taxa from Chile and from Seymour Island).

Just ventral to the cotyles, the dorsal surface of the tarsometatarsus is excavated by the lateral and medial infracotylar fossae (Figure 2.21b). These are smaller and shallower than in other avians, although distinct in some taxa, such as *Eudyptes*, *Megadyptes*, *Spheniscus*, *Marambiornis*, and some *Palaeudyptes*. The three metatarsal shafts are usually prominent, distinctly grooved, and straight. However, the shaft of metatarsal two is distinctly medially curved in Paraptenodytidae and in crown-penguins. In *Anthropornis*, the medial edge of this metatarsal is neither straight nor concave, but wavy in outline. The remaining metatarsals are always straight, except in *Archaeospheniscus lopdelli* and *Dunroonornis*, in which all three curve medially and give the bone a convex lateral margin. In *Wimanu*, the fourth metatarsal is deflected

posteriorly similar to penguin outgroups. Proximally, the medial edge may form a distinct convexity or a V-shaped groove in some extinct species. This surface contains the tubercle for attachment of the *m. tibialis cranialis*, which is distinct in most birds, but varies both in shape and in location in penguins. It is generally absent in penguins, present as a small, elongate process in Paraptenodytidae and many crown-penguins, and prominent and round in *Wimanu* and in the clade (Australodyptinae + *Eudyptes* + *Megadyptes*). The tubercle lies somewhat distally on metatarsal three, but proximally in most paraptenodytids and distally in some pygoscelids.

Ventrally, the trochleae of penguins are rectangular and enlarged, the third of them the most (Figure 2.21c). They are particularly enlarged in Australodyptinae, a clade comprising nearly all palaeodyptids, and *Wimanu*. The trochlea of metatarsal three is enlarged beyond the other two in all penguins except Paraptenodytidae and in Procellariiformes. The second trochlea is medially inflected in all taxa except *Eudyptula* and *Paraptenodytes*, whether or not the second metatarsal is curved medially. If so inflected, it may have a strongly concave medial border, as in numerous palaeodyptids. In penguins, this trochlea extends only as far as that of metatarsal four and not as far as that of metatarsal three. However, the second metatarsal is longer than the fourth in the clade (Spheniscidae + Palaeospheniscus). Only in *Delphinornis gracilis* is the fourth metatarsal longer than the second. The intertrochlear distance is small in most penguins, but widened somewhat in *Megadyptes*, some *Eudyptes*, and some *Spheniscus*, as well as in a few extinct species. The two intertrochlear incisions are generally equal in size, although the lateral is larger in *Megadyptes* and most *Eudyptes*. The collateral ligament

foveae, which indent the second and fourth metatarsal trochleae medially and laterally, are reduced in penguins.

Dorsally, the lateral and medial intermetatarsal grooves and vascular foramina were historically instrumental in determining penguin phylogenetics and taxonomy (e.g., Simpson, 1946; Marples, 1952; Myrcha et al., 2002). The lateral intermetatarsal groove is deep in penguins, although lost in some outgroups, and is shallowed in *Wimanu*, *Paraptenodytes*, the clade (Spheniscidae + *Palaeospheniscus*), and Australodyptinae (Figure 2.21e). The groove also shallows distally in *Delphinornis*, *Duntroornornis*, and most *Palaeodyptes*. Like the lateral groove, the medial groove is generally deep. This occurs in Palaeodyptidae, *Wimanu*, and a clade of paraptenodytids, and is deepened in Spheniscidae. Both grooves are absent in all outgroups and in some *Duntroornornis* and *Palaeospheniscus* species.

One vascular foramen lies proximally in each intermetatarsal groove, and one lies distally in the lateral groove (Figure 2.21a, c). The lateral intermetatarsal foramen is ubiquitous (except in '*Nucleornis hendeyi*' and possibly *Eretiscus tonii*), and often opens plantarly as well, although the plantar opening is absent in *Marambiornis* and *Paraptenodytes*. The dorsal opening is small in most species and large in *Aptenodytes*, some *Delphinornis*, *Mesetaornis*, *Tasidyptes*. It lies proximally, although the opening lies far distally in both *Aptenodytes* and Procellariiformes and in between these two locations in *Eudyptula*, some *Spheniscus*, and a number of extinct species. The foramen is oval in all outgroups and extant species, but circular in a number of extinct taxa. In some species of *Delphinornis*, some of *Palaeodyptes*, and some of *Palaeospheniscus*, the lateral

foramen lies in a pit deeply excavated into the lateral groove. The other proximal vascular foramen lies medially, but is lost in *Eretiscus*, some *Palaeospheniscus*, *Spheniscus chilensis*, and Procellariiformes. The opening is small in most taxa, but only forms a pit in the taxa *Chubutodyptes*, some *Delphinornis*, *Dunroonornis*, and *Palaeodyptes*. It is enlarged in some *Aptenodytes*, some *Archaeospheniscus*, *Delphinornis larseni*, and *Mesetaornis* (modified from Bertelli and Giannini, 2005). The plantar opening of this foramen is present in all genera except *Palaeodyptes*. Medially, a small crista flanks the foramen diagonally in *Eudyptula*, *Spheniscus*, *Delphinornis*, *Ichthyopteryx*, and *Palaeospheniscus* (Myrcha et al., 2002).

The two proximal foramina are the same size in penguins, although the lateral is larger in a clade containing most palaeodyptids, in the clade (Spheniscidae + *Palaeospheniscus*), in the clade (*Paraptenodytes* + *Marambiornis*), and in most outgroups. In *Anthropornis* and a few small clades, the medial is favored in size. These two foramina lie close together in penguins, but are widely separated in *Anthropornis*. They lie somewhere in between in the great majority of species (Myrcha et al., 2002). Plantarily, the medial foramen opens near the medial hypotarsal crest, in relation to which it lies medially in penguins. This positioning differs, however, and may occur with the foramen lying lateral or ventral to the crest. Finally, the distal vascular foramen is autapomorphic within penguins, being present only in *Marambiornis*, *Mesetaornis*, some *Delphinornis*, and *Wimanu*.

Proximally, the plantar surface of the tarsometatarsus contains the medial and lateral hypotarsal crests, which are slender in most species, but robust in *Eudyptula*,

*Spheniscus*, *Inguza*, and *Palaeudyptes* (e.g. Figure 2.21a, e). The crests form a distinct sulcus for passage of the flexor tendons in *Paraptenodytes* and in some outgroups (modified from Myrcha et al., 1990; Clarke et al., 2003). Their total size is smaller than in the outgroups, however, although they are enlarged in a clade of palaeudyptids (including *Archaeospheniscus*) and in Spheniscidae. A third, intermediate, crest is present only in *Marambiornis*, *Paraptenodytes*, and Procellariiformes (Myrcha et al., 1990). The crests are generally parallel and extend along the proximal third of the bone. They converge ventrally to a V in the clade (Spheniscidae + *Palaeospheniscus*) and in *Paraptenodytes*, although this character is lost a number of separate times. The medial crest is vertically elongate and longer than the lateral one, which lies horizontally. The medial crest slants slightly towards the medial margin in the extinct taxa *Delphinornis*, *Korora*, *Spheniscus urbinai* only. The hypotarsal crests are often divided by deepened hypotarsal grooves, which are present in nearly all species as well as some outgroups. They are usually wide, but are narrow in *Ichtyopteryx*, ‘*Inguza*’, *Mesetaornis*, *Palaeudyptes*, and *Palaeospheniscus*. A lateral pit, or lateral parahypotarsal fossa, flanks the lateral crest in most paraptenodytids and in *Eretiscus* and *Korora*. The supratrochlear fossa is present in some taxa (Australodyptinae, *Eudyptes*, and *Archaeospheniscus*), where it is shallow and lies dorsal to the medial intertrochlear incision, on the plantar surface of the bone.

*Pedal Phalanges.* The pedal phalanges in penguins are typical of other avians. There are three phalanges present on digit two, four on digit three, and five on

digit four. All are tubular, straight, and fairly short. The hallux is absent, as in all outgroups (Mayr and Clarke, 2003).

## **Discussion**

Although phylogenetic and morphological work historically concentrated on the variation present within a few skeletal elements only, notably the humerus and tarsometatarsus, it is shown here that phylogenetic variation is present in nearly all elements of the penguin skeleton. While there are certainly more phylogenetically informative characters in bones such as the tarsometatarsus, even those such as the ribs or laterosphenoid vary among species. This is important because identification and naming of extinct species generally proceeded using only two bones, with numerous taxa erected solely from single elements. This problem may not always be solved, as the majority of penguin fossils are isolated, non-comparable elements. However, based on the results of this work, I recommend that formal naming of extinct taxa should at least attempt to identify characters from all available elements. Additionally, nearly all the diagnoses of extant species exclude osteological characters. There is indeed much more variation within the integument and behavior of extant taxa than within their osteology, but it is here seen that living genera and even species may be differentiated using a number of skeletal elements, and future revision should incorporate this fact into the diagnoses of extant taxa.

Interspecific variation in penguins is much lower than that between various genera, which are all osteologically distinct. Recent work in phylogenetics showed that the category 'genus' is not always monophyletic, especially within avians, but it seems

that the taxonomy of living penguins is one example that does accurately reflect natural groups. Future phylogenetic work will show that the six penguin genera are indeed monophyletic, although this assumption is probably vastly incorrect for extinct taxa (Triche, Chapter 3). It is more difficult to differentiate penguin species using osteology alone, however, and the overlap in variation between some species suggests that genera such as *Eudyptes* and *Spheniscus* are only recently separated evolutionarily. Additionally, although this study did not examine sufficient samples of each species to quantify all such variation, enough was observed in the material available to suggest that much intraspecific variation exists within penguins. Future work on the extent of osteological variation should quantify the precise morphological limits of these species and help determine sub-specific and specific taxonomic categories.

It is shown here that, while penguins do form an anatomically conservative group, this clade also possesses much morphological variation, particularly within extinct taxa. While some extinct species, such as the palaeospheniscids, are more similar to extant taxa, the variation of others, such as *Parapterodytes*, the palaeoeudyptids, and especially *Wimanu*, includes a broad size range, differing body proportions, and much variation in the more minor anatomical structures of various skeletal elements. Because major variation exists between living species and the older extinct penguins, not so much within the extant group, Spheniscidae, as well as Sphenisciformes, is probably monophyletic and the group as a whole probably agrees well with the stratigraphy of the rock record. Within the living penguins, variation is on a much smaller scale, including such things as

smaller ranges in the size of elements, but not presence or absence of structures or elements or much similarity to penguin outgroups.

The osteological morphology and variation of penguins is now described, both for living and extinct species. It should now be possible to incorporate should now be able to incorporate much more anatomy and morphological detail into the cladistic matrices of future morphology-based phylogenetic work. This description may also serve in fossil identification, allowing determination of whether a fossil specimen is or is not a penguin and to which living or extinct species it belongs. Future work on penguin anatomy should include more detailed description of particularly complete, extinct taxa (e.g., *Wimanu*; Ando, pers. comm.), and analysis of the variation among problematic, sub-specific taxa (e.g., the *Eudyptula minor* complex). Additionally, more specific comparison of penguin anatomy with that of their prospective outgroups, combined with similarly detailed description of such outgroups, should allow determination of where penguins fit within the avian tree. This completed description of the osteology and character states of penguins is an important step towards placing these fascinating birds in the broader context of avian, phylogenetic history.

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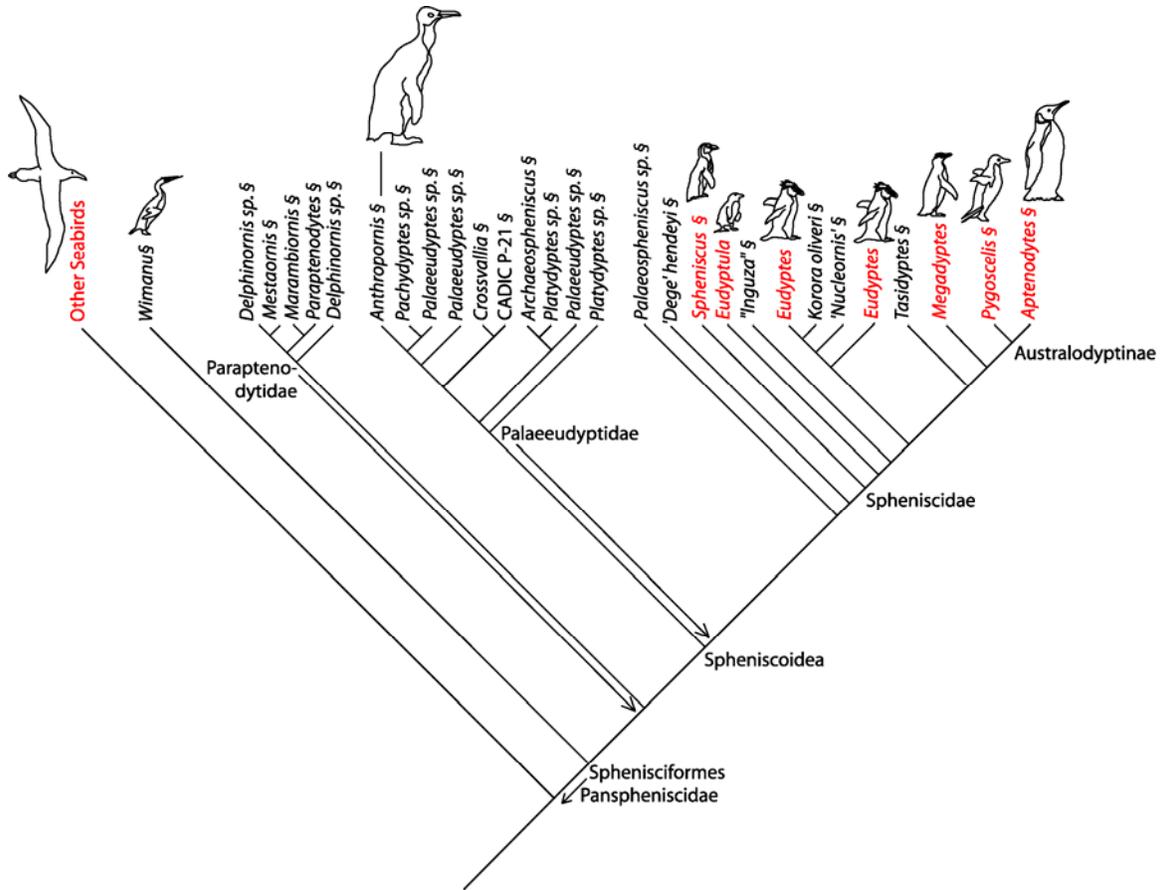
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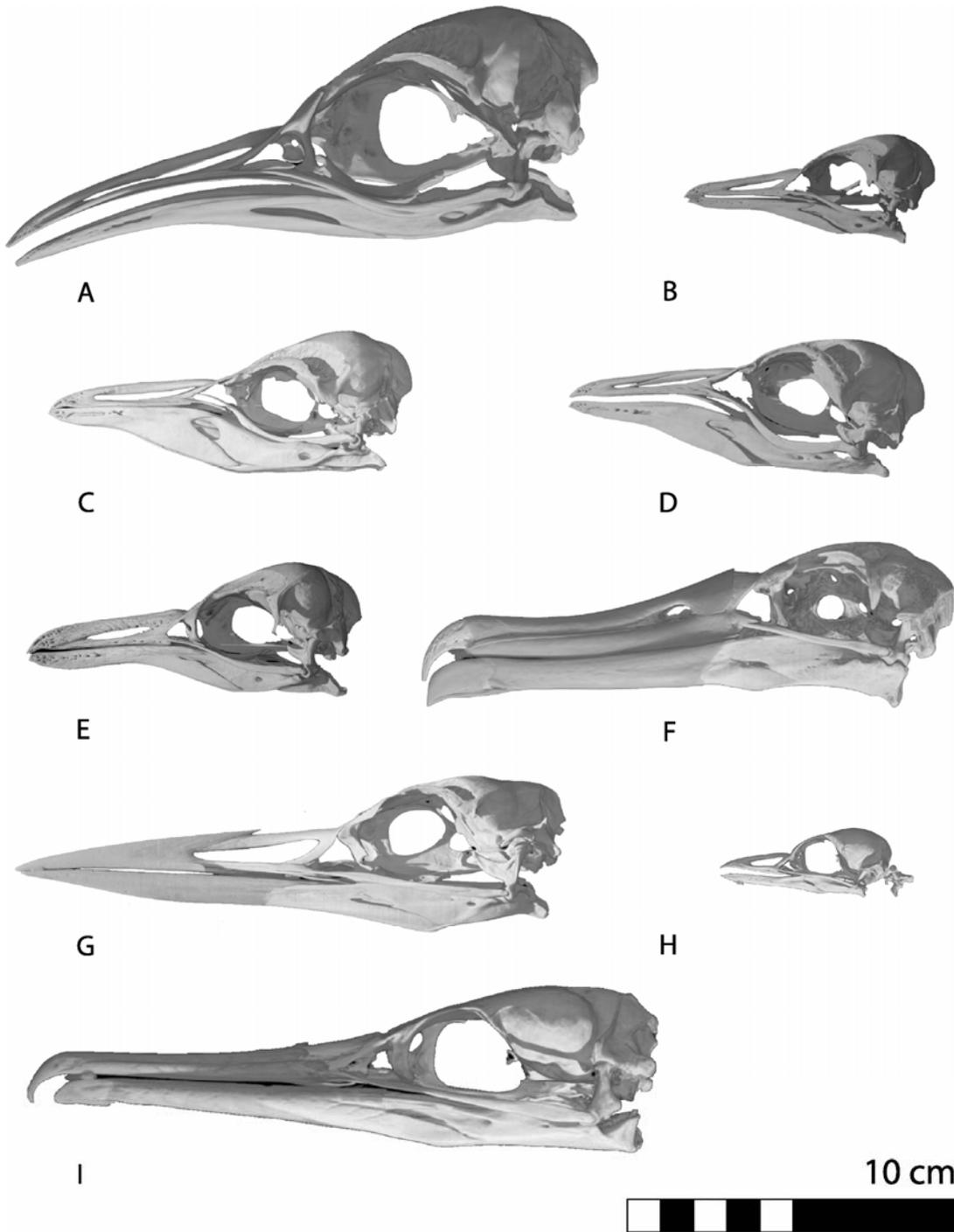
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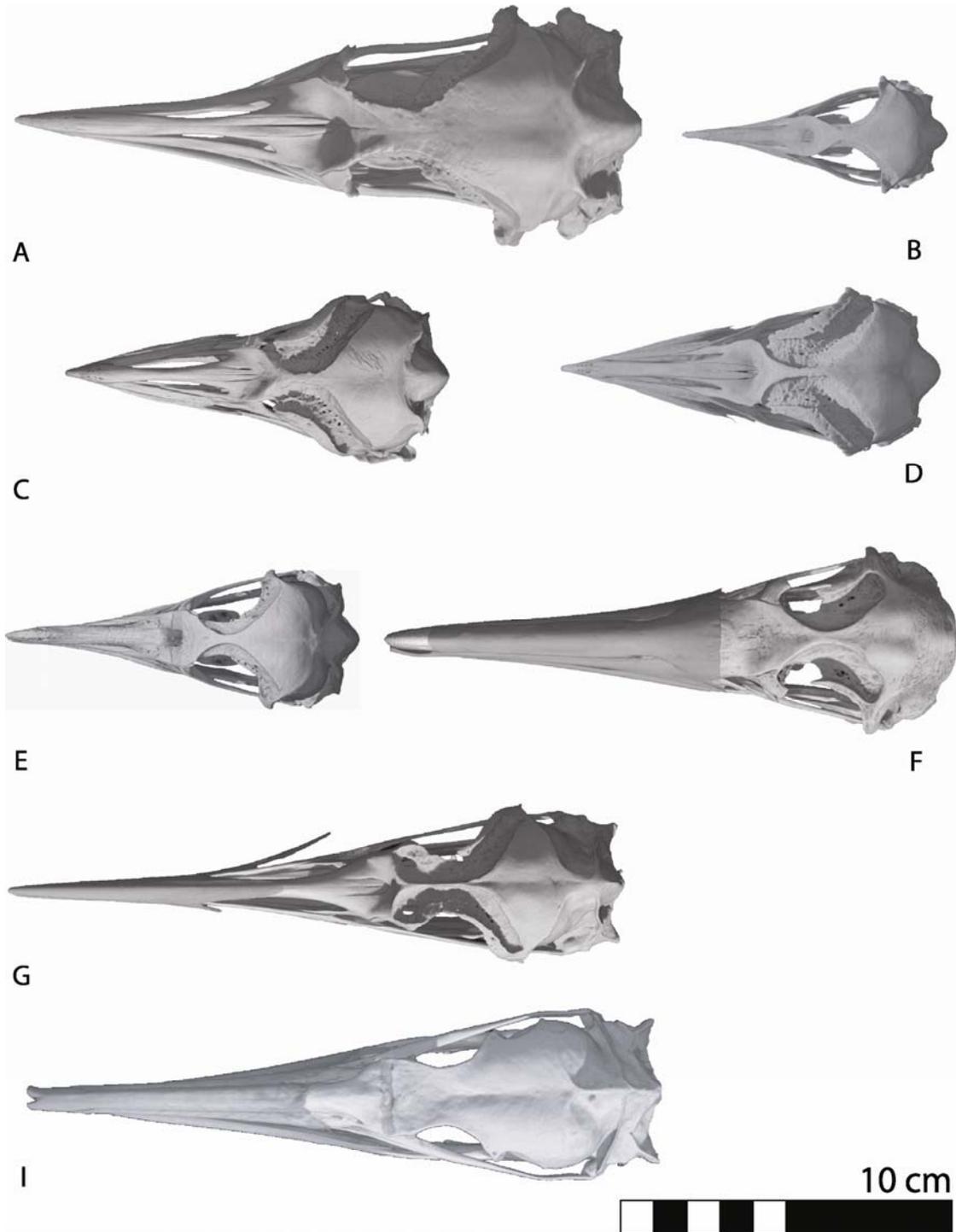
**Figure 2.1. Phylogeny of Extinct and Extant Penguin Species.** Simplified from a cladogram depicting the relationships of all penguin species (Triche, Chapter 3). Extinct taxa are indicated by §, extant taxa are in red. Arrows indicate stem-based names, all other names are node-based.



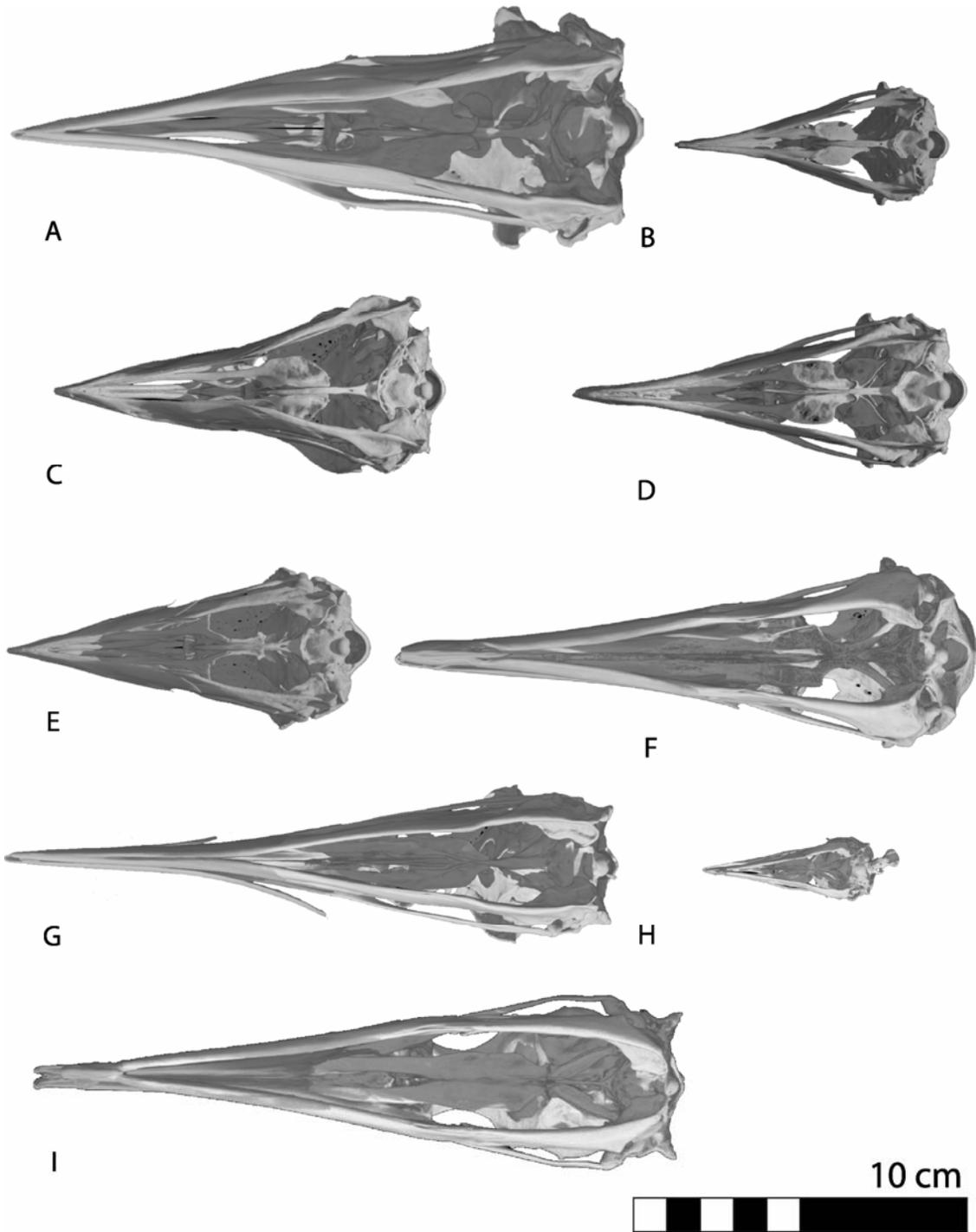
**Figure 2.2. Lateral View of CT Scans of Outgroup and Spheniscid Skulls.** A. *Aptenodytes forsteri*. B. *Eudyptula minor*. C. *Pygoscelis adeliae*. D. *Pygoscelis antarctica*. E. *Spheniscus demersus*. F. Procellariiformes: *Diomedea immutabilis*. G. Gaviidae: *Gavia immer*. H. Podicipedidae: *Podilymbus podiceps*. I. Phalacrocoracidae: *Phalacrocorax pencillatus*.



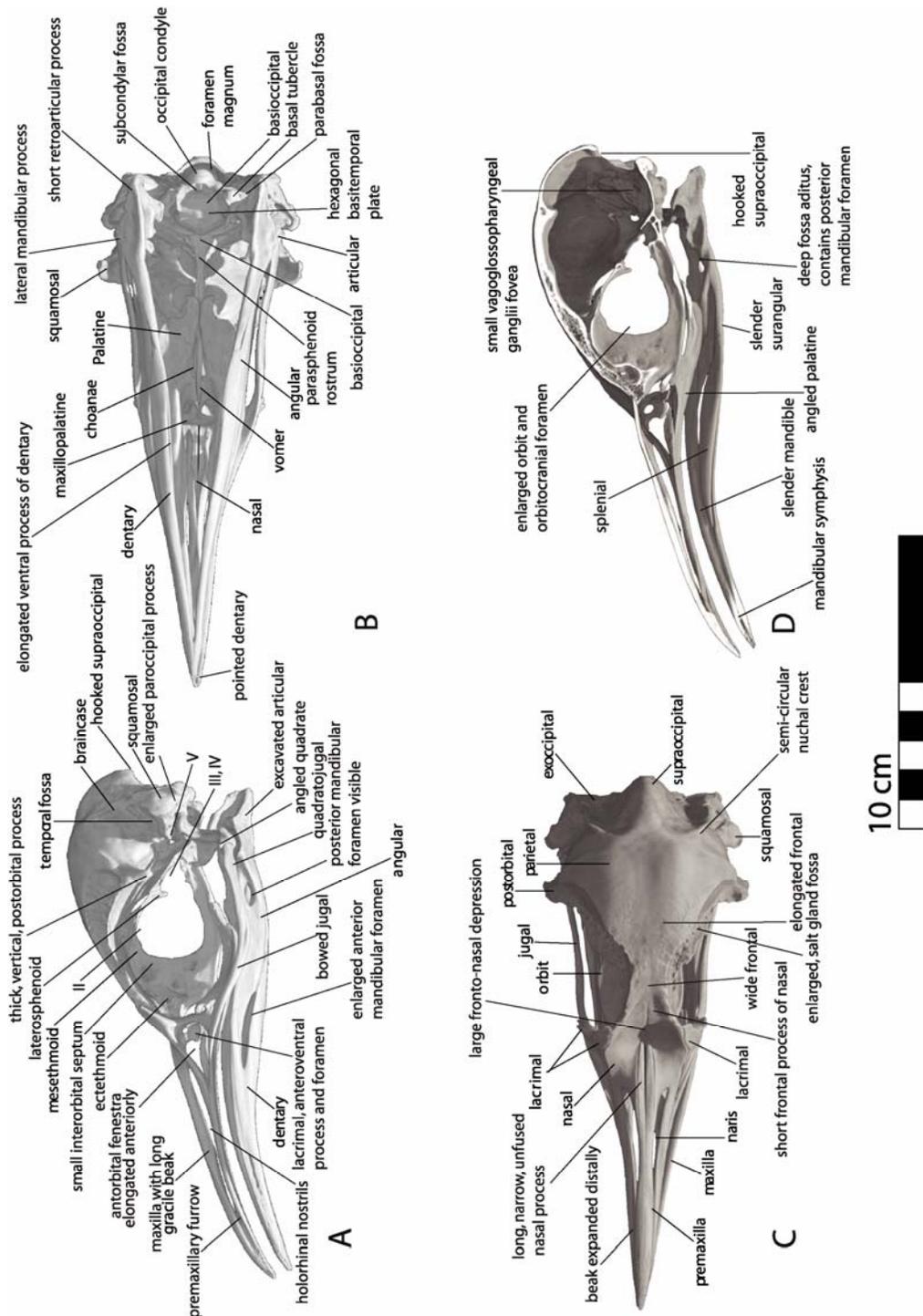
**Figure 2.3. Dorsal View of CT scans of Outgroup and Spheniscid Skulls.** A. *Aptenodytes forsteri*. B. *Eudyptula minor*. C. *Pygoscelis adeliae*. D. *Pygoscelis antarctica*. E. *Spheniscus demersus*. F. *Diomedea immutabilis*. G. *Gavia immer*. H. *Podilymbus podiceps*. I. *Phalacrocorax pencillatus*.

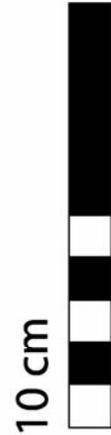
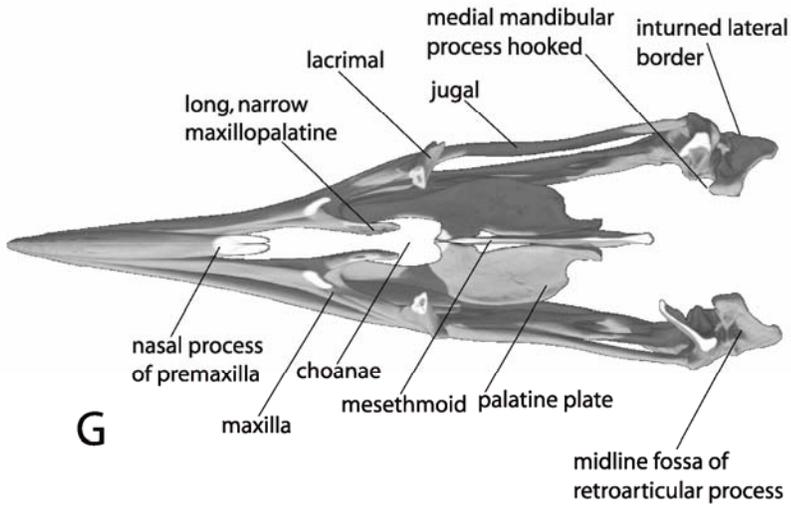
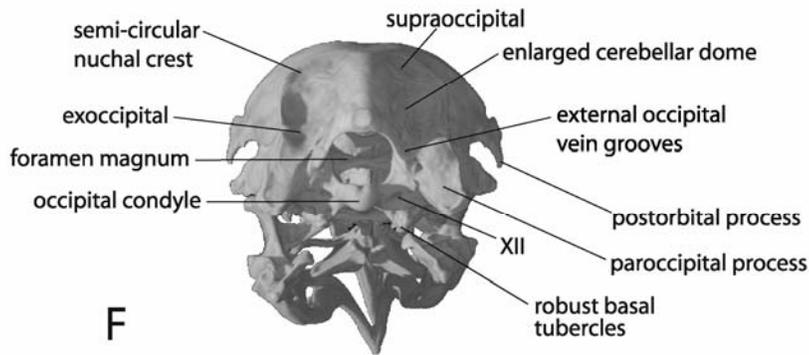
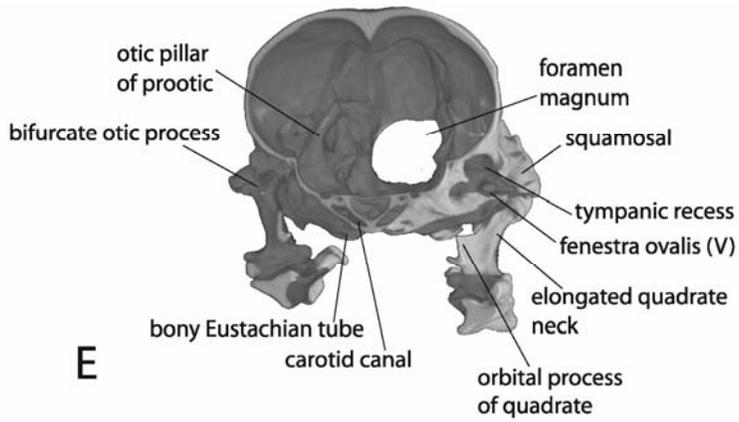


**Figure 2.4. Ventral View of CT Scans of Outgroup and Spheniscid Skulls.** A. *Aptenodytes forsteri*. B. *Eudyptula minor*. C. *Pygoscelis adeliae*. D. *Pygoscelis antarctica*. E. *Spheniscus demersus*. F. *Diomedea immutabilis*. G. *Gavia immer*. H. *Podilymbus podiceps*. I. *Phalacrocorax pencillatus*.

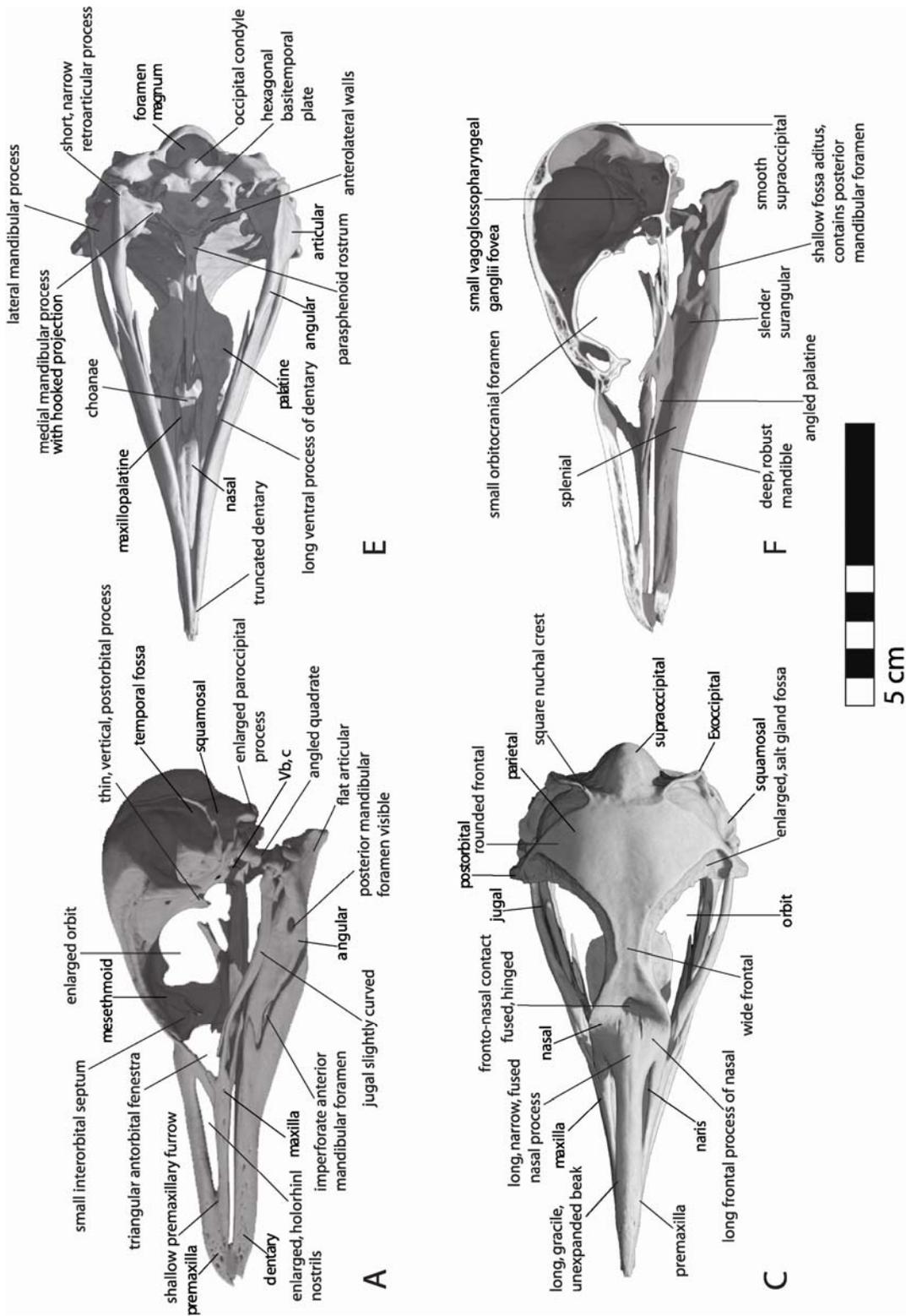


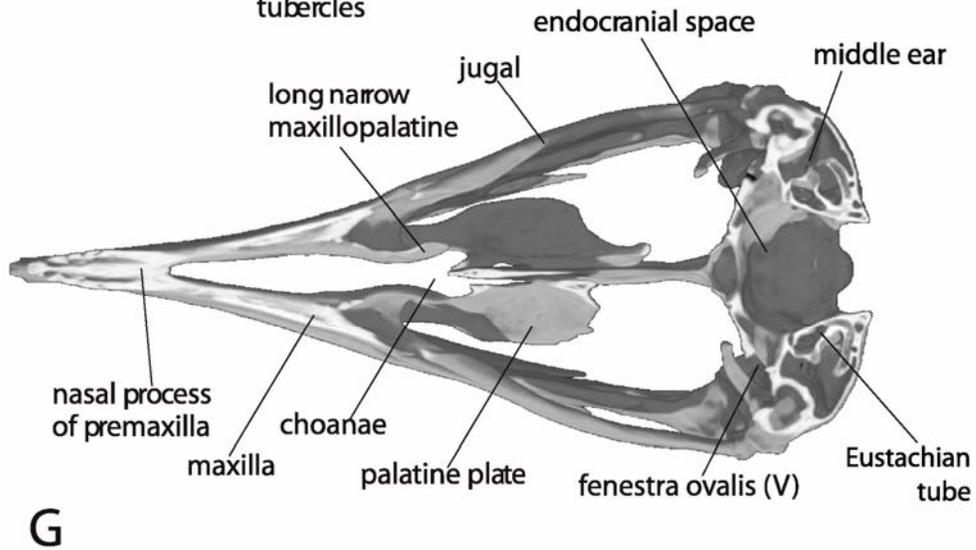
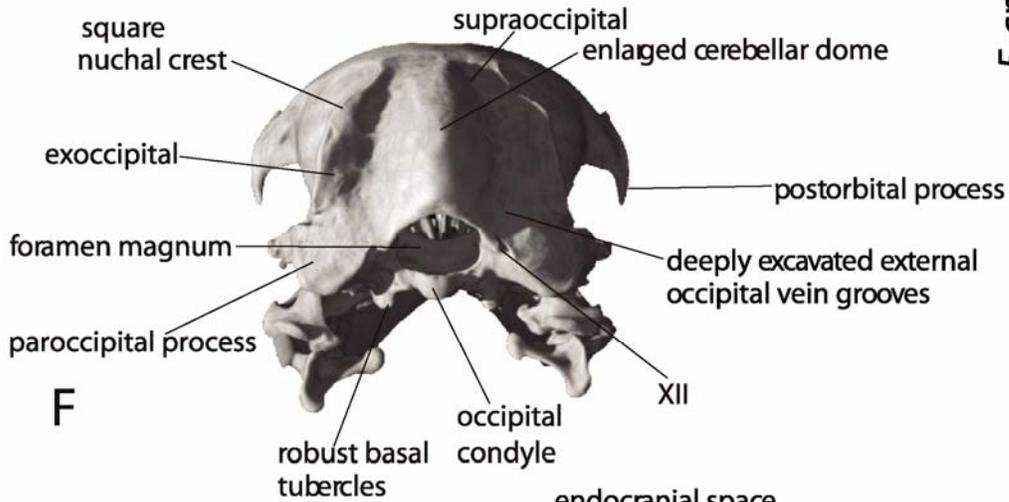
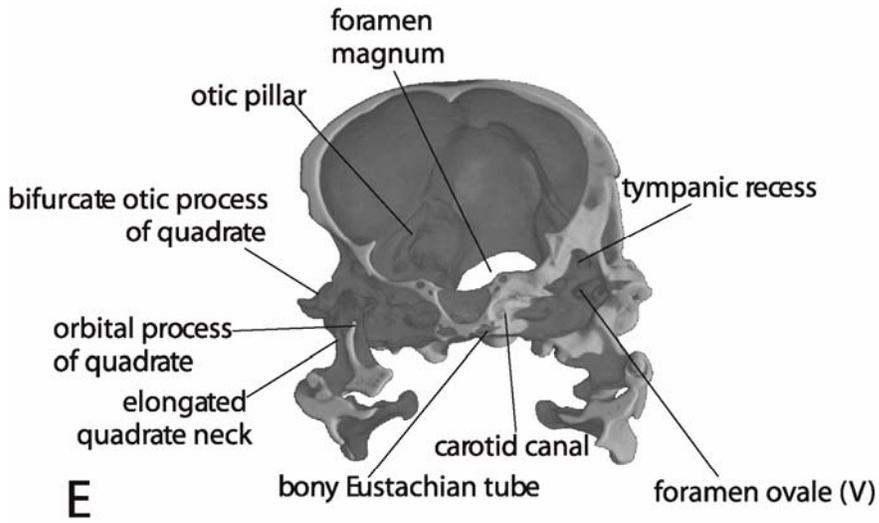
**Figure 2.5. Seven-view of Skull of *Aptenodytes forsteri*.** A. Lateral view. B. Ventral view. C. Dorsal view. D. Sagittal cut-away, showing lateral view of braincase and nasal passage. E. Coronal cut-away, showing anterior view of braincase at level of Eustachian tubes. F. Posterior view. G. Horizontal cut-away, showing dorsal view of palate.



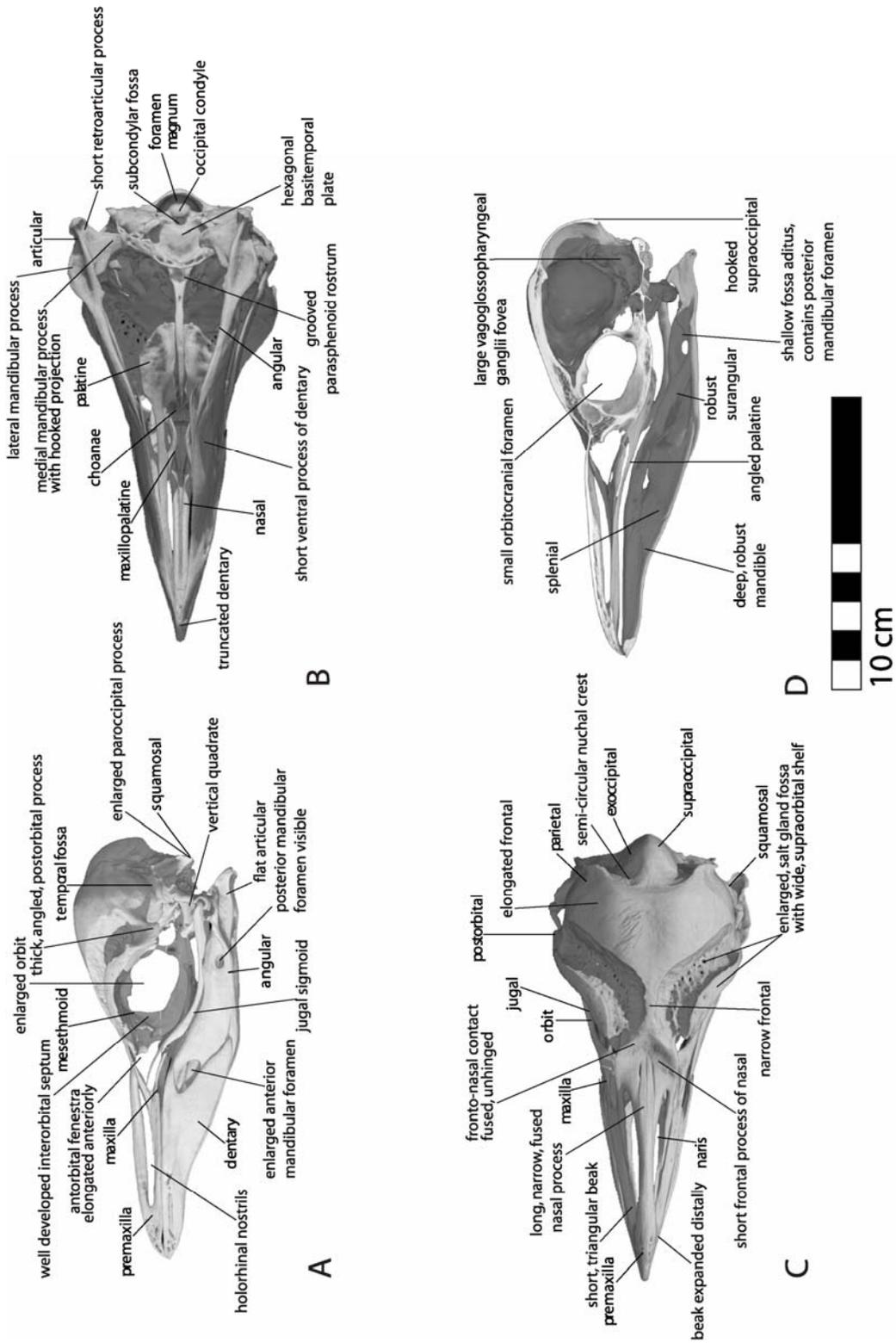


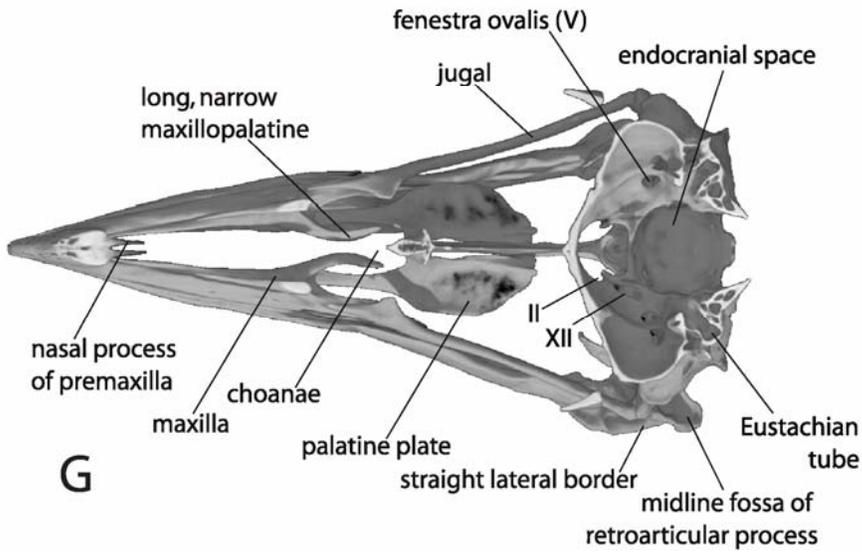
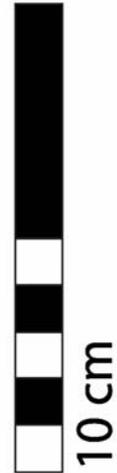
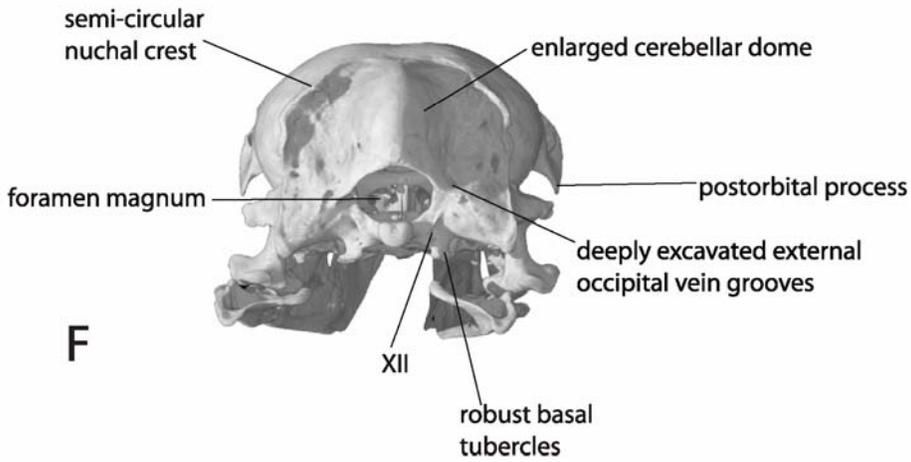
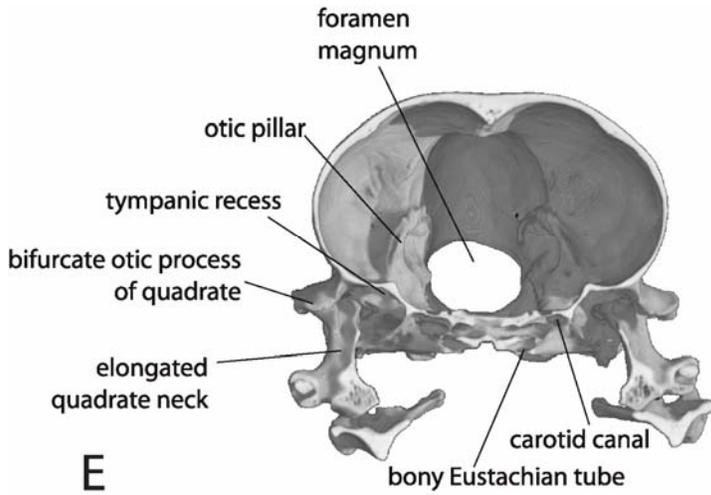
**Figure 2.6. Seven-view of Skull of *Eudyptula minor*.** Views as for Figure 2.5.



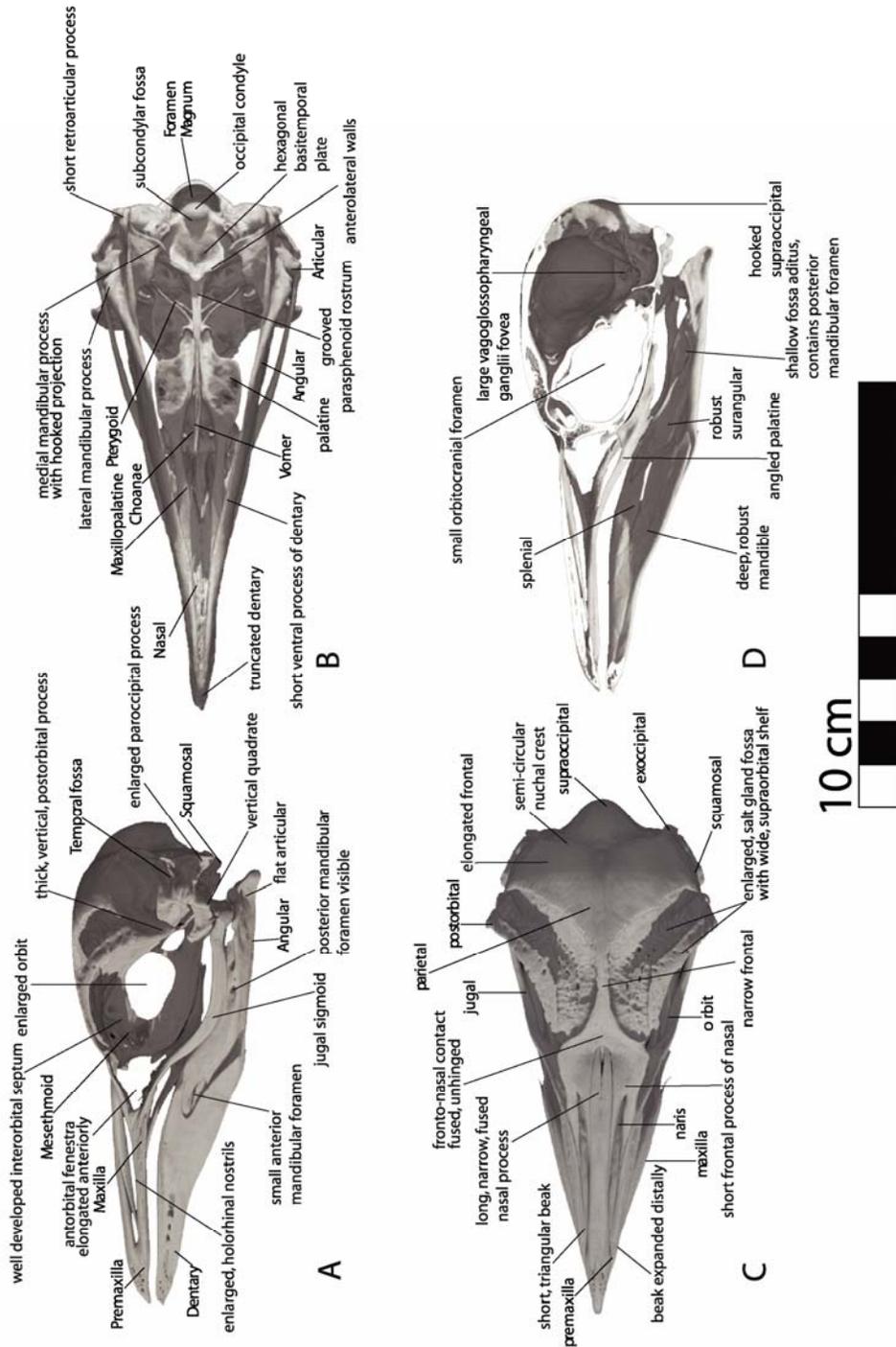


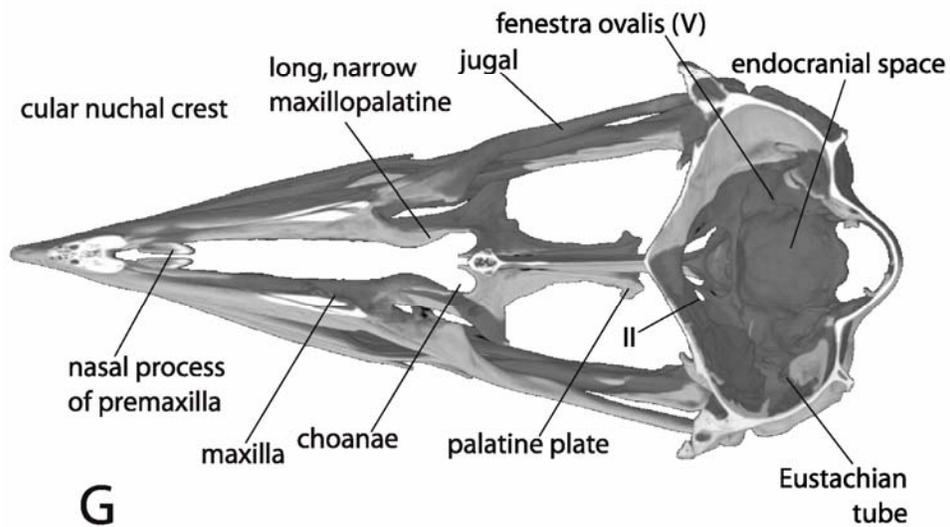
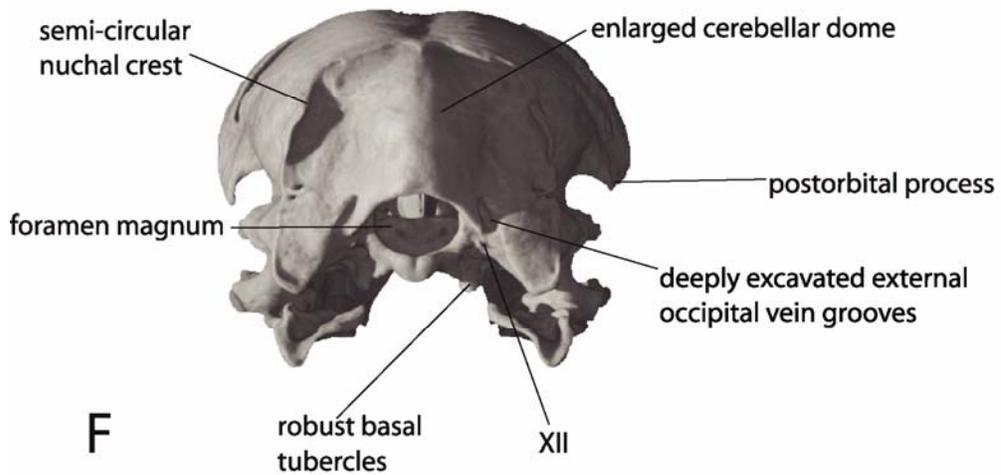
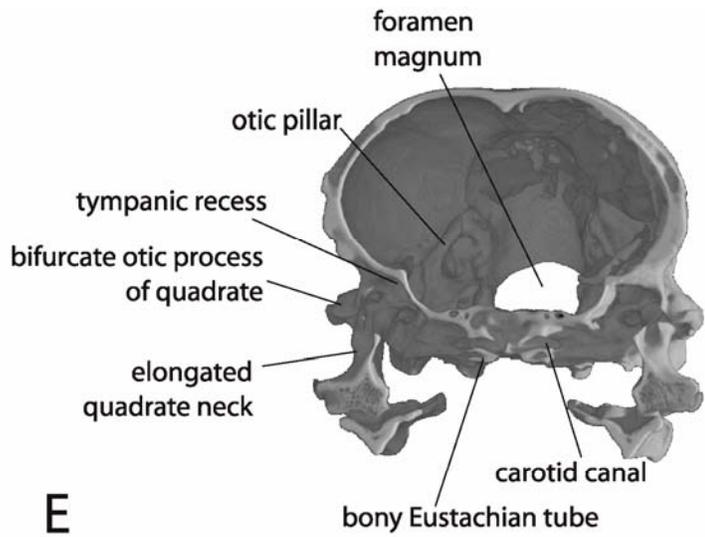
**Figure 2.7. Seven-view of Skull of *Pygoscelis adeliae*. Views as for Figure 2.5.**



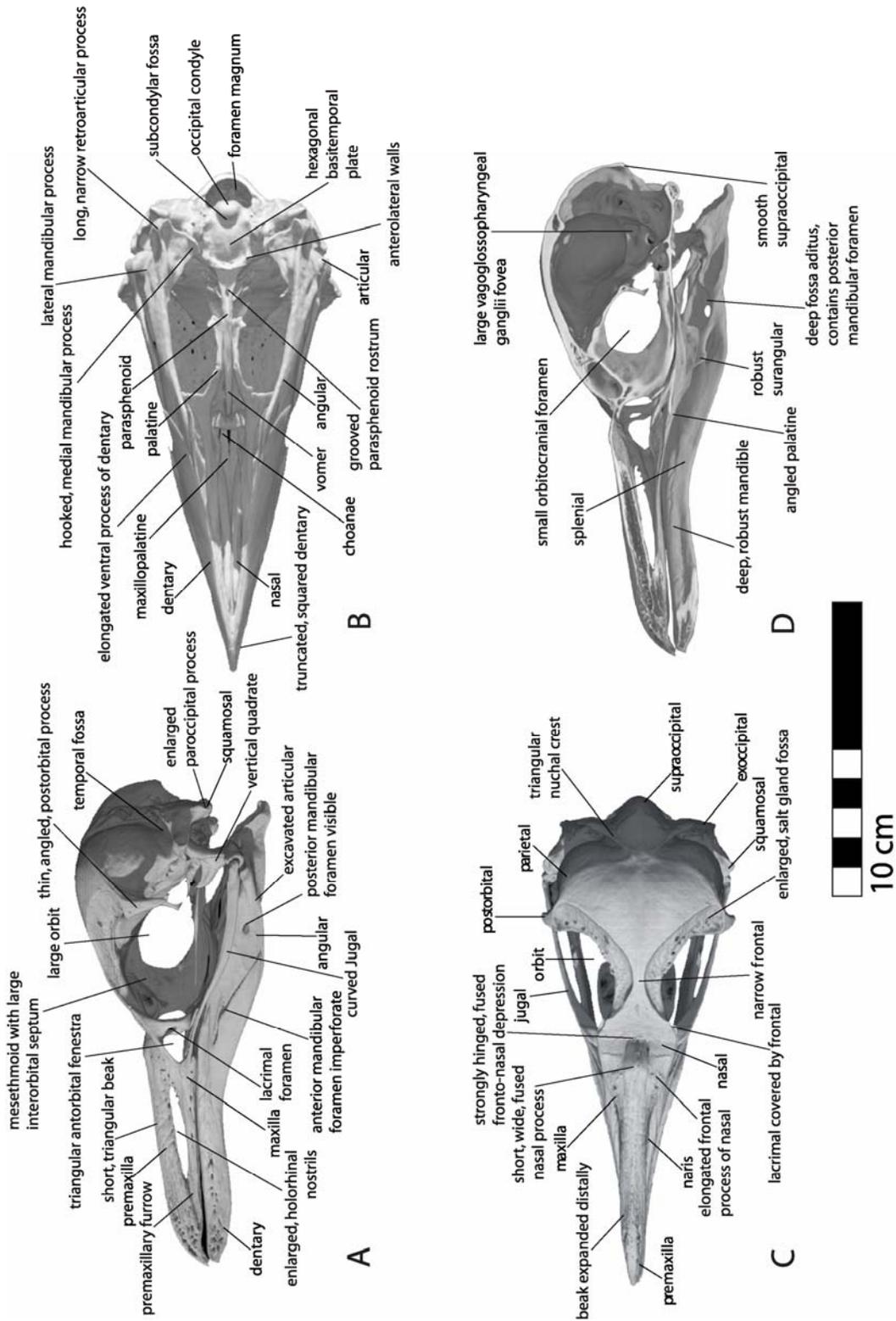


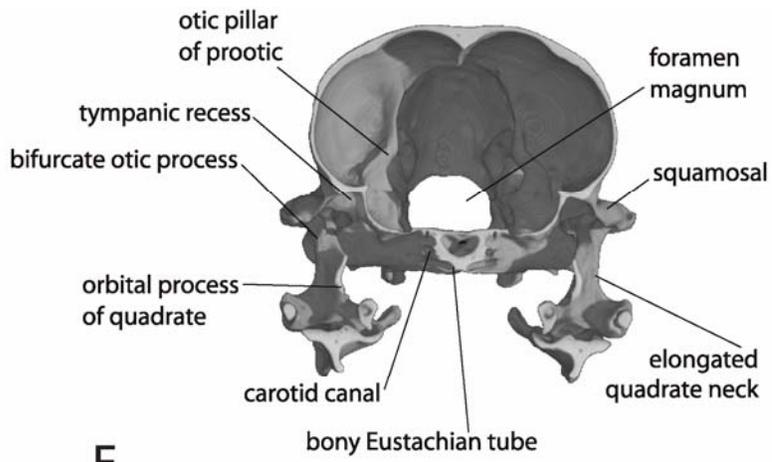
**Figure 2.8. Seven-view of Skull of *Pygoscelis antarctica*.** Views as for Figure 2.5.



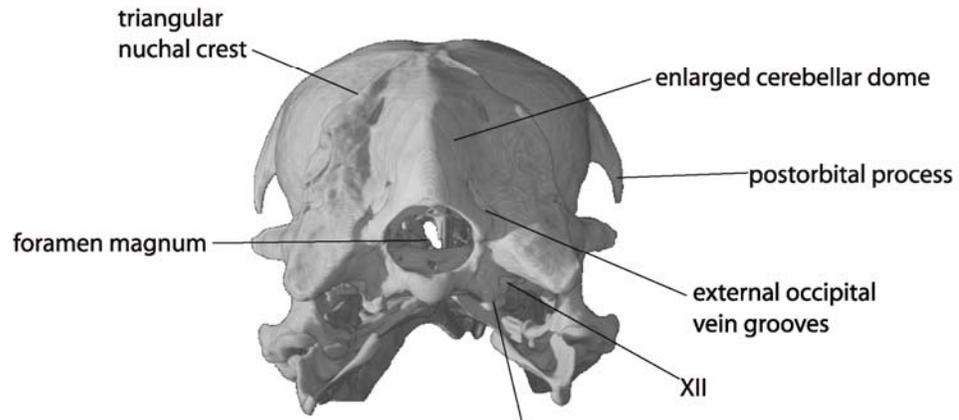


**Figure 2.9. Seven-view of Skull of *Spheniscus demersus*.** Views as for Figure 2.5.





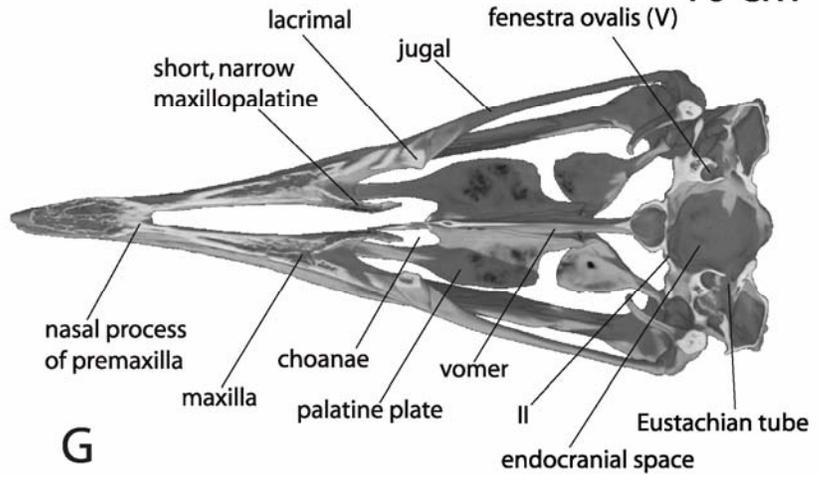
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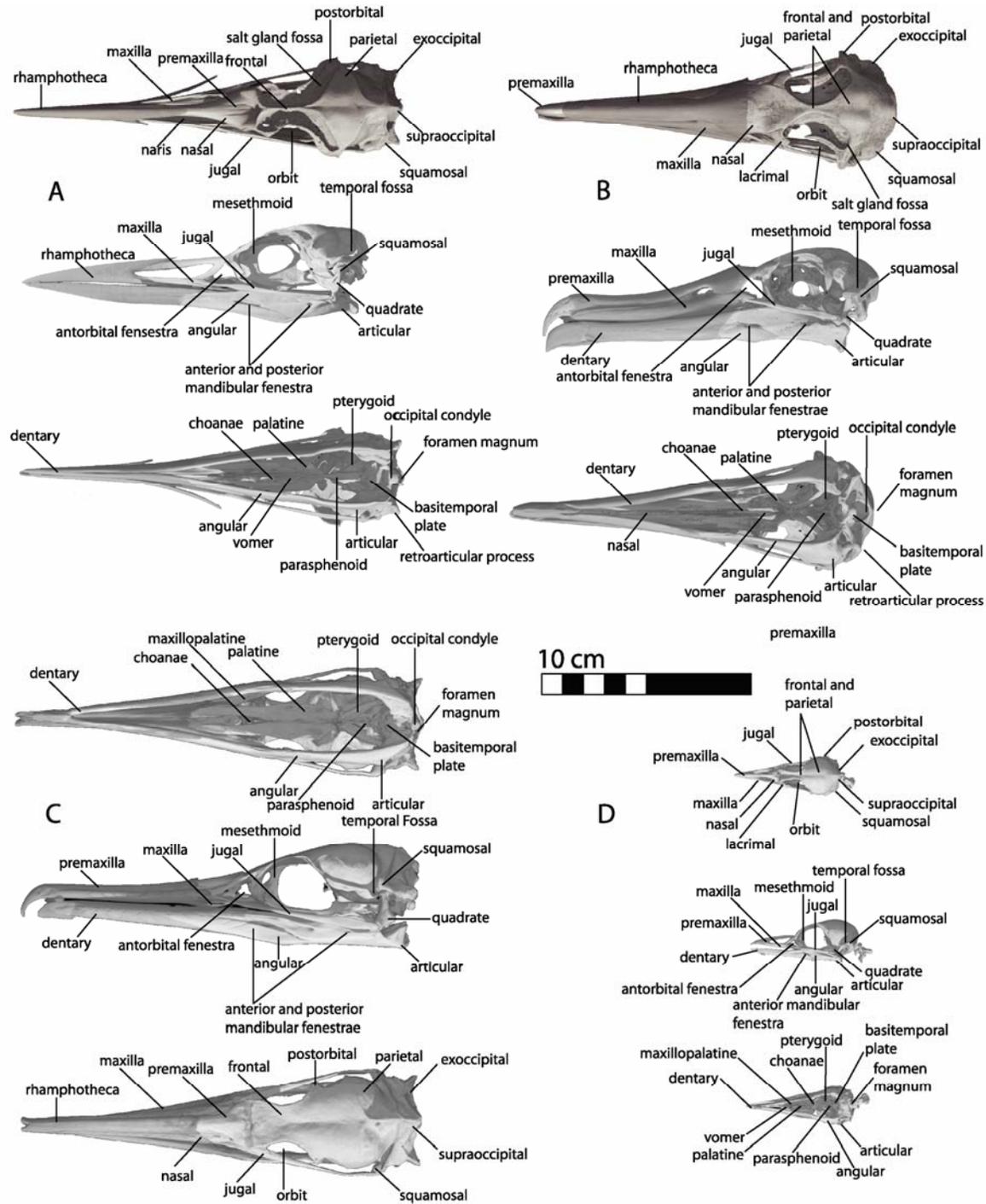


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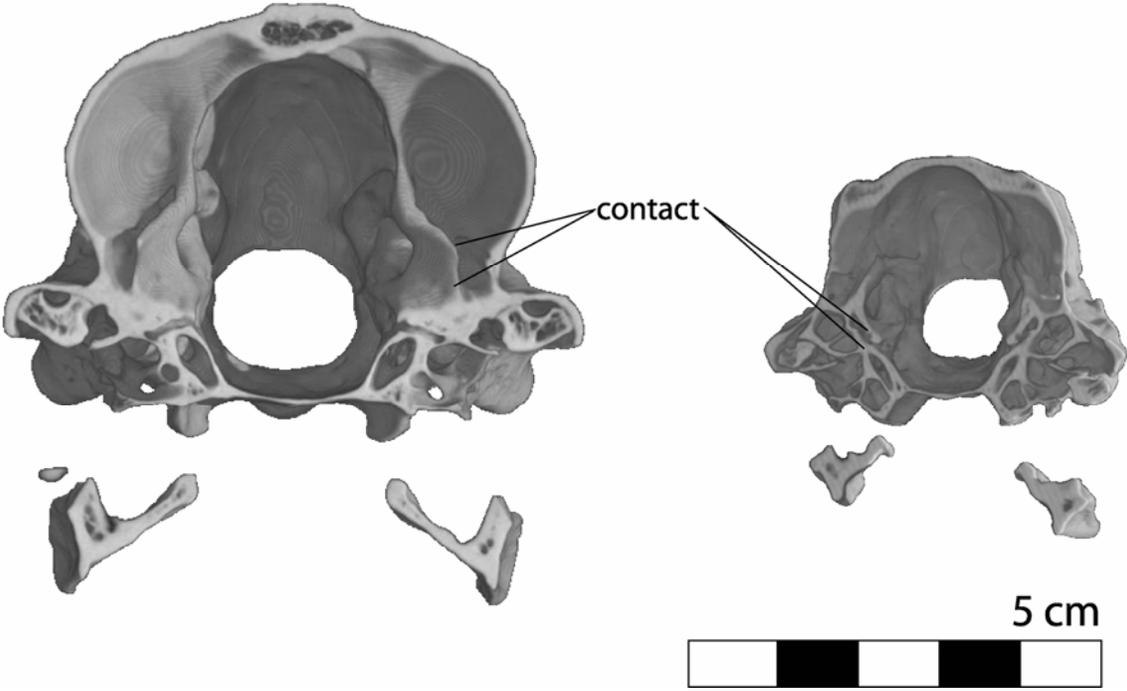


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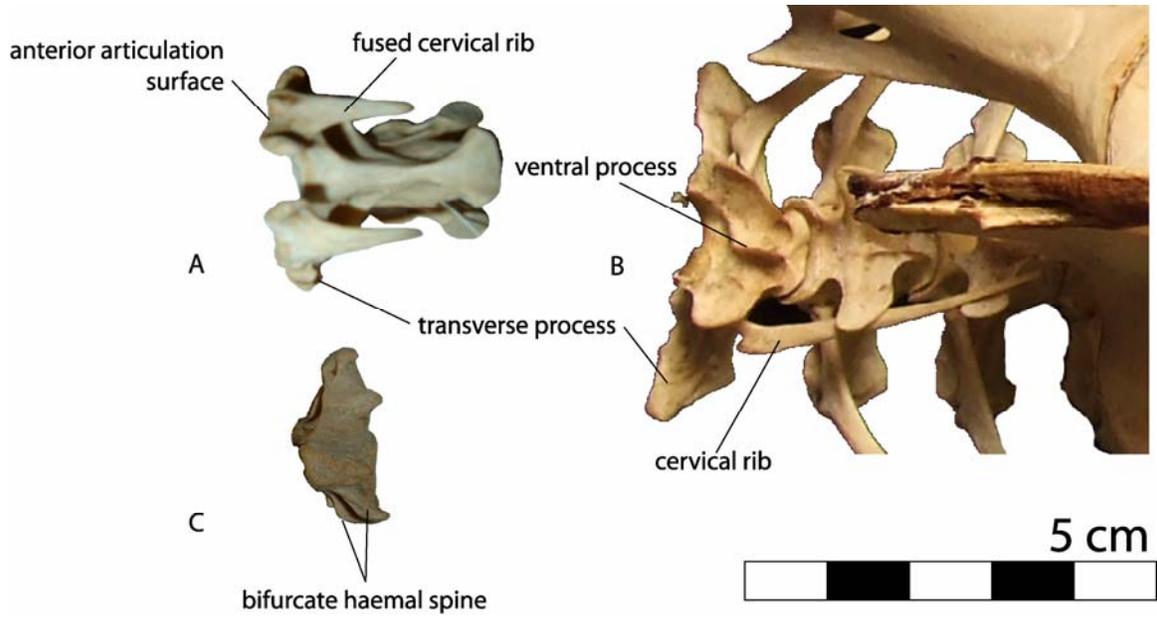
**Figure 2.10. Dorsal, Lateral, and Ventral Views of Skulls of Outgroup Specimens. A.** *Gavia immer* (TCWC 13300). **B.** *Diomedea immutabilis* (FLMNH 313780). **C.** *Phalacrocorax pencillatus* (TMM M-1180). **D.** *Podilymbus podiceps* (TMM M-7139).



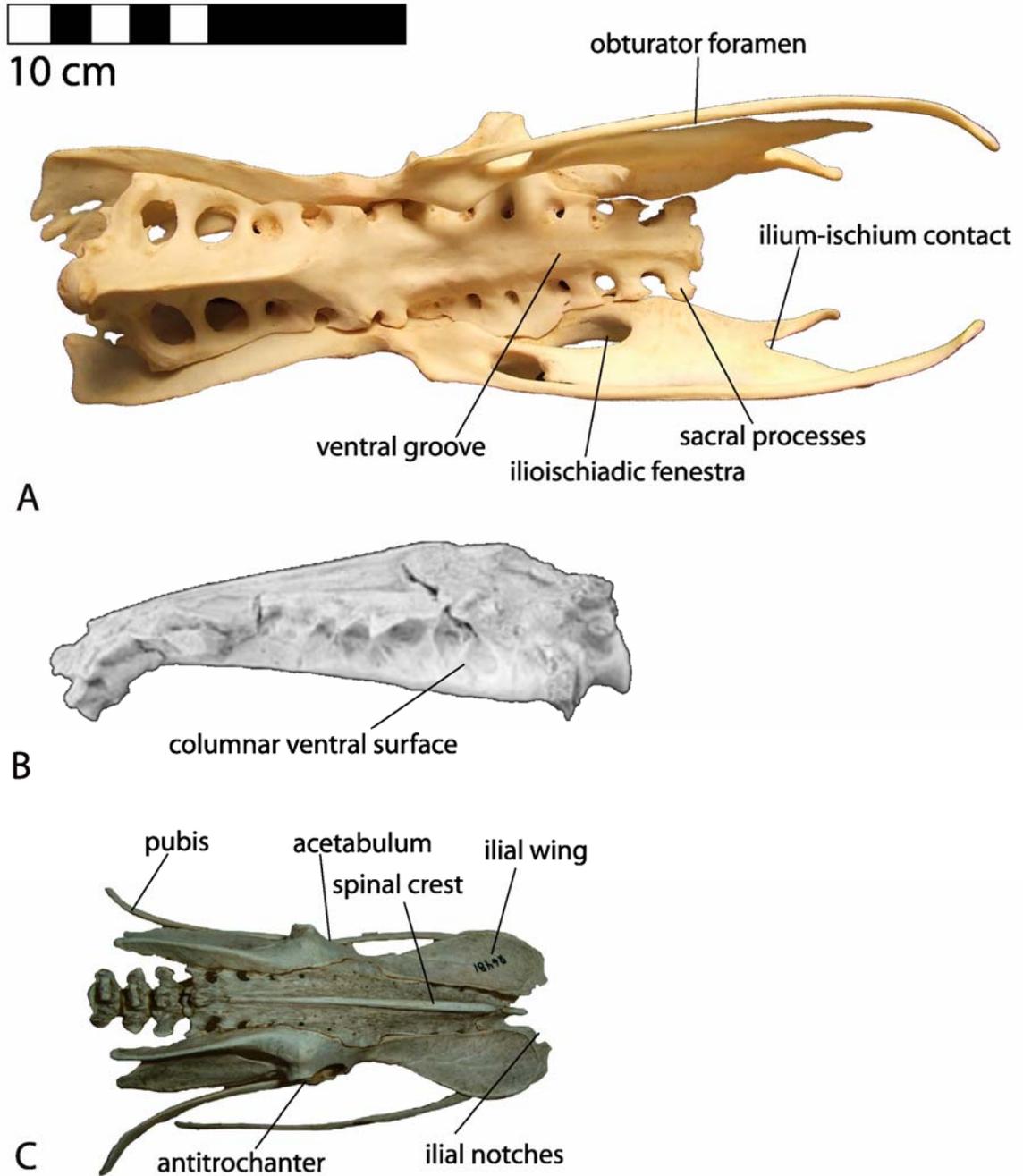
**Figure 2.11. Internal, Anterior View of Braincase of *Aptenodytes forsteri* (left) and *Spheniscus demersus* (right). View indicates prootic-squamosal contact.**



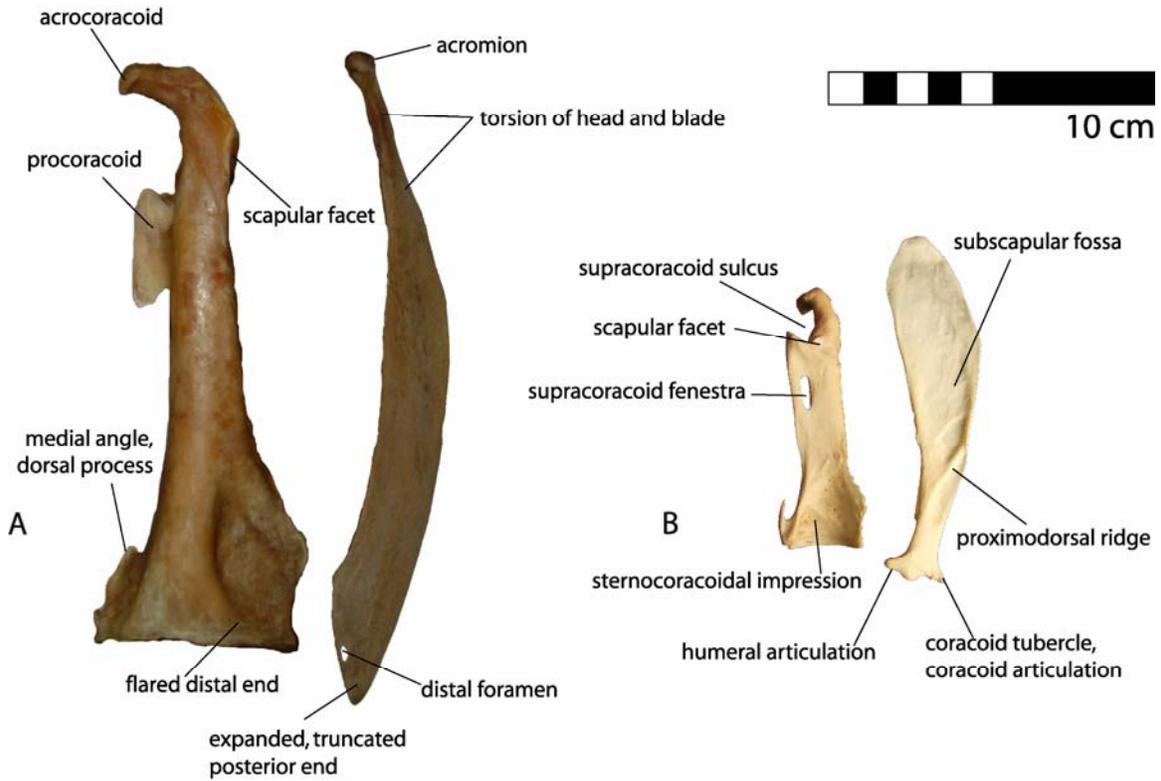
**Figure 2.12. Cervical and Caudal Vertebrae.** A. Dorsal view of cervical (*Aptenodytes patagonicus*, AMNH 1623). B. Ventral view of cervical (*Eudyptes pachyrhynchus*, OM 309). C. Lateral view of free caudal (*Aptenodytes patagonicus*, AMNH 1623).



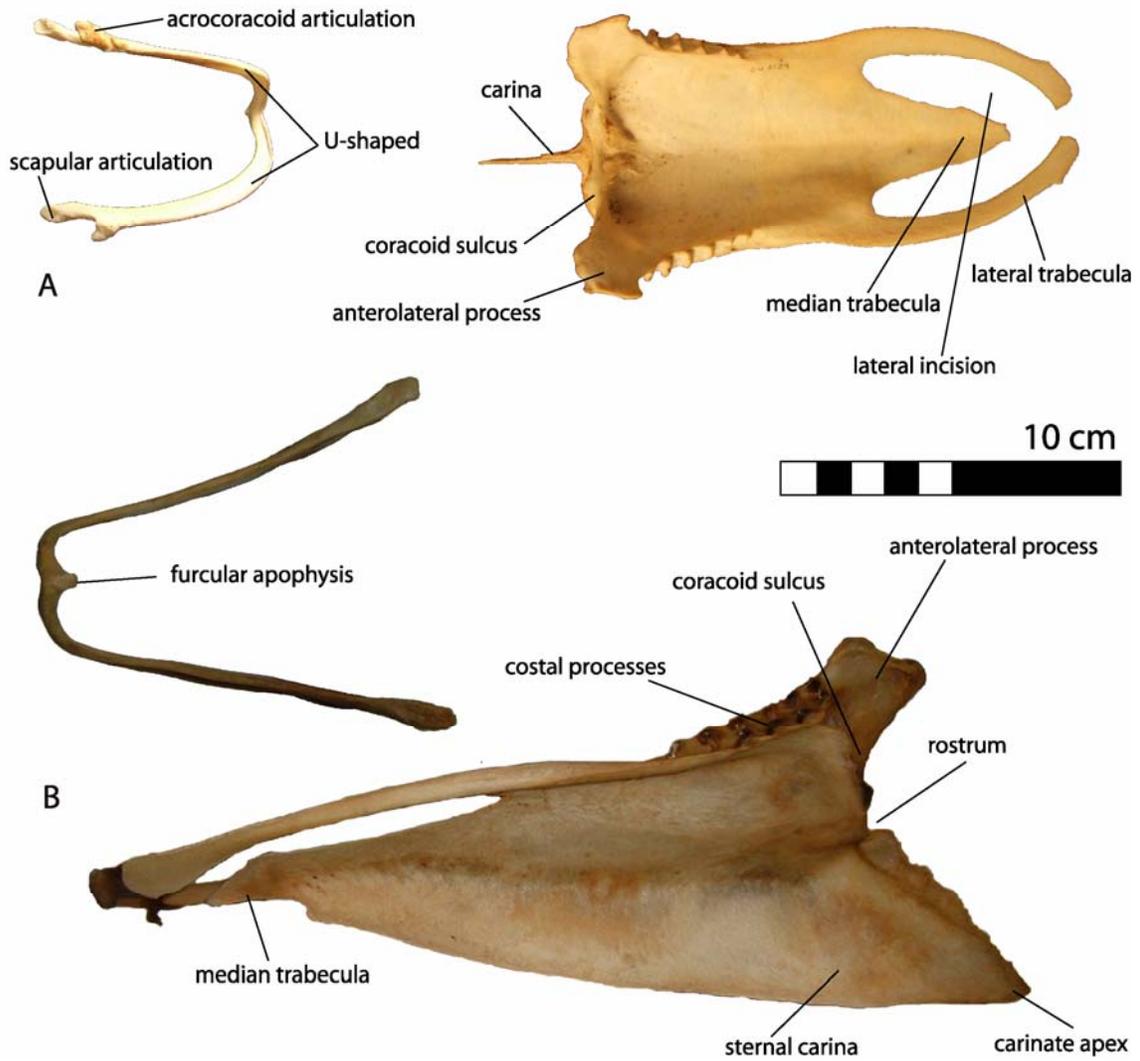
**Figure 2.13. Sacrum and Os Coxae.** A. Ventral view (*Spheniscus humboldti*, CM2129). B. Lateral view (*Wimanu tuatahi*, CM zfa35). C. Dorsal view (*Spheniscus magellanicus*, AMNH 26481).



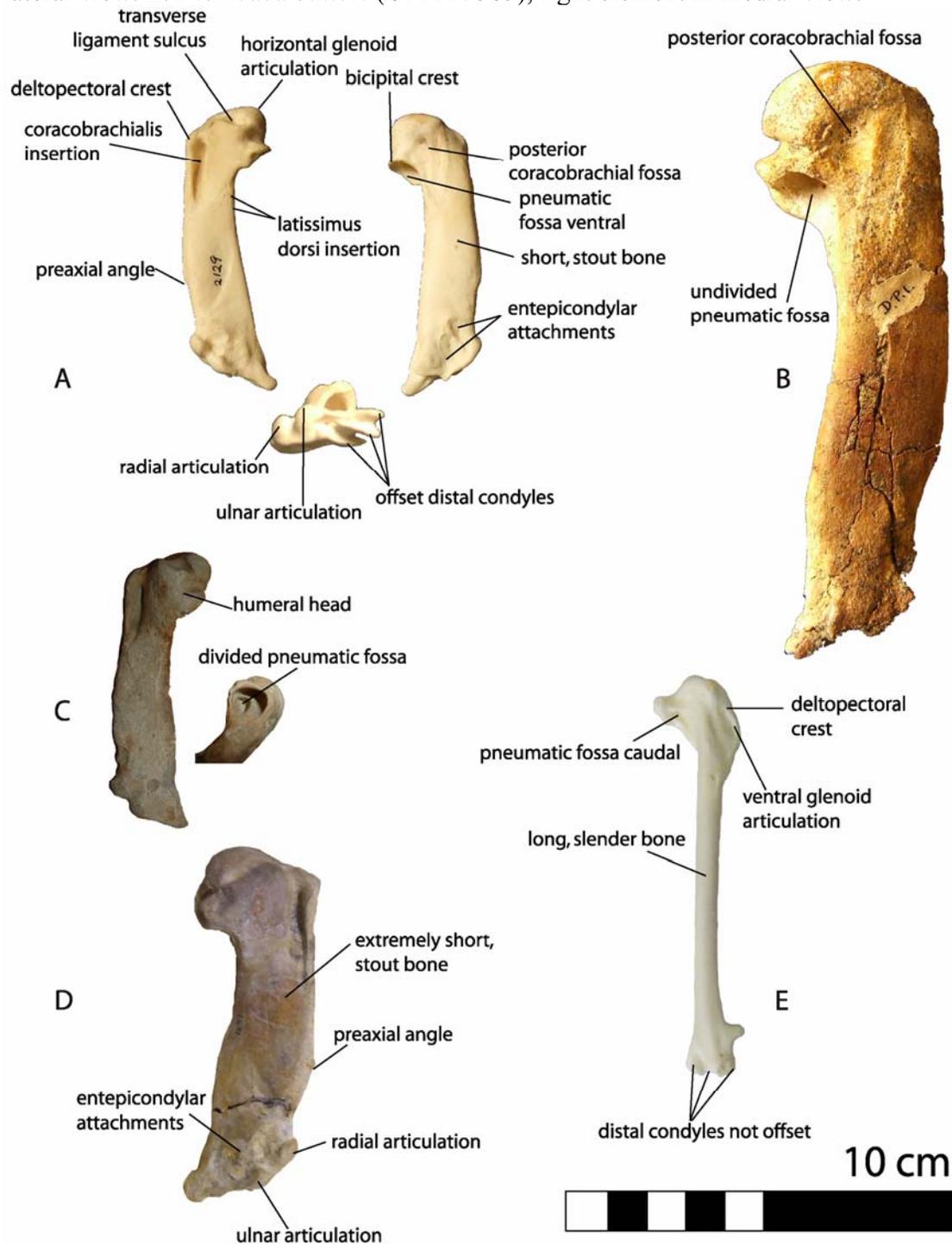
**Figure 2.14. Scapulae and Coracoids.** A. *Aptenodytes patagonicus* (AMNH 27330), right coracoid in anterior view (left) and right scapula in lateral view. B. *Spheniscus humboldti* (CM 2129), left coracoid in posterior view and left scapula in medial view.



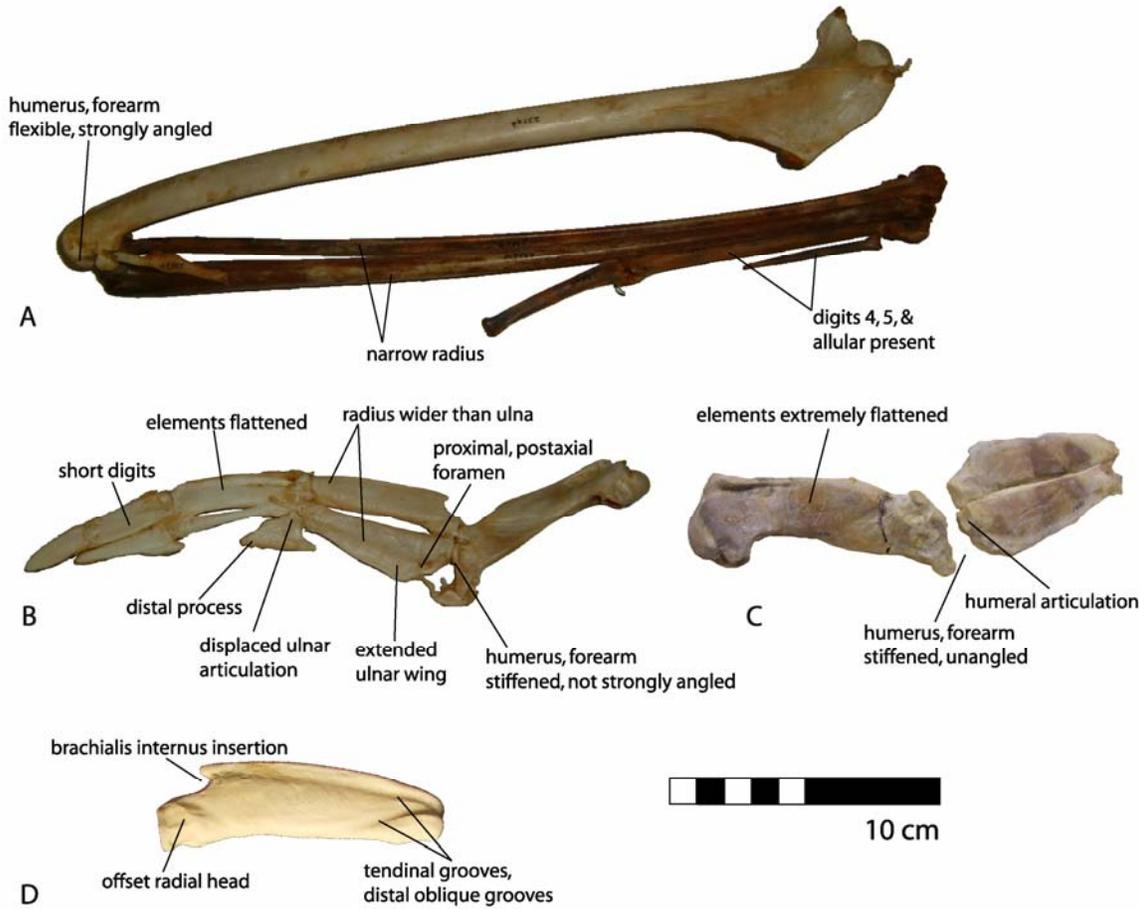
**Figure 2.15. Furculae and Sterna.** A. *Spheniscus humboldti* (CM 2129), dorsal views. B. *Aptenodytes patagonicus* (AMNH 27330), ventral view of furcula, ventral and lateral view of sternum.



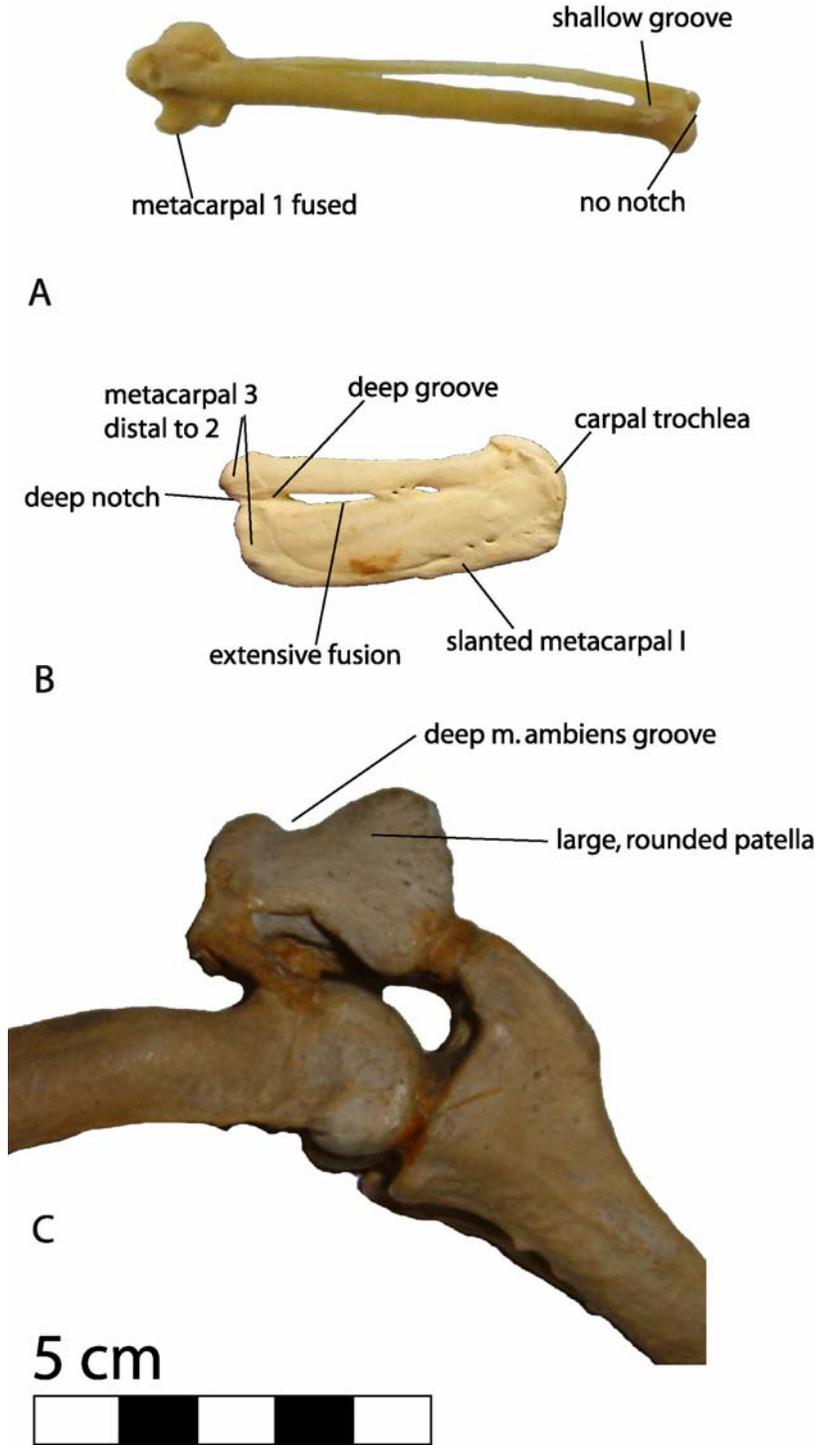
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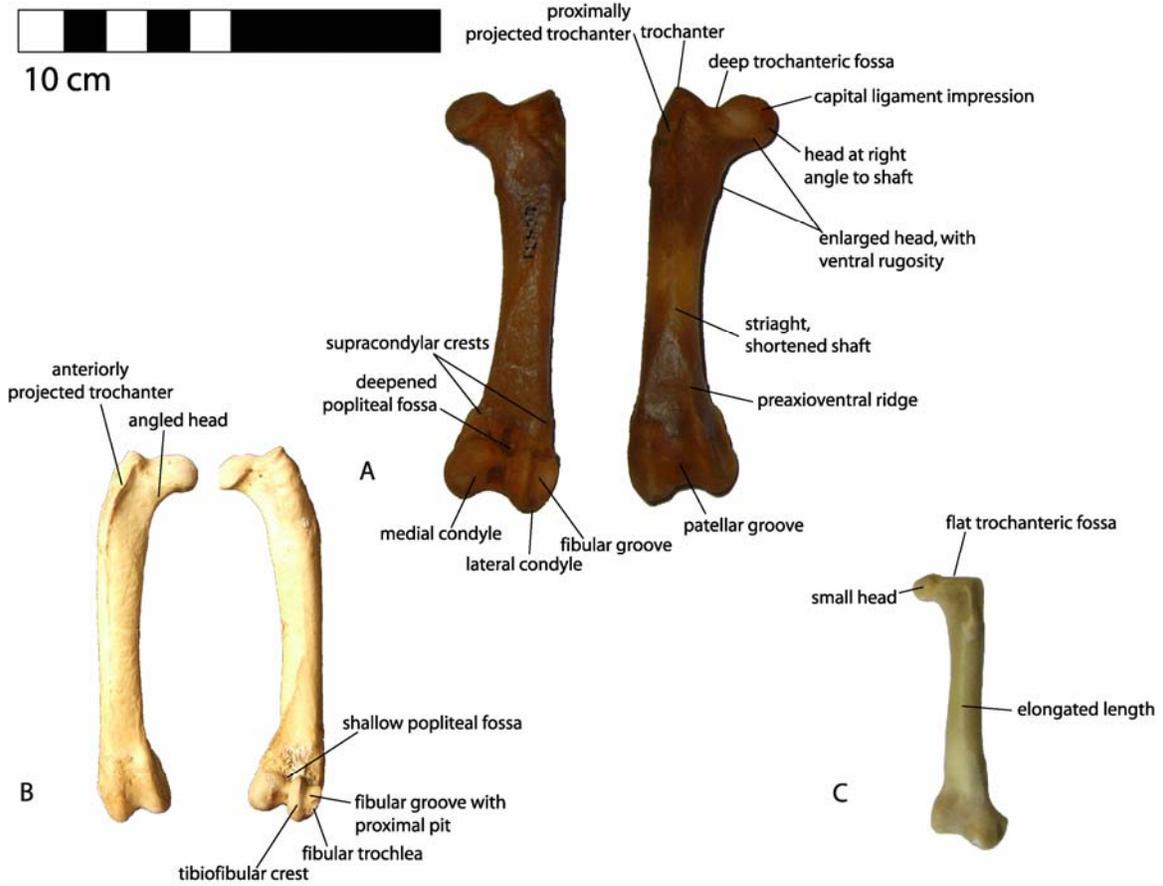
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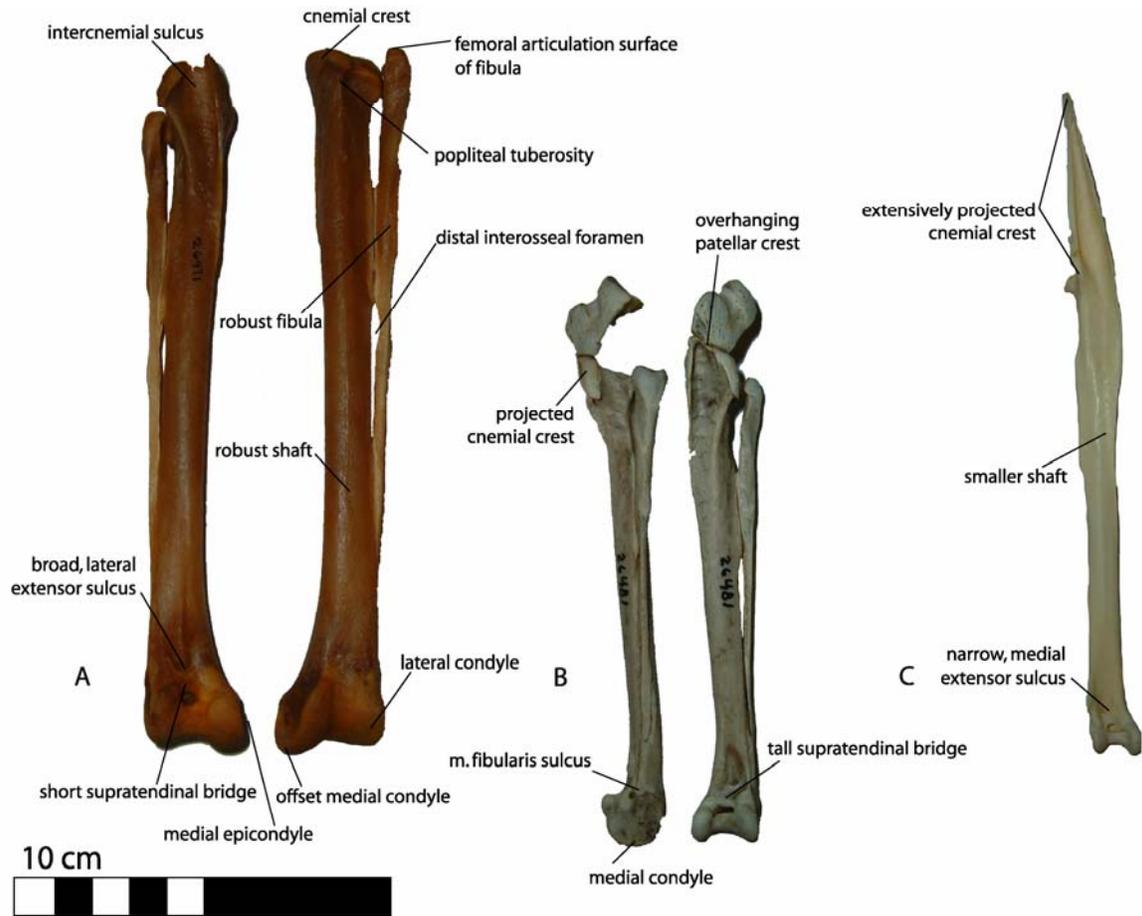
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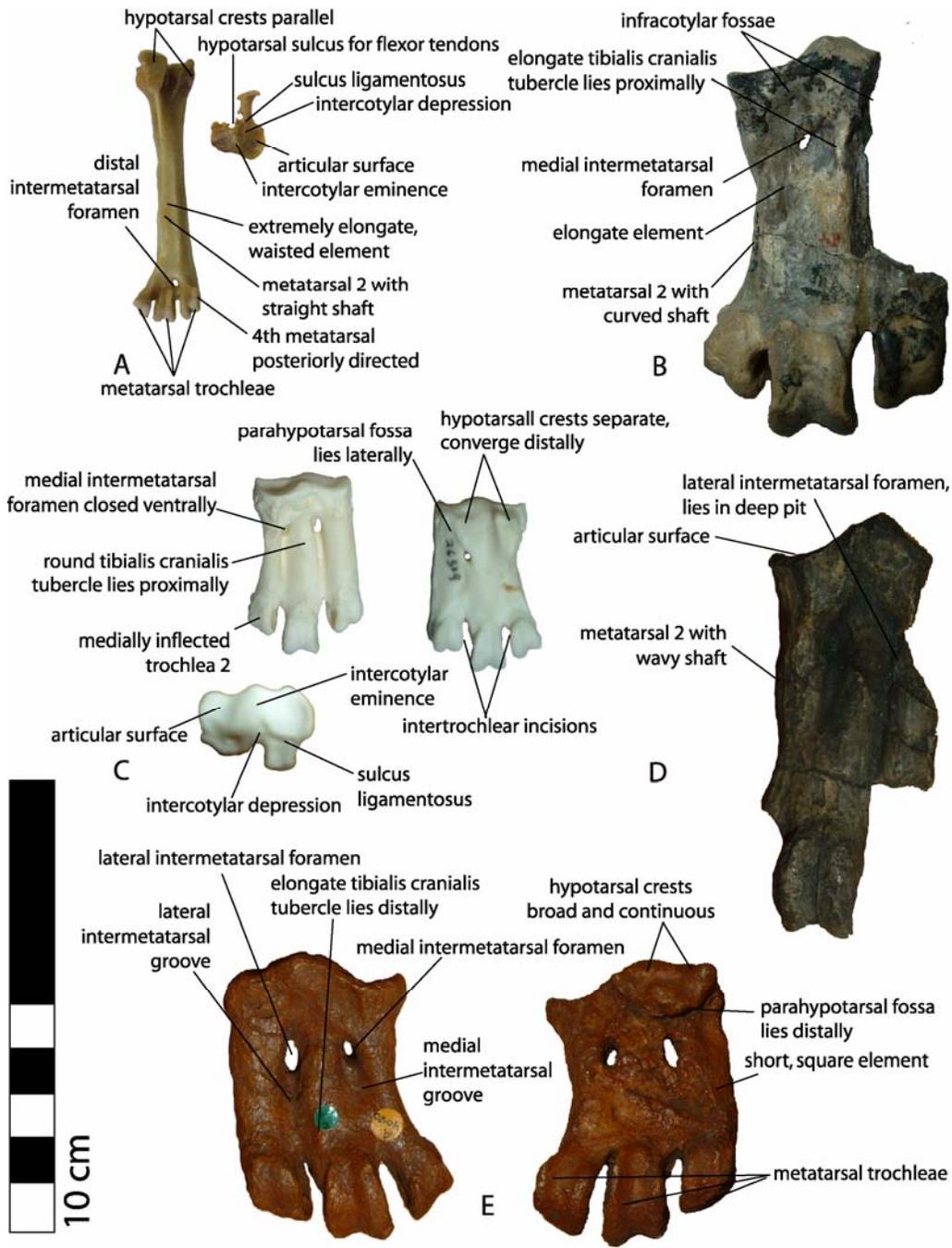
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**Figure 2.20. Tibiotarsi and Fibulae.** A. *Aptenodytes patagonicus* (AMNH 26471), right element, anterior and posterior views. B. *Spheniscus magellanicus* (AMNH 26481), left element, lateral and anterior views. C. *Gavia stellata* (AMNH 4974), right element, anterior view.



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### **Chapter 3: A New Perspective on Penguin Phylogeny: the effect of missing data and the application of phylogenetic nomenclature**

“But it is paleontological data, in conjunction with a study of the Recent biota, that allow us to see [the branches of the history of life] as spatiotemporally bounded individual entities. This is the revised ontology that seems so crucial if we are to sharpen our ideas about the true nature of life’s history and the evolutionary processes that have shaped that history.”

—Eldredge and Novacek, 1985

#### **Abstract**

The potential importance of missing data in systematic analyses was long observed and debated. The effect of such incompleteness, including excluded taxa, excluded types of characters (e.g., analysis of only molecular or only morphological data), and missing data owing to non-preservation, is explored here using the phylogeny of penguins. Cladistic methods were only recently applied to penguin phylogeny, resulting in systematic hypotheses of extant species and part of the large diversity of extinct taxa, although no study included all extinct taxa. It is clear that penguins belong to Aves (birds) and derived Neornithes (living birds), but their relationships with other neornithines remain contentious. That hinders further conclusions regarding penguin evolutionary history, although their excellent fossil record suggests that such analyses would be highly productive. The penguin fossil record is long, extending to the late Early Paleocene (62.4 mya), and penguin fossils are known from every Gondwanan continent except India and every continent currently inhabited. Although most are isolated long bones, every skeletal element is known. Such diversity is not always included in systematic analyses, however, either because older works relied on the well-known and commonly preserved humerus and tarsometatarsus for descriptions and species diagnoses, or because recent research often focuses on smaller-scale questions such as the value of integumentary data in avian (bird) phylogenetics or the placement of a few well-known, extinct taxa.

I here use a previous description of penguin skeletal anatomy based on Computed Tomography (CT) scans and direct observation of all extant and all diagnosable extinct species to reconstruct penguin phylogeny. Combination of that dataset with published myological, integumentary, and behavioral data results in a matrix of 503 systematic characters, which greatly enlarges the previous amount of character data applied to penguin relationships. Parsimony analysis results in the recovery of a highly resolved, well-supported phylogeny, including a monophyletic crown-clade and two separate clades of extinct species. Further analysis of the data partitions supporting this phylogeny indicates that different partitions support different levels of relationship e.g., the

osteological partition informs higher-level taxa, while behavioral characters serve to separate species. Additionally, I show that missing data drastically affects the recovered topology, as does outgroup choice. I also suggest that incorporating the maximum amount of data from the maximum number of sources, including all taxa (both extinct and Recent), all available character data, and all potential outgroups, results in the most well-resolved phylogenies because this insures inclusion of all potentially relevant character states and relationships. Future work should integrate extensive, published molecular data with my results to further increase the completeness of this dataset.

Using the phylogeny hypothesized here, I revise sphenisciform taxonomy, applying phylogenetic nomenclature to penguins for the first time. I formally define the names Panspheniscidae (the total group), Sphenisciformes (currently known penguins), and Spheniscidae (the crown-group), and diagnose the taxa that they represent. I apply the names Palaeudyptidae and Paraptenodytidae to the newly discovered clades of extinct penguins and coin the additional names Spheniscoidea (Spheniscidae + Paraptenodytidae) and Australodyptinae (*Aptenodytes* + *Pygoscelis*).

## **Introduction**

Recent phylogenetic analyses of penguins (Aves: Sphenisciformes) greatly clarified the relationships of extant species, but no previous analysis examined all extinct and living taxa. Although penguins long fascinated scientists and laypeople alike, with particular attention deservedly paid to their ecology and impressive cold-adapted physiology (e.g., Stonehouse, 1975; Emslie and McDaniel, 2002; Meyer-Rochow and Gall, 2003; Peck et al., 2006), it was only in the last year that cladistic analyses of penguin phylogeny that include extinct species appeared. A comprehensive phylogeny of extinct penguins is important in view of extensive recent discoveries of new fossil material (Slack et al., 2006; Walsh and Suarez, 2006; Ksepka and Bertelli, 2007; Clarke et al., 2007; Triche, Chapter 1) and because of the potential effect of such a phylogeny on current disputes over the timing of origin of modern birds (Dyke and van Tuinen, 2004; van Tuinen et al., 2006; Triche, 2006).

Penguins belong to the clade Aves (Figure 3.1). They also belong to a number of less inclusive groups within Aves, namely Neornithes, Neognathae, and Neoaves (Cracraft and Clarke, 2001). Although penguins, or Sphenisciformes (colloquially sphenisciforms), are certainly neoavian, their exact relationships with other birds remain contentious. They probably are most closely related to other living seabirds, although various studies disagree as to whether or not that assemblage is monophyletic, and as to which of the various seabird clades is the sister taxon of Sphenisciformes. A number of cladistic treatments of living penguins are published (e.g., O'Hara, 1989; Bertelli and Giannini, 2005; Ksepka et al., 2006). Only one dataset, however, is applied to more than one extinct species (Ksepka et al., 2006; Clarke et al., 2007), although another will be proposed shortly (Ando, pers. comm.).

Extant penguins, of Spheniscidae (colloquially spheniscids), breed in Patagonia, Tierra del Fuego, Peru, Chile, South Africa, Seymour Island in Antarctica, New Zealand, and Australia. The penguin fossil record is one of the longest of any known extant bird lineage and perhaps the longest within Neoaves (Fig. 2; Vickers-Rich, 1976; Slack et al., 2006). The record extends from the late Early Paleocene, approximately 62.4 mya, through numerous Holocene remains known from e.g., Tasmania, the sub-Antarctic islands, Chile, and other locations (Slack et al., 2006). This early occurrence greatly surpasses the records of all other Gondwanan avians (Vickers-Rich, 1976; Bochenski, 1985; Fordyce et al., 1986), and highlights the importance of penguins to broader analyses of avian evolutionary patterns (Dyke, 2001). Penguin fossils are also known from every Gondwanan continent except India, owing to the fact that they are highly

dispersible but dependent on cold-water currents that restrict them to remain south of the equatorial climate barrier. Fossils come from every major area currently inhabited (Simpson, 1971a, 1971b, 1972; Vickers-Rich, 1980; Olson, 1983; Fordyce, 1991; Stucchi, 2002; Clarke et al., 2003; Emslie and Correa, 2003; Clarke et al., 2007). Dense associations of penguin fossils only occur locally, however and, although globally widespread, are known only from several, discrete localities (Fordyce and Jones, 1990). Additionally, most extinct species are known from disassociated bones, and these single, skeletal elements often are not comparable between named taxa. Most penguin fossils are long bones, notably humeri and tarsometatarsi, but every skeletal element is known from the fossil record, including a number of nearly complete skulls (Zusi, 1975; de Muizon, 1981).

The current total of extinct penguin species includes fifty-nine named taxa, of which the two known species of *Wimanu* are the oldest. Even ignoring its extreme age, that genus is remarkably complete and includes nearly all skeletal elements (Slack et al., 2006). A third Paleocene species, *Crossvallia* from Seymour Island, is slightly younger in age and much less well known (Tambussi et al., 2005). Most remaining extinct penguin species come from New Zealand, Seymour Island, and Patagonia, and include what were traditionally seen as three distinct, unrelated, morphological groups. These are the palaeospheniscids of South America, the palaeudyptids of New Zealand and Seymour Island, and a group of extant species and their few close relatives (e.g., Simpson, 1946; Marples, 1952, 1953). Authors traditionally placed these extinct species into a number of

separate, subspecific categories, although that classification scheme was later abandoned (Simpson 1946, 1971b).

The present work attempts to integrate the abundance of fossil material with that of extant species to propose a comprehensive phylogenetic hypothesis. The main drawback to previous studies of penguin phylogeny was missing data, arising from the use of inadequate taxon sampling, small numbers of systematic characters, single types of systematic data, and incomplete specimens. While the last of these may be unavoidable in work on extinct penguins, remaining incompleteness is here addressed by vastly expanding the amount of data analyzed. Osteological, myological, integumentary, soft part, and behavioral data make up a phylogenetic character matrix, which also includes all diagnosable extinct and extant taxa and a greatly enlarged number of systematic characters. My analysis does not include molecular data because I am primarily concerned with the relationships of extinct taxa and because a number of recent works previously examined the molecular phylogeny of extant spheniscids (Bertelli and Giannini, 2005; Baker et al., 2006; Ksepka et al., 2006). Additionally, molecular data will be combined with the matrix presented here in future work, and previous hypotheses based on molecular characters are used here as a constraint tree to examine the relationship between such previous hypotheses and the morphological work presented here. Those previous studies also included morphology, but osteological characters played a reduced role. The purpose of new systematic characters proposed here is to maximize information from the previously underrepresented osteological dataset and to create a matrix now extensively scorable for extinct penguins. Recent work on the

phylogeny of Neornithes shows that greatly expanding the number of characters in a matrix (to 2,954) does result in well-resolved phylogenetic reconstructions that allow the untangling of previously controversial relationships (Livezey and Zusi, 2006, 2007). Even systematic studies of large groups do not generally include more than 100-200 characters, despite the wealth of systematically variable anatomy present in most higher taxa. Greatly increasing the number of characters, however, tends to increase the resulting phylogenetic resolution, at least when the characters are independent and represent additional evidence of synapomorphies for the examined taxa.

I performed a number of additional analyses that build on the original phylogenetic results obtained from my matrix, in order to determine the effect that incompleteness and missing data have on penguin phylogeny reconstruction. I also examine the topology of my hypothesized phylogeny in comparison with previous analyses, discuss resulting conclusions regarding character evolution in Sphenisciformes, and revise the taxonomy of extinct and extant penguins. The last such revision greatly predates the application of modern phylogenetic methods, and penguin systematics will benefit from being brought up to date with current evolutionary ideas, including the definition of phylogenetic nomenclature applicable to penguin clades.

### **Review of Previous Phylogenetic Literature**

Most older studies concerning penguins were limited to morphological description (e.g., Coues, 1872; Gervais and Alix, 1877; Jullien, 1882), whereas those that did address systematics reached contradictory conclusions (e.g., Gregory, 1934; Lowe 1933, 1939; Simpson, 1946). Some recent taxonomic revisions also lacked a phylogenetic

framework (Kinsky and Falla, 1976; Myrcha et al., 2002; Jadwiszczak 2006), while other work included only extensive reviews (Fordyce and Jones, 1990; Fordyce, 1991), and proposals of potential systematic characters (Verheyen, 1958; Zusi, 1975). The past few years, however, witnessed a proliferation of cladistic analyses of extant penguins. Some addressed their placement within Neoaves (Cooper and Penny, 1997; Livezey and Zusi, 2001, 2006, 2007; van Tuinen et al., 2001; Mayr and Clarke, 2003; Slack et al., 2003; Mayr, 2004, 2005), while a smaller number addressed extinct species (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Baker et al., 2006; Bertelli et al., 2006; Walsh and Suarez, 2006; Ksepka et al., 2006).

#### **Placement of Sphenisciformes**

Most authors today agree that penguins lie within Neoaves, but there is still no consensus regarding their relationships with other neoavians. Most hypotheses, however, suggest an extant clade of seabirds as their sister taxon (Figure 3.3). Because Aves and Neoaves contain so many species, analyses of the entire group vastly under-sample most included higher taxa, include one species of penguin at most (e.g., Livezey and Zusi, 2006, 2007) or may even exclude penguins altogether (e.g., Mindell et al., 1997), and often exclude many other, possibly influential, seabird clades. These seabirds invariably cluster together in analyses using either molecules or morphology, but it is uncertain whether that reflects actual relationship or convergent evolution related to the constraints of their aquatic habitat (Livezey and Zusi, 2001). It is often assumed that convergence in both datasets is affecting the placement of seabirds within Neoaves, however the broader

issue is lack of adequate sampling to produce a large tree that may then be used to test whether or not ‘seabirds’ are convergent or monophyletic.

Proposed penguin sister-taxa, based on both molecular and morphological analyses, include part or all of the tubenoses (albatrosses and petrels, or Procellariiformes; Simpson, 1946; Sibley and Ahlquist, 1990; Cooper & Penny, 1997), tubenoses followed by loons (Gaviidae; Van Tuinen et al., 2001; Livezey and Zusi, 2001, 2006, 2007), or a paraphyletic tubenose clade (McKittrick, 1991; Figure 3.3). They also include loons (Olson, 1985b), loons plus grebes (Podicipedidae; Cracraft, 1982, 1988; Sibley and Ahlquist, 1990; Mayr and Clarke, 2003), loons followed by grebes (Ho et al., 1976), and loons plus grebes plus flamingos (Phoenicopteridae; Mayr, 2004; Figure 3.3).

One of the most unexpected sister group hypotheses is the extant Ciconiidae (storks; Slack et al., 2003). That hypothesis is vulnerable to the criticism that it relies on a maximum likelihood analysis of an entire mitochondrial genome that included no other seabird species, only members of Paleognathae, Galloanseres, and four Neoavians almost certainly unrelated to penguins. While that study was intended to examine penguin relationships specifically, only avian phylogeny in general, the exclusion of all previously hypothesized sister taxa of penguins does still call into question the proposed sister-taxon statement. A subsequent work built on that dataset failed to place storks anywhere near penguins, which group, as usual, in the midst of a clade of seabirds (Slack et al., 2006). A second unique suggestion for the sister taxon to penguins is the extinct Plotopteridae, a group of flightless seabirds known from the Tertiary of the North Pacific (Mayr, 2005). That study examined a large number of extant and extinct seabird clades with

morphological data, but supported the Plotopteridae-Sphenisciformes clade with only three synapomorphies among a large number of proposed convergent and plesiomorphic characters (Mayr, 2005). Also, some character coding used a putative plotopterid specimen that may actually be a frigatebird (Mayr, 2005), because its phylogenetic placement was not examined in any other analysis. The remainder of the plotopterid coding was based on a few, somewhat misleading figures (e.g., Olson and Hasegawa, 1979), which illustrate only portions of the relevant anatomy and, in my opinion, do not present sufficient detail for use in character coding. The analysis also failed to include any extinct penguin and one of the six extant penguin genera. That method almost certainly excludes any basal sphenisciform character states that might or might not indicate true relationships with plotopterids. The morphology of plotopterids and penguins is otherwise generally agreed to be convergent, coinciding with the fact that penguins are exclusively Southern Hemisphere birds and Plotopterids are known only from the Northern Pacific Ocean (Olson and Hasegawa, 1979). However, no test included an adequate sample of taxa to determine whether the two groups are really convergent or if their wide geographic separation influenced ideas about their relationships, as is common in paleontology (Bever, 2005; Bell and Bever, 2006).

The variety of conclusions about penguin phylogeny probably stems from the various sampling problems outlined above. Analyses of penguin relationships suffer from a number of sampling biases, both regarding systematic data and taxon choice. These include use of only a small number of systematic characters, inadequate sampling of different character types (e.g., osteological, behavioral, or molecular datasets), lack of a

broad outgroup sample or assumption of an untested outgroup, and light sampling within the ingroup, especially among extinct taxa. The placement of penguins also was only examined in the context of broader analyses that were never specifically focused on the penguin problem. Consensus on the relationships of penguins probably thus includes a true relationship with other seabirds, but not with storks or pterosaurs.

### **Extant Species**

Cladistic approaches to the phylogeny of extant penguins were attempted only recently, and remain somewhat problematic because proposed relationships conflict. Researchers recognize from sixteen to eighteen extant species, depending on whether *Eudyptes schlegeli* or *Eudyptula minor albosignata* are considered as species or subspecies (Williams, 1995; Davis and Renner, 2003; Giannini and Bertelli, 2004), and continue to debate the numbers of recognized subspecies of other *Eudyptes* and *Eudyptula* species (e.g., Kinsky and Falla, 1976). Additionally, various authors proposed phylogenies that incorporate every possible relationship between the six extant genera (Figure 3.4).

The first phylogeny proposed for living penguin species was an evolutionary hypothesis based on overall similarity and never actually diagrammed as such (Figure 3.4; Simpson, 1946). That was basically the only such work for forty years, until the advent of cladistic methods. The first cladistic analysis of penguin relationships was an unpublished Ph.D. dissertation including sixteen morphological characters and all proposed extant species (Figure 3.4; O'Hara, 1989). Also published that year was a morphometric study of all extant penguins, which included a resulting phenetic

hypothesis of relationship (Figure 3.4; Livezey, 1989). An allozyme analysis later examined the relationships between three extant species in the genus *Spheniscus* (Figure 3.4; Grant et al., 1994), and a behavioral phylogeny of four extant species grouped penguins with petrels (Figure 3.4; Paterson et al., 1995). More recently, a supertree analysis of procellariiform phylogeny included ten extant penguins in its data set (Figure 3.4; Kennedy and Page, 2002). Penguins formed a monophyletic outgroup to Procellariiformes, but some unexpected relationships resulted within Sphenisciformes, including complete lack of resolution in the strict consensus tree and presence of two non-monophyletic genera in the more-resolved Adams consensus tree. Although collapse of resolution is inherent to strict consensus trees, these results are also artifactual because the original source trees contained numerous non-overlapping taxa. That problem, which is widespread in supertree analyses, results in a proliferation of artifactual polytomies and reduces the utility of the method for reconstructing species-level relationships (Kennedy and Page, 2002; Gatesy et al., 2004).

The first cladistic analysis of all extant species examined breeding characters and the unique integumentary structure of penguins (Figure 3.4; Giannini and Bertelli, 2004). The authors subsequently integrated their dataset into a combined morphological and molecular analysis (using mDNA-12S and cyt B) to recover a similar topology (Figure 3.4; Bertelli and Giannini, 2005). The morphological and molecular data partitions are divergent when analyzed separately, however, suggesting that the number of molecular characters is swamping the included morphology. That study is the only one to expressly test the monophyly of the Sphenisciformes, which was strongly supported, and the only

one to combine molecules and morphology, including osteological and integumentary characters, to examine penguin phylogeny (Bertelli and Giannini, 2005). No study has yet explicitly tested the monophyly of a penguin genus or any other taxon within penguins. Finally, a molecular analysis of all eighteen proposed species used numerous genes, including RAG-1, mtDNA-12S, rDNA-16S, COI, and cyt B, in support of a new phylogeny including divergence time estimates (Figure 3.4; Baker et al., 2006). The resulting topology is identical to that of the previous combined analysis, although it differs in most respects from the result recovered using morphology alone (Bertelli and Giannini, 2005). Current agreement on extant spheniscid relationships seems to support the sister taxon relationship of a crested penguin clade (*Eudyptes* + *Megadyptes*) and a *Spheniscus-Eudyptula* clade. More research, however, is required to explain the relationships of the two Antarctic genera, *Aptenodytes* and *Pygoscelis*, as well as the conflicting morphological and molecular signals present in penguins.

### **Extinct Species**

Various authors dealt with the phylogeny of extinct penguin species nearly since their discovery, which occurred contemporaneously with Darwin's popularization of the theory of evolution (Huxley, 1859). Published cladistic analyses, however, only addressed extinct penguins in the context of an extant species phylogeny. Generally, phylogenies examining extinct penguins were informal and consisted of short appraisals of the degree of similarity between various faunas or species. Simpson, for example, proposed an evolutionary phylogeny of extinct species that included a number of separate, and highly specialized, extinct lineages, none of which were directly ancestral

to modern species (Simpson, 1946). Simpson concluded that modern species had evolved from some as-yet undiscovered penguin ancestor (Simpson, 1946, 1971b, 1972). Within extinct penguin lineages, he found the most similarity between two New Zealand taxa, a *Pachydyptes-Platydyptes* group and the genus *Palaeudyptes*, all of which are more distantly related to *Anthropornis* of Seymour Island. These anthropornithine and palaeudyptine groups were distinct from the palaeospheniscine species known from Patagonia. The only similarity Simpson noted between the faunas of the two continents is that the Patagonian group included the New Zealand genera *Dunroonornis* and *Korora* (1971b). Although the palaeospheniscines were not closely related to extant Spheniscinae, they were the only group of penguins that Simpson thought might be more closely related to the crown-group, a view shared by Marples (Simpson, 1946).

Marples, in all his classifications, noted the probable phylogenetic affinities between species from Australia, New Zealand, and Seymour Island, as opposed to the separate Argentinian lineage and the derived, extant species (Marples, 1953). That hypothesis was only formalized as a subfamilial taxonomy, never a phylogenetic tree. He also agreed with Simpson that the Australasian group was not ancestral to modern species, but differed in linking the Argentinean group with the extant clade, despite the presence of a few morphological differences (Marples, 1952). Marples' conclusions differed from Simpson's when he separated the Palaeudyptine penguins from the Argentinean *Paraptenodytes* (Simpson, 1971b).

Other non-cladistic work includes a functional analysis of penguin skull structure that examined extant species and the few extinct species then known from cranial

remains (*Parapterodytes antarctica* and *Palaeospheniscus novaezealandiae*; Zusi, 1975). Zusi found support for a monophyletic crown clade, but none for the placement of either taxon (Zusi, 1975). Recent proposals also suggested that crown-group penguins originated in the Eocene of Seymour Island (Baker et al., 2006; Triche, Chapter 4), which in turn points to small extinct species such as *Delphinornis* as the ancestors of modern penguins (Jadwiszczak, 2006).

The first cladistic analysis to include an extinct penguin (Slack et al., 2006) integrated the oldest known penguin, *Wimanu*, into a previous analysis of Aves (Mayr and Clarke, 2003). The only other extinct penguin taxa included in the matrix were *Wimanu*, *Platydyptes*, and ‘*Palaeudyptes*’, as the analysis was used specifically to examine the potential position of *Wimanu* as a stem-penguin (Slack et al., 2006). Results showed *Wimanu* to be the unambiguous sister taxon to other Sphenisciformes, with all penguins nested within a clade also containing Gaviidae, Podicipedidae, and Procellariiformes. Although the analysis was narrow in scope, including only three of the great number of extinct penguin species, it is noteworthy in marking the first cladistic treatment of an extinct penguin.

Several subsequent studies also focused on analyzing the positions of single extinct taxa. In a second cladistic analysis, for example, *Parapterodytes antarcticus* formed the sister taxon to a monophyletic Spheniscidae (Bertelli et al., 2006). The matrix they used was identical to that of that in their previous work on extant penguin phylogeny (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005), with the addition of one modified character. Their analysis examined only one of three named species of

*Paraptenodytes*, owing to a focus on description of the cranial anatomy of a particularly well-preserved specimen of *Paraptenodytes antarcticus* and to their suspicions that that genus is not monophyletic. The sister-taxon status of *Pygoscelis antarcticus* was highly supported, both by relative support values, a large number of synapomorphies shared with Spheniscidae, and by the relatively complete scoring of the extinct taxon. However, addition of more extinct taxa to, or combined analysis of, these two taxa will undoubtedly modify the topology of the penguin stem-group and ingroup.

The third cladistic study of extinct penguins again examined the relationships of a single taxon, the new species *Pygoscelis grandis*. Bertelli et al. (2006) concluded that study focused on post-cranial characters and did not include all living penguin species or any additional extinct taxa. The topology of the resulting cladogram is identical to that of O'Hara (1989) and to the morphological tree of Bertelli and Giannini (2005), although it does not include the genus *Megadyptes*, which forms the only incongruence between these other two cladograms. The new species lies within a monophyletic *Pygoscelis* clade, but support for this node is low (bootstrap value of 58%), suggesting to the authors that the clade may have evolved relatively recently or may even be paraphyletic, with its constituent taxa not having diverged enough to provide a robust phylogenetic signal.

Finally, work by Acosta Hospitaleche on Argentinian material includes a new phylogenetic hypothesis resulting from a morphometric analysis of three South American taxa (*Paraptenodytes antarctica*, *Palaeospheniscus biloculata*, and an unnamed new genus, MEF-PV 100), as well as fourteen extant species. That work placed *Palaeospheniscus biloculata* as the sister taxon to extant *Aptenodytes*, and the other two

extinct taxa as subsequent outgroups to crown penguins (Acosta Hospitaleche, 2004). A second analysis examines these fossils as well as a new taxon, *Madrynornis*, in a cladistic analysis based on the matrix of Bertelli and Giannini (Acosta Hospitaleche et al., 2007). That work also suggests that *Paraptenodytes* is the sister-taxon of the crown-clade and upholds the placement of *Palaeospheniscus*, while the new *Madrynornis* is recovered as the closest relative of extant *Eudyptes*.

Two analyses exist that include numerous extinct penguin taxa, representing a vast advance in phylogenetic knowledge. The first examined 32 extinct and 18 extant taxa using tarsometatarsal morphology (Triche, 2005). It resulted in a highly resolved, if somewhat weakly supported, phylogeny. After the removal of six particularly incomplete taxa, the topology included a monophyletic crown-clade, five monophyletic extant genera (because *Spheniscus* proved to be paraphyletic), and resolution of one extinct clade of Antarctic species and one of New Zealand species. That study was the first cladistic treatment of extinct penguins and remains the largest such work available, although it is not yet published.

Finally, another entry in the plethora of cladistic penguin work appearing in 2006 was the second analysis of multiple species of extinct penguins (Ksepka et al., 2006). The matrix used was nearly identical to that of previous analyses of extant species by two of the same authors (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Bertelli et al., 2006), with the addition of 26 novel characters to account for all anatomical variation observed in extinct taxa. The analysis included nine taxa examined directly and an additional nine taxa coded from the literature. The resulting cladogram recovered a

mostly pectinate arrangement of extinct taxa leading up to a monophyletic crown-clade. Bremer support values suggested low support for most nodes, but the consensus tree was reasonably well resolved. A modification of this dataset supported a subsequent analysis that examined the relationships of two new Peruvian species amongst other extinct taxa and resulted in a similar phylogeny (Clarke et al., 2007). The conclusions section below will elaborate on the results of those works, in comparison with the present study.

## **Materials and Methods**

### **Taxa**

This analysis examines all extant species and all extinct species that are diagnosable, including nearly all named and a few unnamed extinct penguin taxa. Species and specimens examined, including outgroup taxa, are listed in Appendix 3.1. Extant taxa utilized include all eighteen proposed species. Although the specific status of *Eudyptula minor albosignata* remains contentious, it was coded as a separate terminal taxon to account for the possibility of its being a valid species. Multiple specimens were examined for each extant species, although only two osteological specimens were available for three of the rarer taxa. Samples included specimens from as wide a geographic and ontogenetic range as possible.

Most extinct taxa were examined and scored personally in museum collections, but a few were only accessible by coding from the literature and are listed separately in Appendix 3.1. Extinct taxa included in the analysis comprise forty eight species out of fifty seven currently named taxa. The new extinct taxa *Icadyptes*, *Madrynornis*, *Perudyptes*, and *Tonniornis* were not included because these taxa were named and

described just after completion of the current analysis (Tambussi et al., 2006; Acosta Hospitaleche et al., 2007; Clarke et al., 2007). The remaining eight species are extremely incomplete and of dubious taxonomic validity and are thus not considered here. Three other unnamed, but at least specifically distinct taxa, are included. All remaining undescribed species were excluded from this analysis. Successful efforts were made to examine every known specimen of all extinct taxa, except when specimens examined from the literature were only partially figured or described. South African genera are listed using quotation marks because these taxa are probably not generically distinct from *Spheniscus*, but systematic revision of included genera is beyond the scope of the current work. Numerous fossil elements of penguins probably represent juvenile specimens and are thus non-comparable in phylogenetic analysis, but no ontogenetic transformation data for these birds are currently available. That is probably particularly problematic in regards to the Seymour Island specimens, where size classes that may reflect only ontogenetic variation were previously used to diagnose different species. Until further study clarifies the ontogenetic age of these isolated elements, however, all specimens must be assumed to be derived from adult individuals.

Outgroups include the four most commonly proposed penguin sister taxa, or Procellariiformes, Gaviidae, Podicipedidae and Phalacrocoracidae. Coding included four procellariiform species from two of the four extant families, two of the five extant gaviid species, five podicipedids from three of six extant genera, and four phalacrocoracids from one of two living genera. Procellariiforms are most often taken to be the sister taxon of penguins, although much of that work relies on a nearly identical dataset (e.g., Bertelli

and Giannini, 2005; Ksepka et al., 2006). Podicipedidae is probably the sister taxon to Phoenicopteridae (storks; Mayr, 2004), but is still examined here in order to include potentially important outgroup variation. Originally, I included all outgroups in an unconstrained analysis, then analyzed each group separately to avoid the unnecessary assumption that Procellariiformes is the sister-taxon of penguins and to test whether choice of outgroup affected the ingroup topology.

### **Characters**

The character matrix for this analysis resulted from the compilation of numerous independent datasets, in an effort to approach total evidence and to analyze the largest possible sample of character data. This matrix now equals the size of small molecular datasets, and in future may be profitably combined with such data to thoroughly sample all available character sources. I scored 503 osteological (67% of the matrix), myological (6%), integumentary (15%), and behavioral (12%) characters. The largest proportion of characters (43%) in the matrix resulted from new examination of osteological specimens and codification of previous literature, while a smaller percentage of osteological characters came from existing cladistic analyses. Remaining characters were taken from original examination of museum specimens, proposed as novel characters based on previous descriptive literature, and modified from previously proposed characters extracted from existing cladistic analyses. About one third of these data are cranial (36%) and about two thirds are postcranial (64%) characters. Other datasets compiled in the matrix include myological characters adapted from descriptive literature and other soft part and integument characters taken from the literature and from previous analyses, and

behavioral characters taken from previous analyses with additional scoring from the literature (Boswall and MacIver, 1975; Budd, 1975; Conroy, 1975; Reilly and Balmford, 1975; Warham, 1975; Yeats, 1975). Until recently, there was no detailed, modern description of the penguin skeleton, despite numerous, complete, fossil remains and an abundance of extant specimens. Therefore, to provide a phylogenetically informed, morphological basis for comparisons among species, a comprehensive description of extinct and extant penguin osteology was recently completed, and is used as the main basis for describing systematic characters in the current analysis. The description will soon be published elsewhere (Triche, Chapter 2). Osteological description from previous works, especially those describing extinct species (e.g., Simpson, 1946; Marples, 1953; Jadwiszczak, 2006), are also used here to integrate anatomy known from extinct taxa with that from extant species. Appendix 3.3 lists all characters with associated literature, when applicable, and illustrations of characters not figured elsewhere. Appendix 3.4 presents the scored matrix for this dataset. Terminology for character descriptions comes from the *Handbook of Avian Anatomy: Nomina Anatomica Avium* (Baumel and Witmer, 1993), but was anglicized for convenience. Additional terminology specific to penguins comes from taxon-specific sources (Simpson, 1946; Marples, 1952; Myrcha et al., 2002).

All continuous variation was transformed into discontinuous characters using bins (for measurements) and fractional estimates (for ratios). Binary characters were generally preferred, although 46% of the matrix is multistate. This is mainly owing to my combining of purportedly correlated characters, and to extreme variability in the non-osteological characters that is often coded into as many as six states. For example, the

color of the bill of immature penguins may be black, red and black, red, yellow, or gray, which variation was already coded as a single character in the literature. The number of states in such characters was often reduced from previous analyses because only some of these states are present in the taxa included here. Although the initial analysis coded all characters as unordered, 47 characters (9%) were ordered in a subsequent run to determine the potential effect on tree topology (listed in Appendix 3.3), the effects of which are discussed below. These include only characters that are morphoclines or spatial clines (e.g., length of an element or the degree of elaboration of a structure). Although some phylogenetic studies exclude autapomorphic characters on the basis of their irrelevance for determining relationships, all such characters are included here for diagnosis of terminal taxa and correct calculation of tree support values.

The percentage of data scored for each taxon is listed in Appendix 3.2. Numerous extinct penguin taxa are notoriously incomplete, owing mainly to lack of knowledge of numerous elements of the skeleton rather than to poor preservation of elements that are known. Completeness of the taxa included ranges from 98.2% in three extant taxa to 2.0% in *Palaeospheniscus gracilis*. These percentages are noticeably higher, however, when considering only the amount of potentially scorable data, or osteology. These figures also more accurately reflect, for example, the completeness of taxa in the analysis that included only osteological data.

### **Analyses**

This cladistic matrix allowed me to run a number of different analyses that examine phylogeny with various subsets of taxa, and to investigate the effect of character

removal and ordering on tree topology. Search methodology is described below, followed by a discussion of the types of analyses run. I ran all analyses using the parsimony search algorithm of PAUP 4.01b10 (Swofford, 1991) to reconstruct phylogeny, and examined all trees, including reconstruction of character states and changes, in MacClade 4.06 OSX (Maddison and Maddison, 2000). Owing to the size of the matrix (74 taxa and 503 characters), an initial branch and bound search terminated prematurely after about 8 minutes run time. Therefore, only heuristic searches were further utilized. Searches were run with '?' indicating missing data, multi-state codings interpreted as polymorphic characters, and character reconstruction using DELTRAN. Each search included 1000 branch-swapping replications (TBR), swapping on the best trees only. The analysis started via random stepwise addition with a random addition sequence, holding one tree at each step. After an initial search determined that 52 separate tree islands, or local most parsimonious optima, exist for this dataset, the analysis was rerun to thoroughly sample this tree-space. I here searched by saving only ten trees that were one step longer than the shortest originally found. This original heuristic search used unrooted trees with no topological constraints. A bootstrap analysis of 1000 replicates was also run on the original, heuristic search with 10 random addition searches per replicate. The search was performed five times, all of which resulted in the same outcome.

The original run included the entire matrix with all characters unordered, all taxa included, and four taxa defined as outgroups (Procellariiformes, Gaviidae, Podicipedidae, and Phalacrocoracidae). The next two runs included 1) addition of some ordered characters, and 2) binary characters only, with all multi-state characters excluded.

Further runs partitioned the matrix into its component data types. These runs analyzed the taxa using characters from all morphology (osteology, integument, and soft parts), only osteology, only the tarsometatarsus, only the humerus, only myology, only the integument and soft parts, and only behavior. Runs including only the tarsometatarsus or the humerus tested the robustness of the common methodology of reliably diagnosing penguin taxa using single osteological elements and the converse, that analysis of these single, morphologically complex, elements may allow recovery of a highly resolved phylogeny. The runs including only myology, only the integument, and only behavior were run originally with all taxa, then again with only extant taxa because they are completely unscorable in extinct species but may allow determination of which data sets are affecting which aspects of the extant topology.

Finally, a number of runs examined the effect of taxon removal and outgroup specification, all using the entire, unordered, matrix. The first removed all outgroups from the matrix to exclude the possibility that long-branch attraction stemming from an abundance of scorable data (e.g., behavioral characters) or convergence of e.g., behaviors in extant taxa might affect reconstruction of relationships among penguins. The next returned each outgroup individually, to examine the change in ingroup relationships in the presence of single outgroups. Further runs constrained the ingroup to be monophyletic and removed incomplete taxa. This latter analysis included two runs, the first with taxa scored for less than 5% of the matrix removed, the second removing taxa less than 10% complete. These resulted in the removal of four and twenty-one of the 69 penguin taxa, respectively. Safe taxonomic reduction, or the removal of taxa with

identical character codings (Wilkinson, 1995), is not feasible with this dataset because no such taxa exist and therefore was not performed. The closest available species are *Pygoscelis tyreei* and *P. papua*, which differ in only two characters. Finally, an analysis was run with a backbone constraint based on the topology common to previous analyses of molecular data (Bertelli and Giannini, 2005; Baker et al., 2006; Ksepka et al., 2006).

Determination of patterns of character evolution involved reconstruction of ancestral states in MacClade, using both synapomorphies present at each node and terminal and changes in characters throughout the tree viewed by each osteological element or by myological, integumentary, or behavioral partition. This procedure allowed examination of changes that occur in various clades as well as changes that occur through evolution in each partition of data.

Lastly, a systematic revision of taxonomy and nomenclature is performed in concordance with the phylogeny proposed here. Linnean taxonomy, including ranks, is abandoned, and formal clade and taxon names are defined following the tenets of phylogenetic nomenclature (e.g., Rowe, 1987; de Queiroz and Gauthier, 1990, 1992).

## **Results**

### **Heuristic search**

The original analysis resulted in one most parsimonious tree (MPT) with a length of 2117 steps. The tree is fully resolved, although not well supported by tree support values (CI: 0.3602, RI: 0.5754, RCI: 0.2147). This MPT is shown in Figure 3.5a-b, along with bootstrap and Bremer support values and tree statistics. All recovered clades are also numbered for ease of discussion (Figure 3.5a-b). The following section begins

with the original search, describes all discovered penguin clades, proceeds through an analysis of character support, and ends with discussion of the various other runs performed. Clade names discussed here are formalized in the Systematic Revision below.

The MPT indicates that penguins are most closely related to either Phalacrocoracidae or to a clade including all other outgroups (Figure 3.5a). Further testing of the sister-taxon of penguins must await a thorough, phylogenetic analysis of these outgroups. All known penguins lie within the group Panspheniscidae, a stem-based clade whose name is defined here as all taxa more closely related to crown-penguins than to their outgroups. The Paleocene penguin *Wimanu* is recovered as the basal-most panspheniscid and a monophyletic genus (clade 2). This branching event marks the origin of the clade Sphenisciformes, which includes *Wimanu* + Spheniscidae. The two names (Panspheniscidae and Sphenisciformes) hence denote identical taxonomic content, for the time being at least, although the future discovery of more basal penguins will change this content (after Clarke et al., 2003; Ksepka et al., 2006).

The next branching event within penguins produced the clades Parapterodytidae and Spheniscoidea, which are first recognized in this paper (Figure 3.5a). This clade (clade 3) therefore includes all known penguins except *Wimanu*, although it is expected that discovery of additional stem-penguins will add to this complement. One of the descendants of this node is Parapterodytidae, which includes a paraphyletic *Delphinornis* and a monophyletic *Parapterodytes* (clade 8). The clade is known mainly from Seymour Island, although *Parapterodytes* is exclusively South American. The non-monophyly of *Delphinornis* is not surprising, as this taxon was erected solely on size-classes from an

enormous collection of Seymour Island tarsometatarsi, as were the other paraptenydytids *Mesetaornis* and *Marambiornis* (Myrcha et al., 2002). Because the Seymour Island bones are completely disassociated, the taxa erected from these collections may be synonymous and do not necessarily represent distinct species. Additionally, unexplored ontogenetic variation, especially in size, may be mistakenly influencing the assignment of elements and obscuring the relationships between species. Although such taxa are undoubtedly similar and probably do form a clade, hypotheses of relationship between paraptenydytid species should be considered preliminary.

The sister-taxon of Paraptenydytidae, or Spheniscoidea, includes all remaining penguins (Figure 3.5a). The disparity between the appearance of this clade in the rock record in the Late Paleocene and the implied time of origination of Paraptenydytidae in the fossil record results in a long ghost lineage for the latter. However, the majority of both the basal spheniscoids (or Palaeudyptidae) and nearly all paraptenydytids occur in rocks of the same age. Although both clades contain species from the La Meseta of Seymour Island, this does not explain why both groups suddenly appear at this particular time, after such a long gap in both much abundance and nearly all diversity. Such patterns will be further examined in subsequent publications (Triche, Chapter 4).

Spheniscoidea may be divided into two clades, Palaeudyptidae and Node 30 (Figure 3.5a), which includes the much larger crown-clade, Spheniscidae (see Figure 3.5b) and a number of successive stem-spheniscids. Palaeudyptidae includes a large number of extinct species known mainly from New Zealand and Seymour Island, Antarctica. Palaeudyptidae is first known from the Paleocene, as evidenced by the

Antarctic taxon *Crossvallia*, but only diversified dramatically in the Eocene. The clade includes a basal bifurcation followed by the further branching into two large clades (Clades 13 and 19, Figure 3.5a). The former contains a clade of two *Archaeospheniscus* species (clade 18) and a number of other, poorly known taxa, while the latter includes a *Crossvallia*-CADIC clade (28) and a monophyletic *Anthropornis* (clade 24). Finally, *Archaeospheniscus*, *Palaeudyptes*, *Pachydyptes*, and *Platydyptes*, which are all common, New Zealand palaeedyptids, are also all shown to be paraphyletic genera.

Seven stem-taxa are more closely related to Spheniscidae than to Palaeedyptidae (Figure 3.5a). While most of these are younger in age than any more basal penguin, *Ichtyopteryx*, *Palaeospheniscus spp.*, and *Dunroonornis* do all serve to extend the geologic age of the crown-clade. These species range from the Oligocene through the Pliocene in age. The oldest, *Ichtyopteryx*, is also the basal-most stem-spheniscid (clade 30, Figure 3.5a), and predates the remaining group by about 10 million years. The remaining stem-spheniscids are predominantly New Zealand species, indicating that the ancestral crown penguin may be a New Zealand species similar to such forms as *Marplesornis* or *Dunroonornis*. Alternatively, various South American *Palaeospheniscus* taxa also lie within this stem-group and within crown-clade spheniscids, suggesting a closer link of the crown with South America. This second hypothesis is better supported by the greater relative completeness of the *Palaeospheniscus* taxa in this analysis.

The penguin crown-clade, Spheniscidae, contains 33 taxa, only about half of which (18 species) are extant (clade 37, Figure 3.5b). Nine of the extinct members of this

clade, however, are either congeneric with extant taxa or often considered as such (e.g., the South African genus '*Inguza*'; Olson, 1983). All nominal, extant genera are monophyletic except *Eudyptes* (clade 48), which includes the South African '*Nucleornis*', the Argentinian *Chubutodyptes*, and the New Zealand *Korora*. Regarding relationships among the extant groups, the two Antarctic genera, *Aptenodytes* and *Pygoscelis*, are sister taxa and specify the clade Australodyptinae, whereas the remaining four extant genera form successive outgroups to this clade. *Megadyptes* is the extant sister taxon to Australodyptinae, followed by *Eudyptes* (together forming clade 47), *Eudyptula* (clade 45, together forming clade 44), and *Spheniscus* (clade 38, together forming clade 37). These relationships are generally similar to previous morphological analyses (Figure 3.4; Walsh and Suarez, 2006; Bertelli and Giannini, 2006; Ksepka et al., 2006), lending further support to the current accepted view of penguin evolutionary history. The only difference in the cladogram proposed here is the pectinate arrangement of genera, as opposed to the previously recovery of a sister-taxon relationship between crested penguins (*Eudyptes* and *Megadyptes*) and a *Spheniscus-Eudyptula* clade (Bertelli and Giannini, 2006; Ksepka et al., 2006). All morphological hypotheses, including that recovered here, differ from all molecular work, however, in the placement of Australodyptinae (Baker et al., 2006; Bertelli and Giannini, 2006).

Relationships within these extant genera are also all resolved (Figure 3.5b). The single, extinct species of *Aptenodytes* is most closely related to *Aptenodytes patagonicus*, which agrees with their close geographic relationship. The Emperor penguin (*Aptenodytes forsteri*) forms the outgroup to the other two, completing a monophyletic

*Aptenodytes*. *Pygoscelis adeliae* is the basal-most member of the pygoscelid species, while the other two extant species, *Pygoscelis antarctica* and *P. papua* form a clade with the two extinct species, *P. grandis* and *P. tyreei*, as successive outgroups. This result also agrees with geography because *Pygoscelis adeliae* is by far the most southerly of this otherwise sub-Antarctic and temperate clade. The topology disagrees with previous work, however, which places either *Pygoscelis papua* outside a clade uniting *Pygoscelis adeliae* and *P. antarctica* (Walsh and Suarez, 2006), or the Chinstrap outside an Adelie-Gentoo clade (Bertelli and Giannini, 2005; Ksepka et al., 2006). The fact that all possible relationships are now proposed for pygoscelid species concurs with the suggestion that these penguins only recently diverged from other extant penguins and are not differentiated enough to allow great phylogenetic resolution (Walsh and Suarez, 2006). *Spheniscus* species include a sister-group relationship between *Spheniscus magellanicus* and *S. mendiculus* (clade 42) and between *Spheniscus demersus* and *S. humboldti* (clade 41), the latter of which also includes the extinct *Spheniscus chilensis* (clade 40). Most previous work instead supports grouping *Spheniscus demersus* and *S. magellanicus* apart from *Spheniscus mendiculus* and *Spheniscus humboldti* (Kennedy and Page, 2002; Bertelli and Giannini, 2005; Ksepka et al., 2006).

Extant ‘crested penguins’ include *Eudyptes* and *Megadyptes* and are not monophyletic. The rare and endangered Yellow-Eyed penguin (*Megadyptes*) is the extant sister-taxon of Australodyptinae (together forming clade 57), followed by the only known Tasmanian penguin, the extinct *Tasidyptes* (clade 56, Figure 3.5b). It is suggested that the two may be congeneric or even conspecific, and this question warrants further study (van

Tets and O'Connor, 1983). Within the remaining 'crested penguins', the Royal (*Eudyptes schlegeli*) and Macaroni (*Eudyptes chrysolophus*) penguins form a clade (clade 55), as would be expected considering that the former is sometimes classified as a subspecies of the latter. The outgroup to this clade is the Rockhopper penguin (*Eudyptes chrysocome*), while these three together (clade 54) form the sister taxon of a clade including the Erect-crested penguin (*Eudyptes sclateri*), its three extinct relatives, and the Snares Island crested penguin (*Eudyptes robustus*, clade 50). Finally, the Fiordland crested penguin, *Eudyptes pachyrhynchus* diverged as the most basal *Eudyptes* penguin (clade 48). The first of these three-taxon groups is distributed widely throughout the Southern Ocean, while *Eudyptes sclateri* and *E. robustus* are restricted to islands offshore from New Zealand. The topology within *Eudyptes* is exactly that of some recent, morphological, analyses (Bertelli et al., 2005; Ksepka et al., 2006), but differs widely from other morphological and molecular studies (Baker et al., 2006; Walsh and Suarez, 2006).

It is seen here that the large amount of incompleteness shown by many of these taxa does not inhibit recovery of their phylogenetic relationships. However, a bootstrap analysis run on the original, unmodified matrix shows that most nodes received support values under 50%, especially extinct clades. A number of nodes are highly supported, including the outgroups, *Wimanu*, a clade of two unnamed New Zealand '*Palaeoeudyptes*' species (OM C47.23A and OM C47.25), and most extant clades. Additionally, the consistency and retention indices for the MPT's (0.4836 and 0.5792, respectively) are no lower than expected, considering the large size of the analysis (Sanderson and Donoghue, 1989). In fact, the correlation between CI and the number of taxa included in an analysis

suggests that the expected CI for this analysis would be 0.35, slightly lower than that obtained. It appears that use of a large matrix and extensive analysis does here result in great resolution of penguin relationships.

### **Character Analysis**

Of the original 503 characters, 449 were parsimony informative, while the rest serve to diagnose the terminal taxa. This results in a ratio of about seven characters per terminal taxon, which is twice as many as that used in most other recent penguin analyses (e.g., about 3.5 in Ksepka et al., 2006; about 2.3 in Walsh and Suarez, 2006; about 3 in Slack et al., 2006; and about 5.3 in Bertelli and Giannini, 2005). More data, via a greater number of characters, only leads to improved resolution of relationships if it contains the particular character states or combinations thereof that comprise synapomorphies *a posteriori* (e.g., Donoghue et al., 1989). However, this large character-to-taxon ratio should suggest better support for the cladogram hypothesized here because including a large number of characters is the best way to insure that such synapomorphies are discovered and that good phylogenetic resolution results. This is especially important because the number of taxa examined in this analysis is nearly double that used in previous penguin work, and large numbers of characters are essential in resolving analyses of large numbers of taxa (e.g., Hill, 2005). All extant species are at least 90% completely scored, except for the outgroup taxa Gaviidae, Podicipedidae, and Phalacrocoracidae, which are 60-80% complete owing to lack of published information on, for example, behavioral characters (Appendix 3.2). Many extinct taxa are much less complete than this, but mainly owing to the lack of knowledge of numerous elements, not

to poor preservation of elements that are known. This is important because it generally allows scoring of numerous characters from diagnostic, although single, elements. Particularly complete extinct taxa include *Palaeudyptes antarcticus*, *Palaeudyptes marplei*, *Palaeospheniscus bergi*, *Palaeospheniscus patagonicus*, *Paraptenodytes antarcticus*, and *Paraptenodytes robustus*, *Pygoscelis grandis*, *Spheniscus urbinai*, and *Wimanu tuatahi*. The completeness of these taxa is particularly informative because they are spread throughout the penguin phylogeny and include representatives of the earliest sphenisciform genus, of both Paraptenodytidae and Palaeudyptidae, and of extant genera.

Figure 3.6a and b illustrate character support for the MPT from my original analysis. All unambiguous synapomorphies are indicated on this tree for all large clades, while all changes for all nodes and all terminals are listed in the Systematic Revision section and in Appendix 3.5, respectively. Character support for important clades is discussed below. Functional interpretation of this character evolution is mentioned when available. However, the functional purpose of most evolutionary changes is not known because most of the characters analyzed here are new and not yet analyzed in any functional context.

**Sphenisciformes.** Currently, Panspheniscidae and Sphenisciformes contain the same taxa because there is no known penguin more plesiomorphic than *Wimanu*, and character support for the two clades is identical. Nineteen synapomorphies support the clade Sphenisciformes (Figure 3.6a), including cranial characters such as loss of pneumaticity, which allows the evolution of swimming via increased bone density,

deeply excavated temporal fossae, which allows for a larger jaw musculature and potentially different feeding habits (e.g., Ksepka and Bertelli, in press), and presence of a bifurcate quadrate head. Additionally, penguins evolved bifurcate haemal spines and lost two sacral vertebrae, retaining twelve. Within the pectoral skeleton, they gained a supracoracoid fenestra and a shortened humerus with an inturned head and a large, deep, pneumatic fossa. This shortened sacrum and humerus may have served to shorten and streamline their body for swimming. Their pelvic skeleton evolved a fused ilio-sacral connection, a straight femur, and a greatly shortened tarsometatarsus.

An additional sixteen synapomorphies support the slightly smaller clade that excludes the stem-penguin *Wimanu* (Clade 2, Figure 3.6a). These involve many characters of the pectoral girdle and limb, such as evolution of a change in the coracoid from flared to rod-like, a more strongly bent forearm, and a number of humeral characters. In this clade, the humerus becomes shorter and stouter in relation to the remaining forelimb skeleton, widens distally to an equal width throughout, undergoes displacement of the distal tendinal grooves from the shaft, and evolves a deep, oblong fossa for insertion of the *pectoralis primus* muscle, rather than the shallow groove present in *Wimanu* and all outgroups. Additionally, the tibiotarsus is shortened and the tarsometatarsus changes shape from a waisted hourglass to a rectangle, while the trochlea of its fourth digit rotates anteriorly to lie in the same vertical plane as the other two, and its distal intermetatarsal foramen opens to form the external adductor groove.

Most of the apomorphies diagnosing the nodes Sphenisciformes and Clade 2 may be correlated with adaptation to a swimming body plan from the flying type present in

sphenisciform outgroups. They mainly concentrate on the post-cranial skeleton, but also include skull adaptations that allow better swimming via solid, heavier bones and loss of pneumaticity, and utilization of different feeding mechanisms via enlarged jaw adductor musculature (characters 1 and 2).

Character distributions may also be mapped onto the phylogeny to characterize the morphology of the ancestral sphenisciform. This procedure reconstructs the ancestral penguin as having already lost all skeletal pneumaticity, including the pneumatic foramen of the humerus and all cranial pneumaticity. The bird had gained temporal fossae that were deeply excavated dorsally, nearly to the midline, but did not yet contain a deepened ventral section. It also possessed a long, gracile beak with small, holorhinal nostrils, but had not yet evolved a deepened, more robust mandible or a retroarticular process. The bird's tympanic recess was deeply excavated and it had evolved a large paroccipital process and a laterally compressed vomer free from the palatine. However, this original sphenisciform had not yet evolved an enlarged cerebellar dome, a styliiform process of the supraoccipital, a eustachian tube enclosed with bone, a dorsally visible lacrimal, or a triangular pterygoid. The vertebrae of the ancestral penguin were reduced in number to 42, those of the synsacrum to 12, and those of the caudal series to eight. The hallux and the 4<sup>th</sup>, 5<sup>th</sup>, and allular digits typical of other birds had already been lost, as had the heterocoely of the posteriormost thoracic vertebra. This bird had evolved a flattened coracoid with an elongate lateral process and a small supracoracoid fenestra, and a sternum with the coracoid sulcus continuous across the midline and only one lateral incision. The humerus of the ancestral penguin had a large, square head and a large, deep

pneumatic fossa, but lacked the horizontal articulation, distally widened shaft, sigmoid shape, and bipartite pneumatic fossa seen in more derived penguins. This element, and the other wing bones, were extremely flattened (contra Ksepka et al., 2006), although the limbs were not heavily pachyostotic. Finally, the ischiopubic fenestra was not yet open posteriorly and the ilio-sacrum was completely fused in the adult, not sutured, as in some extant species.

A number of character states reconstructed for the ancestral penguin are intermediate between those of more derived penguins and of penguin outgroups, as one might expect. For example, the supraorbital salt gland fossa was present, but did not contain the lateral shelf known in most extant species; the angle between the forearm and the humerus was much smaller than in other extinct penguins, resulting in a more strongly bent arm, but much less so than in all outgroups; the cnemial tibiotarsal crest was long, but not as elongate as in procellariiforms; and all metatarsals were fused, as in derived penguins, but also uncurved and with a posteriorly deflected trochlea on metatarsal four, as in all outgroups. The ancestral penguin was small, with skull and humeral lengths in the smallest range of any known species (115 mm or less and 70 mm or less, respectively). Its wing proportions were also different than those of more derived clades of penguins, with a longer forearm in comparison with the humerus. Leg proportions varied as well, with a proportionately thicker femur and narrower, longer tarsometatarsus, in comparison both with the tibiotarsus and with the femur. These characteristics indicate that the ancestral penguin, while noticeably adapted for

swimming, had not evolved many of the fully aquatic, osteological specializations of derived penguins.

**Paraptenodytidae.** One of the clades of entirely extinct penguins, Paraptenodytidae, comprises a small group of small-sized penguins that may be differentiated from all other species by one synapomorphy, in which the lateral hypotarsal crest of the ventral surface of the tarsometatarsus is more prominent than the medial. This clade and *Archaeospheniscus* are the only penguins that possess this trait.

**Spheniscoidea.** Only one unambiguous synapomorphy supports the clade Spheniscoidea, the sister taxon of Paraptenodytidae (Figure 3.6a). Spheniscoids lost the sigmoidal humerus present in all earlier penguins in favor of a straight bone and are smaller, especially in terms of tarsometatarsal size. Palaeudyptidae, one of the members of Spheniscoidea, underwent a large amount of evolution, but remaining, stem-spheniscid, spheniscoids evolved few synapomorphies. However, much character evolution occurred within the other large clade of spheniscoids, or Spheniscidae.

**Palaeudyptidae.** The clade Palaeudyptidae possesses only nine unambiguous synapomorphies, and the clades within it are generally even more weakly supported (Figure 3.6a). This group of extinct species possesses a posteriorly-grooved synsacrum and a humerus with an abrupt projection at the preaxial angle. Within palaeudyptids, the monophyletic group including *Anthropornis* and most *Palaeudyptes* and *Pachydyptes* species (clade 21) is supported by two synapomorphies, including a lengthened humerus indicative of an enlarged body size. In general, most palaeudyptids were larger than extant penguins and other spheniscoids. It appears, therefore, that penguins evolved from

a medium-sized bird, small for a penguin at about a meter in standing height. The extinct clade Palaeedyptidae evolved greatly enlarged size twice, in the group circumscribed by *Anthropornis* and *Palaeedyptes antarcticus*, and in the clade containing *Archaeospheniscus*. Finally, Spheniscoidea maintained the plesiomorphic size of Sphenisciformes, with some much smaller, derived members. Previous authors suggested that *Crossvallia* was part of the radiation of enormous, extinct penguins and that the evolution of drastically increased size may have occurred twice in penguin history (Tambussi et al., 2005). That hypothesis presented no phylogenetic framework, however, only assumed that *Crossvallia* is not related to other giant penguin species. My phylogeny suggests not only that *Crossvallia* was not actually as large as the ‘giant’ penguins but also that it is the sister taxon to these giant forms. One may interpret the character data, therefore, as an evolutionary cline ranging from ancestrally small palaeedyptids, through the larger *Crossvallia* and the ‘Tierra el Fuego’ species, to the largest known penguins, which form a single monophyletic group.

**Spheniscidae.** Three unambiguous synapomorphies support the penguin crown-clade, Spheniscidae (Figure 3.6b). These include loss of the elongated lateral process of the coracoid, a reduced dorsal extension of the medial angle of this bone, and loss of a sigmoid humerus. Taxonomic incompleteness may be affecting the monophyly of the crown-clade because, although all extant species are completely known, a number of included extinct taxa are not. Lack of knowledge of behavioral, integumentary, and myological data from those species may be masking the synapomorphies that support the clade.

The basal-most clade of spheniscids includes seven species in the monophyletic *Spheniscus*, which all share two synapomorphies. One of these is cranial, a well-developed interorbital septum, while the other is presence of a dorsoventrally thin acrocoracoid process. The number of synapomorphies supporting the monophyly of each remaining extant genus is much larger than that for *Spheniscus*, reaching 58 in the extant genus *Eudyptula*. This weak support for *Spheniscus* penguins suggests that the genus, like *Pygoscelis*, may be relatively little differentiated and hence relatively recently evolved.

The remaining four extant genera of penguins form a monophyletic group supported by thirteen synapomorphies (Figure 3.6b, clade 47). These include: temporal fossae that lie far apart and are only weakly hollowed; large, holorhinal nostrils; a slightly hinged nasofrontal contact); a dorsally visible lacrimal; a retroarticular process longer and narrower than the articular surface of angular; a medial mandibular process of the articular that has an accessory midline fossa; a medium-width proximal end of the coracoid; a humerus with a distal, trochlear process extending past the humeral shaft; a capital groove of the humerus that is shallow and wide; a small, distally closed fossa between the insertions for the *supracoracoideus*; a triangular or fan-shaped *deltoideus major*; pinkish dorsal surface of feet; and a December molting season. The prevalence of cranial characters, as opposed to other skeletal elements, as synapomorphies of this clade probably arose because cranial material remains unavailable for nearly all extinct taxa outside this clade. Within this group, 5 synapomorphies (0 cranial), support the monophyly of *Eudyptes*, while 28 (12 cranial) support *Pygoscelis*, 3 (0 cranial) support *Aptenodytes*, and 42 support *Megadyptes* (see Appendix 3.5 for complete list).

The Antarctic genera are united in the clade Australodyptinae (Figure 3.6b), which is supported by three unambiguous characters that include: tibiotarsal sulcus for *m. fibularis* absent or small; intercotylar eminence of tarsometatarsus small, narrow, not raised; and medial intermetatarsal foramen with a medially bordering crista present.

### **Data Partitions**

Figure 3.7 illustrates the taxonomic levels at which these data partitions support various penguin clades. For example, *Spheniscus* is supported by many data types, including myology and osteology, but only the *Spheniscus demersus*-*S. mendiculus* group is recovered using behavioral characters. All such partitions are discussed below.

The first modification of the matrix, which differed by ordering a number of characters, resulted in a massive polytomy in the strict consensus of resulting trees, but nearly complete resolution in the Adams consensus of these trees. Spheniscidae remained monophyletic, and relationships among extant genera were identical to those in the original analysis, but the relationships of more basal lineages were different. Relationships within Palaeudyptidae nearly all dissolved with addition of ordered characters, and the species within this clade nested either as outgroups to Paraptenodytidae or as numerous pectinate outgroups to Spheniscoidea.

Analysis of only binary characters resulted in even less similarity to the original tree topology. For example, the crown-clade was no longer monophyletic, many extant genera were split apart, and even the placement of *Wimanu* was not as expected, forming a non-monophyletic genus nested within Sphenisciformes. The extreme reduction in resolution upon addition of ordered, and especially upon removal of multi-state

characters, occurred because many important synapomorphies happen to be multistate and were thus removed. This highlights the importance of including all types of character data because *a priori* analysis cannot determine which character or which character type will serve as a synapomorphy that is important for the analysis.

Taxon choice, both for outgroups and ingroups, was examined next. First, the analysis was run without any outgroup taxa, to exclude possible convergent morphology with these other seabirds. Unfortunately, this procedure also excludes important outgroup character polarizations. The analysis recovered Palaeudyptidae in an almost identical position as that of the original analysis, but all resolution within Paraptenodytidae was lost, with most of its included taxa lying basally within Sphenisciformes. The recovered phylogeny also placed the extinct palaeudyptids as the sister taxon to the extant crown-clade. This group, Spheniscidae, remained monophyletic, but its internal relationships were completely reversed. The most divergent result was, again, the placement of *Wimanu*, which lay well-nested with Palaeudyptidae. Obviously, outgroup comparison is necessary to polarize the character states of this stem-penguin. *Wimanu* in particular shows a mosaic of characters known from more derived penguins and from various outgroups. It is not surprising that the derived characters pull the taxon further into Sphenisciformes when these outgroups are removed.

Following this test, each outgroup was reincluded in the analysis separately. Inclusion of only Gaviidae resulted in recovery of nearly identical relationships as the original search, at least within Spheniscidae and its immediate outgroups. The only minor difference was the reversal of the placement of *Eudyptula* and *Spheniscus*. Relationships

among extinct species, however, were highly altered. The composition of Paraptenodytidae was mostly concordant, although *Paraptenodytes* did fall outside this clade, closer to the crown-group. Half of the species contained within Palaeudyptidae were relocated to lie either within or as outgroups to Paraptenodytidae. Analysis of only Podicipedidae resulted in the same crown-clade topology as using Gaviidae, while the extinct species were altered somewhat similarly. In this case, Paraptenodytidae completely dissolved, with some species nesting within the crown-clade and some remaining as its outgroups. Palaeudyptidae remained mostly intact, although it did split into two clades rather than one united group. Analyzing Procellariiformes separately resulted in the retention of both extinct clades, but recovery of Paraptenodytidae within Palaeudyptidae. The crown-clade here was similar to that of the original run, with the exception that species previously recovered as stem-Spheniscidae form a clade that lies in a polytomy with Australodyptinae and *Eudyptes*.

Finally, examining Phalacrocoracidae alone gives almost exactly the same results as the original run, with the two sole exceptions that *Paraptenodytes* lies within Palaeudyptidae, not Paraptenodytidae and that the *Crossvallia*-CADIC clade emerges from Palaeudyptidae to lie in a polytomy between both this group and remaining Sphenisciformes. This may indicate that Phalacrocoracidae is particularly important in reconstructing the relationships of penguins, although it should be reiterated that this study is not intended to determine the sister-taxon of penguins and does not include all data pertinent to such a question. However, this analysis does suggest that the potential sister-taxon status of Sphenisciformes and Phalacrocoracidae should be further examined.

Evidence from analysis of these various outgroups indicates that choice of different proposed penguin sister taxa greatly influences relationships within Sphenisciformes. This is to be expected, as authors repeatedly suggested that the predominant cause of uncertain sphenisciform relationships is convergence in seabird evolution. It seems, therefore, that the best method to overcome such convergence is the inclusion of numerous outgroups, not only a sole probable sister-taxon of penguins. Because of the variable effect of outgroup choice, care must be taken when interpreting previous analyses of penguin relationships, both extant and extinct (e.g., Bertelli and Giannini, 2005; Slack et al., 2006; Walsh and Suarez, 2006; Ksepka et al., 2006). Most of this previous work included only one outgroup, or two at most, although many of the analyses did use numerous species to code these outgroups. A larger, supermatrix approach could potentially eliminate this incomplete outgroup sampling while retaining the broad species coverage gained by considering the outgroups from all of these studies.

The next analyses examined the effects of constraining the ingroup to be monophyletic. The first of these resulted in the retention of a monophyletic ingroup and Palaeudyptidae, but movement of Paraptenodytidae to form a polytomy with Phalacrocoracidae and remaining sphenisciforms. Paraptenodytidae in this case was more closely related to the penguin outgroups than was *Wimanu*. Phalacrocoracidae is therefore resolved as the penguin sister-taxon, both of which are then most closely related to Procellariiformes, then Podicipedidae, then Gaviidae. This order is not congruent with the nested relationships most often recovered for penguin, which are generalized as (((penguins), Procellariiformes), Gaviidae), Podicipedidae, Phalacrocoracidae). The fact

that changing only this one setting, ingroup constraint, results in completely different outgroup relationships, in conjunction with consideration of the results of the previous outgroup analysis, demonstrates that the relationship of penguins to their relatives remains contentious and requires further study (contra, e.g., Bertelli et al., 2006; Ksepka et al., 2006). These authors asserted that Procellariiformes is probably the sister taxon of penguins and that this conclusion is well tested and common to most analyses, but they included only Gaviidae as a second, potential outgroup. Additionally, taxon sampling within procellariiforms was extensive, using eleven species, while only one gaviid was included. Although this method is probably more than sufficient to polarize characters for reconstruction of relationships within penguins, it does not adequately examine their relationships to other seabirds and should not be used to conclude that the placement of penguins is well tested.

Next, sphenisciform relationships were examined with the removal of various incomplete taxa, both at the 95% incomplete and 90% incomplete levels. The first of these runs removed the following species: *Anthropodytes gilli*, *Marplesornis novaezealandiae*, *Orthopteryx gigas*, *Palaeospheniscus gracilis*, *Pseudapterodytes macreei*, and CADIC P-21. In addition to these, the second run removed the following taxa: *Chubutodyptes bilocolata*, *Crossvallia unienwillia*, *Delphinornis arctowski*, *D. gracilis*, *D. larseni*, *Duntroonornis parvus*, *Eretiscus tonii*, *Ichtyopteryx gracilis*, *Korora oliveri*, *Marambiornis exilis*, *Mesetaornis polaris*, 'Nucleornis' *insolitus*, *Palaeodyptes klekowskii*, *Palaeospheniscus wimani*, *Platydyptes amiesi*, *Pygoscelis tyreei*, *Spheniscus megaramphus*, and *Tereingaornis moisleyi*. Removal of all taxa 95% or more incomplete

resulted in nearly exactly the same relationships as the original run. The only major difference is that this topology places *Crossvallia* within Paraptenodytidae, rather than Palaeedyptidae, probably because its hypothesized sister-taxon, CADIC P-21, was removed. Because this analysis removes excessively incomplete taxa, its results suggest high confidence in the proposed topology of penguin relationships. Removal of additional taxa of slightly higher completeness resulted in loss of resolution within Palaeedyptidae, suggesting that some of these less complete taxa retain important character states for reconstructing relationships among other, more complete species. In this respect, it is important that the current work analyses all extinct taxa, rather than just fairly complete species, because such partial data does seem to include character states and combinations indicative of higher relationships (Donoghue et al., 1989).

In addition to removing incomplete taxa, an analysis was also performed using a pruned set of taxa, by removing all but the most complete species of every genus found to be monophyletic in the original analysis. This left 48 ingroup taxa and one outgroup (Procellariiformes) in the analysis. This includes many more taxa than there are penguin genera because many extinct genera are here hypothesized to be para- or polyphyletic. The pruned tree is almost fully resolved, but recovers a number of different relationships within extant species. For example, the crown-clade is not monophyletic and the extant genera in fact form a succession of outgroups to a clade of extinct Miocene taxa. Further, *Tasidyptes* does not group with *Megadyptes* as expected, and the relationships between genera are completely different. Extinct species, on the other hand, retain almost all relationships found in the original analysis, with the exception that Paraptenodytidae and

Palaeudyptidae are sister taxa. This highlights the fact that taxon choice, even among well-known, extant species, is extremely important in phylogenetic analysis, and that the common practice of using only a single penguin species in larger analyses is not warranted.

To analyze the efficacy of this new matrix regarding extant taxa alone, all extinct taxa were removed in the next run. A single most parsimonious tree was recovered. This tree contained the same outgroup relationships as previous analyses and nearly identical relationships between all extant genera and all extant species. The only exception was *Eudyptula*, which lies basally within Spheniscidae, rather than nested above *Spheniscus*. This topological similarity probably results from the fact that the large number of behavioral, integumentary, and myological characters scorable only for living species are swamping any potential osteological similarity between extant and extinct taxa that would appear in a more global run.

Finally, I ran an analysis identical to the original heuristic search with the addition of a molecular backbone constraint tree imposed. The topology utilized is common to analyses of penguin phylogeny based on molecular data (Bertelli and Giannini, 2005; Baker et al., 2006; Ksepka et al., 2006):

((*Aptenodytes forsteri*, *Aptenodytes patagonicus*), ((*Pygoscelis adeliae*,  
*Pygoscelis antarctica*, *Pygoscelis papua*)), ((((*Eudyptes sclateri*, (*Eudyptes*  
*pachyrhynchus*, *Eudyptes robustus*)), (*Eudyptes schlegeli*, *Eudyptes*  
*chrysolophus*)), *Eudyptes chrysocome*), *Megadyptes antipodes*), (((*Spheniscus*

*humboldti*, *Spheniscus mendiculus*), (*Spheniscus magellanicus*, *Spheniscus demersus*)), (*Eudyptula minor*, *Eudyptula minor albosignata*))))))

The analysis ran using 1000 replicates of random stepwise addition in a heuristic search and resulted in ten MPT's with a score of 2598. The strict consensus of these trees is almost completely resolved and nearly identical to their Adams consensus tree.

Additionally, relationships among extinct taxa are very similar to those obtained by the original analysis. The main differences include recovery of Palaeoeudyptidae as the sister taxon of Paraptenodytidae and loss of a sister-taxon relationship between *Megadyptes* and *Tasidyptes*. The MPT's recovered using this molecular constraint are also significantly longer than those recovered originally, suggesting that the molecular data is not wholly congruent with that used in this analysis.

The last type of analysis to be run examined the effect that different data partitions have on different taxa and levels within penguin phylogeny. In this case, all outgroups and ingroup species were retained, as were all original settings. Running the analysis using only morphological characters (87% of the total data) resulted in similar crown-clade relationships as the original analysis. Exceptions included the placement of *Eudyptula*, which formed the sister-taxon to Australodyptinae, and the crested penguins, which here formed a clade including *Eudyptes*, *Megadyptes*, and *Tasidyptes*. Both these relationships were suggested previously in many morphological and molecular analyses, implying that different behavioral characters are now responsible for separating these clades (e.g., Simpson, 1946; Bertelli and Giannini, 2005; Baker et al., 2006). Nearly all higher level relationships were also similar to the original run, with the exception of the

members of stem-Spheniscidae. These taxa now lie outside Spheniscoidea, as part of a polytomy with Palaeudyptidae. Analysis of osteological characters alone resulted in a slightly different topology, in that all relationships supported in the original run were upheld except that of *Aptenodytes*, which lies basally within Spheniscidae, and the repeated appearance of a ‘crested penguin’ clade. It is not surprising that osteology, and morphology in general, agree with the results obtained using all data, as these partitions form the vast majority of the total dataset. Osteology, considered alone, supports nearly every node on the proposed sphenisciform cladogram. The high resolution and congruent relationships obtained using osteological data supports the use of fossil data, even if remains are somewhat incomplete, when included within a broader systematic framework.

Even smaller partitions were tested next, utilizing only the tarsometatarsus and only the humerus. These are the two most commonly preserved elements of the penguin skeleton, and are additionally thought to be individually diagnostic to species level in extinct taxa. Incomplete extinct taxa, especially avians and especially specimens known from single elements, are often not diagnostic to such low taxonomic levels, however, and their applicability should be tested before assuming so (Clarke, 2004). Therefore, reconstructing sphenisciform phylogeny using only one of these elements tests whether or not it is possible to use either element as the sole diagnostic tool for isolated, extinct specimens. Not surprisingly, both analysis of only tarsometatarsal and of only humeral characters resulted in strict consensus cladograms showing absolutely no resolution whatsoever. Adams consenses, although not fully resolved, do show much greater

resolution. Ignoring the taxa for which the ankle bone remains unknown, tarsometatarsal analysis recovered Palaeudyptidae and Paraptenodytidae. Spheniscidae is not monophyletic because a clade consisting of about half the members of Palaeudyptidae nests just above a basal *Pygoscelis*, as the sister-taxon to remaining spheniscids. In the humeral analysis, more taxa show no resolution owing to lack of this element, but resolution among the remaining species is high. Relationships are again different, with a non-monophyletic crown-clade and numerous non-monophyletic extant genera. It appears from these two analyses that extant species may be differentiated using either element, but that numerous extinct species cannot and should not be diagnosed using only the humerus or the tarsometatarsus. Specimens consisting of single elements may probably be diagnosed to larger clades within Sphenisciformes, such as Spheniscoidea or Palaeudyptidae, but not to genus or species level.

When only integumentary and soft part characters are analyzed, the resulting strict consensus cladogram is entirely unresolved, except for the recovery of a monophyletic *Pygoscelis*, in which *Pygoscelis adeliae* and *Pygoscelis papua* are derived relative to *Pygoscelis antarctica*. In the Adams consensus tree, integumentary characters support the monophyly of all extant genera as well as that of Spheniscidae, although this is obviously an artifact of the lack of integumentary data in extinct taxa. Relationships between genera are completely incongruent with those recovered in the original analysis and much more similar to the molecular signal present in previous works (e.g., Bertelli and Giannini, 2006; Ksepka et al., 2006). A basal trichotomy between *Aptenodytes*, *Spheniscus*, and the remaining genera forms the clade Spheniscidae. The more derived clade resolves

*Eudyptula* and *Megadyptes* as sister taxa, with no further resolution present between this group, *Eudyptes*, and *Pygoscelis*. All species-level relationships are identical to the original analysis, excepting *Pygoscelis*. Myological data, on the other hand, results in slightly more resolution. The genera *Spheniscus* and *Aptenodytes* form unambiguously monophyletic clades, and the latter is reconstructed as the sister-taxon to *Pygoscelis* in the clade Australodyptinae. All remaining genera are ambiguous with regard to monophyly, although a subset of *Eudyptes* does also form a clade. Finally, analyzing behavioral characters alone completely resolves all ingroup taxa. No closer relationship with any outgroup taxon appears, but all extant genera are monophyletic, excepting *Spheniscus*, and all intergeneric relationships are identical to those of the original search. A number of intrageneric topologies differ from the original result, however, notably the relationships within *Spheniscus* and its paraphyletic inclusion of *Megadyptes*.

Results from the separate analysis of these data sets indicate that various types of data are phylogenetically informative at different levels of relationship. Osteological characters in particular seem to contain much information about higher-level relationships, while smaller morphological partitions such as myological and integumentary characters support lower-level clades, i.e. species, and behavior supports generic relationships. Integument is particularly informative at the intrageneric level, for example within *Pygoscelis*, while myology supports higher, intergeneric relationships. Osteological and behavioral data are responsible for the incongruence with molecular phylogenies of extant penguins, whereas signal from the integumentary and myological characters is congruent with this molecular data. Although data other than osteology

inherently does not inform relationships among extinct taxa, various levels of taxonomic relationship among these species are supported by different partitions within the osteological data. In particular, the placement of various congeneric species as members of extant taxa derives support from numerous data types, and is thus highly supported. These members include *Tasidyptes*, *Pygoscelis grandis* and *Pygoscelis tyreei*, *Aptenodytes ridgeni*, *Chubutodyptes*, ‘*Nucleornis*’, and all extinct *Spheniscus sp.* Within non-crown taxa, the following relationships are notably well supported by numerous types of data: *Palaeospheniscus bergi* + *Palaeospheniscus gracilis*, a monophyletic *Paraptenodytes*, *Mesetaornis* + *Delphinornis arctowski*, a monophyletic *Archaeospheniscus*, a monophyletic OM C-47, a monophyletic *Anthropornis*, a monophyletic *Wimanu*, Sphenisciformes, and Sphenisciformes minus *Wimanu*. Recovered monophyly of these groups, as well as of extant genera by nearly all types of data suggests much stronger support for these hypothesized clades than had they been proposed using one type of data alone. For example, the monophyly of Sphenisciformes is supported by morphological, osteological, tarsometatarsal, and binary characters, as well as by analysis excluding 95% and 90% incomplete taxa.

### **Systematic Revision**

This section revises the current taxonomy of extinct and extant penguins using an explicit phylogenetic framework. Taxonomic names are defined for clades recovered in cladogram presented here (Figure 3.5) and diagnosed using synapomorphies from the single MPT (character number and polarity indicated in parentheses), according to the principles of phylogenetic taxonomy (Rowe, 1987; de Queiroz and Gauthier, 1990, 1992;

Rowe and Gauthier, 1992; Joyce et al., 2004; Sereno, 2005). Figures illustrating all systematic characters are referenced in Appendix 3.3. All named taxa above the generic level are either new or converted clade names. Although all species analyzed here do form diagnosable taxonomic units, I only define those names that refer to highly supported clades, either in terms of large numbers of synapomorphies, many types of data partitions, or stable placement recovered by many types of analysis. This results in a large number of diagnosed, but unnamed, clades, which is currently unavoidable owing to the fragmentary nature of the penguin fossil record. Such clades are numbered as in Figure 3.5a-b, which also shows the specific content of each clade. Only named clades are therefore defined. Additionally, only clades that received unequivocal support are diagnosed. Clades not diagnosed for this reason include: Node 16, 47, 49, 52, 53, 62.

Following recent attempts to initiate a system of phylogenetic nomenclature, exhaustive debate about the utility, logic, and methodology, or lack thereof, of this new system has consumed the systematic community (e.g., Benton, 2000; Schuh, 2003; Cantino and de Quieroz, 2006; etc.). In a hopeful, although perhaps impossible, attempt to navigate this often contentious and acrimonious debate, I will here incorporate the potentially most promising aspects of phylogenetic nomenclature into the current, Linnaean system. The code regulating phylogenetic nomenclature is yet to be published, but I here follow PhyloCode recommendations for naming clades to maximize their continuity upon future implementation of this code (e.g., rankless taxonomy, ‘pan-’ stems for total clade names; Cantino and de Quieroz, 2006). I restrict such guidelines to taxa above the generic level, however, while those below are revised in accordance with the

ICZN (ICZN, 1999). I do not convert any generic name to a clade name because the rationale and procedure for conversion of generic and specific names is under revision and not yet formalized (Cantino and de Quieroz, 2006). A number of clades recovered here undoubtedly comprise monophyletic genera (e.g., *Archaeospheniscus*, *Spheniscus*, *Aptenodytes*), but conversion of these names should await the adoption of a universal methodology.

Although one of the many recommended methods of defining a taxonomic name involves the use of apomorphies (Cantino and de Quieroz, 2006), I choose to avoid such definitions here. As a rationale, and using the Paleocene penguin *Wimanu* as an example, I will point out three, among many, difficulties inherent in apomorphy-based definitions (Rowe, 1987; Rowe and Gauthier, 1992; Padian et al., 1999; Gauthier and de Quieroz, 2001; Sereno, 2005). First, it may be fairly certain that *Wimanu* did not fly, but differentiating between flighted and non-flighted bird species is difficult and will become more so as earlier, more plesiomorphic penguins are discovered. If the apomorphy ‘lack of flight’ serves as the specifier for Sphenisciformes, it will be difficult to assign such species to this clade because there are no identified morphological correlates to diving even in many extant birds (e.g., grebes). Additionally, although many complex apomorphies are difficult to define precisely, ‘flight’ presents a particular difficulty in that it is a behavior, not a morphology, and thus cannot be observed directly in extinct organisms. In regards to penguins specifically, these birds utilize the same mechanism to ‘fly’ underwater as do most other birds in air. An example of problems resulting from this apomorphy-based definition involves a recent description of newly discovered cranial

and humeral material from Seymour Island (Jadwiszczak, 2006). That work was unable to diagnose these remains even to Sphenisciformes because of lack of certain elements, although the material almost certainly belongs to this clade. A node-based name will unequivocally exclude from Sphenisciformes all penguins shown by all relevant data to be more plesiomorphic than *Wimanu*. The new cranial material, in this case, would then be assignable to Sphenisciformes.

Secondly, apomorphy-based names do logically fulfill the criteria required of a phylogenetic definition but do not add to the purpose of node-based names but do add unnecessary complexity to their definitions. Both types of definition function by tying a clade to a taxonomic specifier, be it '*Wimanu*' or 'the first penguin that couldn't fly', i.e. *Wimanu*. Apomorphy-based names, however, add another step to the identification of this specifier: 'Sphenisciformes → 'lack of flight' → *Wimanu*' rather than 'Sphenisciformes → *Wimanu*'. While the specifier used in an apomorphy-based definition will change with the discovery of more plesiomorphic taxa, the definition will always require such a specifier and will never require additional, character-based information. Modifying a specifier with character data (apomorphies) is thus detrimental both to the objective of separating definition and diagnosis and to maintaining simplicity in phylogenetic nomenclature (Rowe, 1987; Sereno, 2005).

Finally, the loss of flight in penguins probably occurred quickly, owing to the functional difficulty of being able to both fly and swim (Simpson, 1946). The future discovery of a flighted penguin is therefore probably not likely. This would make assigning taxa to an apomorphy-based 'Sphenisciformes' easier, but it would also mean

that there will never be any panspheniscids that are not also sphenisciforms. A node-based Sphenisciformes will be of more taxonomic use, however, because this term and the total-clade should attain differing taxonomic compositions with future fossil discoveries. Because the purpose of naming taxa is to identify groups about which one wishes to speak, using two names to circumscribe identical taxonomic content is not only unnecessary but will also hinder discussion about this group. It would be more beneficial to apply the names Panspheniscidae and Sphenisciformes to groups with content that differs both currently and in the future (Sereno, 1999).

SYSTEMATICS  
AVES Linnaeus, 1758  
NEOAVES Sibley et al., 1988  
PANSPHENISCIDAE Triche 2007 new clade name

**Definition:** The stem-based total clade of the crown-clade Spheniscidae.

**Diagnosis:** Skeletal pneumaticity lost (1, 1 → 0); temporal fossae excavated nearly to midline (2, 1 → 0); otic process of the quadrate bifurcate (54, 1 → 0); 12<sup>th</sup>-13<sup>th</sup> cervicals, transverse process elongated laterally (133, 0 → 1); haemal spines of vertebrae small and bifurcate (137, 3 → 1); number of synsacrals reduced to 12 (139, 3 → 0); length of coracoid 81mm-120mm (151, 0 → 1); small supracoracoid fenestra of the coracoid (165, 0 → 2); acromion process of scapula does not extend anteriorly past coracoid articulation (184, 2 → 1); humerus reduced to 101-140 mm in length (203, 3 → 2); glenoid surface of humerus lies horizontally (206, 0 → 1); cranial edge of distal end of humerus bumpy in outline (213, 0 → 1); bicipital crest of humerus wide, lies on proximoventral side of shaft (220, 1 → 0); proximal end of ulna widened and flattened horizontally (240, 1 → 0); keel

of os coxae robust (263, 1 → 0); iliosacrum unfused (271, 0 → 1); tarsometatarsus reduced to half femoral length (275, 2 → 0); femur straight (280, 0 → 1); femur, angle of head with shaft about 90° (281, 1 → 0).

**Occurrence:** Early Late Paleocene to Holocene of Antarctica, South America, South Africa, Australia, and New Zealand.

**Discussion:** Previous authors suggested the term Pansphenisciformes for this clade, but did not formally define it (Clarke et al., 2003). The intent of these authors was for the term to correspond to “the penguin stem-clade” or “a name for all taxa more closely related to extant penguins than to any other extant avian taxa” (Clarke et al., 2003, pp. 3), and thus to include all penguins. My purpose here is to maintain the intent of this previous definition, although the name is changed from Pansphenisciformes to Panspheniscidae to conform to current recommendations (Cantino and de Quieroz, 2006) to create total group names by adding ‘pan-‘ to the crown-clade name (Spheniscidae, not Sphenisciformes; sensu Jadwiszczak, 2006).

Node 1: SPHENISCIFORMES Sharpe 1891 [Triche 2007] converted clade name

**Definition:** The least inclusive, node-based clade that contains *Wimanu tuatahi* and *Aptenodytes forsteri*.

**Emended Diagnosis:** Currently as for Panspheniscidae.

**Occurrence:** Currently as for Panspheniscidae.

**Discussion:** All known panspheniscids currently fit this definition, therefore no difference exists between the diagnoses for the two groups. As for Panspheniscidae,

previous authors originally proposed Sphenisciformes, but did not formally diagnose or define the term (Clarke et al., 2003). Although they suggested that Sphenisciformes be applied as the name for “all parts of this lineage [Panspheniscidae] with a loss of aerial flight homologous with that of extant penguins” (Clarke et al., 2003, pp. 3), the term is here defined as a node-based name owing to difficulties with apomorphy-based definitions, as discussed above.

Node 2: *Wimanu* Jones, Ando, and Fordyce, 2006 (in Slack et al., 2006)

**Type Species:** *W. tuatahi*, Jones, Ando, and Fordyce, 2006 (in Slack et al., 2006)

**Included Species:** *W. manneringi* Jones, Ando, and Fordyce, 2006 (in Slack et al., 2006)

**Emended Diagnosis:** Limb bones heavily pachyostotic and rigid (14, 1 → 0); last thoracic vertebra weakly opisthocoelous (134, 2 → 1); ventral surface of synsacrum columnar (142, 0 → 2); proximal carpometacarpal articulation flat (251, 1 → 0); (285, 0 → 1); extensor sulcus of tibiotarsus narrow and medial (297, 0 → 3); metatarsals two and four straight (312 & 315, 0 → 1); tarsometatarsus with massive trochleae, especially trochlea three, and shallow intermetatarsal grooves (320, 1 → 2; 324 & 326, 0 → 1).

**Occurrence:** Late Early Paleocene (60.5-61.6 mya) to early Late Paleocene (58-60 mya) of basal to upper Waipara Greensand, New Zealand.

**Discussion:** The genus *Wimanu* was formally named in 2006, although it was discovered 20 years previously, and a forthcoming description will undoubtedly add to the morphological information now available (Ando, in prep). It is certain at present, however, that *Wimanu* is the oldest known penguin as well as the most plesiomorphic. Phylogenetically, the genus is currently the basal-most member of Sphenisciformes and

of Panspheniscidae. It is, therefore, indispensable to cladistic work on penguins, to polarization of penguin morphological characters, and to future determination of penguin outgroups.

Node 3: Unnamed

**Diagnosis:** Anterior articulatory surface of vertebrae robustly protruding (129, 0 → 1); distal end of coracoid straight (155 0 → 1); proximal edge of scapula medially concave (180, 2 → 1); humerus shortened and stout, with a width to height ratio of about 1:4 (202, 0 → 1); head of humerus reduced (204, 0 → 1); width of humeral shaft subequal throughout (207, 0 → 1); distal angle of humerus about 120° (211, 2 → 0); distal tuberosities and tendinal grooves of humerus displaced from shaft (212, 0 → 2); humeral insertion for *pectoralis primus* a deep, oblong fossa (230, 0 → 1); *brachialis internus* insertion of radius sharply concave (236, 1 → 0); radius with tendinal grooves and distal oblique grooves for *extensor metacarpus radialis brevis* deep (237, 1 → 0); articulatory surface of ulna hollowed for humerus (242, 1 → 0); proximal portion of femur composed of head and trochanter (276, 1 → 2); length of tarsometatarsus reduced from 51-69 mm to 35-50 mm (305, 2 → 1); tarsometatarsal body thickened, not waisted (306, 0 → 1); fourth tarsometatarsal trochlea in same transverse plane, not displaced posteriorly (321, 1 → 0).

**Occurrence:** Late Paleocene to Holocene of Antarctica, South America, South Africa, Australia, and New Zealand.

**Discussion:** *Wimanu* is by definition a sphenisciform, but the genus is much more plesiomorphic than other penguins and shares a number of character states with penguin

outgroups. The number of synapomorphies supporting clade 3, therefore, is large, only three fewer than the number supporting Sphenisciformes.

Node 4: PARAPTENODYTIDAE Simpson 1946 [Triche 2007] converted clade name

**Definition:** The most inclusive, stem-based clade containing *Paraptenodytes antarcticus* but not *Aptenodytes forsteri*.

**Diagnosis:** Acrocoracoid process rests on bent neck (156, 0 → 1); intercotylar depression small (310, 0 → 1); lateral intermetatarsal foramen large, about 4.2-6.3mm, and proximal and circular (327, 2 → 3; 328, 1 → 3).

**Occurrence:** Late Eocene to Late Miocene of Seymour Island, Antarctica and Patagonia, Argentina.

**Discussion:** This clade is supported by three unambiguous synapomorphies, as well as 24 equivocal characters. The probability that the composition of this clade may change is high, both because of this low character support and because the taxa included are very poorly known. Although paraptenodytids should remain outside the larger Spheniscoidea and distinct from Palaeudyptidae, their internal relationships will probably change with discovery of additional material pertaining to these species. As with Palaeudyptidae, this clade name is taken from Simpson's sub-familiar classification (originally Paraptenodytinae) and converted here to a clade name (Simpson, 1946). The clade currently contains two of the three species of *Delphinornis*, as well as the genera *Marambiornis*, *Mesetaornis*, and the namesake of the group, *Paraptenodytes*. The latter

now synonymizes all species originally placed within Paraptenodytinae by Simpson. The definition is based on *Paraptenodytes antarcticus* because this species is one of the most complete and well described extinct penguins known and was always recovered lying outside the crown-clade (Bertelli et al., 2006). All paraptenodytids except *Paraptenodytes* are small, Seymour Island taxa known certainly only from tarsometatarsi. This fact suggests that the close relationship between *Delphinornis*, *Marambiornis*, and *Mesetaornis*, as well as these three with *Paraptenodytes*, may be artifactual, but this hypothesis may only be tested with recovery of further, potentially associated, material. The polyphyly of *Delphinornis* may also be questioned owing to the dissociated, incomplete remains of these three species.

#### Node 5: Unnamed

**Diagnosis:** Sulcus ligamentosus of the tarsometatarsus absent (308, 1 → 0); tibialis cranialis tubercle raised onto metatarsal 3, lies proximally (317, 0 → 2); lateral intermetatarsal groove does not shallow distally (325, 0 → 1).

**Occurrence:** As for Paraptenodytidae.

**Discussion:** Unambiguous character support for this clade relates entirely to the tarsometatarsus, as this is the only element known for the majority of included taxa. Morphology analyzed alone also supports the group, but no other type of analysis. Support for this clade is therefore considered to be too low for formal naming.

#### Node 6: Unnamed

**Diagnosis:** Tarsometatarsal trochleae massive (320, 1 → 3).

**Occurrence:** Late Eocene of Seymour Island, Antarctica.

**Discussion:** Only one unambiguous synapomorphy supports this relationship, which is therefore not formalized. Additional, equivocal support also comes entirely from the tarsometatarsus and includes: intercotylar depression deep (310, 1 → 2); lateral foramen smaller than medial (332, 0 → 2). Several separate analyses do support these species as sister-taxa, however, including various morphological partitions and various types of pruning.

#### Node 7: Unnamed

**Diagnosis:** Lateral intermetatarsal foramen forms a pit only (no plantar opening; 327, 3 → 1); presence of three, large, hypotarsal crests (339, 3 → 0).

**Occurrence:** As for Paraptenodytidae.

**Discussion:** This clade is also differentiated from the previous group by the presence of the lateral intermetatarsal foramen lying in a deeply excavated pit (329, 1 → 0), but only as an equivocal synapomorphy. As with other paraptenodytids, tarsometatarsal morphology and morphology analyzed alone form the only other support for this clade.

Node 8: *Parapterodytes* Ameghino, 1891  
**Type Species:** *P. antarcticus* Moreno and Mercerat, 1891  
**Included Species:** *P. robustus* Ameghino, 1895

**Synonymy:** *Metancylornis* Ameghino, 1905  
*Isotremornis* Ameghino, 1905  
*Arthrodytes* Ameghino, 1905

**Emended Diagnosis:** Limb bones heavily pachyostotic and rigid (14, 1 → 0); tarsometatarsus with second metatarsal straight distally (318, 0 → 1), shallow lateral intermetatarsal groove (324, 0 → 1), plantar opening of the medial intermetatarsal foramen lying lateral to the medial hypotarsal crest (334, 1 → 0), hypotarsal crests very robust, forming marked sulcus for passage of all flexor tendons (336, 0 → 2).

**Occurrence:** Late Oligocene to middle Late Miocene of Chubut and Santa Cruz, Argentina.

**Discussion:** The clade *Parapterodytes* is also support by the following equivocal character data: shaft of metatarsal two curved (312, 1 → 0). A number of unique morphologies, particularly of the skull, also characterize *Parapterodytes antarcticus*. These are unfortunately unknown in other parapterodytid species because they lack such elements and thus cannot serve as diagnoses for this clade. When better, comparable material is found relating to this group, the diagnosis of *Parapterodytes* may be expanded to include such cranial apomorphies.

#### Node 9: Unnamed

**Diagnosis:** Medial intermetatarsal foramen of tarsometatarsus, plantar opening lies lateral to medial hypotarsal crest (334, 1 → 0); distal intermetatarsal foramen of tarsometatarsus absent and external adductor groove open (335, 1 → 0).

**Occurrence:** Early Late Paleocene to Holocene of Antarctica, South America, South Africa, Australia, and New Zealand.

**Discussion:** This node includes the clade Spheniscoidea and the species *Delphinornis gracilis*. The latter thus forms a polyphyletic genus because all other delphinornids lie within Paraptenodytidae.

#### Node 10: SPHENISCOIDEA Triche 2007 new clade name

**Definition:** The least inclusive, node-based clade containing *Palaeudyptes antarcticus* and *Aptenodytes forsteri*.

**Diagnosis:** Medial intermetatarsal foramen of tarsometatarsus smaller than lateral (332, 1 → 0).

**Occurrence:** Early Late Paleocene to Holocene of Antarctica, South America, South Africa, Australia, and New Zealand.

**Discussion:** The specifiers for this clade are chosen because the crown-clade is definitionally stable and because *Palaeudyptes antarcticus* is the most well known of the palaeudyptid penguins. It is intended that Spheniscoidea continue to serve as the node-based name that includes Spheniscidae and Palaeudyptidae, even if the taxonomic complement of these sub-clades changes. Equivocal character data (4 synapomorphies)

also supports Spheniscoidea, among which are: tarsometatarsal trochleae all small (320, 1 → 0); lateral intermetatarsal groove of tarsometatarsus does not shallow distally and remains deep throughout (325, 0 → 1); medial intermetatarsal foramen of tarsometatarsus smaller than lateral (332, 1 → 0); presence of two large hypotarsal crests (339, 3 → 2); and medial hypotarsal crest more prominent than lateral (340, 1 → 0).

Therefore, although relationships within Paraptenodytidae or Spheniscidae may change, support for Spheniscoidea is high and suggests continued recovery of the clade in future analyses. Choice of the ending –oidea in the name Spheniscoidea is meant to reflect its placement as more inclusive than Spheniscidae and less inclusive than Sphenisciformes, not any rank-based connotation.

Node 11: PALAEEUDYPTIDAE Simpson 1946 [Triche 2007] converted clade name

**Definition:** The most inclusive, stem-based clade containing *Palaeudyptes antarcticus* but not *Aptenodytes forsteri*.

**Diagnosis:** Proximal end of coracoid medium in width laterally (161, 0 → 1); elongate process of this proximal end absent (163, 1 → 0); humerus with transverse ligament sulcus on proximal end deep, short, and round (216, 0 → 2); proximal head of radius distinctly offset from shaft (238, 0 → 1); metacarpal three of carpometacarpus with widened flange/wing distally (257, 0 → 1); length of tarsometatarsus elongated to 51-69 mm (305, 1 → 2); intercotylar eminence of tarsometatarsus large, wide, and raised (309, 1 → 0); distal end of second metatarsal inflected medially, with a strongly concave medial border (318, 0 → 2); medial intermetatarsal foramen forms only a pit (330, 2 → 1).

**Occurrence:** Late Paleocene to Middle Miocene of Seymour Island, Antarctica; Patagonia and Tierra del Fuego, Argentina; the South Island of New Zealand, and Australia.

**Discussion:** Many synapomorphies also support the monophyly of nodes within Palaeudyptidae (e.g., clade 13), but the name Palaeudyptidae is placed at this node because it is the most inclusive group of spheniscoids lying outside the crown-clade. This clade name is modified from an earlier, sub-familial taxon based on the genus *Palaeudyptes* (Simpson, 1946). Sub-familial ranks are not used here, but the name Palaeudyptidae is chosen for clade conversion to maintain usage of a historically important name and because the genus *Palaeudyptes*, as historically constituted, lies entirely within this clade, although it is paraphyletic. Palaeudyptidae is by far the largest clade of extinct penguins, with 20 included species (figure 3.5a). These taxa are further divided by a basal split between *Platydyptes-Wimanornis* (clade 29), followed by a major division between an *Archaeospheniscus* group and a *Anthropornis* group.

#### Node 12: Unnamed

**Diagnosis:** Second metatarsal of tarsometatarsus with curved shaft (312, 0 → 1); tibialis cranialis tubercle of tarsometatarsus (316, 1 → 2); tarsometatarsal trochleae massive, with metatarsal three enlarged (320, 0 → 2); lateral and medial hypotarsal crests robust (336, 0 → 1).

**Occurrence:** Late Paleocene to Middle Miocene of Seymour Island, Antarctica; Patagonia and Tierra del Fuego, Argentina; the South Island of New Zealand, and Australia.

**Discussion:** This clade includes all palaeodyptids except the *Pachydyptes-Wimanornis* clade. It is therefore as temporally and geographically wide-ranging as Palaeodyptidae. It is supported by four synapomorphies and five equivocal characters.

Node 13: Unnamed

**Diagnosis:** Humerus with greatly expanded cranial edge of distal end (213, 1 → 2); proximal end of ulna widened only (240, 0 → 1); sulcus ligamentosus of tarsometatarsus absent (308, 1 → 0); collateral ligament fovea of metatarsal two pronounced, that of metatarsal four small or absent (323, 2 → 3); lateral intermetatarsal foramen of tarsometatarsus large, about 4.2-6.3mm (327, 2 → 3).

**Occurrence:** Middle Eocene to Middle Miocene of Australia, Seymour Island, and the South Island of New Zealand.

**Discussion:** This clade includes all *Archaeospheniscus* species, although this genus is not monophyletic. Nearly all included species are New Zealand or Seymour Island taxa. The clade is supported by five synapomorphies and five equivocal characters.

Node 14: Unnamed

**Diagnosis:** Degree of flattening of wing bones extreme (11, 1 → 0); distal angle of humerus about 135° (211, 0 → 1); humerus with fossa between insertions for *pectoralis*

*secundus* and *tertius* extending distally as sharp ridge to *latissimus dorsi* insertion (233, 1 → 4); tarsometatarsal width is greater than or equal to half its height (303, 1 → 0); medial intermetatarsal foramen of tarsometatarsus large (330, 1 → 3); medial and lateral intermetatarsal foramina equal in size (332, 0 → 1); and widely separated (333, 2 → 1); medial intermetatarsal foramen lies ventral to medial hypotarsal crest (334, 0 → 2).

**Occurrence:** Middle Eocene to Middle Miocene of Australia, Seymour Island, and the South Island of New Zealand.

**Discussion:** Supported by eight synapomorphies and one equivocal character, this clade includes all species in Clade 13 except *Palaeudyptes gunnari* and has a much higher level of support.

#### Node 15: Unnamed

**Diagnosis:** Preaxial angle of humerus about 155° (210, 2 → 1).

**Occurrence:** Middle Eocene to Middle Miocene of Australia, Seymour Island, and the South Island of New Zealand.

**Discussion:** This group of taxa separates the genus *Archaeospheniscus* in a paraphyletic taxon. It is supported by only a single synapomorphy, as well as six equivocal characters.

#### Node 17: Unnamed

**Diagnosis:** Sigmoid shape of humerus absent (208, 1 → 0).

**Occurrence:** Middle Eocene to Late Oligocene of Seymour Island, Antarctica and the South Island of New Zealand.

**Discussion:** The sister-taxon *Orthopteryx gigas-Platydyptes amiesi* are supported by only one synapomorphy. *Platydyptes* is therefore also a non-monophyletic genus.

Node 18: Unnamed

**Emended Diagnosis:** Distal end of humerus, caudal border, extended trochlear process present, separated from other processes by deep fossa (215, 1 → 3); *brachialis internus* insertion of radius smooth (236, 0 → 1).

**Occurrence:** Middle Eocene to lower Oligocene of Seymour Island and the South Island of New Zealand.

**Discussion:** Other diagnostic, but equivocal, characters supporting the monophyly of these two *Archaeospheniscus* species include: preaxial border of humerus with rounded, angular projection (209, 2 → 1); and distal end of humerus, extended cranial edge of equal width as ulnar condyle (214, 2 → 1). The clade is supported by all data types that apply to extinct taxa except humeral morphology. This is significant in that, although *Archaeospheniscus* is not monophyletic, two of its included taxa are, and are also one of the most well-supported clades of extinct penguins. The robust phylogenetic support for the clade probably results from the fact that its included species are very well known, having some of the highest values of percentage data scored of all extinct species. *Archaeospheniscus* probably originated on Seymour Island, as the older, more plesiomorphic of its species (*Archaeospheniscus wimani*) is known only from that locality. The remaining species are known only from New Zealand, indicating that *Archaeospheniscus* either dispersed to or vicariated there in the Late Eocene.

Node 19: Unnamed

**Diagnosis:** Scapular facet of coracoid shallow and big (166, 0 → 1); glenoid facet of coracoid deep (167, 1 → 0); small, proximal foramen located on postaxial edge of ulna present (243, 0 → 1).

**Occurrence:** Late Eocene to Late Oligocene of Seymour Island, Antarctica; Patagonia, Argentina; the South Island of New Zealand; and Australia.

**Discussion:** This is the other major resolved group of palaeodyptids. It is supported by three synapomorphies and eight ambiguous characters.

Node 20: Unnamed

**Diagnosis:** Preaxial border of humerus with rounded, angular projection (209, 2 → 1).

**Occurrence:** Late Eocene to Late Oligocene of Seymour Island, Antarctica; Patagonia, Argentina; the South Island of New Zealand; and Australia.

**Discussion:** This clade is nearly identical to Clade 19, excepting only *Pachydyptes simpsoni*. It is supported by a single synapomorphy and the equivocal character: distal fusion between metacarpal one and metacarpal three deeply grooved (256, 1 → 0).

Node 21: Unnamed

**Diagnosis:** Humeral length 141cm or more (203, 2 → 3); femoral condyles far separated (284, 1 → 0).

**Occurrence:** Late Eocene to Late Oligocene of Seymour Island, Antarctica; the South Island of New Zealand; and Australia.

**Discussion:** Two characters support the monophyly of this taxon, which includes the extinct species *Anthropornis* and most species included in the paraphyletic genus *Palaeudyptes*.

Node 22: Unnamed

**Diagnosis:** Tarsometatarsal length 70 mm and longer (305, 2 → 3); lateral intermetatarsal groove of tarsometatarsus shallows distally (325, 1 → 0).

**Occurrence:** Late Eocene to Late Oligocene of Seymour Island, Antarctica; the South Island of New Zealand; and Australia.

**Discussion:** This clade is supported by two synapomorphies and seven additional, equivocal characters.

Node 23: Unnamed

**Diagnosis:** Lateral and medial hypotarsal crests slender (336, 1 → 0)

**Occurrence:** Late Eocene to Late Oligocene of Seymour Island, Antarctica; the South Island of New Zealand; and Australia.

**Discussion:** This group of extinct penguins includes *Anthropornis* and most *Palaeudyptes* species, and is supported only by a single tarsometatarsal synapomorphy.

Node 24: *Anthropornis* Wiman, 1905  
**Type Species:** *A. nordenskjoldi* Wiman, 1905  
**Included Species:** *A. grandis* Wiman, 1905

**Synonymy:** *Pachypteryx* Wiman, 1905

**Emended Diagnosis:** Femoral trochanter projected far proximally (282, 3 → 0); shaft of metatarsal two of the tarsometatarsus wavy in outline (312, 1 → 2); medial intermetatarsal foramen small but larger than lateral intermetatarsal foramen and widely separated from it (330, 1 → 2; 332, 0 → 2; 333, 2 → 0).

**Occurrence:** Early Miocene of Seymour Island, Antarctica and of southern Australia.

**Discussion:** *Anthropornis* is one of the better known extinct penguin taxa, one of the most derived palaeudyptids, and one of the largest penguins known. The genus ranges throughout the southern hemisphere, with remains known from Antarctica and Australia.

Node 25: Unnamed

**Diagnosis:** Pneumatic fossa of humerus flattened anteroposteriorly (223, 0 → 1); preaxial edge of carpometacarpus notched distally (252, 1 → 0).

**Occurrence:** Late Eocene to Early Oligocene of the South Island of New Zealand.

**Discussion:** This clade of New Zealand species owes its monophyly to the presence of one humeral and one tarsometatarsal character.

Node 26: Unnamed

**Diagnosis:** Wing bones extremely flattened (11, 1 → 0); humerus long and slender (202, 1 → 0); pneumatic fossa of humerus partially divided (227, 0 → 1).

**Occurrence:** Late Eocene to Early Oligocene of the South Island of New Zealand.

**Discussion:** This monophyletic clade of *Palaeodyptes* species is supported by three synapomorphies, the first of which evolved convergently in the ‘*Archaeospheniscus*’ clade (node 14). The additional humeral character serve, however, to differentiate the two clades.

Node 27: OM C47

**Included Species:** OM C47.23A and OM C47.25

**Diagnosis:** Sigmoidal shape of humerus lost (208, 1 → 0); distal, trochlear process of the humerus present, separated from other processes by a deep fossa (215, 1 → 3); *pectoralis secundus* insertion of humerus small and curved (232, 0 → 1); postaxial edge of ulna elongated "like" an olecranon (241, 0 → 1).

**Occurrence:** Waipara Greensand; Late Eocene of the South Island of New Zealand.

**Discussion:** These specimens undoubtedly comprise a new taxon, probably a new genus and species. Their sister taxon relationship is extremely well supported, and their closest relative is another *Palaeodyptes* species, *Palaeodyptes marplei*. The genus *Palaeodyptes*, however, is almost certainly polyphyletic, indicating that OM C47 should probably not be placed within *Palaeodyptes*, and that revision of the ‘*Palaeodyptes*’ complex is required before formally naming or defining these species.

Node 28: Unnamed

**Diagnosis:** Limb bones heavily pachyostotic and rigid (14, 1 → 0).

**Occurrence:** Late Paleocene to Middle Eocene of Seymour Island and southernmost South America (Tierra del Fuego).

**Discussion:** The single diagnostic synapomorphy of this clade is homoplastically present in *Wimanu*. However, neither *Crossvallia* nor CADIC possess any of the remaining synapomorphies that support *Wimanu*, which may thus still be differentiated. This clade is not named because of its low amount of support, because both taxa remain fairly incomplete and because one included species remains unnamed. The taxonomic complement of this clade suggests that the lineage originated in the Late Paleocene on Seymour Island, where it is represented by *Crossvallia*, then dispersed northwards to southernmost South America, evolving into the species represented by the unnamed CADIC P-21.

Node 29: Unnamed

**Diagnosis:** Ectepicondylar attachments of humerus round and lateral (218, 1 → 2); lateral intermetatarsal groove of tarsometatarsus shallow (324, 0 → 1).

**Occurrence:** Early Late Eocene to late Oligocene of Seymour Island, Antarctica and the South Island of New Zealand.

**Discussion:** These sister taxa share only two synapomorphies, although these do include both the humerus and the tarsometatarsus.

Node 30: Unnamed

**Diagnosis:** Collateral ligament foveae of tarsometatarsus pronounced (323, 2 → 0).

**Occurrence:** Late Eocene to Holocene of Antarctica, South America, South Africa, Australia, and New Zealand.

**Discussion:** The seven taxa that lie within Spheniscoidea but outside Spheniscidae are generally poorly known and hence the clades that contain them are not named here. These include: *Ichtyopteryx*, two species of *Palaeospheniscus*, 'Dege', *Duntroonornis*, *Marplesornis*, and *Tereingaornis*. Phylogenetic definition of these taxa remains premature until either better palaeospheniscine material becomes available or a detailed taxonomic revision of palaeospheniscines in particular is completed. This poor preservation is unfortunate because these taxa are the probable closest relatives of extant spheniscids and thus should most closely represent the morphology of the ancestral crown-penguin. Further, equivocal character support may include 24 additional synapomorphies. There is also much temporal incongruence present at this node, suggesting either that more crown-group stem taxa remain to be found or that incomplete taxa are biasing the reconstruction of the cladogram topology. The most basal stem-spheniscid, *Ichtyopteryx*, is known from the Late Eocene of New Zealand, while additional stem species do not appear until the Late Oligocene, around ten million years later. Further discovery of fossil remains of this species could potentially affect relationships among stem-spheniscids drastically because the amount of data scored in the matrix for *Ichtyopteryx* is only about 7%.

Node 31: Unnamed

**Diagnosis:** Tarsometatarsus length 34 mm or less (305, 1 → 0); second metatarsal of tarsometatarsus shorter than the third and longer than the fourth (319, 1 → 0).

**Occurrence:** Late Oligocene to Holocene of Antarctica, South America, South Africa, Australia, and New Zealand.

**Discussion:** Only one character supports this clade, which is not surprising considering the preservation of these stem-spheniscid taxa. It is identical to Clade 30 with the removal of *Ichtyopteryx*.

Node 32: Unnamed

**Diagnosis:** Lateral intermetatarsal groove of the tarsometatarsus shallow (324, 0 → 1); lateral intermetatarsal foramen proximal and circular (328, 1 → 3); (330, 2 → 1).

**Occurrence:** Late Oligocene to Early Miocene of Patagonia, Argentina. Possibly from the Middle Miocene of Chile and of Peru.

**Discussion:** As discussed above, definition of this taxon will remain premature until further material becomes available. As reconstructed here, *Palaeospheniscus* is a polyphyletic taxon, with representatives lying within extant Spheniscidae and as the outgroup to Spheniscidae. The two taxa discussed here are united by only three synapomorphies and are known mainly from unassociated, appendicular, skeletal elements. Potential, equivocal support includes nineteen additional characters.

Node 33: Unnamed

**Diagnosis:** Preaxial border of humerus with rounded, angular projection (209, 2 → 1); fibular groove of femur large (286, 2 → 1); width of tarsometatarsus greater than or equal to half its height (303, 1 → 0).

**Occurrence:** Late Oligocene to Early Miocene of Patagonia, Argentina. Possibly from the Middle Miocene of Chile and of Peru.

**Discussion:** These outgroups to Spheniscidae share with them only three characters, one of which (303, 1 → 0) evolved convergently in the '*Archaeospheniscus*' clade.

Node 34: Unnamed

**Diagnosis:** Tarsometatarsal trochleae all small (320, 0 → 1).

**Occurrence:** Late Oligocene to Early Miocene of Patagonia, Argentina. Possibly from the Middle Miocene of Chile and of Peru.

**Discussion:** These three outgroups to Spheniscidae share only one additional character.

Node 35: Unnamed

**Diagnosis:** Preaxial border of humerus straight (209, 1 → 0).

**Occurrence:** Early Oligocene to late Pliocene of the South Island of New Zealand.

**Discussion:** The sister taxa *Duntroonornis* and *Marplesornis* are united by one unambiguous synapomorphy, as well as nine ambiguous ones.

Node 36: Unnamed

**Diagnosis:** Coracoid 80mm in length or less (151, 1 → 0).

**Occurrence:** Late Oligocene to Early Miocene of Patagonia, Argentina. Possibly from the Middle Miocene of Chile and of Peru.

**Discussion:** This taxa includes Spheniscidae and its sister-taxon, *Tereingaornis*. They are supported only by a single coracoid synapomorphy.

Node 37: SPHENISCIDAE Bonaparte 1831 [Triche 2007] converted clade name

**Type Species:** *Spheniscus* Brisson

**Definition:** The least inclusive, node based crown-clade containing *Aptenodytes forsteri*, *Spheniscus demersus*, *Eudyptula minor*, *Eudyptes pachyrhynchus*, *Megadyptes antipodes*, and *Pygoscelis adeliae*.

**Emended Diagnosis:** Elongate lateral process of proximal end of coracoid absent (163, 1 → 0); dorsal extension of medial angle of coracoid small (169, 0 → 1); sigmoid shape of humerus absent (208, 1 → 0).

**Occurrence:** Late Oligocene to Holocene of Argentina, Chile, Peru, both islands of New Zealand, South Africa, Australia, and Antarctic and sub-Antarctic coasts and islands.

**Discussion:** Extant penguins were traditionally grouped within the family Spheniscidae and the subfamily Spheniscinae (Simpson, 1946). In traditional taxonomic revisions, all extinct penguins are also classified within Spheniscidae, which was always taxonomically identical to the Order Sphenisciformes. The only previous discussion of phylogenetic systematics as applied to penguins, however, recommended that Spheniscidae be formally applied to “the clade comprised of the most recent common

ancestor of all extant penguins and all of its descendants” (Clarke et al., 2003, pp. 3) because all extant species were traditionally grouped in this family. Additionally, nearly all work on extant penguins uses the term Spheniscidae (e.g., Coues, 1872; Watson, 1883; O’Hara, 1989; Mayr, 2005; Baker et al., 2006), crown-clades generally take ‘family’ names, and Spheniscidae Bonaparte 1831 takes precedence over Spheniscinae Simpson 1946. Because traditional and conventional usage thus prefers the term Spheniscidae, the former is used here as the definition for extant, or crown-group penguins. It should remain as such in future analyses and should continue to include all six extant genera.

Although the crown-clade is monophyletic, only three synapomorphies unambiguously support Spheniscidae, and no equivocal characters. This is unexpected for an extant clade, especially as many more types of data (e.g. myological, behavioral) are available for Spheniscidae. Low amounts of support for the clade may arise owing to its inclusion of numerous poorly known fossils, and may not necessarily indicate that the extant clade is poorly supported.

Node 38: *Spheniscus* Brisson, 1760

**Type Species:** *S. demersus* Linnaeus, 1758

**Included Species:** *S. chilensis*, *S. humboldti*, *S. magellanicus*, *S. megaramphus*, *S. mendiculus*, and *S. urbinai*

**Emended Diagnosis:** Interorbital septum well-developed (37, 0 → 1); acrocoracoid process thin dorsoventrally 159 (1 → 0); .

**Occurrence:** Late Miocene of Peru and Chile to Holocene of South Africa, Peru, Argentina, Chile, and sub-Antarctic and Galapagos Islands.

**Discussion:** The genus *Spheniscus* is supported by two synapomorphies, by all data types except behavior, which is to be expected in a clade containing extinct species, by the presence of several, highly supported sub-clades, and by a bootstrap value of 79, one of the highest of all recovered clades. Further, equivocal, support for *Spheniscus* includes 44 additional characters.

Node 39: Unnamed

**Diagnosis:** Retroarticular process longer and narrower than articular surface (119, 1 → 3); tarsometatarsus with medial cotyle of tibiotarsal articular depressed (311, 0 → 1).

**Occurrence:** Late Pliocene to Holocene of South Africa, Peru, Argentina, Chile, and sub-Antarctic and Galapagos Islands.

**Discussion:** In addition to the two unambiguous synapomorphies that support this clade, 3 additional characters provide equivocal support for the node, including data from the myological, integumentary, and osteological partitions. In general, the morphology of the two species of *Spheniscus* not included within this clade is much different than that of those included, especially in regards to size. A group comprising all extant species is thus expected, although the placement of *Spheniscus chilensis* may be less well-supported. There is no detailed description of *Spheniscus chilensis*, although it is known from abundant remains and numerous skeletal elements. This limits the ability to code the species and hence reduces confidence in its phylogenetic placement.

Node 40: Unnamed

**Diagnosis:** *Latissimus dorsi* insertion of the humerus small and round (229, 1 → 3); carpometacarpus with a deep, distal notch separating metacarpals two and three (255, 1 → 0).

**Occurrence:** Late Pliocene to Holocene of South Africa, Peru, and Chile.

**Discussion:** Two unambiguous, skeletal synapomorphies support a clade containing these three *Spheniscus* species. Geographically, the clade is more restricted than its parent, further supporting its monophyly and suggesting that it originated in Chile with subsequent dispersal by the Jackass Penguin to South Africa.

Node 41: Unnamed

**Diagnosis:** Preaxial border of humerus with abrupt angular projection (209, 1 → 2); lateral, supracondylar crest of femur absent, medial crest unprojected (283, 1 → 2).

**Occurrence:** Holocene of South Africa, Peru, and Chile.

**Discussion:** Most previous analyses of *Spheniscus* phylogeny recovered a *Spheniscus demersus*/*S. magellanicus* clade (e.g., Bertelli and Giannini, 2005; Baker et al., 2006; Walsh and Suarez, 2006). This discrepancy is probably owing to the much larger amount of character data used here, with osteological data now comprising as large a partition as other, integumentary and behavioral characters. In particular, various analyses of different data partitions here show that morphology alone, osteology alone, and use of only binary characters support the clade, while integument, myology, and behavior do not. The clade is also robust to changes in outgroup selection and various types of

pruning, and received a bootstrap support value of 77, one of the highest in the entire cladogram. All of these sources of data suggest that higher confidence may be placed in this clade than in a previously proposed *Spheniscus demersus*/*S. magellanicus* group.

Node 42: Unnamed

**Diagnosis:** Radius and ulna of equal width (13, 2 → 0); posterior end of paroccipital process extends laterally (97, 3 → 2); dentary straight, half the mandibular length (115, 2 → 0); 43 vertebrae present (128, 0 → 1); 9 caudal vertebrae present (135, 1 → 2); procoracoid process of coracoid large but short (164, 0 → 2); supracoracoid fenestra large (165, 2 → 3); acromion process of coracoid distinctly hooked laterally, doesn't extend anteriorly past coracoid articulation (184, 1 → 0); transverse ligament sulcus on proximal end of humerus deep, short, and round (216, 3 → 2); radiale rectangular and wedge-shaped (244, 2 → 1); dark lateral band present on flanks of immature plumage (424, 0 → 1).

**Occurrence:** Holocene of Chile, Argentina, the Falkland and Galapagos Islands.

**Discussion:** As with *Spheniscus demersus* and *Spheniscus humboldti*, the support for the *Spheniscus magellanicus*/*S. mendiculus* clade arises from morphological, particularly osteological data. Also as above, it appears that the disagreement between this and previous analyses (e.g., Bertelli and Giannini, 2006) stems from swamping of osteological data by molecular, behavioral, and integumentary characters.

Node 43: Unnamed

**Diagnosis:** Skull length of 171 mm or more (6, 0 → 3); beak longer than remainder of skull (8, 1 → 2); premaxilla with marked groove distal to nostril elongated (16, 1 → 2); posterior, orbital section of frontal elongated laterally (41, 0 → 1).

**Occurrence:** Late Miocene of Peru.

**Discussion:** Four unambiguous synapomorphies support this clade, as well as the osteological and morphological data sets analyzed independently, many of the different outgroup comparisons, and the geographic and temporal proximity of its component species. It may be diagnosed primarily by great similarity to extant *Spheniscus* species combined with greatly enlarged size. The ubiquity of cranial synapomorphies arises because both *Spheniscus megaramphus* and *Spheniscus urbinai*, uncommonly among penguins, are known from various cranial remains.

Node 44: Unnamed

**Diagnosis:** Temporal fossae far apart, at least the width of the cerebellar prominence, only weakly hollowed, and narrow (2, 0 → 1); nostrils holorhinal and enlarged (17, 0 → 2); nasofrontal contact slightly hinged (26, 3 → 2); lacrimal visible dorsally (29, 0 → 1); retroarticular process longer and narrower than articular surface of angular (119, 1 → 2); medial mandibular process of articular, accessory midline fossa present (125, 0 → 1); proximal end of coracoid medium in width laterally (161, 2 → 1); humerus with distal, trochlear process extending past humeral shaft (215, 1 → 0); capital groove of humerus shallow and wide (222, 1 → 0); fossa between insertions for *supracoracoideus* small,

closed distally (233, 1 → 0); *deltoideus major* triangular or fan-shaped (347, 1 → 0); dorsal color of feet pinkish (441, 0 → 1); molt season in December (504, 0 → 1).

**Occurrence:** Late Oligocene to Holocene of Argentina, both islands of New Zealand, South Africa, Antarctica, Australia, and Antarctic and sub-Antarctic coasts and islands.

**Discussion:** The fact that 13 unambiguous synapomorphies support this clade is indicative of strong support for a clade of extant taxa that excludes *Spheniscus*. This clade also is not named, however, as it includes *Eudyptes* in the present analysis but often excludes this genus in other work.

Node 45: *Eudyptula* Bonaparte, 1856

**Type Species:** *Eudyptula minor* Forster, 1781

**Synonymy:** *Aptenodytes minor* Forster, 1781

**Emended Diagnosis:** Flattening of wing bones less extreme (11, 0 → 1); tip of premaxilla deflected downward, uncompressed (15, 0 → 1); nasopremaxillary suture completely fused (22, 0 → 1); elongated frontal process of the nasal (28, 0 → 1); anteroventral emargination of the ectethmoid absent (36, 1 → 0); postfrontal process of frontal thin and vertical (42, 2 → 0); position of mandibular articulation lies anterior to otic articulation (46, 0 → 1); pterygoid condyle of the quadrate confluent with quadrate body (50, 1 → 0); posterior half of the eustachian tube covered with bone (88, 1 → 2); orbitocranial fonticuli of laterosphenoid, one large and one small (89, 2 → 0); paroccipital process curves onto lateral surface of exoccipital (96, 0 → 1); paroccipital process of exoccipital, with ventral end extending laterally (97, 3 → 2); narrow, posterolateral fenestra ovalis (101, 1 → 0); surangular slender (117, 1 → 0);

pseudotemporal tubercle of the angular elongated (121, 0 → 2); articular surface of articular, lateral border longitudinal (122, 1 → 0); lateral surface of articular nearly flat (123, 0 → 1); medial surface of articular, anteroventral fossa present and large (124, 0 → 1); last thoracic vertebra opisthocoelous (134, 2 → 0); procoracoid process large but short (164, 0 → 2); supracoracoid fenestra forms notch only (165, 2 → 1); medial surface of scapula hollowed for ribs (178, 1 → 0); proximal edge of scapula not thickened (181, 0 → 1); robust spine present on sternal rostrum (192, 1 → 3); median trabecula both notched and perforated (200, 0 → 2); *supracoracoideus* insertion on humerus both small and straight (232, 0 → 2); *brachialis internus* insertion of radius flat and short (236, 0 → 2); foramen present on radiale (245, 0 → 1); carpometacarpal length 40mm or less (250, 1 → 0); pubis straight, equally deep throughout (273, 3 → 2); medial supracondylar crest of femur strongly projected medially, lateral crest absent (283, 1 → 0); popliteal fossa of femur shallow, not discrete (287, 0 → 1); patella shallowly grooved for tendon of *m. ambiens* (289, 2 → 1); medial condyle of tibiotarsus deflected medially, does not project further than lateral condyle (296, 0 → 3); intercotylar area of tarsometatarsus deep (310, 1 → 2); second metatarsal of tarsometatarsus straight, with straight distal end (312, 1 → 0; 318, 0 → 1); lateral intermetatarsal foramen of tarsometatarsus both oval and medially proximo-distal (328, 1 → 2); hypotarsal crests parallel (338, 1 → 0); *m. deltoideus propatagialis*, superficial and deep layers undivided (346, 1 → 0); *deltoideus, major, caput caudal* intermediate in length (348, 0 → 1); *flexor perforatus digitis 4*, rami two-three and rami one-two both free (357, 0 → 1); *flexor perforatus digitis 4*, rami 2-3 free, rami 1-4 free (359, 1 → 0; 360, 1 → 0); longitudinal grooves present on culmen

only (388, 0 → 2); bill not deeply grooved (374, 1 → 0); nostril tubes present in chick only (391, 0 → 1); throat pattern white (407, 0 → 1); second down, collar present (421, 0 → 1); flipper, underside, dark elbow patch absent (429, 1 → 0); underside and upperside of leading edge of flipper both white (430, 1 → 0); leading edge of flipper, upperside white (431, 0 → 2); white line connecting leading edge of flipper with white belly present (432, 0 → 1); dorsum color light bluish-grey (435, 0 → 2); feet, dorsal color is white/flesh (441, 1 → 3); feet, dark soles present (444, 0 → 1); creche small, 3-6 birds (450, 2 → 1); time of return from foraging is after dark (456, 1 → 2)

**Occurrence:** Coasts and offshore islands of south Australia, Tasmania, both islands of New Zealand, and Chatham and Stewart Islands.

**Discussion:** The monotypic *Eudyptula* contains only the *Eudyptula minor* subspecific complex. This species includes six currently accepted subspecies: *Eudyptula minor minor*, *E. m. albosignata*, *E. m. chathamensis*, *E. m. variabilis*, *E. m. iredalei*, and *E. m. novaehollandiae*. None of these subspecies are diagnosable using osteological characters and are thus none are re-diagnosed here, nor are any elevated to specific status. This genus is extremely apomorphic as compared with other extant penguins, including 58 unambiguous and 26 equivocal synapomorphies. It is also supported by the highest bootstrap value recovered, 94, and by more types of analyses than any other penguin clade, including analysis of all data partitions and all types of outgroups.

Node 46: Unnamed

**Diagnosis:** Proximal portion of femur composed of trochanter (276, 0 → 1).

**Occurrence:** Late Oligocene to Holocene of Argentina, both islands of New Zealand, South Africa, Antarctica, Australia, and Antarctic and sub-Antarctic coasts and islands.

**Discussion:** This clade includes the extant genera *Aptenodytes*, *Pygoscelis*, and the crest penguins *Eudyptes* and *Megadyptes*, as well as a number of extinct species. It is supported by only one synapomorphy, but also 55 equivocal characters and is thus reasonably well supported.

Node 48: *Eudyptes* Vieillot, 1816

**Type Species:** *Eudyptes chrysocome* Forster, 1781

**Included Species:** *E. chrysolophus*, *E. pachyrhynchus*, *E. robustus*, *E. schlegeli*, and *E. sclateri*, *Chubutodyptes bilocolata*, *Korora oliveri*, *Nucleornis' insolitus*

**Emended Diagnosis:** Preaxial angle of humerus about 155° (210, 2 → 1); femur sigmoidal or bowed (280, 1 → 0); lateral supracondylar crest of femur present, medial crest not projected (283, 1 → 3); tibiotarsus articulation of tarsometatarsus, medial cotyle depressed (311, 0 → 1); tibialis cranialis tubercle prominent and round (316, 1 → 2).

**Occurrence:** Late Oligocene to Holocene of coasts and offshore islands of New Zealand, Chile, Argentina, Antarctica and sub-Antarctic and Antarctic Islands.

**Discussion:** The genus *Eudyptes* is the only non-monophyletic extant genus of penguins, although it would be considered monophyletic if including three extinct species, *Chubutodyptes*, *Korora*, and 'Nucleornis'. These extinct species are too fragmentary, however, to allow robust discrimination from extant *Eudyptes*. The group is supported by

2 additional, equivocal synapomorphies. Much resolution within eudyptids is also recovered and generally agrees with previous work, as discussed below.

Node 50: Unnamed

**Diagnosis:** Posterior section of frontal elongated laterally (41, 0 → 1); zygomatic process of squamosal large (61, 0 → 1); haemal spines present on four caudal vertebrae (136, 1 → 2); anterior process of sternum with broad base (195, 1 → 0); popliteal fossa of femur small (287, 0 → 1); cnemial crests of tibiotarsus project far proximally (293, 0 → 1); fibular sulcus of tibiotarsus small or absent (299, 1 → 0); leading edge of flipper with underside completely dark and wide (430, 1 → 2).

medial surface of articular, anteroventral fossa present, large (124, 0 → 1); medial mandibular process of articular, accessory midline fossa absent (125, 1 → 0); scapular articulation of furcula angled laterally (175, 0 → 1); ectepicondylar attachments of humerus oval and dorsal (218, 1 → 0); femur, angle of head with shaft greater than 90° (281, 0 → 1); collateral ligament foveae, metatarsal two of tarsometatarsus, small or absent, that of metatarsal four pronounced (323, 2 → 1); gape, margin markedly fleshy (398, 0 → 2)

**Occurrence:** Late Oligocene of New Zealand and Patagonia, Late Pliocene of South Africa, and Holocene of New Zealand and its sub-Antarctic islands.

**Discussion:** Geographically and temporally, this clade is highly disjunctive. The extant species, for example, have no known fossil record, probably because they inhabit only the sub-Antarctic islands surrounding New Zealand, while *Chubutodyptes* is known only

from the Early Miocene of Argentina and *Korora* only from the late Oligocene of New Zealand. This disjoint distribution is probably caused either by a poor crown-clade fossil record, which is seen in numerous extant groups, or by the incorrect phylogenetic placement of *Chubutodyptes* or *Korora*, as discussed below. One additional, equivocal synapomorphies support the monophyly of this clade, as does separate analysis of integumentary and of morphological data.

Node 51: Unnamed

**Diagnosis:** Length of tarsometatarsus 35-50 mm (305, 0 → 1).

**Occurrence:** Late Oligocene of New Zealand and Patagonia, Late Pliocene of South Africa, and Holocene of New Zealand and its sub-Antarctic islands.

**Discussion:** Only one synapomorphy supports this group, along with 49 ambiguous characters. This is probably because most of the included taxa are very poorly known, especially *Chubutodyptes*, with only about 6% of its anatomy scored. This fact, along with lack of much support for the clade, suggests that additional material or further examination of these incompletely described extinct taxa may overturn the relationship hypothesized here.

Node 52: Unnamed

**Diagnosis:** Intercotylar eminence of tarsometatarsus small, narrow, not raised (309, 0 → 1); tibiotarsus articulation of tarsometatarsus with medial cotyle depressed (311, 1 → 0); Tibialis cranialis tubercle of tarsometatarsus small and elongate (316, 2 → 1); Lateral

intermetatarsal groove of tarsometatarsus shallows distally (325, 1 → 0); and medial one shallow (326, 2 → 1); medial intermetatarsal foramen, medially bordering crista present (331, 0 → 1); hypotarsal crests with lateral pit present on lateral ridge (337, 0 → 1).

**Occurrence:** Late Oligocene of New Zealand and Patagonia, and Holocene of New Zealand and its sub-Antarctic islands.

**Discussion:** These three taxa share seven equivocal synapomorphies only, with a similarly disjunct distribution as Clades 50 and 51.

#### Node 53: Unnamed

**Diagnosis:** Capital groove of humerus shallow and tapered caudally (222, 2 → 1).

**Occurrence:** Late Oligocene of New Zealand and Holocene of New Zealand and its sub-Antarctic islands.

**Discussion:** The sister taxa *Korora* and '*Eudytes sclateri*' share only one equivocal synapomorphy.

#### Node 54: Unnamed

**Diagnosis:** Orbitocranial fonticuli of laterosphenoid, one large and one small present (89, 2 → 0); fenestra ovalis of prootic single (102, 1 → 0); vertebra with dorsal, crested arch lying longitudinally absent (132, 3 → 2); radiale rectangular, wedge-shaped (244, 3 → 1); (246, 1 → 0) femur, head small, no rugosity present (277, 1 → 2); head plumes heading backward, drooping, sparse (413, 1 → 2); immature plumage, throat pattern is mottled (423, 2 → 1); nest construction season is spring or autumn (505, 0 → 1).

**Occurrence:** Holocene of Chile, Argentina, sub-Antarctic and Antarctic islands.

**Discussion:** The distribution of these three *Eudyptula* species is congruent with their monophyly, as they are the only eudyptids known from South America. Recovery of this clade also accords well with previous suggestions that *Eudyptes schlegeli* is a subspecies of *Eudyptes chrysolophus*, and with work by other authors suggesting that *Eudyptes pachyrhynchus* lies outside the remainder of *Eudyptes*. The group is supported only by a few other types of analyses and by the nine unequivocal characters used as its diagnosis.

Node 55: Unnamed

**Diagnosis:** Premaxilla tip deflected ventrally, not laterally compressed (15, 0 → 1); lacrimal extensively visible dorsally (29, 1 → 2); posterior mandibular foramen not visible medially or laterally (108, 0 → 1); medial surface of articular, anteroventral fossa present, large (124, 0 → 1); acrocoracoid process of coracoid, rests on bent neck (156, 0 → 1); humerus 71-100 mm in length (203, 0 → 1); pneumatic fossa of humerus circular (223, 2 → 0); supratendinal bridge of tibiotarsus short (298, 0 → 1); gape, margin markedly fleshy (398, 0 → 2); head plumes orange, present on forehead (412, 2 → 3; 414, 0 → 1); rump distinctly whitish (440, 0 → 1).

**Occurrence:** Holocene of Chile, Argentina, sub-Antarctic and Antarctic islands.

**Discussion:** Eleven equivocal synapomorphies in addition to the twelve unambiguous characters, as well as suggestions of conspecificity and recovery in analyses using morphology, osteology, integument, and others, all support this sister-taxon relationship.

#### Node 56 Unnamed

**Diagnosis:** Tibialis cranialis tubercle of the tarsometatarsus prominent and round (316, 1 → 2); trochleae of tarsometatarsus as follows: second metatarsal shorter than third, as long as fourth (319, 0 → 1).

**Occurrence:** Early Miocene to Holocene of the South Island of New Zealand, Antarctica, and Antarctic and sub-Antarctic coasts and islands.

**Discussion:** Twenty-eight additional synapomorphies, including a large number of behavioral similarities, and the recovery of the clade when extant taxa are analyzed alone, all support this group, which includes the extant genera *Megadyptes*, *Pygoscelis*, and *Aptenodytes*.

#### Node 57: Unnamed

**Diagnosis:** Medial and lateral intermetatarsal foramina of tarsometatarsus equal in size (332, 0 → 1); lateral and medial hypotarsal crests slender (336, 1 → 0).

**Occurrence:** Early Miocene to Holocene of the South Island of New Zealand, Tasmania, Chile, Patagonia, the Antarctic Peninsula, and sub-Antarctic and Antarctic coasts and islands.

**Discussion:** These taxa are united by only synapomorphies, as well as the ambiguous character: supracoracoid fenestra forms a notch only (165, 2 → 1).

Node 58: Unnamed

**Diagnosis:** Length of tarsometatarsus less than one quarter that of tibiotarsus (304, 1 → 0); lateral intermetatarsal groove of tarsometatarsus shallow (324, 0 → 1); hypotarsal crests of tarsometatarsus parallel (338, 1 → 0).

**Occurrence:** Early Miocene to Holocene of the South Island of New Zealand, Tasmania, Chile, Patagonia, the Antarctic Peninsula, and sub-Antarctic and Antarctic coasts and islands.

**Discussion:** This clade comprises Australodyptinae and one species of *Palaeospheniscus*. This latter, polyphyletic genus thus composes the sister taxon of Australodyptinae and one of its most derived members. The clade is supported by only three synapomorphies, all related to the tarsometatarsus, as the *Palaeospheniscus* species is known only from this bone.

Node 59: AUSTRALODYPTINAE Triche 2007 new clade name

**Definition:** The least inclusive, node-based crown-clade containing *Pygoscelis adeliae* and *Aptenodytes forsteri*.

**Diagnosis:** Tibiotarsal sulcus for *m. fibularis* absent or small (299, 1 → 0); intercotylar eminence of tarsometatarsus small, narrow, not raised (309, 0 → 1); medial intermetatarsal foramen, medially bordering crista present (331, 0 → 1).

**Occurrence:** Early Miocene to Holocene of the South Island of New Zealand, Tasmania, Chile, Patagonia, the Antarctic Peninsula, and sub-Antarctic and Antarctic coasts and islands.

**Discussion:** This clade is here formalized, as other clades of extant penguins are not, because an *Aptenodytes/Pygoscelis* clade is often recovered in analyses of penguin phylogeny and availability of a name for this group will thus aid taxonomic communication, even if the clade does not continue to be recognized. Additional support for the clade includes one equivocal synapomorphy, recovery of the clade using integumentary and behavioral data alone, and geographic congruence, as these are the only two genera of penguins known from the Antarctic. The clade also includes three extinct taxa, *Eretiscus tonnii*, *Palaeospheniscus patagonicus*, and *Pseudaptenodytes macreei*.

Node 60: *Pygoscelis* Wagler, 1832

**Type Species:** *Pygoscelis papua* Forster, 1781

**Included Species:** *P. adeliae*, *P. antarctica*, *P. grandis*, and *P. tyreei*

**Emended Diagnosis:** Jaw depressed from level of basitemporal plate (10, 0 → 1); premaxillary groove distal to nostril absent (16, 1 → 0); interorbital septum well developed (37, 0 → 1); jugal strongly curved, sigmoid shape in lateral view (44, 2 → 3); caudal mandibular condyle of quadrate absent (48, 1 → 0); quadratojugal cup of quadrate present and small (49, 2 → 1); orbital process of quadrate very long (55, 1 → 2), with distal end truncated vertically (57, 1 → 2); medial surface of quadrate somewhat excavated (59, 1 → 0); parasphenoid rostrum with weak ventral longitudinal groove (85, 0 → 1); fenestra ovalis opens narrowly, posterolaterally (101, 1 → 0); lateral surface of articular nearly flat (123, 0 → 1); ventral surface of synsacrum grooved (142, 0 → 1); acrocoracoid process rests on bent neck (156, 0 → 1); procoracoid process large but short

(164, 0 → 2); proximal edge of scapula not thickened (181, 0 → 1); lateral trabecula of sternum thin and vertical (198, 1 → 0); radius with deep tendinal grooves, shallow oblique grooves (237, 1 → 3); ilioischadic foramen not occluded dorsally (265, 0 → 1); head of femur with large, with prominent ventral rugosity (277, 1 → 0); capital ligament on femoral head broad and deep (278, 1 → 0); femoral shaft sigmoidal (280, 1 → 0); patella perforate (289, 2 → 0); supratendinal bridge of tibiotarsus tall (298, 1 → 0); distinct dark axillary patch of triangular shape (438, 0 → 1); flanks, extension of dorsal dark cover into leg distinct, reaching tarsus (439, 1 → 0); tail length medium, quills distinctly developed but no surpassing feet extended caudally (444, 0 → 1); tail stiff (445, 0 → 1).

**Occurrence:** Late Miocene to Holocene of Chile, the Antarctic Peninsula, and sub-Antarctic and Antarctic islands.

**Discussion:** Additionally, the monophyly of *Pygoscelis* is supported by 27 equivocal characters, as well as a number of additional analyses, including separate analysis of morphology, osteology, and numerous outgroup modifications. Notable among pygoscelid synapomorphies is the presence of a stiffened tail, from which the genus acquires its common name, Brush-Tailed Penguins.

#### Node 61: Unnamed

**Diagnosis:** Capital groove of the humerus deep and wide (222, 0 → 2).

**Occurrence:** Late Miocene to Holocene of Chile and sub-Antarctic and Antarctic Islands.

**Discussion:** A single synapomorphy and separate analysis of morphological characters support this clade, indicating medium support only. Some authors place *Pygoscelis adeliae* as the sister taxon to *Pygoscelis antarctica*, while some recover an extant topology similar to that recovered here, but the extinct pygoscelids, *Pygoscelis grandis* and *Pygoscelis tyreei*, are both always hypothesized to lie outside the crown-group (Emslie and Correa, 2003; Bertelli and Giannini, 2005; Walsh and Suarez, 2006). Weak support for the topology presented here, as well as the disagreement in the literature, supports the hypothesis that pygoscelids diverged little from other extant penguin species (Walsh and Suarez, 2006). Exclusion of *Pygoscelis adeliae* from a clade of remaining pygoscelids leave a more northerly, sub-Antarctic group. This may indicate that pygoscelids evolved in Antarctica and then dispersed northward, eventually reaching northern Peru.

Node 63: Unnamed

**Diagnosis:** Tibialis cranialis tubercle raised onto metatarsal 3, lies very distally (317, 0 → 1).

**Occurrence:** Late Miocene to Holocene of the sub-Antarctic and Antarctic Islands.

**Discussion:** The sister-taxa *Pygoscelis antarctica* and *P. papua* also share a single synapomorphy. It may be expected that relationships among pygoscelid species may change with future analysis because of the low amount of support for these taxa

Node 64: Unnamed

**Diagnosis:** Deep notch separating digits two and three of the carpometacarpus (255, 1 → 0); proximal portion of femur composed of trochanter, not head (276, 0 → 1); extensor sulcus of tibiotarsus broad, lateral, and large (297, 1 → 0); lateral intermetatarsal foramen absent (327, 2 → 0).

**Occurrence:** Early to Middle Miocene of Patagonia and New Zealand, Holocene of Antarctica and sub-Antarctic and Antarctic Islands.

**Discussion:** The three extinct species most closely related to *Aptenodytes* are largely temporally incongruent with this extant genus. Both *Palaeospheniscus patagonicus* and *Eretiscus* are known from the earliest Miocene of Argentina, while the earliest record of *Aptenodytes* is Late Pliocene and the genus is known only from New Zealand and Antarctica. This does not affect the topology of these relationships, but the presence of only four synapomorphies supporting the clade, and the fact that only one of the extinct species is well known (*Palaeospheniscus patagonicus*), does indicate that this node is not robust.

Node 65: Unnamed

**Diagnosis:** Lateral and medial hypotarsal crests robust (336, 0 → 1).

**Occurrence:** Late Miocene to Holocene of the sub-Antarctic and Antarctic Islands.

**Discussion:** The taxa *Aptenodytes* and *Eretiscus* form this clade, which is supported by only one synapomorphy, probably owing to the extremely poor preservation of *Eretiscus*.

Node 66: *Aptenodytes* Miller, 1778  
**Type Species:** *Aptenodytes patagonicus* Miller, 1778  
**Included Species:** *A. forsteri* and *A. ridgeni*

**Emended Diagnosis:** Articular surface of tarsometatarsus large and rectangular (307, 1 → 0); tarsometatarsus 35-50 mm in length (305, 0 → 1); lateral intermetatarsal foramen large, about 4.2-6.3mm (327 (1 → 3)).

**Occurrence:** Late Pliocene to Holocene of New Zealand, Antarctica, and the Antarctic and sub-Antarctic islands.

**Discussion:** Size is particularly important in differentiating *Aptenodytes* from other extant penguins, including data on the length of the humeri and the tarsometatarsi. Two additional characters equivocally support this node, as well as an extensive number of different analyses. These include morphology, osteology, integument, myology, behavior, and nearly all variations of outgroup and ingroup choice. This node thus has one of the highest levels of support of all Spheniscidae and is second only to *Eudyptula* in number of analyses in which it is recovered.

Node 67: Unnamed

**Diagnosis:** Lateral larger than medial intertrochlear incision of the tarsometatarsus (322, 1 → 2); medial intermetatarsal foramen, medially bordering crista absent (331, 1 → 0).

**Occurrence:** Late Pliocene to Holocene of New Zealand and the Antarctic and sub-Antarctic islands.

**Discussion:** Although geographic data supports the sister-taxon status of this clade, as both these taxa are sub-Antarctic, while *Aptenodytes forsteri* is Antarctic in distribution,

support is fairly low in terms of number of synapomorphies, two, bootstrap support, and number of other analyses supporting the node. Morphology and osteology, when examined alone, however, do recover this relationship.

#### Node 68: Unnamed

**Diagnosis:** Pneumatic fossa of humerus flattened anteroposteriorly (223, 0 → 1); lies caudally on shaft (226 1 → 0); and contains a nearly longitudinal partition that angles anterolaterally, with its ventral division excavated into a distinct pit (228, 0 → 2).

**Occurrence:** Early Miocene to Late Miocene of Patagonia.

**Discussion:** The monophyly of the *Palaeospheniscus patagonicus*-*Pseudapterodytes macreei* clade is supported by three synapomorphies and seventeen equivocal characters, suggesting high confidence in this relationship.

## Discussion and Conclusions

### Comparison with Previous Work

Comparing the phylogeny presented here with previous proposals illustrates a number of differences, mainly between the morphological and molecular datasets. The first cladistic analysis to examine phylogeny among extinct penguins resulted in a very different topology, with Australodyptinae lying basally within Spheniscidae and other extant taxa more derived, a failure to recover Parapterodytidae, and a reconstruction of Palaeodyptidae with a very different taxonomic complement (Triche, 2005). It concurs with the phylogeny presented here in the similar placement of *Wimanu* and in recovery of

a polyphyletic *Palaeudyptes*, but also found non-monophyly of *Anthropornis* and *Paraptenodytes*. That phylogeny was, however, based entirely on tarsometatarsal characters and thus almost certainly presents a biased picture of penguin evolution, both by using a much smaller character set and by excluding all extinct species not known from the ankle bone.

Work presented here agrees fairly closely with that performed on South America extinct and extant species alone (Acosta Hospitaleche, 2004; Acosta Hospitaleche et al., 2007). These analyses placed *Palaeospheniscus biloculata* as the sister taxon to *Aptenodytes*, which is similar to the topology presented here that places a number of *Palaeospheniscus* species within and just outside Spheniscidae. Additionally, Acosta Hospitaleche always recovers a monophyletic Australodyptinae and identical relationships among extant taxa, with the sole exception of a paraphyletic *Eudyptes* (2004) or *Pygoscelis* (2007). The two other extinct species included here are crown penguin outgroups, which is congruent with the present analysis and expected from a matrix including only three extinct taxa.

Phylogenetic analyses of single, extinct, penguin taxa agree exactly with the phylogeny recovered here because no other extinct species are included that might present differing results (Slack et al., 2006; Bertelli et al., 2006; Walsh and Suarez, 2006). The first of these, which examined the placement of *Wimanu*, recovered the species as a monophyletic genus forming the sister-taxon to all other penguins, or their ‘crown + stem-penguins’ (Slack et al., 2006). The second analysis, which found *Paraptenodytes antarcticus* to be the sister-taxon to Spheniscidae (Bertelli et al., 2006),

and the third, which found a monophyletic *Pygoscelis* to include *Pygoscelis grandis* (Walsh and Suarez, 2006), both also accord with the current topology. The analysis presented here is more informative in that it includes all these taxa and is thus able to elucidate relationships between them.

Finally, the only other analysis of numerous extinct penguins is similar in regards to extant topology but different as regards relationships among extinct taxa (Ksepka et al., 2006). It hypothesized Procellariiformes as the sister-taxon to Spheniscidae, with Gaviidae as a subsequent outgroup, which is not incongruent with results found here, but does require further testing, as these authors included twelve procellariiforms, but only two gaviids and no other outgroups. Topological similarities within Spheniscidae included a monophyletic Australodyptinae, a sister-taxon relationship between that group and *Megadyptes*, a basal position for *Spheniscus*, and identical placement of extinct *Spheniscus* species. However, *Eudyptula* was reconstructed as the sister-taxon of *Spheniscus* and the crested penguins (*Eudyptes* + *Megadyptes*) formed a clade, neither of which relationships are recovered here. The discrepancy probably arises either because of my inclusion of numerous extinct, crown-group taxa that affect the reconstruction of basal crown-group character states or because of the much larger size of the matrix utilized here.

Outside Spheniscidae, these authors reconstruct a drastically smaller Palaeodyptidae, which includes only four taxa, as opposed to the 21 recovered here. The difference is caused partially by analysis of different taxon sets, but four of the species here recovered as palaeodyptids do fall outside that clade in the previous work (Ksepka

et al. 2006). Three of these species lie close to Palaeedyptidae, however, and include a palaeedyptine-*Anthropornis* polytomy. That relationship indicates that the different reconstruction is again probably caused by too little character data to resolve the polytomy in prior analyses. The other major extinct clade discovered here, Paraptenodytidae, was never recovered previously (Ksepka et al. 2006). In fact, although four of the seven paraptenodytids recovered here are evaluated in that other phylogeny, none of them lie close to *Paraptenodytes*, and all three are the most basal of all sphenisciforms except *Wimanu*. The difference probably reflects either the excellent preservation of *Paraptenodytes* as compared with other paraptenodytids, my inclusion of numerous, additional, extinct taxa or, again, the larger amount of data analyzed here.

Previous work concluded that gigantism in penguins either evolved multiple times (Ksepka et al., 2006) or once in a paraphyletic grade of extinct species (Clarke et al., 2007). The phylogeny recovered here suggests that gigantism evolved only once, in a monophyletic group that evolved within Palaeedyptidae. Conclusions about the evolution of gigantism should probably not be drawn based on my analysis, however, until it incorporates *Icadyptes* and *Perudyptes*, two of the species reconstructed as attaining giant size.

### **Missing Data**

The present analysis suggests that the use of large numbers of systematic characters and of differing taxon choice greatly affects phylogeny reconstruction. This dataset is vastly larger than any previously used in penguin systematics, and correspondingly results in a high, nearly complete, level of resolution, even of a

seemingly prohibitively incomplete group of birds. Other difficult, phylogenetic problems may benefit from similar application of large datasets including numerous data types (e.g., Livezey and Zusi, 2006, 2007). For example, the question of whether or not extant seabirds are monophyletic or merely convergent may gain resolution from examination of more detailed morphology in a broader, expanded analysis. Phylogenetic resolution decreases when number of taxa is increased without a corresponding increase in characters (e.g., Hill, 2005), and most phylogenetic problems in ornithology include vast numbers of species.

Taxon choice is also shown here to be important for determining phylogenetic topology. Removing incomplete taxa is shown to affect topology when performed in a number of different ways, indicating that all outgroups and all ingroup species should be included, not only the most complete species and a single, hypothetical outgroup. When that is not possible, as with higher-level or larger analyses, more detailed studies should be consulted to determine which species show the most appropriate, plesiomorphic, morphology. That is now possible with penguins: *Spheniscus*, as the basal-most extant taxon, should be included in higher-level analyses, which nearly always previously excluded that genus. Fortuitously, however, that is the only penguin taxon included in the largest and most recent morphological analysis of neornithine phylogeny, an inclusion that should be followed in future analyses (Livezey and Zusi, 2006, 2007). Additionally, single elements, or at least the most commonly preserved humerus and tarsometatarsus, are not diagnostic to species or generally even genus level. They should no longer be used to diagnose or propose new penguin species when known only in isolation.

Finally, the use of multiple data types, not just, for example, integumentary or molecular sources alone, results in topological support at different hierarchical levels. This is important in demonstrating that it is not sufficient to analyze phylogeny with only one type of data, as this may only accurately reflect some relationships. Use of all available data sources (molecules, morphology of all sorts, behavior, etc.) is the only way to include phylogenetic signal from all relationships. Therefore, a more global approach using total evidence, large character matrices, and all taxa possible should improve the quality of future phylogenetic studies, both in terms of resolution and of topological accuracy.

### **Conclusions**

This analysis examines all extant, most named, and a few unnamed extinct penguin taxa. The results of various phylogenetic analyses suggest that taxa pertaining to extant genera are well known and their relationships well resolved, but that much descriptive and systematic work remains regarding older, extinct taxa. Penguin phylogeny is not particularly well supported in any analysis (e.g., confidence or bootstrap values), but its resolution is high in nearly all analyses and in the strict consensus of all MPT's. This phylogeny is probably as robust as could be expected, considering the isolated nature of the fossil remains of this group. It is important to consider this excellent fossil record in analyses of living penguins because character states found within extinct taxa obviously strongly affect the topology of extant genera, as shown by the differences between morphological and molecular analyses. Penguins are shown to be monophyletic, as is the penguin crown-clade, Spheniscidae, and two entirely extinct clades of penguins

lying outside this crown (Palaeedyptidae and Paraptenodytidae). The positions of most extinct taxa are well-resolved, although less resolution applies to Palaeedyptidae. Some fossil remains are probably too fragmentary and isolated to allow much confidence in their phylogenetic placement, however, including *Chubutodyptes*, *Eretiscus*, and *Korora*.

Various modifications of this analysis show that taxon choice, data completeness, and outgroup inclusion are instrumental in resolving penguin phylogeny. Removal of various data types (e.g., integumentary, behavioral, portions of osteology, etc.) greatly changes the recovered topology, as does exclusion of partially incomplete taxa. It is therefore imperative to include as many taxa, extinct and extant, as possible in such phylogenetic analyses, and to incorporate as much and as many types of character data as feasible.

Agreement on penguin phylogeny among this and previous analyses includes a robust, monophyletic crown-clade that ranges temporally at least to the earliest Miocene, based on fossil material, and possibly to the Late Eocene, based on molecular dating and confidence intervals (Baker et al., 2006; Slack et al., 2006; Triche, 2006). Disagreement lies in the relationships of various extinct species and particularly in the paraphyly proposed here for numerous extinct genera, especially the '*Palaeedyptes*' group. Finally, the sister taxon of Sphenisciformes is most likely Procellariiformes, but that requires further investigation and should not yet be assumed in future analyses. Podicipedidae is probably also a valid potential sister-group that should be included in future analyses of penguins, and inclusion of all proposed outgroups should henceforth be attempted.

## **Future Work**

There are numerous areas of research in penguin paleontology and systematics that require future effort. Such work is now provided with a comprehensive phylogeny of extinct and extant relationships. This updates much of the important work performed on penguins prior to the use of phylogenetic systematics and will allow analysis of future discoveries and specimens not included here in an explicitly phylogenetic framework. Much analysis still remains, however, including revision of the *Palaeudyptes* complex and a number of new ‘palaeudyptid’ species from New Zealand, including OM C47. Individual specimens of *Palaeudyptes* species may now be analyzed using this matrix to determine the boundaries of currently named species and the variability of future, unnamed taxa. The ‘*Palaeudyptes*’ complex is certainly paraphyletic, and separate examination of each species using an expanded version of the matrix presented here may allow determination of intraspecific boundaries and of the placement of each taxon within penguin phylogeny. The clade Palaeudyptidae is also in need of more phylogenetic resolution. While some sub-clades are recovered, support within this clade is low and a detailed examination of its character support as well as addition of new, systematic data will be necessary to untangle palaeudyptine relationships.

A number of penguin taxa, including the *Palaeudyptes* group, needs systematic revision not attempted here. This includes potential synonymizing of the *Tasidyptes/Megadyptes* clade, formalizing of the species represented by OM C47 and CADIC P-21, and revised diagnosis of numerous, additional, extinct species. The fauna from Seymour Island was recently thoroughly revised (Jadwiszczak, 2006a, b; Tambussi

et al., 2006), however, some of that systematic revision relied on size categories and referral of unassociated and non-overlapping elements, while the remainder names species using probably non-diagnostic humeral characters rather than phylogenetic analysis. That fauna should be examined element by element using a phylogenetic matrix to determine if these referrals are valid and whether or not the Seymour Island taxa are monophyletic and correctly placed phylogenetically. Detailed description of a number of important penguin fossils is also required, especially *Wimanu* (Ando, pers. comm.), *Crossvallia*, and the South African fauna. Future discoveries, as well as description of these known species, may now focus on what is known to be phylogenetically variable anatomy.

Perhaps the most important area of future research in penguin systematics concerns the relationships of penguins with other avian taxa. Although recent studies, including that presented here, examined numerous outgroups and generally agreed that penguins are most closely related to either Procellariiformes or Gaviidae (Bertelli and Giannini, 2005; Livezey and Zusi, 2006, 2007), that hypothesis was not examined directly, only in the context of interspecific, penguin relationships. This phylogeny and dataset may now be expanded to include other seabird taxa and resolve not only the relationships of penguins to other avians, but also questions regarding the potential monophyly and interrelationships of all seabirds.

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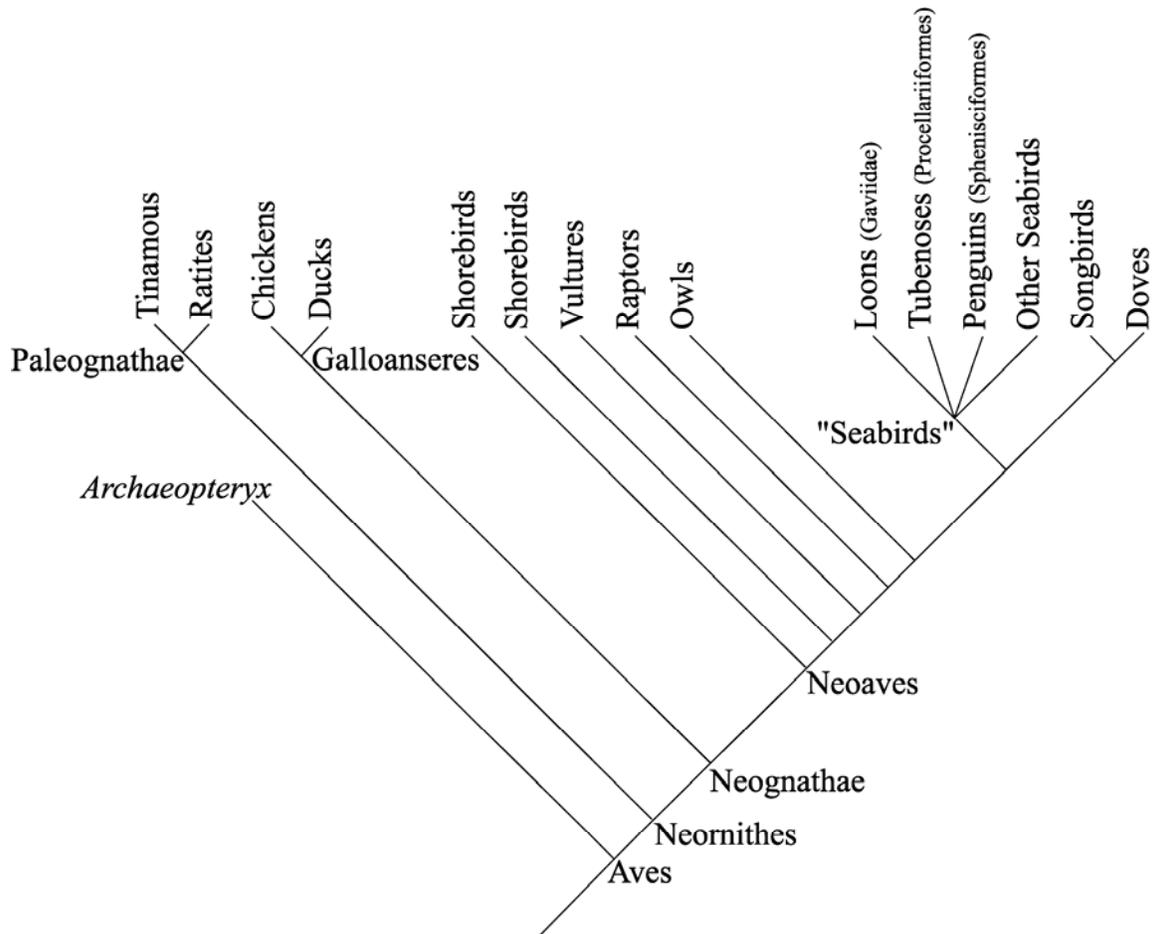
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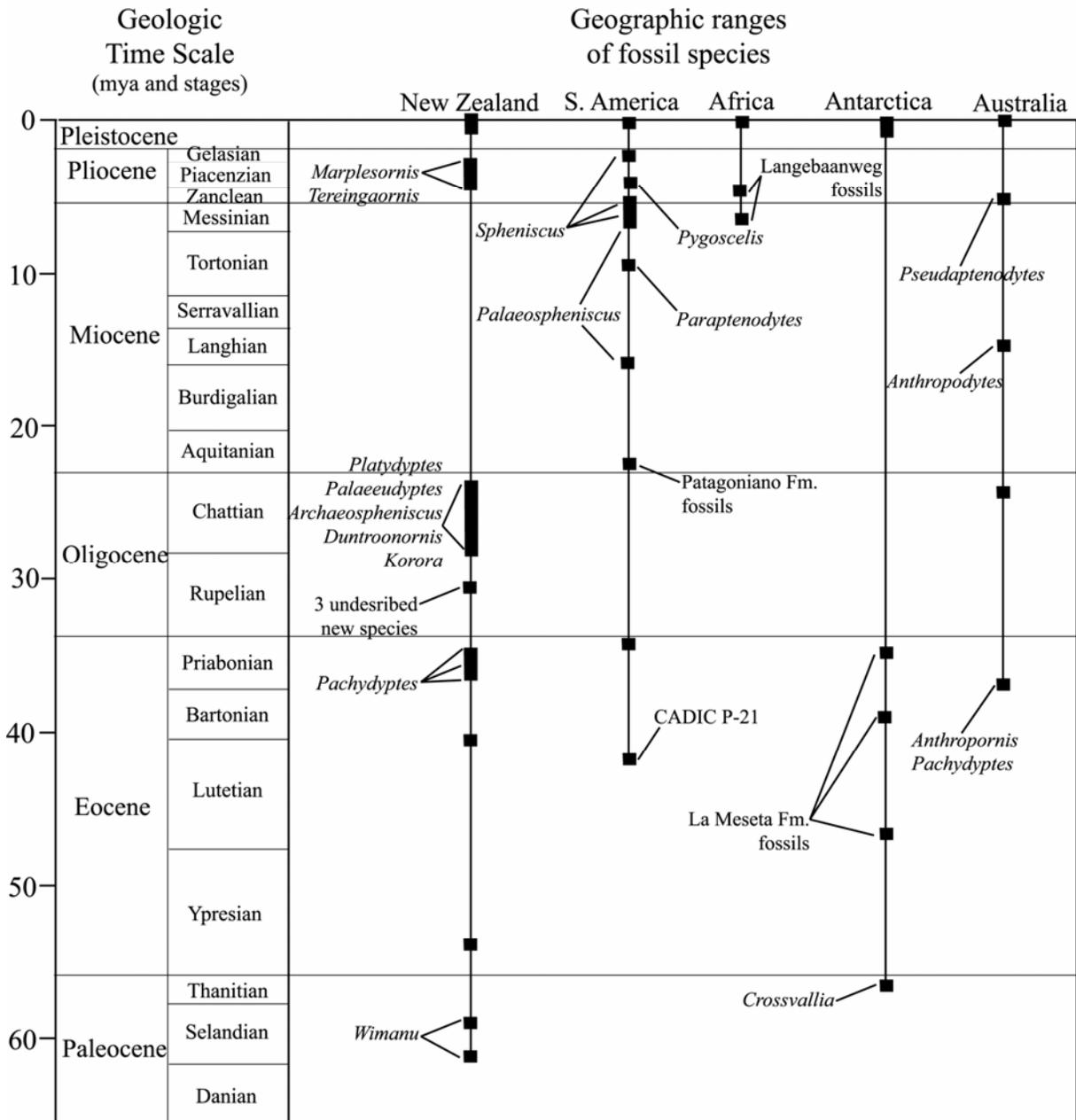
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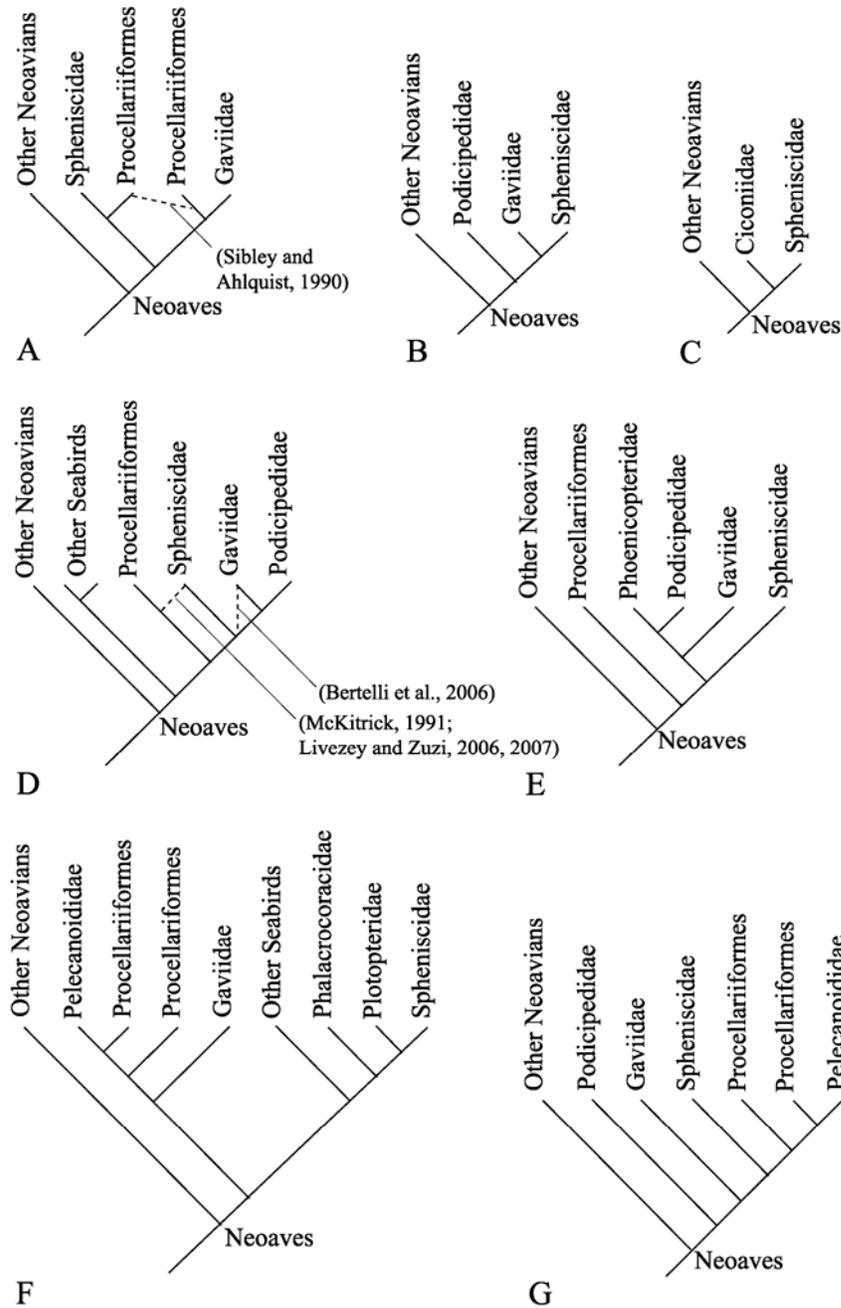
**Figure 3.1. Generalized Relationship of Sphenisciformes to Other, Selected Avians.**  
 After Mayr and Clarke, 2003.



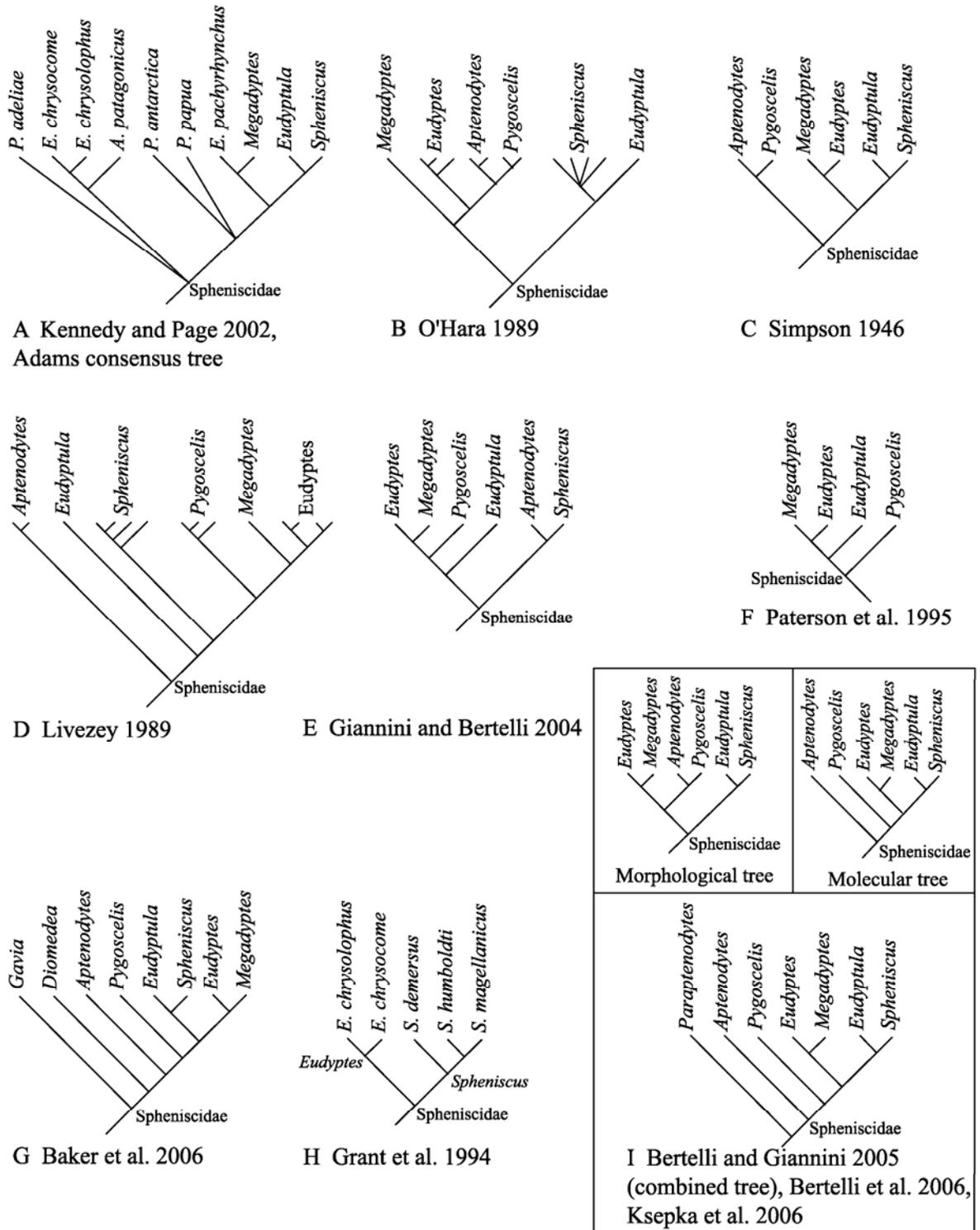
**Figure 3.2. Temporal Distribution of Extant and Extinct Penguin Species.** Plotted against the Cenozoic time scale (after Gradstein et al., 2004). Blocks represent occurrences of penguin remains. Ages determined in millions of years or to stage. Unlabelled blocks denote unnamed or unpublished occurrences and extant species. Inspired by Fordyce and Jones, 1990 (Figure 18.2).



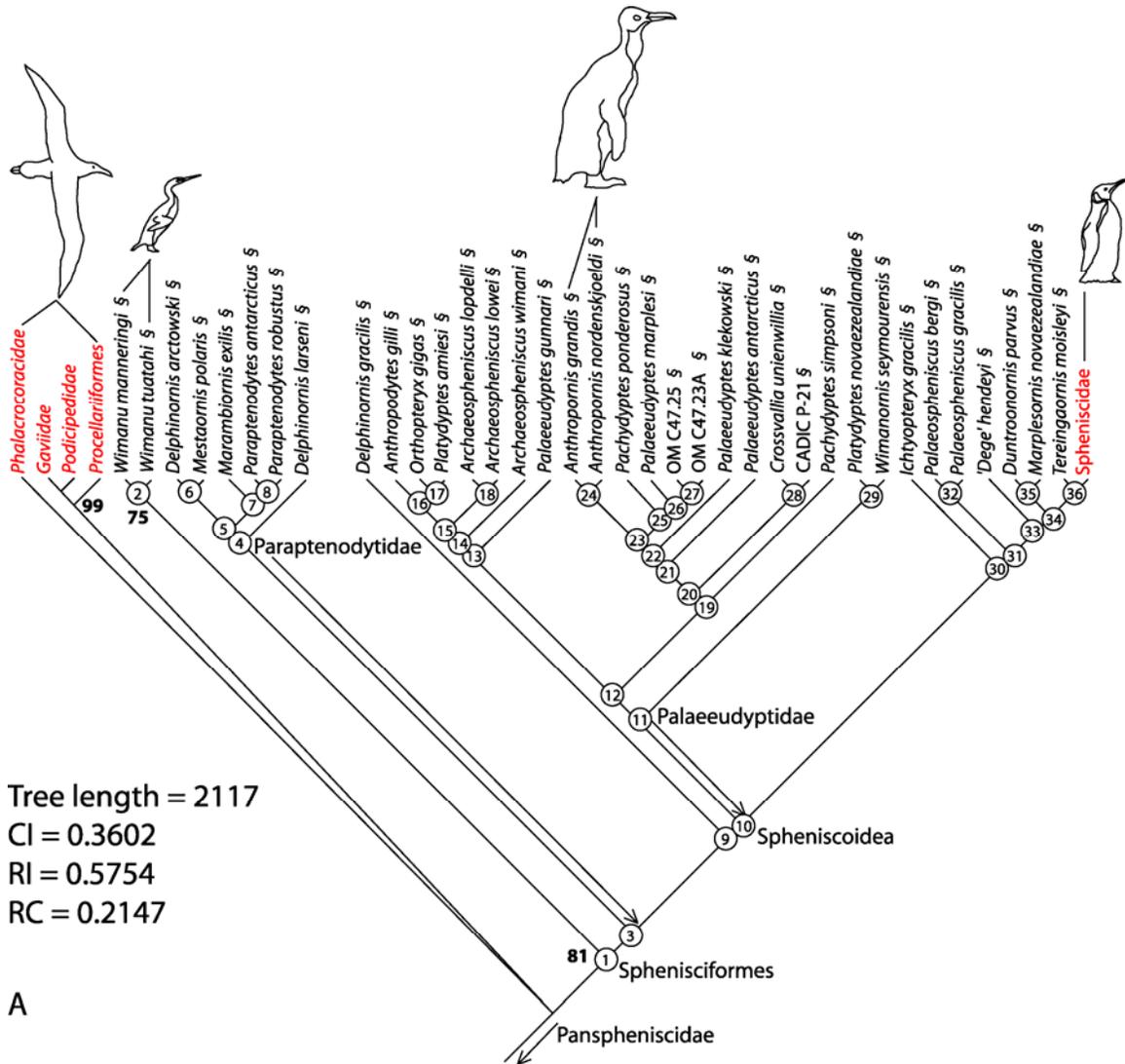
**Figure 3.3. Proposed Relationships between Spheniscidae and Other Neoavians.** A. Topology of Simpson, 1946; Sibley and Ahlquist, 1990; Cooper & Penny, 1997. B. Topology of Ho et al., 1976; Olson, 1985b. C. Topology of Slack et al., 2003. D. Topology of Cracraft, 1982, 1988; Sibley and Ahlquist, 1990; McKittrick, 1991; Mayr and Clarke, 2003; Bertelli et al., 2006; Livezey and Zusi, 2006, 2007. E. Topology of Mayr, 2004. F. Topology of Mayr, 2005a. G. Topology of Van Tuinen et al., 2001; Livezey and Zusi, 2001.

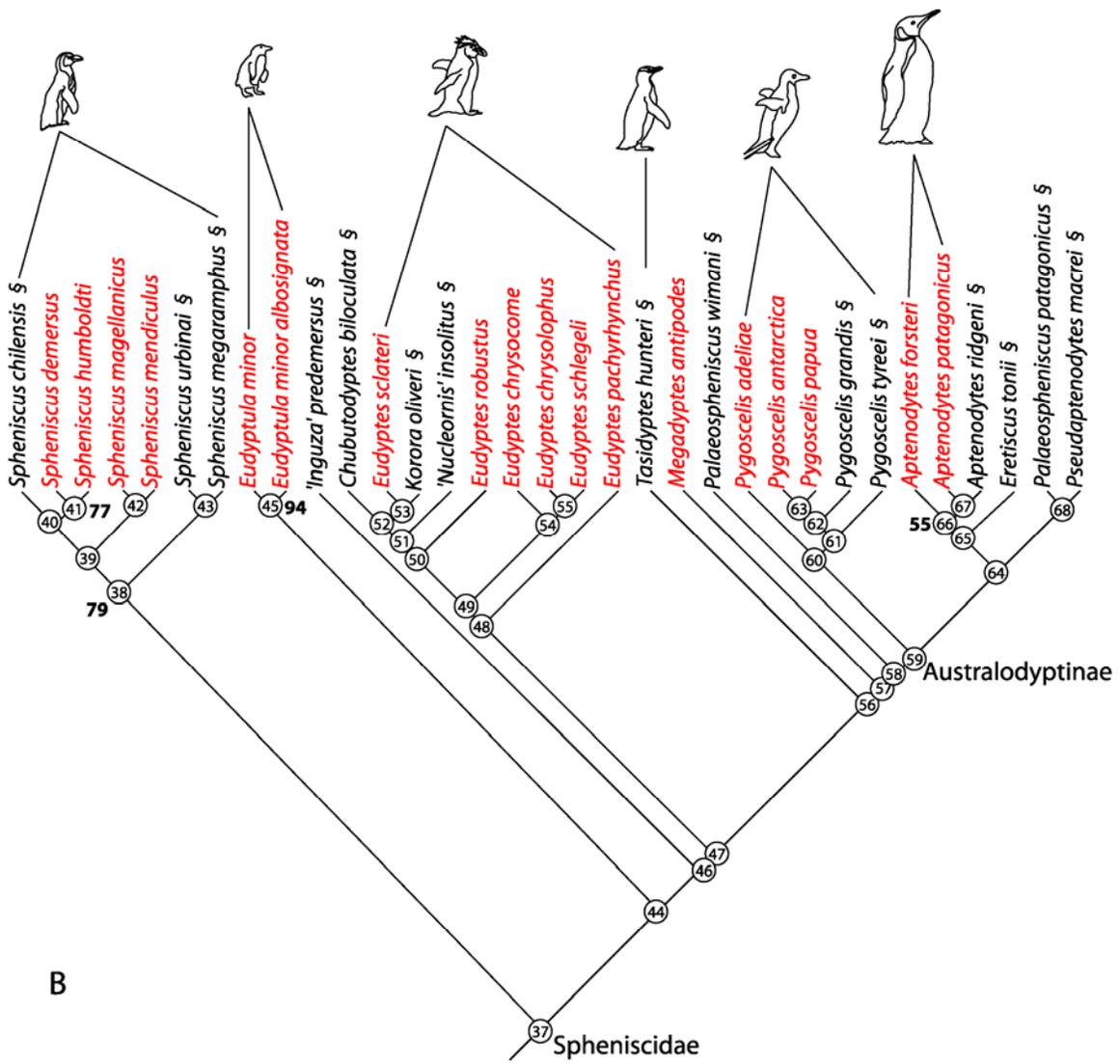


**Figure 3.4. Proposed Phylogenies of Extant Penguin Species.** See text for discussion of data used for each reconstruction.

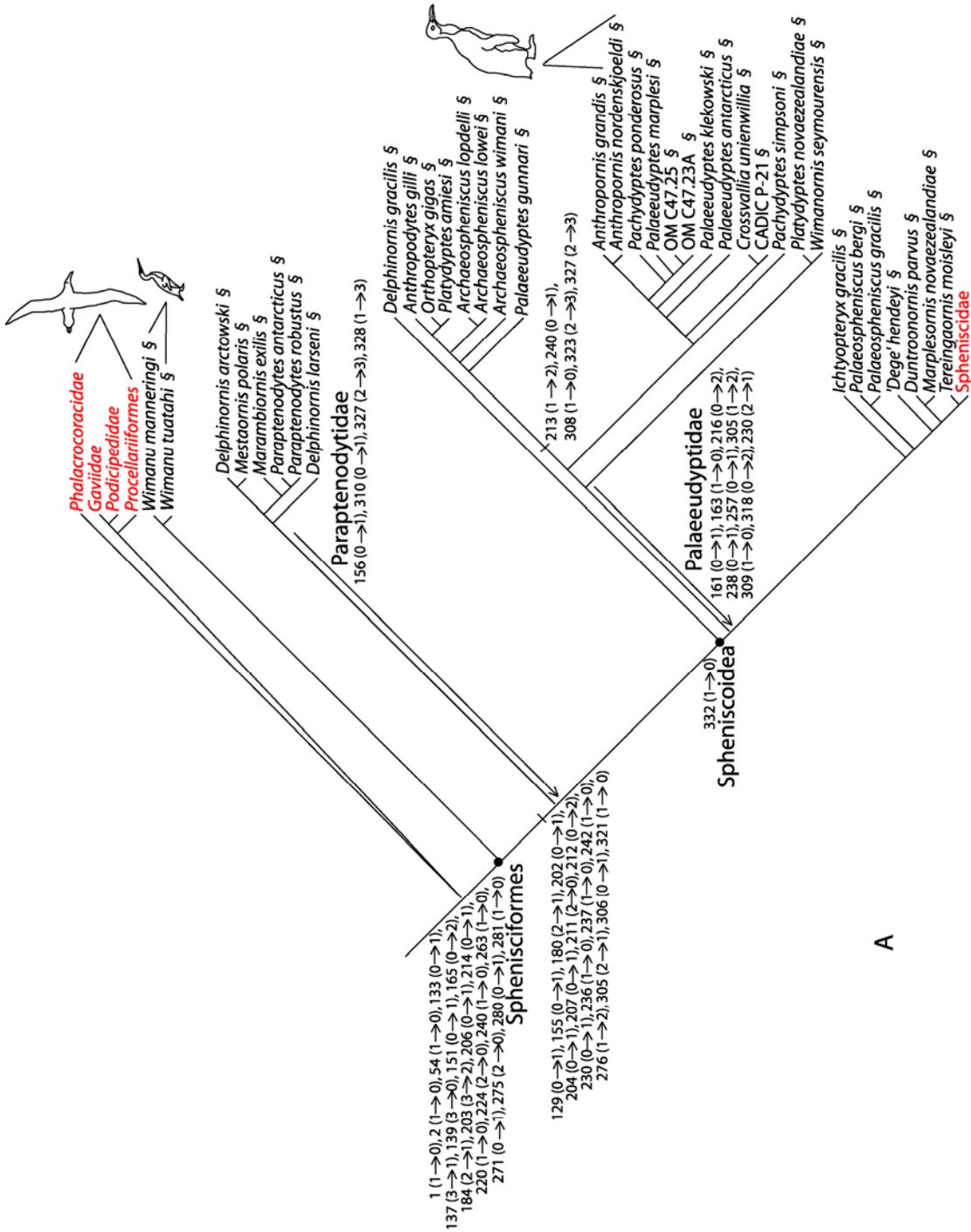


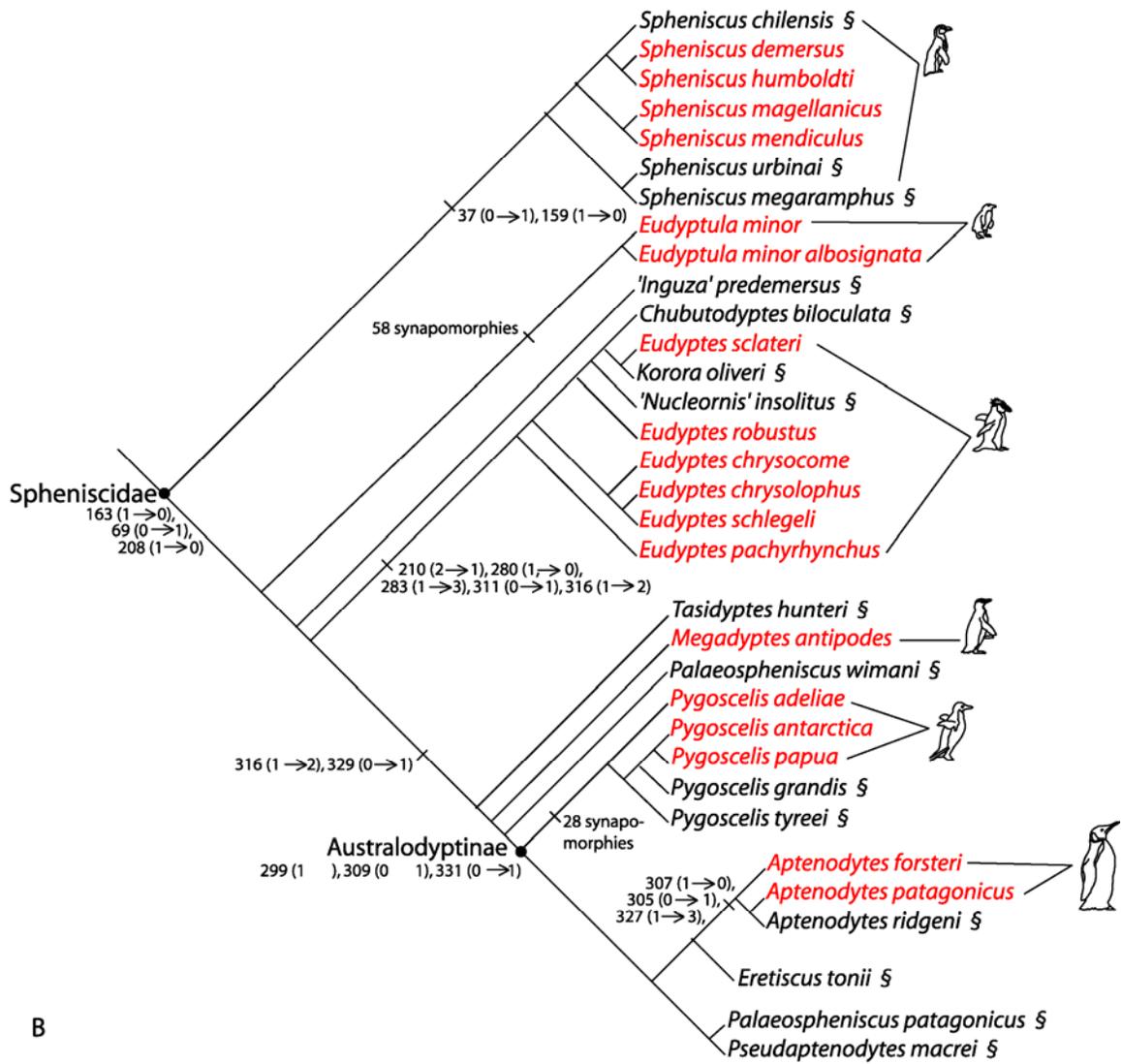
**Figure 3.5. Most Parsimonious Reconstruction of Relationships of Extinct and Extant Penguins.** A. Single MPT. B. Expanded relationships of crown-clade taxa. Small, bold-face numbers indicate bootstrap percentages (only >50% are shown); all clades are numbered in small circles at nodes. Arrows indicate stem-based taxa, all other clade names are node-based. Extant taxa in red, extinct taxa indicated with §.





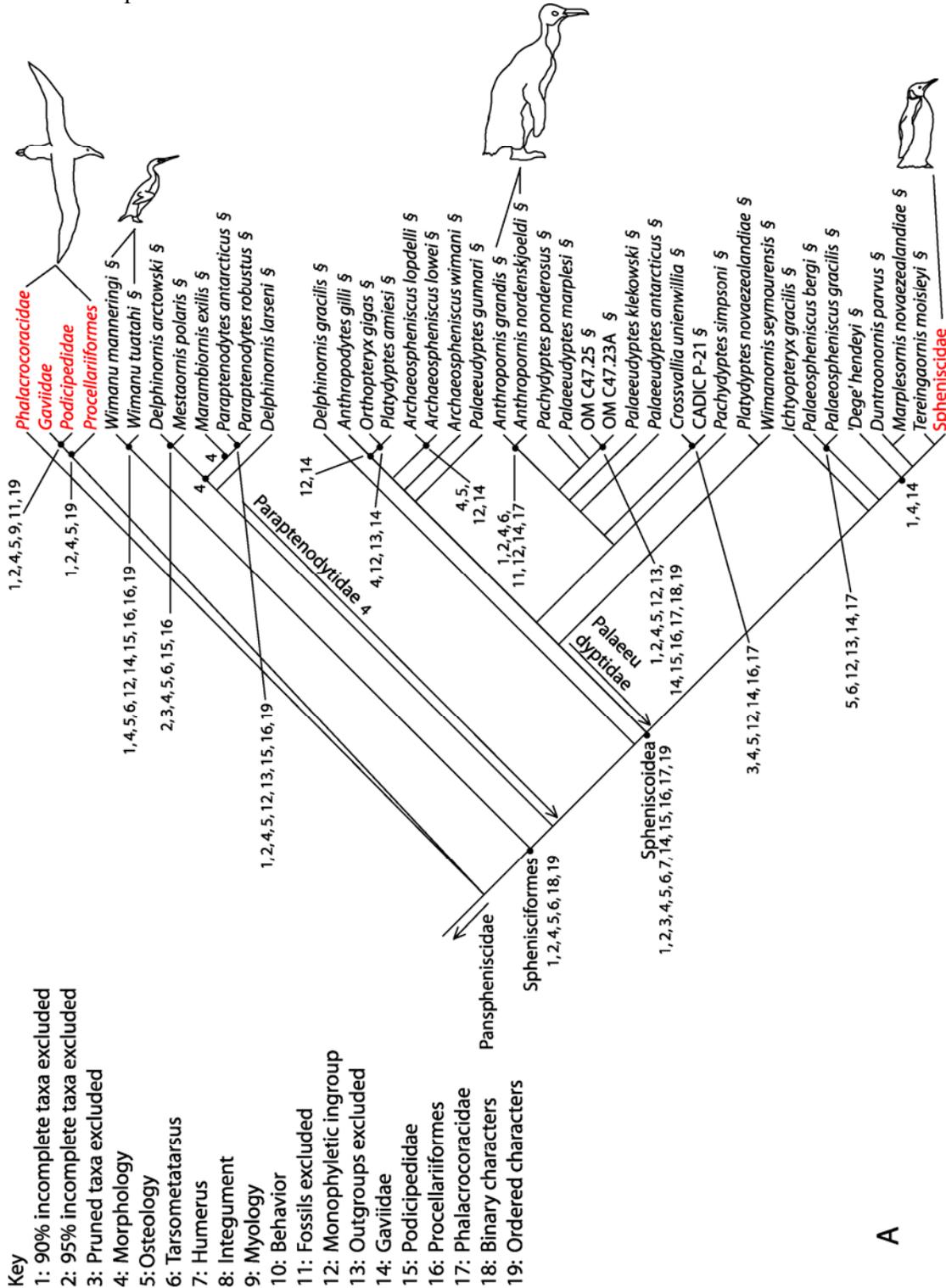
**Figure 3.6. MPT from Original Analysis.** A. Synapomorphies for Panspheniscidae through the clade (*Ichtyopteryx* + Spheniscidae). B. Synapomorphies for Spheniscidae. Unambiguous synapomorphies of major nodes are listed with name or at hatch marks. Synapomorphies for remaining nodes and all terminals are listed in Appendix 3.5. Node-based taxa are indicated with black circles, and stem-based taxa are indicated with arrows.

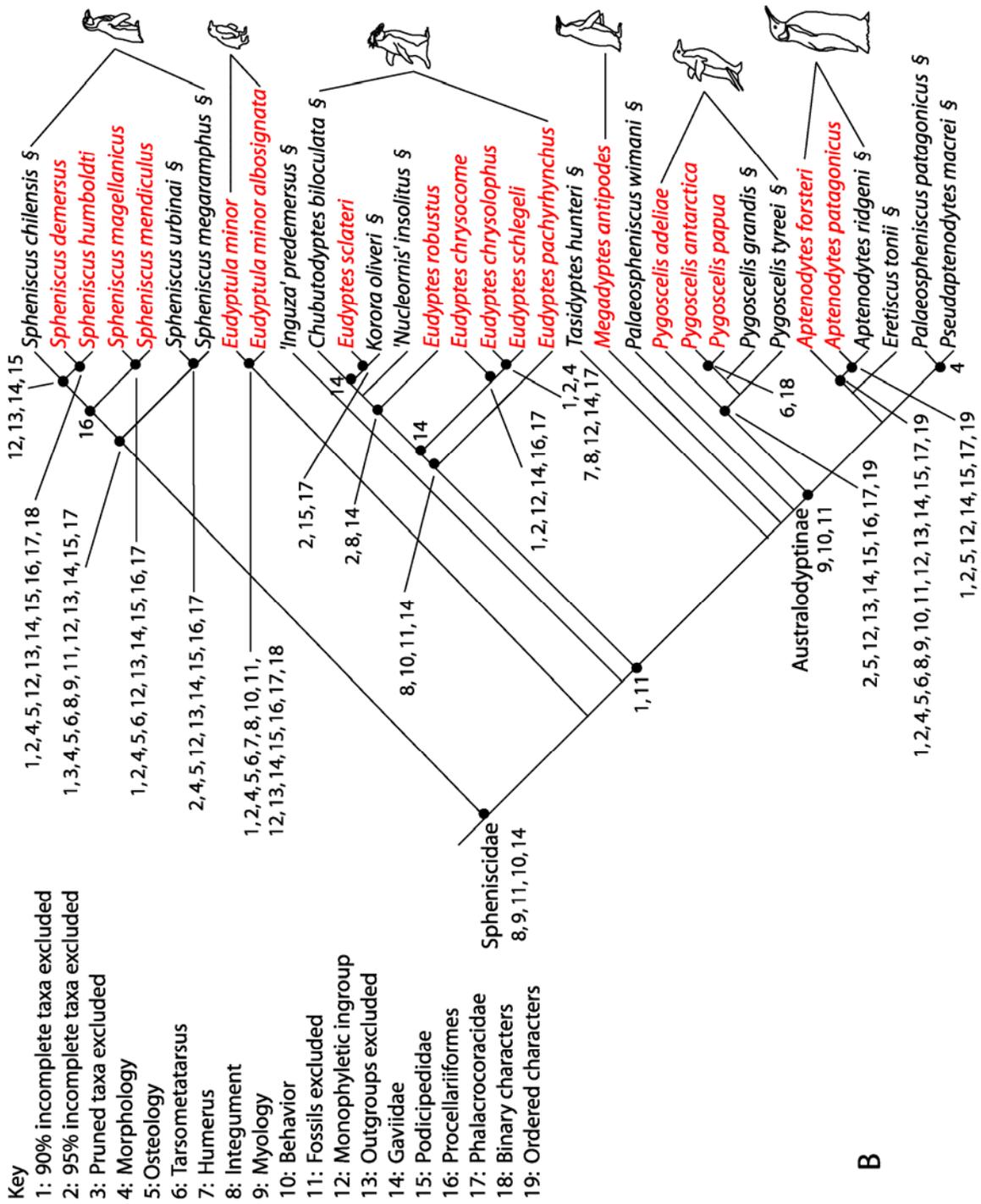




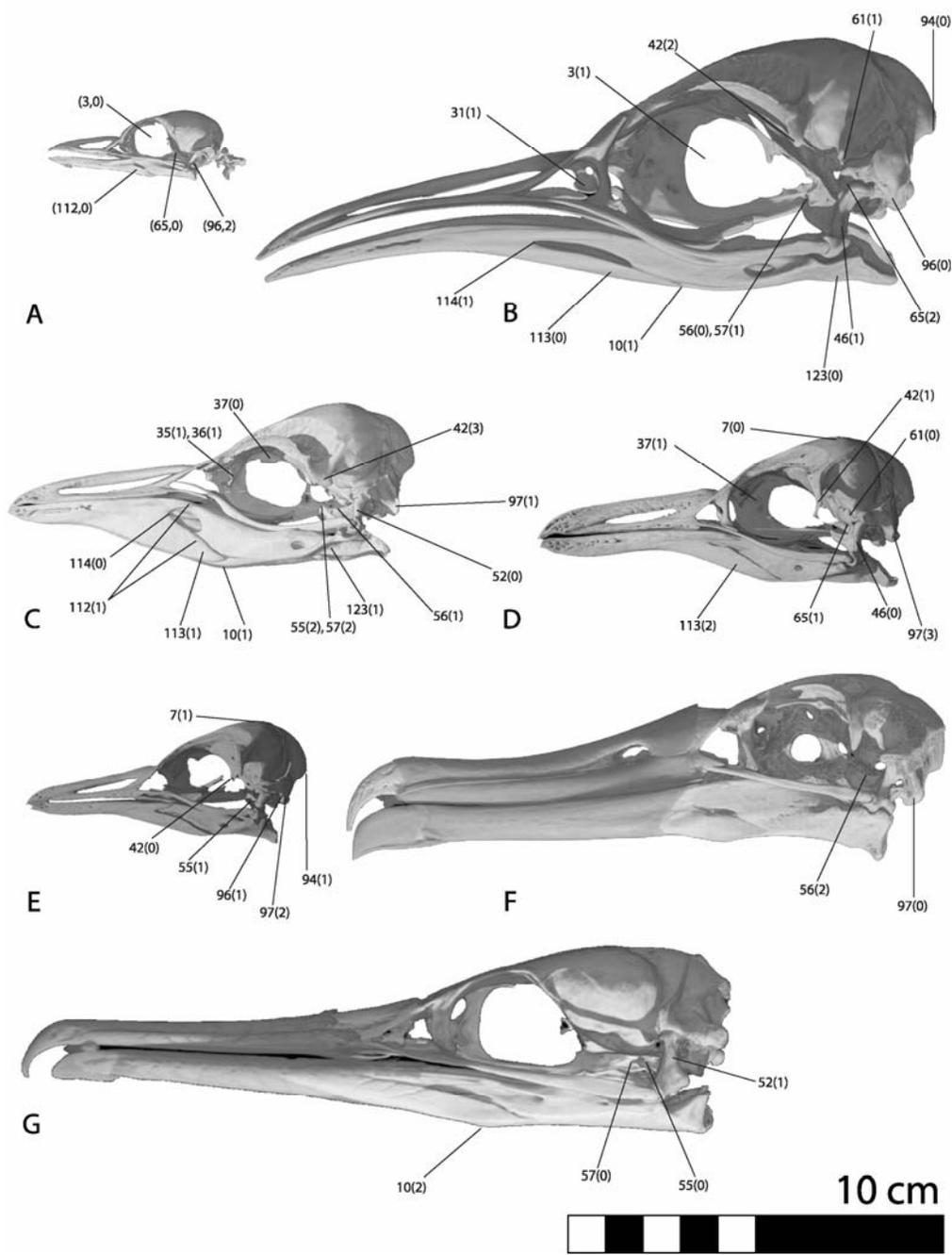
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**Figure 3.7. Original MPT with Type of Support for Recovered Clades.** A. Support is listed for Panspheniscidae through the clade (*Ichthyopteryx* + Spheniscidae). B. Support is listed for Spheniscidae.

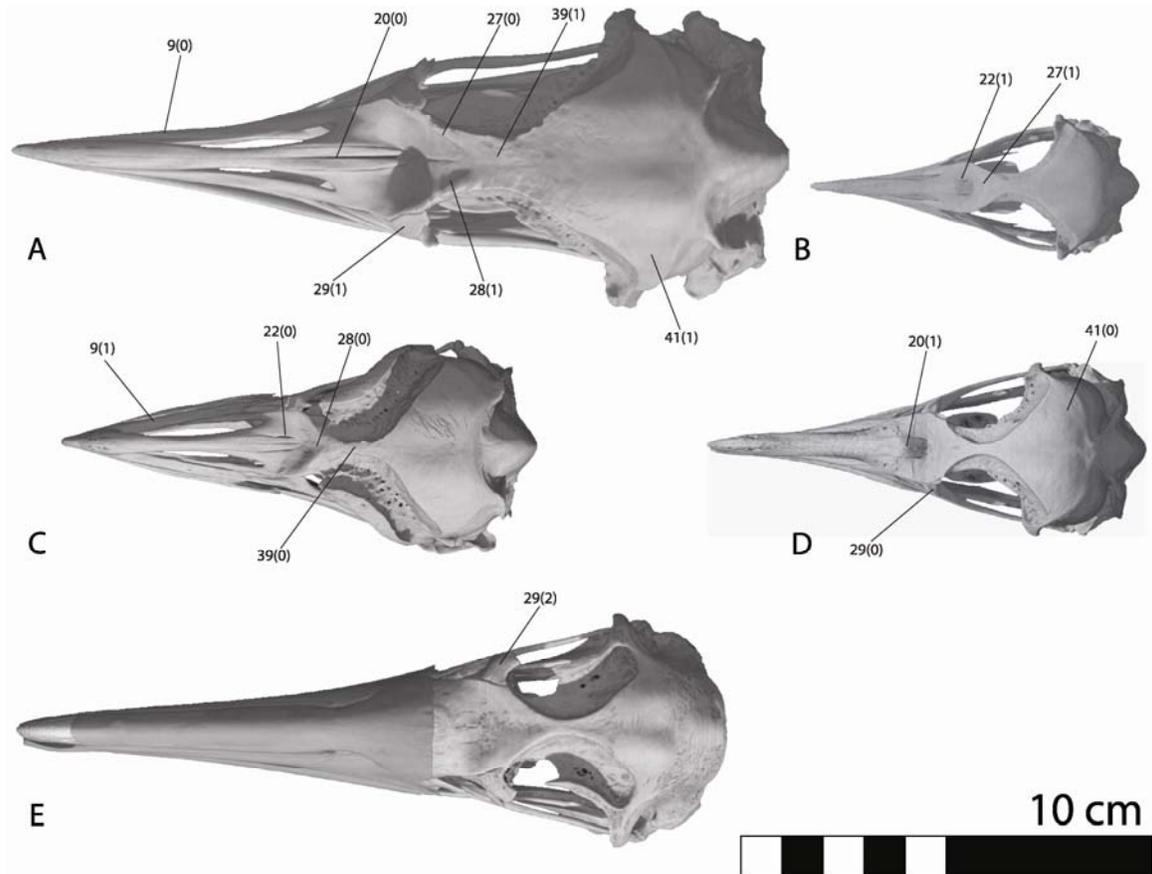




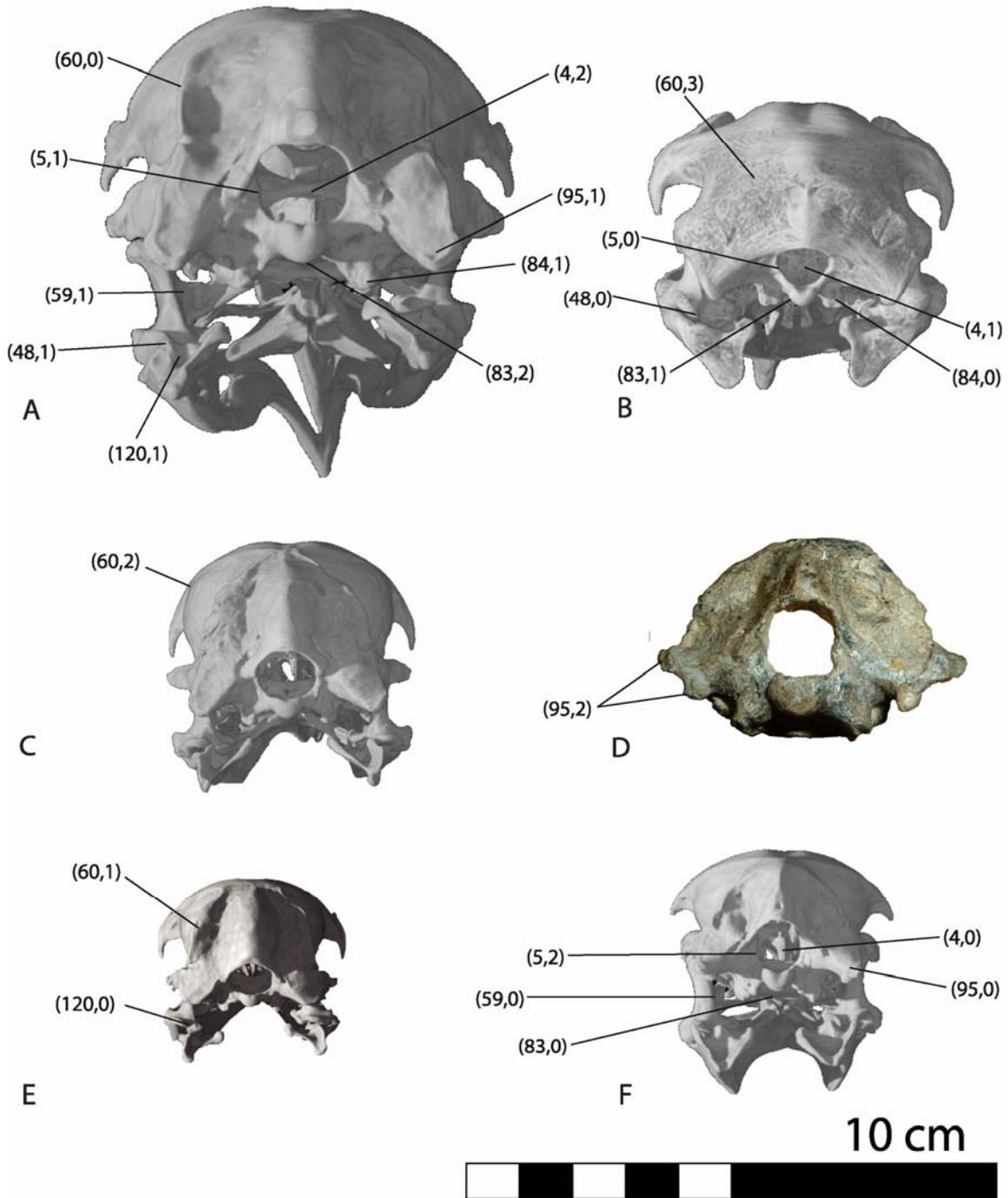
**Figure 3.8. Systematic Characters of the Skull Observed in Lateral View.** A. *Podilymbus podiceps* (TMM M-7139). B. *Aptenodytes forsteri* (UF 22281). C. *Pygoscelis adeliae* (UF 36633). D. *Spheniscus demersus* (UF 21341). E. *Eudyptula minor* (UF 31924). F. *Diomedea immutabilis* (FLMNH 313780). G. *Phalacrocorax penicillatus* (TMM M-1180). Institutional abbreviations as in Appendix 3.1, character states indicated in parentheses.



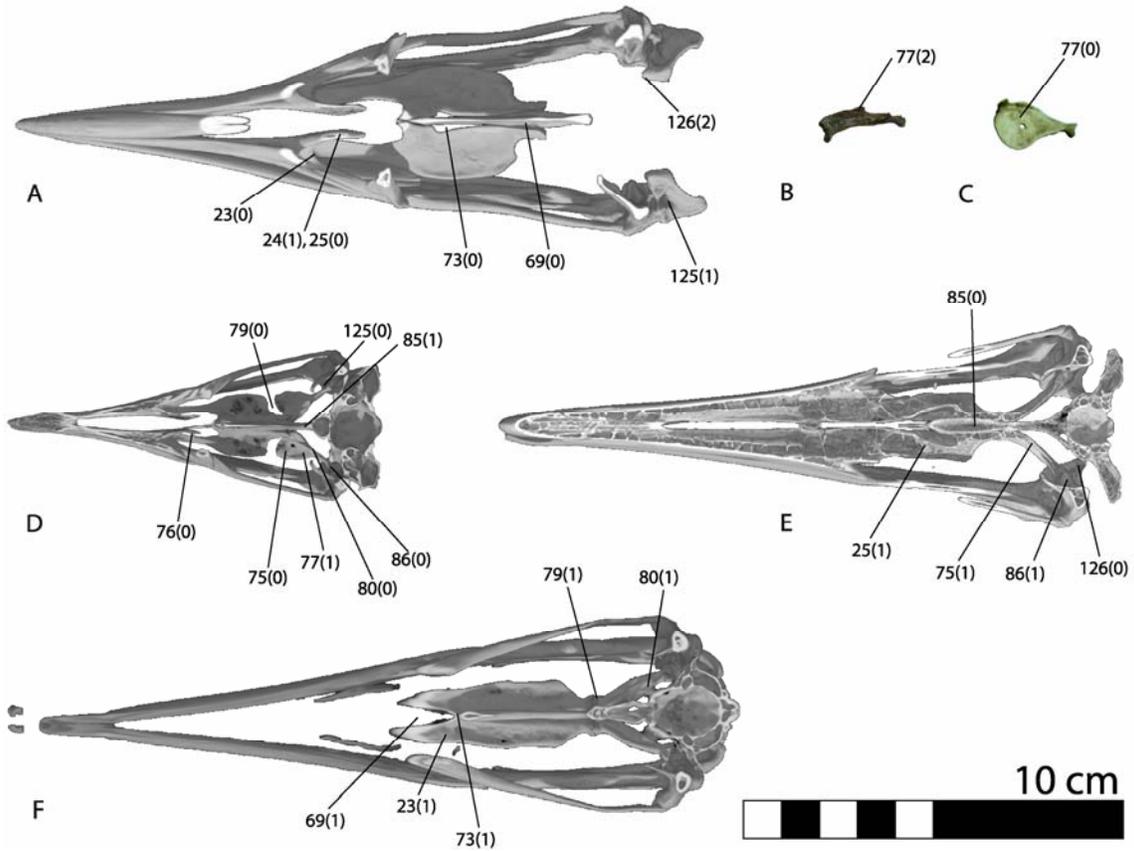
**Figure 3.9. Systematic Characters of the Skull Observed in Dorsal View.** A. *Aptenodytes forsteri*. B. *Eudyptula minor*. C. *Pygoscelis adeliae*. D. *Spheniscus demersus*. E. *Diomedea immutabilis*. Specimens as in Figure 3.8.



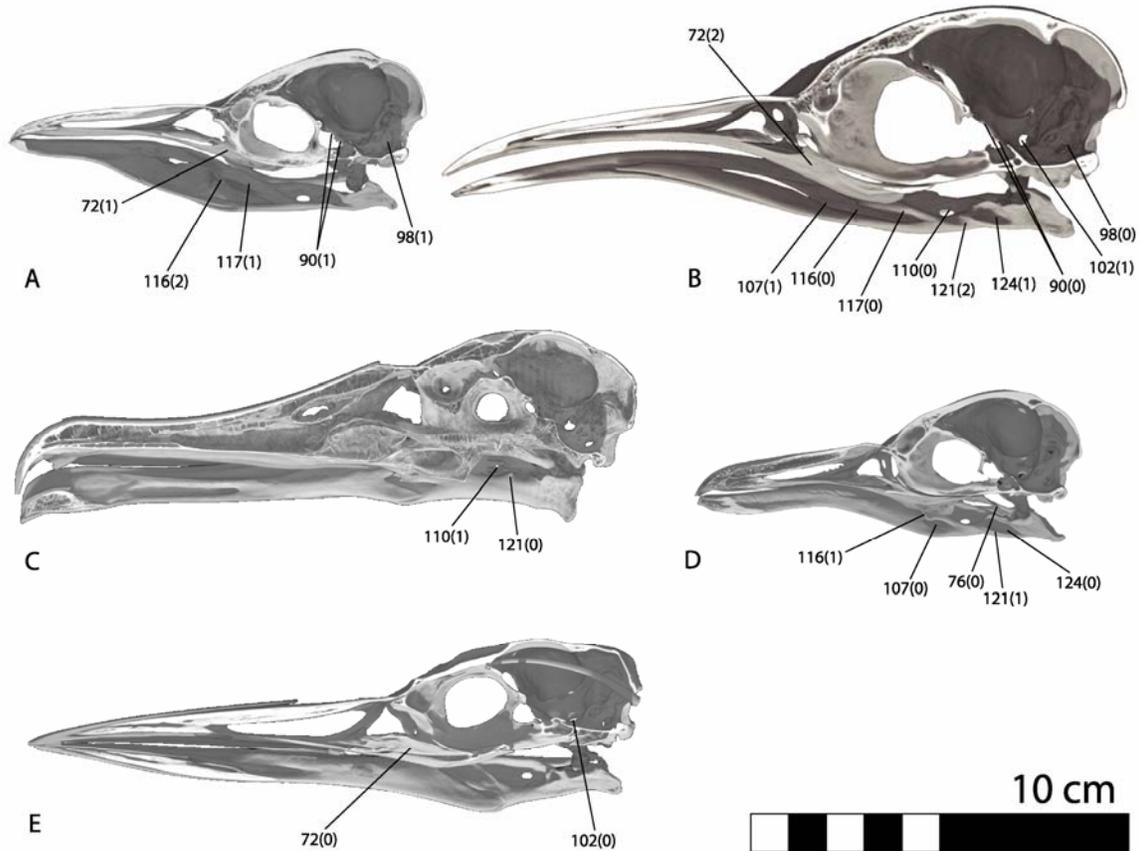
**Figure 3.10. Systematic Characters of the Skull Observed in Posterior View.** A. *Aptenodytes forsteri*. B. *Diomedea immutabilis*. C. *Spheniscus demersus*. D. *Paraptenodytes antarcticus* (AMNH 3338). E. *Eudyptula minor*. F. *Gavia immer* (TCWC 13300). Specimens as in Figure 3.8.



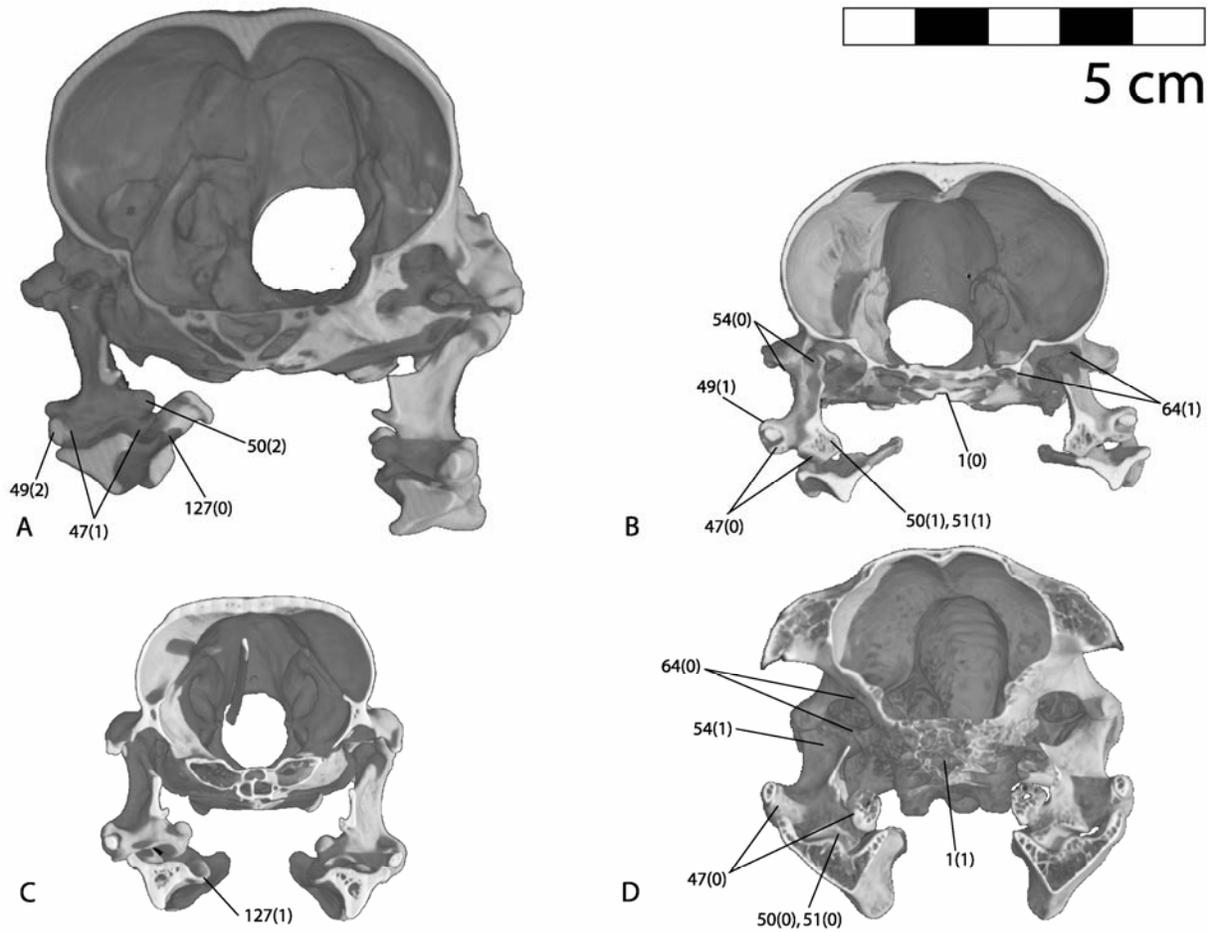
**Figure 3.11. Systematic Characters of the Skull Observed in Dorsal, Cut-away View.**  
 A. *Aptenodytes forsteri*. B. Pterygoid of *Paraptenodytes antarcticus*. C. Pterygoid of *Eudyptes pachyrhynchus* (AMNH 14824). D. *Spheniscus demersus*. E. *Diomedea immutabilis*. F. *Phalacrocorax pencillatus*. Specimens as in Figure 3.8.



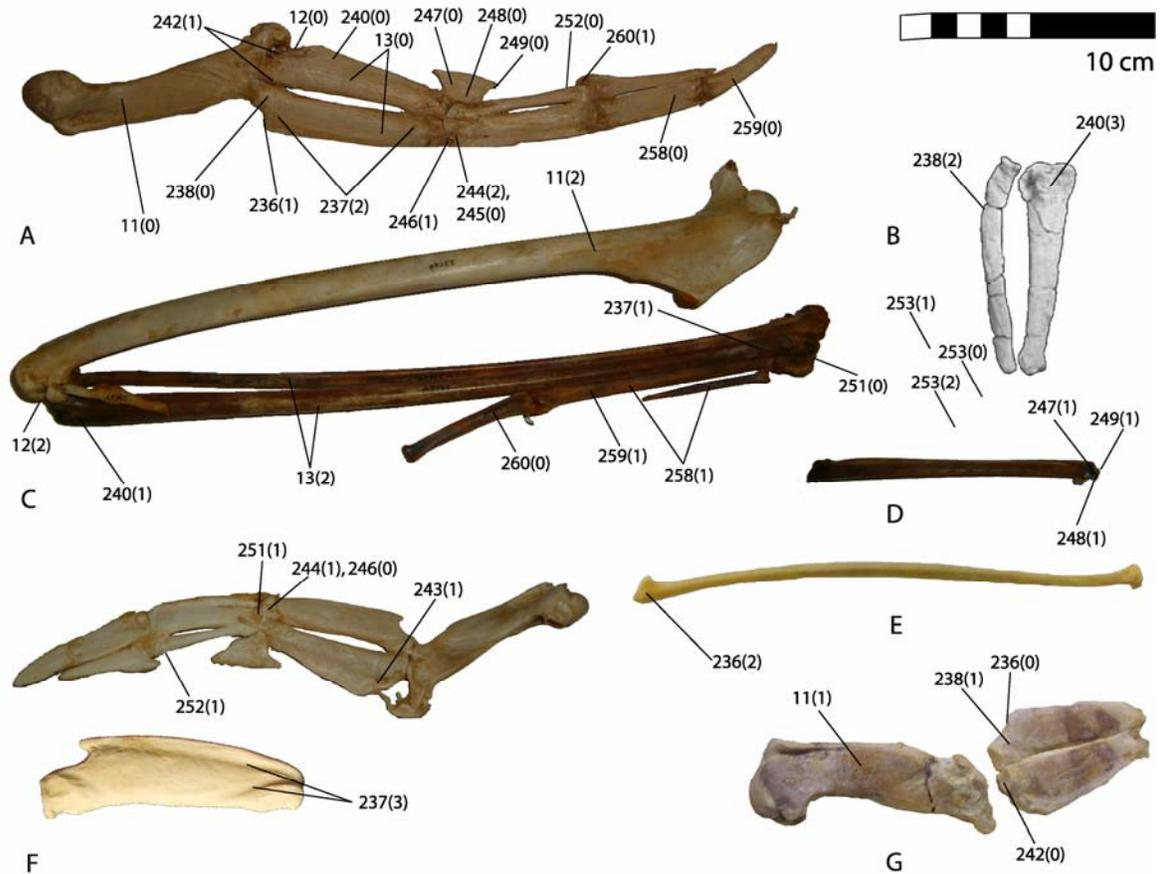
**Figure 3.12. Systematic Characters of the Skull Observed in Lateral, Cut-away View.** A. *Pygoscelis adeliae*. B. *Aptenodytes forsteri*. C. *Diomedea immutabilis*. D. *Spheniscus demersus*. E. *Gavia immer*. Specimens as in Figure 3.8.



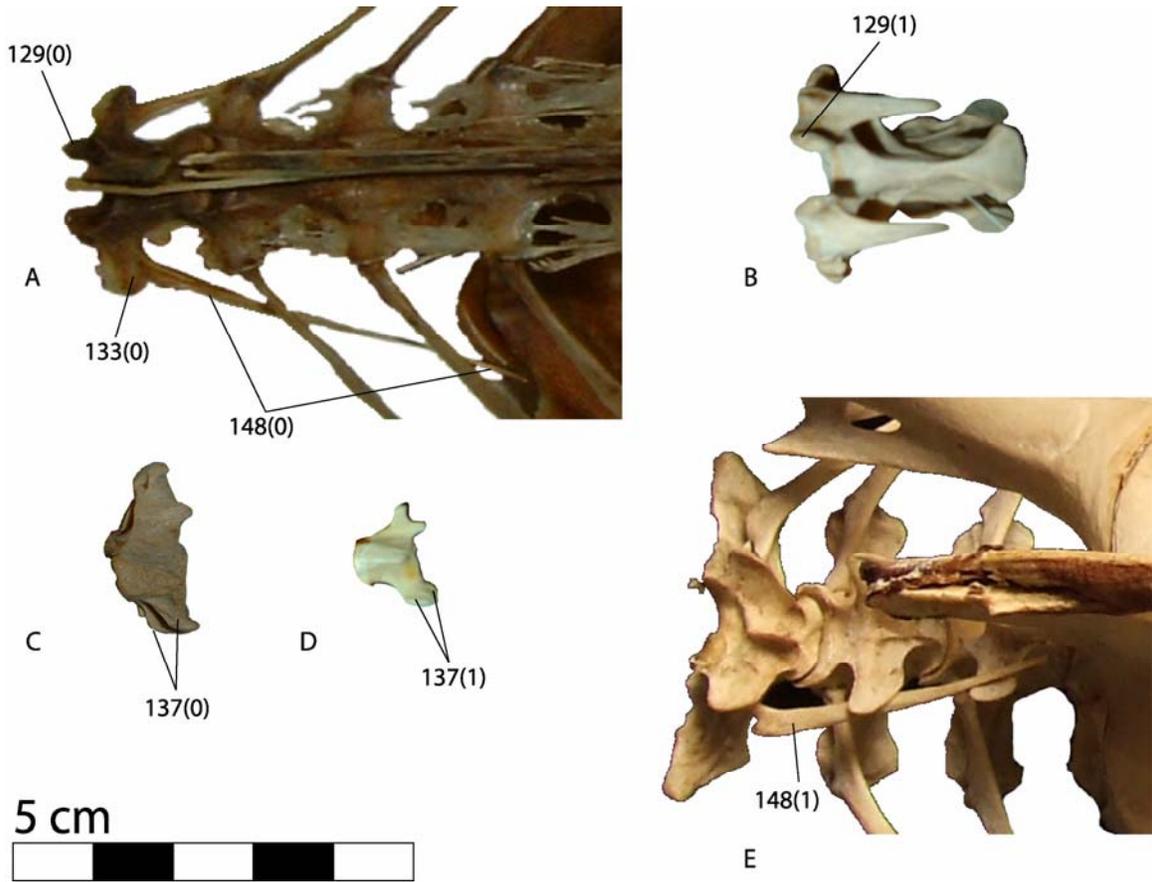
**Figure 3.13. Systematic Characters of the Skull Observed in the Anterior View of Braincase.** A. *Aptenodytes forsteri*. B. *Pygoscelis adeliae*. C. *Gavia immer*. D. *Diomedea immutabilis*. Specimens as in Figure 3.8.



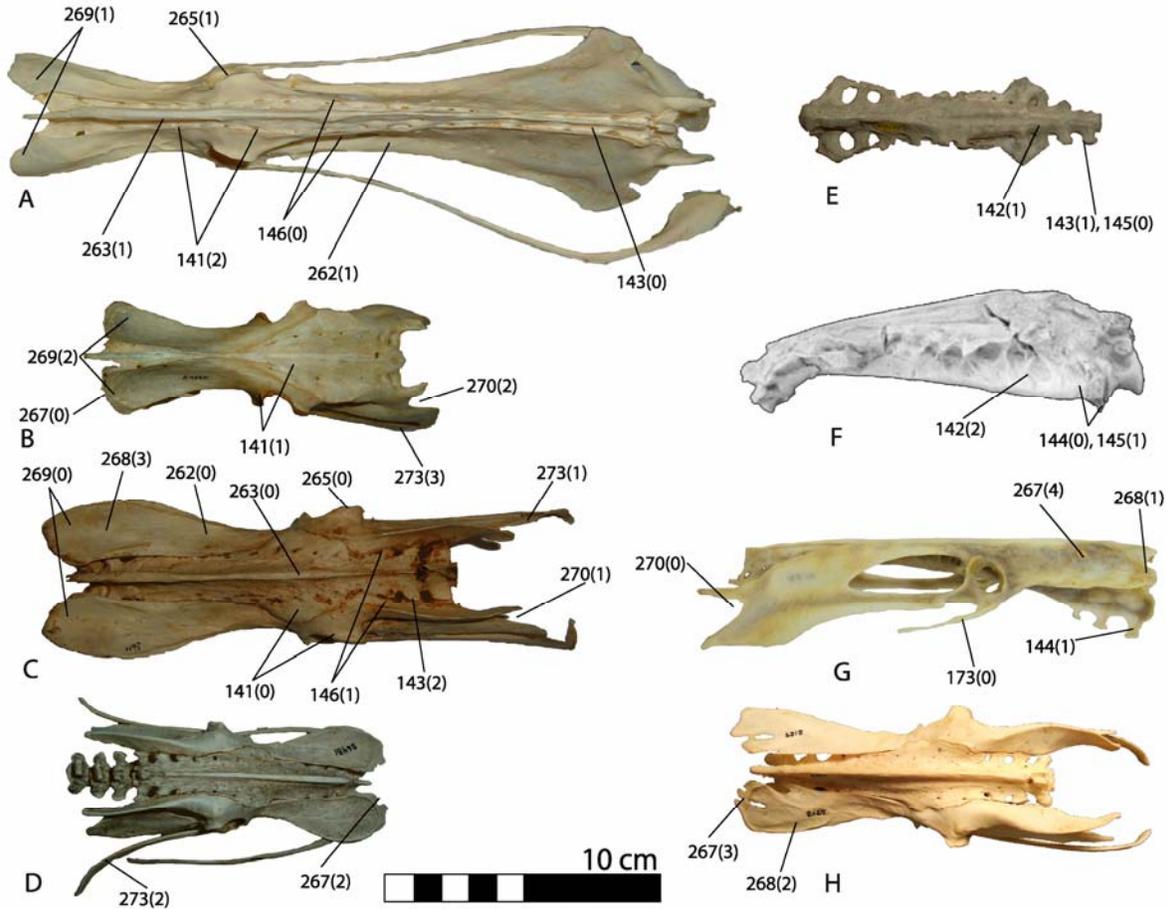
**Figure 3.14. Systematic Characters Observed in Dorsal View of the Humerus, Radius, and Ulna.** A. Left forearm of *Aptenodytes patagonicus* (AMNH 2611). B. Left radius and ulna of *Wimanu tuatahi* (OU 12651, from Slack et al., 2003). C. Right forearm of *Diomedea melamophris* (AMNH 23564). D. Left radius, ulna, radiale, and ulnare of *Aechmorphismus occidentalis* (AMNH 18782). E. Right radius of *Phalacrocorax carbo* (OM AV881). F. Right radius and left forearm of *Spheniscus humboldti* (CM 2129). G. Right forearm of *Platydyptes novaezealandiae* (DM 1451).



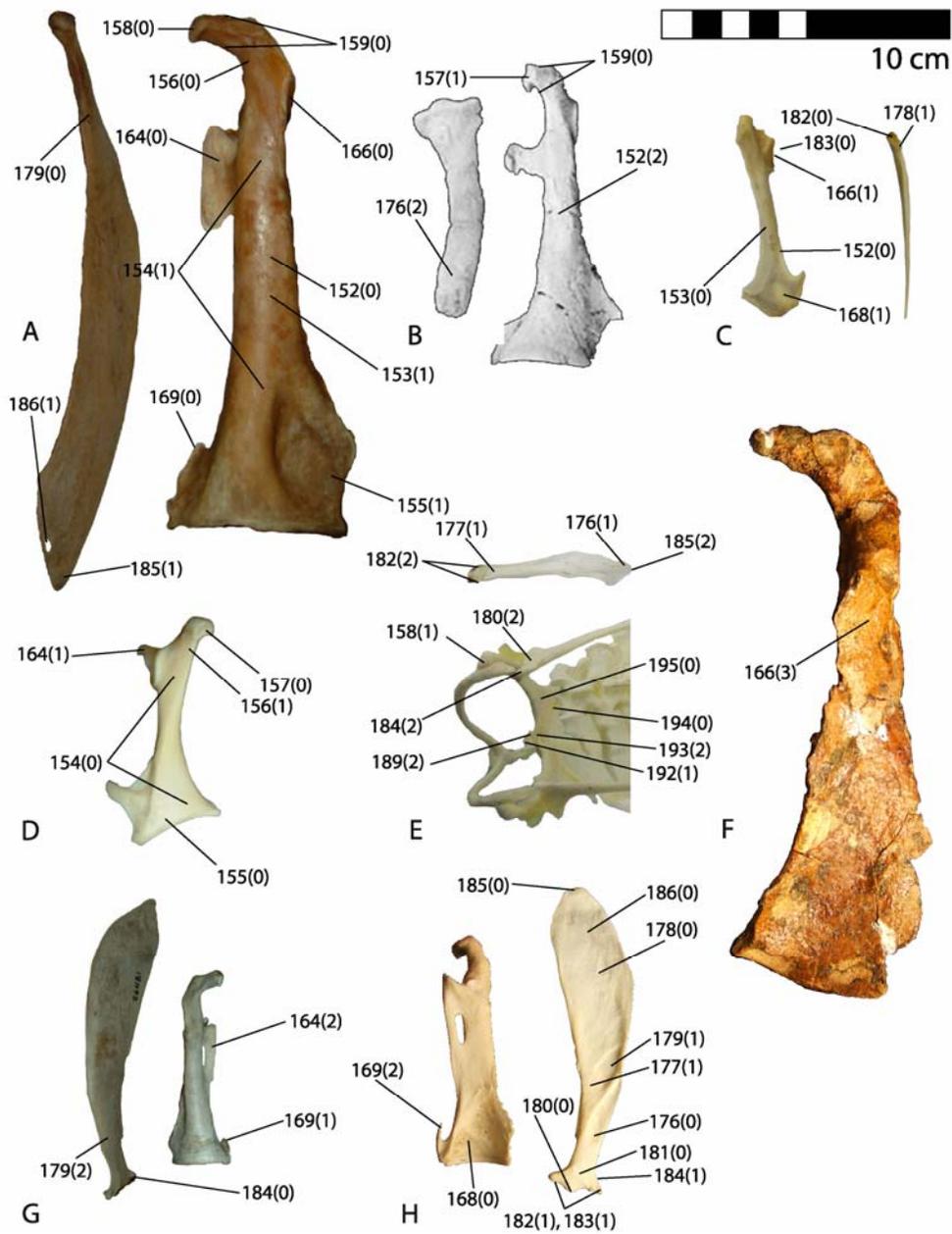
**Figure 3.15. Systematic Characters Observed in the Vertebrae.** A. Cervical of *Aechmorphismus occidentalis* (AMNH 18782). B. Cervical of *Aptenodytes patagonicus* (AMNH 1623). C. Caudal of *Aptenodytes patagonicus* (AMNH 1623). D. Caudal of *Megadyptes antipodes* (AMNH 5615). E. Cervical of *Eudyptes pachyrhynchus* (OM 309). A and E in ventral view, B in dorsal view, C-D in lateral view.



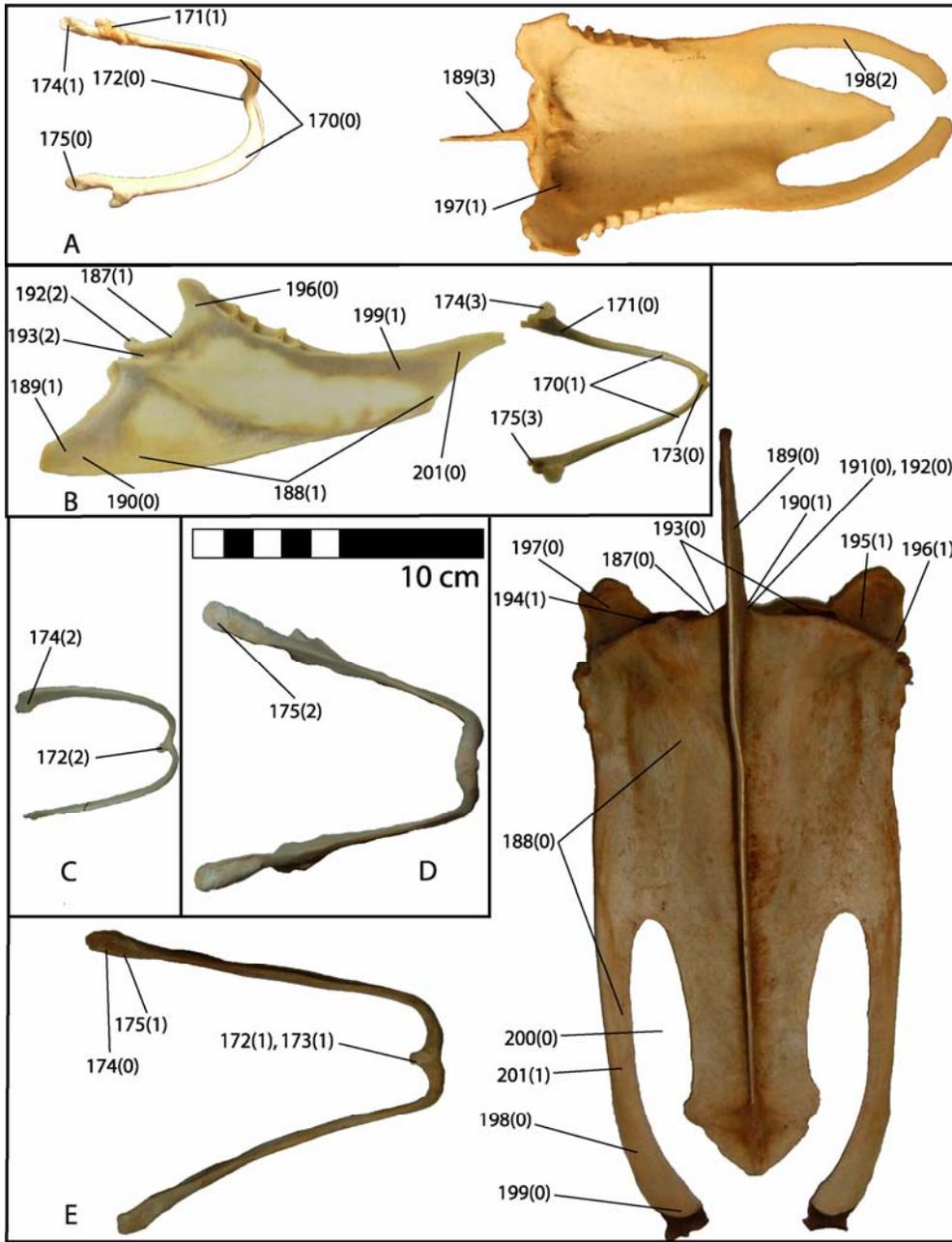
**Figure 3.16. Systematic Characters Observed in the Sacrum and Os Coxae.** A and G. Sacrum of *Gavia stellata* (AMNH 4974). B. Sacrum of *Diomedea melamophris* (AMNH 23564). C. Sacrum of *Aptenodytes patagonicus* (AMNH 1623). D. Sacrum of *Spheniscus magellanicus* (AMNH 26481). E. Sacrum of *Pygoscelis* sp. (NHM A32168). F. Sacrum of *Wimanu tuatahi* (CM zfa35). H. Sacrum of *Spheniscus humboldti* (CM2129). A-D, H in dorsal view, E in ventral view, F-G in lateral view.



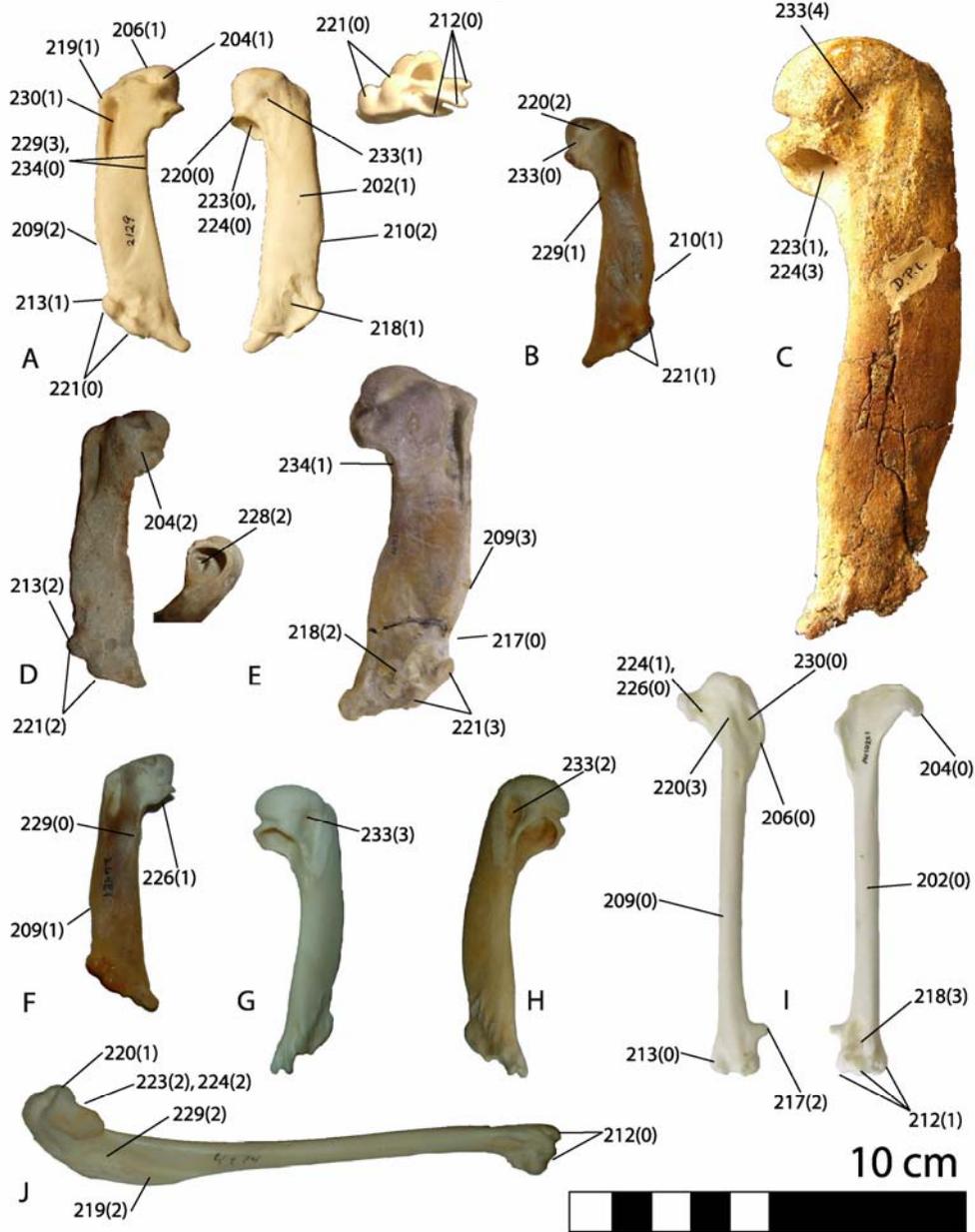
**Figure 3.17. Systematic Characters Observed in the Coracoid and Scapula.** A. *Aptenodytes patagonicus* (AMNH 27330), right elements in anterior and lateral view. B. *Wimanu tuatahi* (CM zfa35), right coracoid in anterior view, left scapula in lateral view. C. *Phalacrocorax carbo* (OM AV881), left elements in posterior view, dorsal views. D. *Gavia stellata* (AMNH 4974), right element in anterior view. E. *Diomedea bulleri* (OM AV585), anterior pectoral skeleton in dorsal view, scapula in medial view. F. OM C47.25, left element in posterior view. G. *Spheniscus magellanicus* (AMNH 26481), left coracoid in anterior view, right in medial view. H. *Spheniscus humboldti* (CM 2129), left elements in posterior and lateral view.



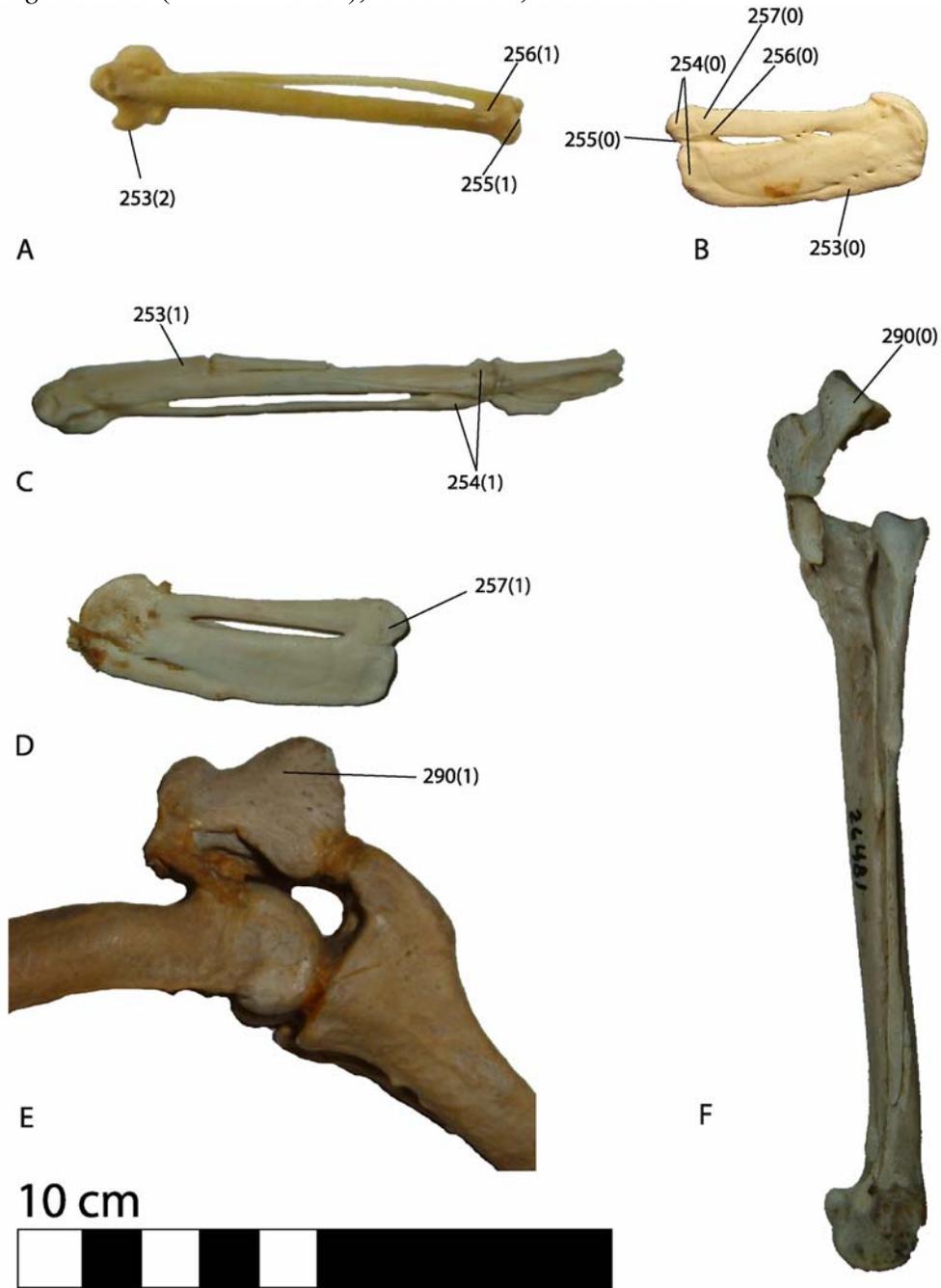
**Figure 3.18. Systematic Characters Observed in the Furcula and Sternum.** A. *Spheniscus humboldti* (CM 2129), dorsal view. B. *Phalacrocorax carbo* (OM AV881), dorsal view of furcula, lateral view of sternum. C. *Gavia stellata* (AMNH 4974), ventral view of furcula. D. *Megadyptes antipodes* (AMNH 5615), dorsal view of furcula. E. *Aptenodytes patagonicus* (AMNH 27330), ventral views.



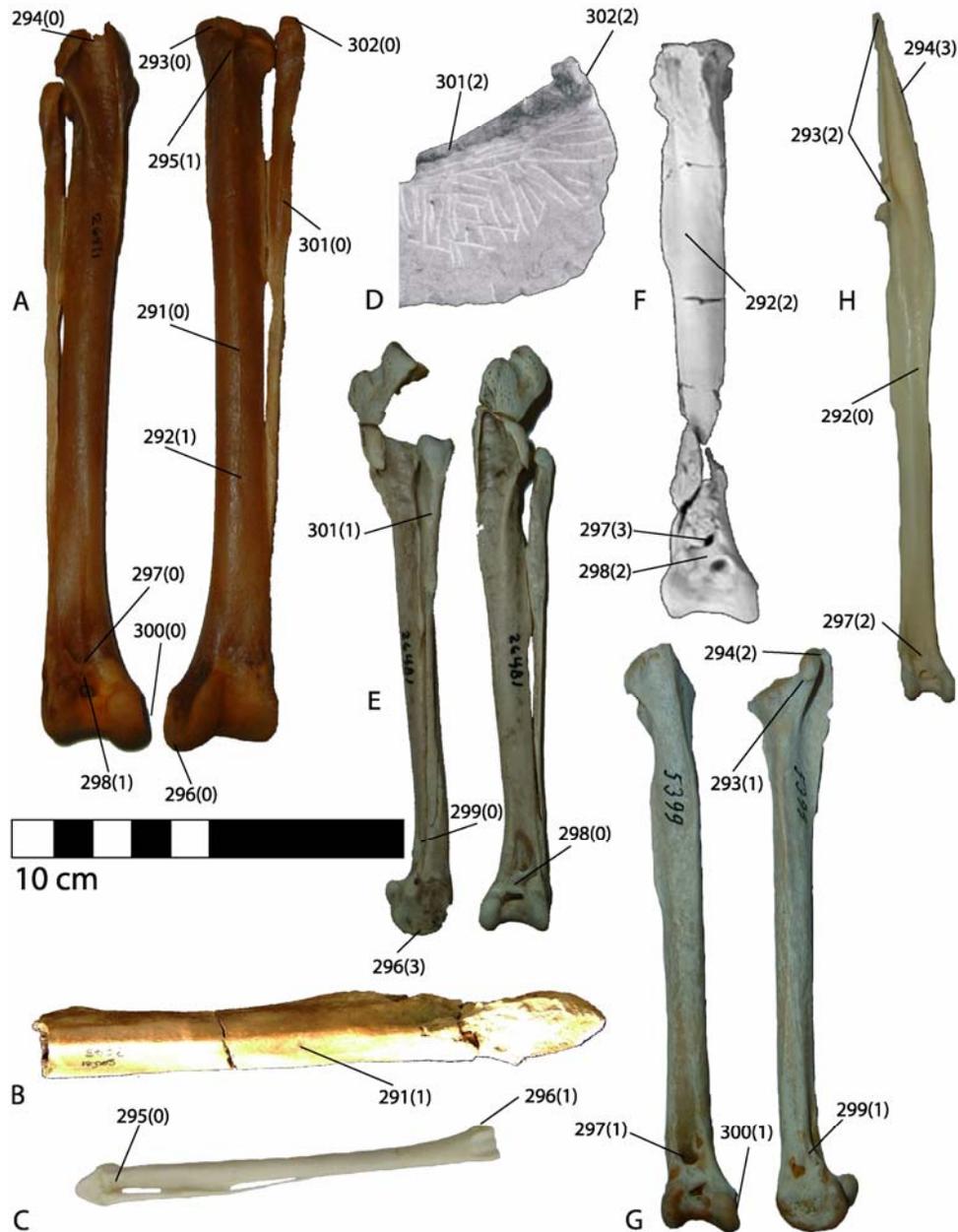
**Figure 3.19. Systematic Characters Observed in the Humerus.** A. *Spheniscus humboldti* (CM 2129), left element in lateral, medial, and distal views. B. *Eudyptes chrysolophus* (AMNH 27338), right element in lateral. C. *Archaeospheniscus lowei* (OM C47.20), left element in medial and lateral views. D. *Palaeospheniscus bergi* (NHM A590), left element in lateral view, with close-up of pneumatic fossa. E. *Platydyptes novaezealandiae* (DM1451) right element in lateral view. F. *Spheniscus magellanicus* (AMNH 26481), left element in lateral view. G. *Eudyptes pachyrhynchus* (AMNH 26508), left element in ventral view. H. *Eudyptes robustus* (AMNH 27678), right element in ventral view. I. *Diomedea bulleri* (OM AV585), right element in medial and lateral views. J. *Gavia stellata* (AMNH 4974), right element in lateral view.



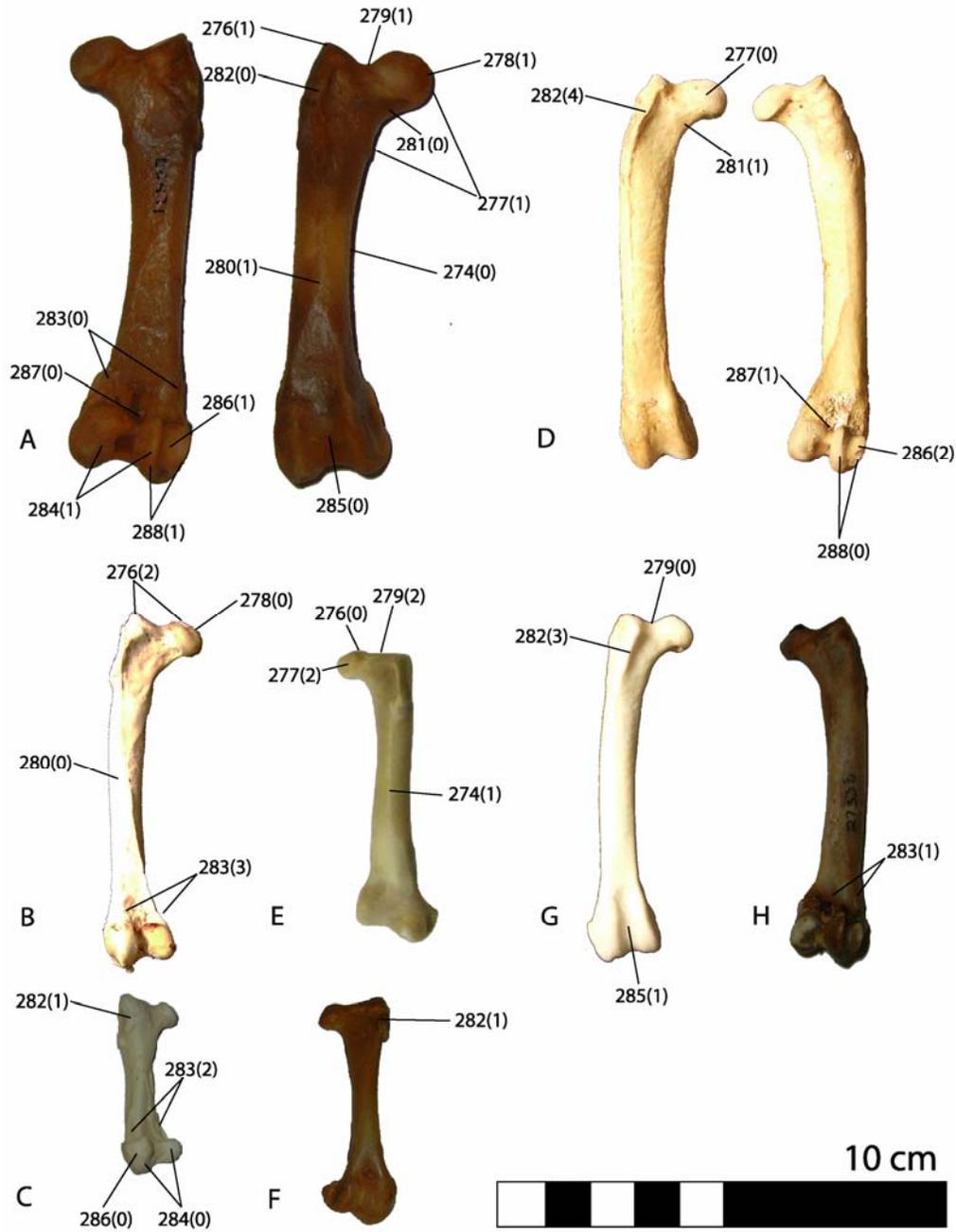
**Figure 3.20. Systematic Characters Observed in the Carpometacarpus and Patella.**  
 A. *Phalacrocorax carbo* (OM AV881), right element in lateral view. B. *Spheniscus humboldti* (CM 2129), right element in lateral view. C. *Gavia stellata* (AMNH 4974), right element in lateral view. D. *Megadyptes antipodes* (AMNH 5615), right element in lateral view. E. *Aptenodytes patagonicus* (AMNH 4383), medial view. F. *Spheniscus magellanicus* (AMNH 26481), left element, lateral view.



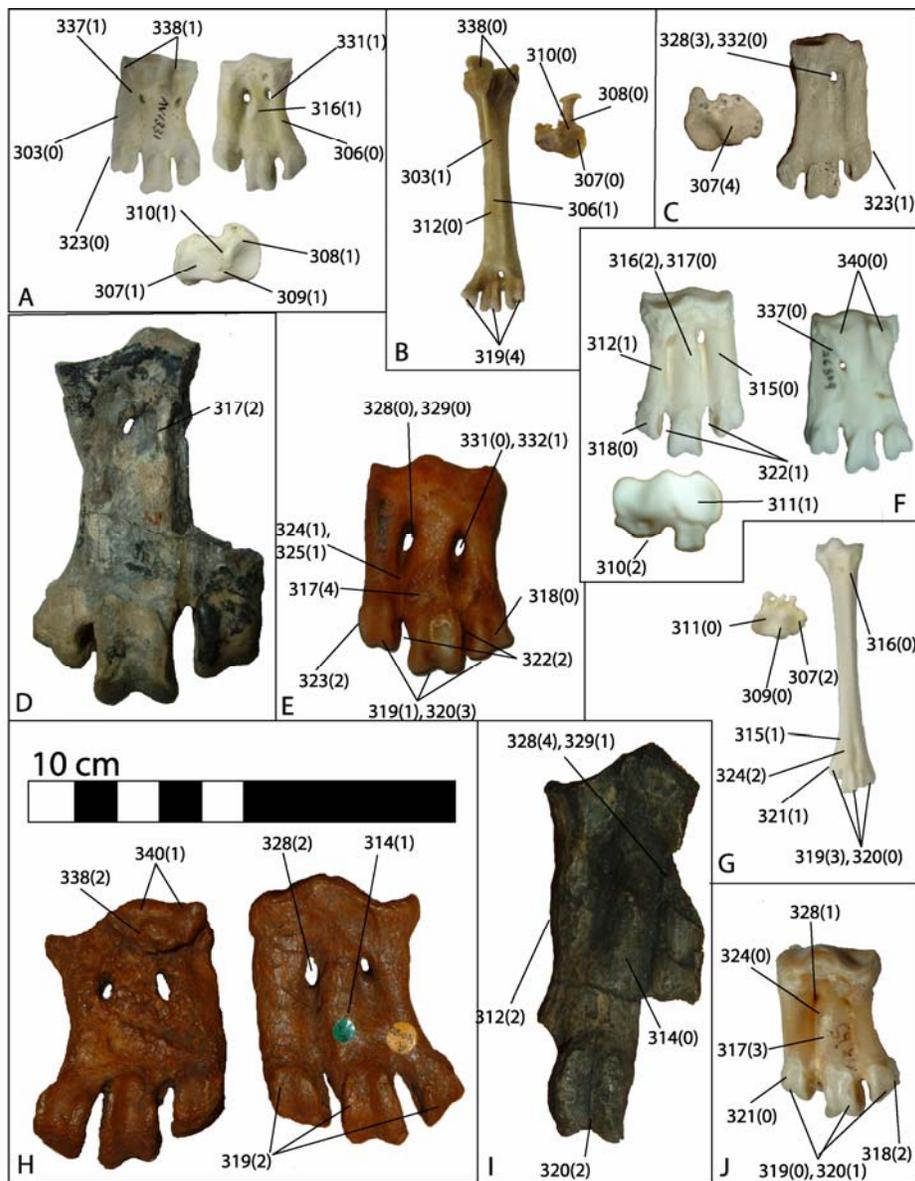
**Figure 3.21. Systematic Characters Observed in the Tibiotarsus and Fibula.** A. *Aptenodytes patagonicus* (AMNH 26471), right element, anterior and posterior views. B. *Palaeudyptes marplei* (OM C50.31 ), shaft. C. *Diomedea bulleri* (OM AV585), left element in posterior view. D. CADIC P-21, right element, lateral view (after Clarke et al., 2003). E. *Spheniscus magellanicus* (AMNH 26481), left element, lateral and anterior views. F. *Wimanu manneringi* (CM zfa35 ), right element, anterior view. G. *Eudyptes schlegeli* (AMNH 5399), right element, anterior and lateral views. H. *Gavia stellata* (AMNH 4974), right element, anterior view.



**Figure 3.22. Systematic Characters Observed in the Femur.** A. *Aptenodytes patagonicus* (26471), right element in posterior and anterior views. B. *Eudyptes pachyrhynchus* (OM 309), left element in posterior view. C. *Gavia stellata* (AMNH 4974), left element in posterior view. D. *Eudyptes sclateri* (OM 764), right element in anterior and posterior views. E. *Phalacrocorax carbo* (OM AV881), left element in anterior view. F. *Podiceps major* (AMNH 5044), left element in anterior view. G. *Spheniscus humboldti* (CM 2129), right element in anterior view. H. *Eudyptes chrysolophus* (AMNH 27338), right element in posterior view.



**Figure 3.23. Systematic Characters Observed in the Tarsometatarsus.** A. *Eudyptes sclateri* (OM AV7861), left element, ventral and proximal views; right element, dorsal view. B. *Phalacrocorax carbo* (OM AV881), right element, ventral and proximal views. C. *Palaeospheniscus bergi* (AMNH A694), left element, proximal and dorsal views. D. *Paraptenodytes antarcticus* (AMNH 3338), left element, dorsal view. E. *Aptenodytes patagonicus* (26471), right element, dorsal view. F. *Eudyptes pachyrhynchus* (OM 309), right element, dorsal, ventral, and proximal views. G. *Diomedea bulleri* (OM AV585), left element, proximal and anterior views. H. *Archaeospheniscus lopdelli* (NHM A4080), right element, ventral and dorsal views. I. *Anthropornis nordenskjoeldi* (NHM R2000), left element, dorsal view. J. *Eudyptes chrysocome* (AMNH 4972), right element, dorsal view.



## **Chapter 4: Origin, Biogeography and Evolution of Penguins (Aves: Sphenisciformes): correlation of fossils and Gondwanan history**

### **Abstract**

Penguins belong to the group Aves (birds), but their relationships within derived birds remain contentious. Recent phylogenetic analyses of penguins clarified the relationships between living and extinct species, lack of which had previously hindered further conclusions regarding penguin evolutionary history. However, the excellent fossil record of penguins suggests that such analyses would be highly productive. The record of penguins is one of the longest of any living bird, extending to the late Early Paleocene (62.4 mya), and is, at least anecdotally, nearly complete, highlighting the importance of penguins to broader analyses of avian (bird) evolution, including such topics as the current debate surrounding the pattern of radiation and extinction of birds across the K-T boundary.

I here use a recent cladistic analysis of extinct and living penguins to examine questions regarding penguin origins, biogeography, and evolutionary history. After calibrating this phylogeny with the geologic time scale, I apply various measures of completeness (e.g., the RCI, SCI, and GER) to quantify the record and to provide more confidence for further analyses. I next apply confidence intervals to the calibrated record to estimate the time in which penguins probably originated. This date probably lies within the latest Cretaceous, whereas the penguin crown-clade probably dates from the Late Eocene or Early Oligocene. This early date of origin of penguins, combined with the derived placement of these birds within Aves, suggests that the origin of a number of extant bird lineages also dates to the Cretaceous. Two major gaps do exist in the penguin fossil record, however, one in the Early Eocene and one in the Middle Miocene, and span much of the earliest history of penguins and most of the temporal range of the crown-clade.

Exploration of the biogeographic pattern of penguins, including analysis of different time slices within penguin history, shows that the group originated in New Zealand and underwent a number of vicariant and dispersal events throughout their history. The two major groups of extinct penguins, however, are West Antarctic in origin, as is the crown-clade. Additionally, the Gondwanan area relationships suggested by penguins are largely congruent with patterns of other Southern Hemisphere taxa. Finally, I correlate the penguin record with historical tectonic and climatic data. This indicates that, subsequent to their Cretaceous origin, penguins underwent a major adaptive radiation in the Late Eocene, probably related to the final separation of Gondwana and to the global cooling event associated with the opening of the Drake Passage, and subsequently declined in diversity throughout the Miocene, probably owing to a correlated warming event.

## **Introduction**

A long tradition of scientific study examines the fascinating, flightless, aquatic birds known as penguins (Aves: Sphenisciformes), but modern, evolutionary analyses of these avians (birds) appeared only recently. Notable additions to the study of penguin evolution include the first cladistic analyses of the relationships between and among living and extinct species (e.g., Bertelli and Giannini, 2005; Triche, 2005; Baker et al., 2006; Ksepka et al., 2006), anatomical descriptions of all penguin taxa (Bertelli et al., 2006; Triche, Chapter 2), reports of numerous, new extinct species (e.g., Clarke et al., 2003; Tambussi et al., 2005; Slack et al., 2006; Clarke et al., 2007), estimations of the date of origin of penguins (Triche, 2006; Baker et al., 2006; Slack et al., 2006), and preliminary, cladistic biogeographic analyses of the group (Triche, 2004; Baker et al., 2006).

The foundation for all subsequent, evolutionary examinations is a well-supported, phylogenetic hypothesis, which was recently provided for penguins (Figure 4.1a; Triche, Chapter 2). Although reconstruction of phylogeny within Sphenisciformes (or sphenisciforms) is now relatively stabilized, the higher-level relationships of penguins and other birds remain contentious. Penguins lie within a number of derived clades within Aves, including Neornithes, Neognathae, and Neoaves, but resolution beyond that level is unclear (Figure 4.1b). Nearly all work on the placement of penguins concludes that they belong to a clade of extant seabirds. It is uncertain, however, whether it is a natural relationship or the result of convergent evolution related to the constraints of an aquatic lifestyle (Livezey and Zusi, 2001; contra Livezey and Zusi, 2006, 2007). Such potential

convergence may occur in both morphological and molecular datasets and affect the placement of all seabirds within Neoaves.

Proposed penguin sister-taxa based on both types of data include part or all of the tubenoses (albatrosses and petrels, or Procellariiformes; Simpson, 1946; Sibley and Ahlquist, 1990; McKittrick, 1991; Cooper & Penny, 1997; Van Tuinen et al., 2001; Livezey and Zusi, 2001, 2006, 2007), loons (Gaviidae; Ho et al., 1976; Olson, 1985b), loons plus grebes (Podicipedidae; Cracraft, 1982, 1988; Sibley and Ahlquist, 1990; Mayr and Clarke, 2003), and loons plus grebes plus flamingos (Phoenicopteridae; Mayr, 2004). Two unexpected suggestions are the extant Ciconiidae (storks; Slack et al., 2003) and the extinct Plotopteridae (Mayr, 2005). The first hypothesis examined avian phylogeny in general, not penguin relationships specifically, and hence included no other seabirds or any previously hypothesized, penguin sister taxon. Subsequent work built on that dataset fails to place storks anywhere near penguins, which group, as usual, in the midst of a clade of seabirds (Slack et al., 2006). The second unique suggestion involves plotopterids, which are a group of Tertiary, flightless seabirds that, like penguins, swam using wing-propelled diving (Mayr, 2005). That study used literature that illustrates only portions of the relevant, plotopterid anatomy and does not present sufficient detail for use in character coding (e.g., Olson and Hasegawa, 1979), and failed to include any extinct penguins, hence almost certainly excluding any basal sphenisciform character states that might or might not indicate relationship with plotopterids. The work recovered weak support for a Plotopteridae-Sphenisciformes clade, amid a large number of convergent and plesiomorphic characters. The morphology of plotopterids and penguins is otherwise

generally agreed to be convergent, coinciding with the fact that pterodactyls are known only from the Northern Pacific (Olson and Hasegawa, 1979).

The variety of conclusions about sphenisciform phylogeny probably stems from a variety of sampling problems, including: small numbers of systematic characters, inadequate sampling of different character types (e.g., osteological, behavioral, or molecular datasets), lack of a broad outgroup sample or assumption of an untested outgroup, and light sampling within the ingroup, especially among extinct taxa. The placement of penguins was also only examined in the context of broader analyses not specifically focused on the penguin problem. Consensus on the relationships of penguins probably thus includes a true relationship with other seabirds, but not with storks or pterodactyls.

Work on phylogeny within penguins (Spheniscidae or spheniscids) underwent a renaissance in recent years, with numerous cladistic analyses appearing recently, but problems remain, especially in regards to extinct species, or Sphenisciformes (sphenisciforms). The six extant genera of penguins are almost certainly all monophyletic, as is Spheniscidae, but various authors recently proposed phylogenies that incorporate every possible relationship between them (e.g., Simpson, 1946; O'Hara, 1989; Bertelli and Giannini, 2005; Baker et al., 2006; Walsh and Suarez, 2006; Triche, Chapter 3). Agreement among much of that work supports the sister taxon relationship of a crested penguin clade (*Eudyptes* + *Megadyptes*) and a *Spheniscus-Eudyptula* clade. More research, however, is required to explain the relationships of the two Antarctic

genera, *Aptenodytes* and *Pygoscelis*, as well as the conflicting morphological and molecular of penguin relationships.

While work on living species is well advanced, most analyses of extinct species are either pre-cladistic or address extinct penguins only in the context of extant species phylogeny. Historically, phylogenies of extinct penguins were informal and consisted of short assessments of the degree of similarity between various faunas. Simpson, for example, proposed an evolutionary phylogeny of extinct species that included a number of separate, and highly specialized, extinct lineages, none of which were directly ancestral to modern species (Simpson, 1946). Within extinct penguin lineages, he found the most similarity between a New Zealand group and a fauna from Seymour Island, Antarctica, which were both distinct from the large group of species known from Patagonia. Other work analyzing crown-clade penguins supports its monophyly (Zusi, 1975) and its possible origination in the Eocene of Seymour Island (Baker et al., 2006; Triche, 2006), which in turn points to small extinct taxa such as *Delphinornis* as the ancestors of modern penguins (Jadwiszczak, 2006).

The first cladistic analyses to include extinct penguins examined the placement of single species by integrating them into previous analyses of extant taxa, generally using few additional characters (Slack et al., 2006; Walsh and Suarez, 2006; Bertelli et al., 2006). These include work on the oldest known penguin, *Wimanu*, which is the unambiguous sister taxon to all other Sphenisciformes (Slack et al., 2006), as well as analyses of *Paraptenodytes antarcticus*, an extremely complete and well-known taxon from Argentina (Bertelli et al., 2006). Other work examined a recently discovered

species, *Pygoscelis grandis*, which lies within a monophyletic *Pygoscelis* (Walsh and Suarez, 2006), and both a morphometric and a cladistic analysis of three extinct, South American taxa (Acosta Hospitaleche, 2004; Acosta Hospitaleche et al., 2007). Only three analyses exist that include numerous extinct penguin taxa, which represent a great advance in phylogenetic knowledge. The first (Ksepka et al., 2006) examined 20 extinct penguins species using a molecular and morphological matrix that is nearly identical to that of previous work on extant species (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Bertelli et al., 2006). The second built on that dataset to analyze the relationships of two newly discovered, extinct, Peruvian species and recovered a nearly identical phylogeny (Clarke et al., 2007). The third, which is used here as the basis for biogeographic and other analyses, examined 51 extinct taxa and numerous outgroups using a large, independent matrix (Triche, Chapter 3). The relationships recovered by these works are congruent in broad outline, including the placement of *Wimanu*, the relationships of extinct species belonging to extant genera, and the monophyly of the crown-group, but the relationships of most older, extinct taxa differ, as does the topology of various extinct clades.

### **Origination Hypotheses**

Numerous authors speculated on the evolutionary origins of penguins, contemplating the probable date, place, and method by which penguins evolved from their seabird ancestors. The debate over the timing of origin of modern birds, or Neornithes, is currently intense and unresolved, with much molecular and some fossil and biogeographic evidence pointing to a Cretaceous origin and initial radiation of modern

birds and the survival of numerous modern lineages across the K/T boundary (Cooper and Penny, 1997; Hope, 2002; Dyke and van Tuinen, 2004; Cracraft, 2000). Much fossil evidence, however, may support a Late Cretaceous origin and a much later, Tertiary radiation of modern birds, with few or perhaps only one modern lineage surviving the K/T extinction (e.g., Feduccia, 2005). The conflict is in some ways more apparent than real, however, because different authors assume different definitions of Neornithes, either stem- or crown-clade based, when discussing the problem (Brochu and Norell, 2001; van Tuinen et al., 2006). The stem-clade Neornithes may well date to the Cretaceous and this period may contain numerous stem-lineages indicative of the modern bird radiation (e.g., stem-penguins), but most crown-group neornithines (e.g., crown-penguins) probably evolved only later, in the Tertiary (Mayr, 2005b; James, 2005). The origination of penguins pertains to the debate by indicating their divergence time from other modern birds and potentially including a Cretaceous representative, as stem-taxa older than the Early Paleocene *Wimantu* remain to be found. If penguins are Cretaceous or even earliest Paleocene in age, their derived phylogenetic placement within Neornithes would constrain the divergence dates of the group to at least the Late Cretaceous (Triche, 2006).

Molecular clock modeling from modern taxa already places the origin of Sphenisciformes in the Late Cretaceous (71 mya) and the origin of the crown-group as early as the Late Eocene (40 mya; Baker et al., 2006). Alternatively, it may be the clade containing all shore- and seabirds that date to the Late Cretaceous, implying that penguins and other included groups originated after the Cretaceous-Tertiary extinction (van Tuinen et al., 2006). The latter study appeared before data about the Paleocene

penguin *Wimanu* was available, however, and therefore probably underestimates the age of that seabird clade (Triche, 2006). The authors also hypothesize that numerous extant aquatic lineages, including penguins, are much younger than other neornithines, possibly owing to slower genetic rates or differential extinction pressures in aquatic environments. However, these dates refer to the appearance of crown-groups, not stem-groups, and ignore the fact that functionally modern, swimming penguins were already present at least in the Eocene (Simpson, 1971). The discrepancy is that the main diversification and radiation of penguins did not occur concurrent with the origination of the crown-group, but much earlier. Numerous problems associated with assuming a molecular clock and the large margins of error reported with these dates also require that they be regarded with caution. Factoring in the age of the oldest known penguin, *Wimanu*, suggests that Neornithes originated at least 90-100 mya, in the Late Cretaceous, and that modern seabirds, including penguins, diverged from other shorebirds by 74 mya, in the Campanian (Slack et al., 2006). Recent analysis of mitogenomic data also upholds this date, placing the date that penguins split from other neoavians at least in the late Cretaceous (Pereira and Baker, 2006). If various sources of data derived from penguins are correct, the Cretaceous origin and presence through the K/T boundary of at least that one lineage of extant neornithines is supported.

### **Biogeographic Hypotheses**

A number of biogeographic observations and hypotheses exist to explain the current and historical distribution of penguins. These birds have probably always been restricted to the southern hemisphere, as they are today, although there is no agreed cause

for the limitation (Cracraft, 1973). Penguins currently range north to central Africa and the equatorial Galapagos Islands, and include three *Spheniscus* species that breed in the tropics (Davis and Darby, 1990). At the other extreme, one of the smallest extant penguins, the 37 cm Adelie (*Pygoscelis adeliae*), lives and breeds solely on Antarctic ice sheets. Also remaining unexplained is the fact that the only other extant Antarctic species is the Emperor (*Aptenodytes forsteri*), which is the largest living penguin species at over a meter in standing height (Stonehouse, 1969). Today, penguins inhabit every Gondwanan continent except India, including breeding populations in Peru, Chile, Argentina, South Africa, New Zealand, Australia, the coasts and offshore islands of Antarctica, and most of the sub-Antarctic islands of the Southern Ocean. Extinct penguins lie entirely within the range and biogeographic provinces of extant species, although some slight differences, such as the former compared with the current ranges of extant genera, do exist.

Although biogeographical analysis, especially in paleobiogeographical contexts, was traditionally descriptive and narrative in nature, analytical, cladistic biogeographic methods are now well established (Erwin, 1981; Nelson and Platnick, 1981; Page, 1988; Morrone and Crisci, 1995; Ronquist, 1997; Lieberman, 2000; Brooks, 2001). Few methods, however, are able to consider vicariance, dispersal, and any sort of time component simultaneously (but see Lieberman, 2003; Upchurch et al., 2002). It is particularly important when considering penguin biogeography because the causal mechanisms underlying sphenisciform patterns probably involve both vicariance and dispersal and certainly include a long geologic history ranging through at least the entire

Cenozoic. Penguins are extremely widespread in distribution and highly vagile in lifestyle. Most regularly migrate thousands of kilometers and some species are distributed throughout the entire Southern Ocean (e.g., the Macaroni Penguin, *Eudyptes chrysolophus*; Davis and Renner, 2003). However, their Gondwanan distribution and extensive fossil record, which extends at least to the Early Paleocene, suggests that the final stages of breakup of Gondwana and subsequent tectonic evolution in the southern hemisphere, such as the emergence of the large, shallow seas that penguins favor, must have affected the distributional patterns of penguins. Many authors noted the pervasive influence of Gondwanan breakup on other southern hemisphere organisms, including *Nothofagus* trees, ratite birds, and marsupial mammals (e.g., Cracraft, 1973; Fordyce and Jones, 1990; Sanmartin and Ronquist, 2004).

Some preliminary work on the subject involved mapping penguin biogeographic distributions onto phylogeny (e.g., Triche, 2004; Bertelli and Giannini, 2005; Clarke et al., 2007). These analyses suggest that either the Australia-New Zealand-Antarctic Peninsula (Bertelli and Giannini, 2005); the 'core of Gondwana', presumably Antarctica (Baker et al., 2006); or Australia-New Zealand (Ksepka et al., 2006) constituted the penguin ancestral area. It is also suggested that penguins invaded the tropical low latitudes at least three times, based in part on Eocene Peruvian penguins (Clarke et al., 2007). The former also inferred a major, early, vicariant split between the living, Antarctic genera and remaining, extant species, followed by numerous, subsequent speciations and dispersal events (Bertelli and Giannini, 2005). The broadness of these hypotheses of ancestral area are probably owing to the use of extant phylogenies and lack

of fossil constraints. Such a drawback also impacts statements concerning vicariance, as extant species are much too young to have been affected by Gondwanan breakup, while extinct species are certainly old enough to have been. Because crown-penguins are monophyletic and highly nested within Sphenisciformes, however, any analysis using only extant species will reconstruct the place of origin of the crown-group, Spheniscidae, not of penguins as a whole.

### **Evolutionary Hypotheses**

As an alternative to or, more appropriately, in conjunction with the effect of tectonics, it is also hypothesized that climate change had a vital effect on the evolution of penguins. For example, extinct species are often found in much warmer environments than extant taxa (e.g., Lowe, 1933; Stonehouse, 1969). The discovery of a Paleocene penguin from Seymour Island highlights that conclusion because the reconstructed Antarctic Paleocene environment included temperate to sub-tropical forests (Feldman and Woodburne, 1988; Francis et al., 2006). That suggests that penguins originated in a much warmer climate and evolved their impressive, cold-adapted physiologies later in their history. It is also suggested that penguins always preferred a temperate climate, and only dispersed from their Antarctic center of origin when the continent glaciated in the Oligocene (Baker et al., 2006) or, alternatively, that penguins were not necessarily tied to cold climates because they had already expanded into very low latitudes by the Eocene (Clarke et al., 2007). Fordyce and Jones (1990) listed major climatic and ecologic events occurring throughout the history of penguins and correlated, for example, the K/T extinction of marine reptiles with the radiation of penguins and other marine vertebrates,

and the Oligocene climatic optimum with an increased abundance of penguins. The decrease in abundance, size, and degree of specialization of extinct species in the Miocene may be related either to concomitant climatic cooling or to competition with or predation by the newly radiating pinnipeds and cetaceans (Stonehouse, 1969; Simpson, 1975; Fordyce and Jones, 1990). Taxon pulses resulting from periodically adverse climatic conditions could also explain the rapid, early expansion of penguins in Seymour Island (Jadwiszczak, 2003).

Similar work examining the effects of climate on extant and Holocene penguins from Antarctica produced conflicting results. Most known Holocene rookeries seem to be abandoned in colder intervals, the Little Ice Age for example, probably owing to lack of sufficient food or an unfavorably large extent of sea-ice (Emslie, 1995; Emslie and McDaniel, 2002; Emslie et al., 2007). However, recent work shows that extant Adelie Penguins expand their distributions as a result of decreasing temperatures and increased continental shelf ice, their preferred breeding location, while extant Chinstrap Penguin populations expand with increasing temperature and are adversely affected when temperatures fall because their preferred habitat is floating sea ice (Trivelpiece et al., 1990; Fraser et al., 1992; Ritchie et al., 2004). All work taken together suggests that correlation of penguin extinctions with climate change may not be so straightforward and points to the difficulty inherent in inferring causation or even basic patterns of penguin evolution, especially when precise data regarding paleoclimate, ice presence and abundance, and ocean productivity remains lacking.

## **Current Investigation**

The present work integrates data from the penguin fossil record and current ideas about penguin phylogeny with information about penguin distributions and climatic and tectonic history in an attempt to explain penguin evolutionary history. I will first examine the completeness of the penguin fossil record in order to determine the level of confidence placed in subsequent analyses. Authors generally assume that the extensive fossil record of penguins is nearly complete, especially considering that penguins are birds. It is certainly the longest and most widespread of any Gondwanan bird, among the longest of all extant neognaths, and possible the longest among Neoaves (e.g., Vickers-Rich, 1976). The contention of high completeness is not tested, however, and should be quantified before using the fossil record as a basis for further analyses.

To examine the quality of the record, and to perform further analyses such as dating the time of origin of penguins and subsequent biogeographic and evolutionary events, penguin phylogeny must be calibrated with the geologic time scale. The method, which was used in paleontology informally for decades as a way of estimating ghost ranges (Norell, 1992), was recently termed ‘minimum age node dating’ (Crepet et al., 2004; Zaragüeta et al., 2004) and utilizes the fact that time may serve as a hierarchical attribute of phylogenies. Temporal data can thus be optimized onto cladograms by dating each node to the age of its oldest daughter taxon, to result in a minimum age by which that node must have diverged. Rather than stratocladistic approaches, which use non-biological criteria to analyze phylogeny, calibrating a previously proposed phylogeny to geologic time still allows introduction of a temporal element to evolutionary studies but

does so *a posteriori* (Hermson and Hendricks, 2006). Once calibrated, phylogeny can yield various measures of the quality of the fossil record. Subsequently, I will apply confidence intervals to penguin history to estimate the time of origin of the group. Neither calibrated phylogenies nor confidence intervals are yet applied to penguins and will provide two independent, fossil-based estimates for comparison with previous, molecular hypotheses of a Cretaceous origination time and an Eocene origin of crown-penguins (Baker et al., 2006; Slack et al., 2006).

I will next examine the historical biogeography of penguins to determine where they originated, whether dispersal, vicariance, or both processes are predominant in the history of the group, and how these patterns change with the addition of time constraints. Penguins constitute an ideal taxon for analysis of southern hemisphere, biogeographic patterns and should provide a robust signal that will be useful in further analyses of the contribution of dispersal and vicariance to southern hemisphere biogeography, as well as in the area relationships of southern continents (e.g., Sanmartin and Ronquist, 2004). Finally, I will synthesize the record of origination, radiation, and extinction in penguin history with tectonic and climatic data from the southern hemisphere Cenozoic to determine whether these two histories are in fact correlated. The temporal length and geographic breadth of the penguin record should allow robust testing of the potential, causal links between these geological and biological processes.

## **Material and Methods**

All analyses performed here use the phylogeny in Figure 4.2 as a basis for investigation. This phylogeny presents the relationships of all seventeen extant penguin

species (Figure 4.2b, those in red), and one sub-species of Little Penguin (*Eudyptula minor*), which is coded as a terminal taxon owing to suggestions that the White-Flipped Penguin (*Eudyptula minor albosignata*) may comprise a separate species. Additionally, the majority of extinct penguin taxa are analyzed, comprising 48 of 57 currently named taxa (Appendix 4.1; Figure 4.2a). Eight, named species were excluded because of extremely poor preservation resulting in dubious taxonomic validity. While it was not possible to include most reports of as-yet unnamed extinct penguins, three unnamed, but specifically distinct species were included in the phylogeny: CADIC P-21, or the Tierra del Fuego penguin (Clarke et al., 2003), and OM C47.23A and OM C47.25, a new, ‘palaeudyptid’ taxon from New Zealand. Finally, the new taxa *Icadyptes*, *Madrynornis*, *Perudyptes*, and *Tonniornis* were not included because these publications just postdated the completion of the current analysis (Tambussi et al., 2006). Penguin outgroups used to polarize phylogenetic, biogeographic and other analyses include Gaviidae, Phalacrocoracidae, Procellariiformes, and Podicipedidae. Although procellariiforms are most likely the sister-taxon of penguins, results from the phylogenetic analysis used here suggest that that question deserves further research. Therefore, numerous proposed outgroups of penguins are included in an attempt to incorporate the true sister-taxon of penguins, as well as other closely related groups.

A matrix of 503 osteological, myological, integumentary, and behavioral characters served as the basis for this phylogeny and resulted in one most parsimonious reconstruction with a completely resolved topology (Figure 4.2). Detailed discussion of this phylogenetic analysis will be published elsewhere shortly (Triche, Chapter 3), but

large clades discussed below are briefly reviewed here. Nomenclature associated with penguins was recently formalized (Triche, Chapter 3) and includes the terms Panspheniscidae (the total group of penguins), Sphenisciformes (*Wimanu* + Spheniscidae), and Spheniscidae (crown-penguins, or the extant clade). Fossil taxa form two completely extinct clades, Palaeudyptidae and Paraptenodytidae, that lie outside the monophyletic crown-group. Spheniscidae contains only extinct species that are congeneric with Recent taxa or probably should be revised as such e.g., the South African species that are probably conspecific with living *Spheniscus* penguins. Within living penguins, the northerly *Spheniscus* genus evolved first, followed by the Little Penguin, then the two genera of crested penguins, *Eudyptes* and *Megadyptes*, and finally the derived clade Australodyptinae, which includes the two, living, Antarctic genera, *Aptenodytes* and *Pygoscelis*.

## **Methods**

**Completeness.** The first analysis performed here examines the completeness of the penguin fossil record using three measures of the goodness of fit of penguin phylogeny with the stratigraphic occurrence of these fossils. To apply these measures, penguin phylogeny is calibrated with the geologic time scale (Figure 4.3; Gradstein et al., 2004). Problems exist regarding the dating of various penguin fossils, usually owing either to certain calibrations of local geologic time scales (e.g., South American Land Mammal Ages) or to imprecise or relative reporting of these dates (e.g., Late Eocene, as opposed to 42 mya). Therefore, dates for calibration were taken as millions of years where available and approximated as the median date of a geologic stage when not.

The first measure calculated is the RCI (Relative Completeness Index), which measures the amount of incomplete stratigraphy present in the record of a taxon (Appendix 4.2; Benton and Storrs, 1994). The method compares the amount of ghost lineage in a phylogeny with the time range actually represented by a lineage, and results range from 100%, indicating a perfectly complete record, to negative values, indicating the presence of more gap than record. Because it measures taxon ranges, the RCI is biased by a point-estimate problem (Siddall, 1998; Wills, 1999). For example, nearly all penguin species are known from a single datum, not ranges, and penguin genera are usually not monophyletic, providing no available higher taxon that might be analyzed in place of species. While this may allow accurate measures of ghost ranges, it also results in vastly artificially reduced ranges for most taxa and great inflation of resulting RCI values. The measure is also biased by tree topology and thus non-comparable among taxa (Siddall, 1998; Wills, 1999).

The second measure utilized is the SCI (Stratigraphical Consistency Index), which is somewhat more sophisticated than the RCI in that it measures both incomplete stratigraphy and incorrect phylogeny (Appendix 4.2; Huelsenbeck, 1994). The SCI is calculated by comparing the number of 'stratigraphically consistent nodes' in a phylogeny with the number that are not. In other words, those bifurcations whose descendant taxa appear later in the rock record than do their sister taxa are consistent with stratigraphy. The resulting measure ranges from 0 to 1, or from a phylogeny that is completely incongruent with stratigraphy to one that matches perfectly. The SCI therefore adds the dimension of cladogram topology and eliminates the point estimate

problem of the RCI. However, the measure remains non-comparable among taxa and biased by the size of the phylogeny of interest (Siddall, 1998; Wills, 1999).

The last measure implemented here is the GER (Gap Excess Ratio), which builds on previous methods to account for the effect of differential tree topologies on missing stratigraphy (Appendix 4.2; Wills, 1999). By measuring the proportion of ghost lineages that are necessitated by the cladogram topology, the GER determines how much of the gap in the record is present because of incomplete stratigraphy and how much is an artifact of phylogeny. That measure also ranges from 0 to 1, and is the only one of the three methods that may be compared between trees.

**Origination.** To determine the date when penguins originated, confidence intervals (CI's) are applied to the penguin record using gap analysis (Appendix 4.2; Strauss and Sadleir, 1989; Bleiweiss, 1998). The method applies an interval of varying confidence level to the beginning and end of an incomplete taxon range in order to estimate the actual duration of that range. In the case of an extant taxon such as penguins, an interval is applied only to the beginning of the taxon range. It is important to note that the applied interval is not an actual estimate of the time of origination of penguins, but a range during which one is nearly certain that penguins originated, whether with 95% certainty, 99% certainty, or other. These confidence intervals, therefore, result only in a maximum age limit to the penguin record, before which they certainly had not evolved.

Gap analysis uses the number of known, fossiliferous horizons compared with the total number of horizons occurring spanned by a taxon, assuming a random distribution of taxa through time, which is obviously not the case for penguins. The first assumption

may be improved, however, by analyzing absolute time rather than geologic horizons, which are rarely of equal length. I therefore calculated CI's using both number of stages, which is the smallest geologic horizon reported for most penguins, and using million year increments. I applied the method here to both Panspheniscidae, to determine the probable origination date of penguins, and to Spheniscidae, to determine that of the crown-group. Because million year increments are more accurate than stages, I used only the former in calculations for Spheniscidae.

**Biogeography.** Answers to a number of biogeographic questions about penguins, such as where they originated, whether they achieve their current distribution through dispersal, vicariance, or both, and how these processes changed through time, come from application of a number of current methods of analysis. Because penguins are likely to have undergone numerous episodes of both vicariance and dispersal, as suggested by various wide-ranging species and their long history of Gondwanan occupancy, methods that favor any one process over another (e.g., Brooks Parsimony Analysis) may not be most applicable. I therefore optimized geography in MacClade to ascertain the center of origin of penguins and their likely history of dispersal and vicariance. Additionally, I analyzed penguin biogeographic patterns in PAUP to recover any supported area relationships. In order to add the often neglected component of time to the commonly studied evolutionary and geographical aspects of biogeography, I divided the penguin record into various time-slices to separate biogeographical signal that may be different at various times within the record (e.g., Upchurch et al., 2002).

Areas or provinces used in the biogeographic analyses include a number of southern hemisphere Provinces: the South Polar; the Magellanic, or the west coast of South America; the Cookian and Antipodean of New Zealand; the combined Australian/Tasmanian; and the South African (Figure 4.4; Zinsmeister, 1979; Kennett, 1980; Case, 1992; Glasby and Alvarez, 1999). I also followed authors who divide the Southern Ocean into a number of separate provinces to accommodate the sub-Antarctic and Antarctic islands ranging from offshore New Zealand to South America. These include the Kerguelan, Bouvet, South Georgian, and Macquarie Provinces. Although all these may be combined as the Southern Ocean Province for the purpose of avian distributions (Chown et al., 1998), all provinces are included here because the widespread nature of the living penguin fauna suggests that division of that province may be useful in untangling the history of extant penguin distributions. Mapping the geographic distributions of penguins onto these biogeographic areas shows them to be widespread and diverse (Figures 4.5-4.7).

For analyses performed in MacClade (Maddison and Maddison, 1987), a taxon-area matrix was constructed using the distribution of all penguin taxa and outgroups in the above-defined Provinces (Figure 4.8a). These fifteen distributional characters were then mapped onto the previously accepted penguin phylogeny to determine their most parsimonious acquisition of geography. While MacClade can make no decision regarding whether these acquisitions represent dispersal or vicariance, it is logical that vicariance results in changes in distribution that are contemporaneous with or postdate historical, tectonic events, while geographic separations that predate tectonic events must be caused

by dispersal. This assumption is valid for penguin taxa because their distributions are separated at the continental scale, meaning that the only vicariant events able to separate penguin taxa are large-scale tectonic breakups. Geographic 'autapomorphies' recognized in MacClade were therefore dated using the time-calibrated penguin phylogeny and inferred to represent vicariance if they matched any associated tectonic splitting events (Kennett, 1980; Lawver et al., 1992; Dingle and Lavelle, 2000; Lawver and Gahagan, 2003).

Time-slice analysis uses the same taxon-area matrix, but prunes various species according to their age. Because it is almost certain that different and potentially conflicting biogeographic patterns occurred throughout the history of any taxon, especially one that spans over 60 million years of geologic history, three partitions within penguin history are analyzed separately to differentiate such patterns. That method divides the geologic range of the taxon of interest into various time-slices and prunes each of all taxa that either did not diverge or are not present in that particular time-slice. MacClade optimization is then performed separately for each time-slice to recover potential vicariant events (e.g., Upchurch et al., 2002; Turner, 2004). Partitions used for penguins include the entire Cenozoic, the Cretaceous through Oligocene, and the latest Miocene to Recent because these time-slices should separate patterns occurring before and after the final separation of Gondwana and contrast them with patterns combined from all times.

Finally, I analyzed a second, area-taxon matrix in PAUP (Swofford, 1991) to examine the relationships between the various areas that penguins inhabit (Figure 4.8b).

Rather than optimizing geographic areas onto penguin phylogeny, that process uses penguin species as ‘characters’ to reconstruct the relationships between areas. The analysis used the DELTRAN optimization and rooted the area cladogram using the Northern Hemisphere (area 15) because it is inhabited only by penguin outgroups. An initial branch and bound and a subsequent heuristic search returned identical results. Although the recovered area cladogram is obviously biased by the use of only one taxon, it does allow proposal of an additional data point to the complement of area cladograms available for the southern hemisphere and will be useful in future work on Gondwanan biogeographic patterns.

**Evolution.** To explore the connection between various penguin evolutionary events and the southern hemisphere abiotic history, I compile dated tectonic and climatic events and correlate them with the time-calibrated penguin phylogeny. Although correlation does not necessarily imply causation, there are a number of well-known causes for organismal radiations and extinctions, which often accompany climatic and tectonic changes. For example, seabird radiations closely track the expansion of cold currents because their prey are easier to locate, more abundant, and more predictably available in cold waters (Warheit, 1992). Additionally, the development of long-term isolation in the Antarctic biota is facilitated by factors such as tectonic breakup, development of deep-water channels, and initiation of the Antarctic Circumpolar Current (Barnes et al., 2006). Factors that commonly cause the extinction of marine taxa, especially in Antarctica, include anoxia, competition and predation, regression and habitat loss, cooling and warming, and reduction in productivity (Peck et al., 2004). All

such causal events may play a role in penguin history and should be examined for correlation with the penguin record.

## **Results and Discussion**

After calibration of phylogeny with geologic time, a number of patterns within the penguin record appear (Figure 4.3). It is seen that penguins range through the entire Cenozoic, with their earliest representative, *Wimanu*, known from the late Early Paleocene. Various penguin outgroups, however, are known from the Cretaceous (e.g., Chatterjee, 2002; Clarke et al., 2005; James, 2005; Mayr, 2005b), suggesting by minimum age node dating that the penguin ghost lineage also extends into the Mesozoic. Following the original appearance of Paleocene penguins, a major, Early Eocene gap obscured nearly 15 million years of the penguin record. The Late Eocene witnessed a burst of penguin diversity, although it is not clear whether this results from a genuine adaptive radiation within penguins, from the abundant preservation of penguins in certain Late Eocene deposits such as the La Meseta Formation of Seymour Island, or from a lack of Early Eocene deposits in the southern hemisphere. The former suggestion gains some support from the fact that both extinct clades of penguins, Palaeudyptidae and Paraptenodytidae, are present and diversify in the Late Eocene, as does one crown-group stem-taxon. Both these lineages of extinct penguins range through the Eocene-Oligocene transition, with a few members extending into the Miocene. The Late Eocene through earliest Miocene therefore comprises the most diverse time in penguin history, with a greater number of species and equal geographic diversity as the extant fauna. The latest

Oligocene also served as the time of origin of crown-clade penguins, at least under a literal reading of the rock record.

Most penguin diversity was extinct by the end of the Oligocene, about 23 mya, and only South America and South Africa contain any reasonable record of Miocene penguins. These remains, however, come only from the earliest and the latest Miocene, with another long, temporal gap stretching through most of the epoch. This hiatus is interesting in that it extends through more than 10 million years of the record of crown-group penguins, suggesting that the record of crown-penguins may be particularly poor. However, most of the older, Early Miocene members of the crown-clade are extremely poorly preserved and also the only factor pulling Spheniscidae back into the latest Oligocene. If their poor preservation caused them to be incorrectly placed phylogenetically, the incongruence between the crown-group and the stratigraphic record would dissolve, but the crown-clade would date only to the Late Miocene. It is at this time that the basal members of extant genera appear in South America and South Africa, with more such taxa known from the Pliocene and Pleistocene.

**Completeness and Origination Time.** Results from the analysis of completeness of the fossil record and origination time of penguins and crown-penguins are listed in Appendix 4.2. One measure of completeness, the RCI, is -377%, indicating that the penguin record has nearly four times as much missing record as recorded history. While this calculation is somewhat discouraging, it is also entirely based on the point estimate problem discussed above. Only nine extinct penguin taxa are known from actual ranges, both because few species are known from more than one deposit and because few extinct

penguin genera are monophyletic. This entirely distorted the calculation of the RCI, and the only real result gained from use of the measure is the conclusion that the penguin record is extremely patchy in terms of species distributions through time.

The second measure calculated, the SCI, is somewhat more promising in terms of completeness. At 48%, the SCI demonstrates that more than half of the proposed phylogeny is in accord with the stratigraphic appearance of penguin taxa. This proportion accords well with those shown previously for other groups, including a number of more preservable taxa than birds, such as tapirs (64%), diapsids (61%), and cystoids (66%; Huelsenbeck, 1994). The penguin record is worse stratigraphically than well preserved groups such as brontotheres (100%), chalicotheres (80%), and some types of graptolites (80%; Huelsenbeck, 1994), but this may also reflect incorrect phylogeny, not just incomplete stratigraphy. The potential that half the penguin fossil record is already known, however, is promising, especially considering that penguins belong to a taxon, birds, that does not preserve as well as other vertebrates and to a geographic region, the southern hemisphere, that remains more poorly explored than the northern.

Finally, a calculated GER of 74.4% shows that the majority of the ghost lineages observed in the penguin record, nearly three quarters in fact, are present owing to the constraints of the proposed cladogram. This is intriguing because it means that either the cladogram used here is drastically incorrect, unlikely in light of the large amounts of character data underlying this phylogeny, or that only about 25% of the penguin fossil record is missing. Taken together, these three measures indicate that the penguin record is good, as expected, but not complete. The record is sporadic, but only inasmuch as any

record would be when analyzed using point estimates. It is also fairly congruent in regards to order of origination, nearly as much so as many groups of higher fossilization potential. Most encouraging of all, nearly the entire missing record of penguins is absent owing to the constraints of a highly non-pectinate cladogram. Assuming the validity of the accepted phylogeny, only 25% of penguin history remains to be discovered. Subsequent analyses regarding dating and other, evolutionary events are considered well supported because of the completeness seen here.

Confidence intervals applied to the penguin record result in a maximum date of origin of 70.65 mya for *Panspheniscidae*. Although younger dates result when using geologic stages, improvement upon the method through use of equal time increments shows 99% confidence that penguins originated no earlier than the Maastrichtian (Late Cretaceous, 71 mya). It is additionally 95% certain that penguins originated somewhat later, about 67 mya, in the latest Cretaceous (mid-Late Maastrichtian). This indicates a short ghost range preceding the appearance of penguins in the geologic record, only 5-8 million years. The crown-group is also dated, resulting in a maximum age of origin of 42.7 mya. More conservatively, penguins originated with 95% confidence only about 35 mya. This results in a preceding ghost lineage of at least twelve and as many as twenty million years, however.

Comparison of these dates with previous hypothesis is possible, but limited, as few previous studies estimated the date of origin of penguins. Those proposed include molecular estimates of 71 mya (Baker et al., 2006) and 67 mya (Slack et al., 2006). These agree well with the confidence intervals of 67 or 71 million years, and both methods are

congruent with minimum age dating that places Panspheniscidae in the Cretaceous on the basis of Mesozoic sister-taxa. These three, independent methods thus all accord extremely closely on the latest Cretaceous as the time of origin of penguins. Only one molecular clock estimate reported a quantitative date for the origin of crown-group penguins, proposing that they evolved around 40 mya (Baker et al., 2006). Others suggested, based on cladogram topology, that crown-penguins extend only back to the latest Miocene (Ksepka et al., 2006), an estimate that agrees more closely with the minimum age node dating shown here. Confidence intervals calculated here again agree with molecular estimates on an Eocene, 40 mya origin for crown-penguins. The discrepancy with the Miocene estimate undoubtedly arises owing to various incomplete, mainly unassociated, Early Miocene fossils that were excluded from the previous work (Ksepka et al., 2006). Additionally, dates given for these fossils are tentative and accompanied by large margins of error. Because the Eocene crown-clade age estimated here is dependent on the phylogenetic placement of these Miocene fossils, the date would change if these taxa were shown to lie in a different phylogenetic position, and this date is therefore the least confident of those proposed here.

**Biogeography.** Optimization in MacClade resulted in recovery of patterns of both dispersal and vicariance throughout the penguin record (Figure 4.9). Biogeographic reconstruction of the area of origin of the total group is based on the distribution of only its most basal taxon and its sister group, therefore the area of origin of penguins as a whole is the least supported aspect of this reconstruction. However, penguins most likely originated in southern New Zealand (Cookian Province), where many extant species,

some outgroups, and the oldest and most basal penguin, *Wimanu*, are all distributed. Subsequently, a major, Late Paleocene vicariation separated the *Wimanu* from all remaining penguins. Although New Zealand initiated separation from Antarctica much earlier, about 85 mya (Lawver et al., 1992), the coastlines and associated shallow seas that penguins favor only appeared between these continents in any abundance in the Late Cretaceous. As opposed to terrestrial organisms, which vicariate quickly after continental separation, vicariant events within marine organisms can only occur much later because their habitats are only newly forming.

Once separated from New Zealand, a number of penguins remained and evolved solely in West Antarctica. These include one both major clades of extinct penguins, Paraptenodytidae and Palaeedyptidae, as well as *Delphinornis gracilis*, the sister-taxon of Palaeedyptidae, and *Ichtyopteryx*, the basal-most stem-spheniscid. Paraptenodytidae is known entirely from Seymour Island, except for one derived member, *Paraptenodytes*, that dispersed to South America in the Miocene. As for Palaeedyptidae, although it is also a West Antarctic clade in origination, a number of palaeedyptids do occur in New Zealand and Australia, probably arriving there via dispersal. These are all much younger species, mainly Oligocene, and therefore lived well after the entire Gondwanan landmass had separated. The New Zealand species include a small clade of ‘*Palaeedyptes*’ species, as well as some *Archaeospheniscus sp.* and *Platydyptes amiesi*. South America also produces some palaeedyptids, at least one of which, CADIC P-21, is slightly too old, about 8 million years, to have arrived via vicariance. The date of opening of the Drake Passage between South America and the Antarctic Peninsula, however, is currently

debated, and could be late enough to have caused a vicariation between CADIC and remaining palaeodyptids (Scher et al., 2006).

Remaining spheniscoids, or Spheniscidae and its stem-taxa, probably had a wide ancestral distribution, spreading throughout much of the Southern Ocean. The only likely area of origination for Spheniscidae is West Antarctica, although this reconstruction is considered equivocal in MacClade. This suggests that the crown-clade was the first group of penguins to disperse from Antarctica, an event that did not occur until the Oligocene. The distributional history of the crown-clade includes a large number of dispersal events, involving species from South Africa and taxa that inhabit numerous Recent, volcanic islands of the Southern Ocean. The derived clade Australodyptinae also spreads widely throughout the Southern Ocean, with an ancestral distribution including Antarctica and the Antarctic Peninsula, as well as most of the sub-Antarctic islands. This widespread original distribution probably indicates that the clade had dispersed widely and repeatedly before its constituent genera evolved as separate lineages.

Results from pruned time-slices indicate that there are two distinct, biogeographic patterns present within penguins and, not surprisingly, that they related to the West Antarctic and New Zealand Provinces. The older time-slice, which ranges from the earliest known penguin through the Oligocene, concurs that New Zealand is the location of origin of Panspheniscidae, lending more support to this hypothesis. However, it also supports West Antarctica as the ancestral area, indicating that the ancestral penguin may have been widespread, inhabiting both areas. This would be entirely plausible geographically, as the two areas were much closer together in the Late Cretaceous. The

biogeographic pattern of this time-slice further suggests that *Wimanu* evolved in one area of this widespread distribution, New Zealand, while Palaeedyptidae evolved in the other, West Antarctica. Analysis agrees that the ‘*Palaeedyptes*’ clade originally suggested to have dispersed back to New Zealand did indeed do so, as did some of the closest relatives of Spheniscidae, *Korora*, *Tereingaornis*, and *Duntronornis*. Alternatively, the fact that the basal penguin species, *Wimanu*, is from New Zealand while nearly all the clades that evolved subsequently are West Antarctic may suggest that *Wimanu* is skewing the results of the analysis.

The second time slice analyzed the crown-clade and its immediate stem-taxa, which are the only penguins that diverged after the final separation of Gondwana. This analysis indicates that penguins underwent dispersal a number of times: three separate events resulted in their arrival in Australia, one allowed the Jackass Penguin to reach South Africa, and all South Ocean Provinces achieved their complement of penguins via dispersal. Additionally, although southern New Zealand is ambiguously supported as the ancestral area of crown-penguins, the West Antarctic Province is unambiguously indicated as their place of origin, suggesting that the ancestral spheniscid was also widespread in distribution. Both extant Antarctic species, however, arrived via separate dispersal at a much later date. Similarly, other Southern Ocean taxa demonstrate Antarctic-Australian links in the Paleocene, but a much depauperate Antarctic fauna today, owing to climate-induced extinctions (e.g., Grande and Eastman, 1986). Because of the harsh, Recent environment present in Antarctica, most previously endemic organisms have either dispersed from the continent or gone extinct (Peck and Barnes,

2006). It is logical, therefore, that penguins should have dispersed from Antarctica following their origination there.

The PAUP analysis resulted in two MPT's of 84 steps (Figure 4.10a, b). Area relationships suggested by penguin distributions include a close relationship between Australia and New Zealand, with Southern New Zealand more closely related to Australia than to the North Island. Additionally, Antarctica groups with the Antarctic and sub-Antarctic islands to the exclusion of all other areas. The Eastern part of the continent is more closely related to Bouvet Province, as they are geographical closer, while Western Antarctica groups with the remainder of the sub-Antarctic islands, including those offshore from New Zealand. Relationships within part of this group are congruent with geography, for example the areas associated with the Scotia Arc, or the oceanographic region connecting the Antarctic Peninsula and southern South America (Georgia, Southern Ocean, and West Antarctica Provinces). However, all other areas within the West Antarctic group lie much further away and are probably associated with West Antarctica because they share a similar climate and organismal diversity.

The two remaining areas, Northern South America and South Africa, are unresolved and lie in a basal polytomy, probably because they contain the fewest penguin species of all areas, and these are endemic, sharing no relationships with other areas. The only difference between the two most parsimonious reconstructions is the placement of the Magellanic Province, which is either associated with Northern South America, as suggested by the fact that they are both on the same continent, or with the Scotia Arc group, as suggested by their similar climatic and oceanographic regimes. The

reconstruction of these two potential relationships is undoubtedly caused by the fact that they are based on only a single group of organisms, penguins.

When compared with area reconstructions from other southern hemisphere taxa, penguin distributions concur with those of chironomid midges and mayflies, polychaetes, and some plant groups, but disagree in part with other Gondwanan plants, consenses of Gondwanan animals, and southern hemisphere tectonic history (Glasby and Alvarez, 1999; Sanmartin and Ronquist, 2004). Particular points of disagreement with other organisms include the relationships of Australia and the Magellanic region, both of which may be more closely related to South America. Differences between penguin biogeography and tectonic reconstructions of Gondwana suggest that some factor other than vicariance, possibly either dispersal or *in situ* speciation, occurred in New Zealand. This is most likely because most Antarctic penguin species inhabit the Antarctic Peninsula, not the continental areas from which New Zealand vicariated, and this geographic separation may be masking the geologic relationship of the two areas.

The highly resolved topology of the reconstruction presented here demonstrates the robust signal of southern hemisphere biogeography present in penguins. It also shows that the area where penguins may be particularly useful in reconstructing biogeographic history relates to the southern ocean islands and that the close biotic associations among these areas may not arise strictly because of geographic proximity, but because of other factors such as similar climatic or oceanographic properties.

**Evolution.** The time-calibrated penguin phylogeny correlates well with a number of southern hemisphere tectonic and climatic patterns (Figure 4.11). If it is correct to

assume a Late Cretaceous origination of penguins, the group would have evolved prior to the Cretaceous-Tertiary extinction and any associated effects (contra Fordyce and Jones, 1990). The cause of penguin originations is thus constrained to a time when Gondwanan continents had not completely separated and lay much closer to each other than currently, when the far southern climate remained warm and wet, and prior to the extinction of other, potentially predatory or competitive, marine reptiles. The obvious conclusion is that penguins originally evolved in fairly warm climates, not the colder areas they inhabit today, and may have originated because of the ongoing separation of Gondwana and the formation and expansion of new, shallow seas between these continents. Much more coastline and shallow, productive ocean existed between these continents in the Late Cretaceous (Clark, 1990), which would have favored an ancestral penguin adapting to an entirely aquatic lifestyle. Penguins then survived the end-Cretaceous extinction, a pattern that may be common to sea- and shore-birds because of similar ecologies (Dyke, 2006) or to aquatic birds in general (e.g., shorebirds, seabirds, and ducks; Feduccia, 1999). Such a pattern would not necessarily impact hypotheses of the timing of radiations among modern birds, be they Cretaceous or Tertiary, only those of the reason for survival across the boundary. Although the mechanisms causing the K/T extinction are now well-explored (e.g., Dingus and Rowe, 1998), the reason behind survival patterns across the K/T boundary remains unexplained, as does the reason penguins were among the survivors.

Although the extinct, palaeodyptid penguins originated, according to a literal reading of the calibrated phylogeny, in the latest Paleocene, nearly simultaneous with the

Paleocene-Eocene Thermal Maximum (Figure 4.11), the group contained only one member for nearly 15 million years. This gap in the penguin record, discussed above, correlates with high, Antarctic temperatures. When climate began to cool around 42 mya, however, as evidenced by the first glaciation and appearance of ice-sheets in Antarctica (Dingle et al., 1998; Dutton et al., 2002; Tripathi et al., 2005), palaeodyptid penguins began to radiate extensively, and both the basal paraptodytid and the basal stem-spheniscid penguins appeared in the record. It was shown that historical seabird radiations are often tied to the availability of cold, nutrient-rich waters (Warheit, 1992), as is extant penguin geographic diversity. For example, the living Humboldt Penguin only maintains its northern distribution owing to the presence of the cold, Humboldt current off the west coast of South America (Davis and Darby, 1990). This historical, explosive, penguin radiation may therefore result from cooling climatic conditions and the commencement of the first really cold conditions of the Antarctic Cenozoic.

Penguin diversity remained high through the end of the Eocene and all of the Oligocene, although it did not increase, while climate across most of Antarctica and certainly on Seymour Island cooled further (Dutton et al., 2002). During that time, two Southern Ocean seaways opened, first the Drake Passage that separates South America from the Antarctic Peninsula, followed by the Tasman Sea, which separates the latter from Australia. These events initiated the formation of the Antarctic Circumpolar Current, which today serves as a major driving force in global climate cycles and served in the past as the cause of glaciations and world-wide cooling (Lawver et al., 1992; Lawver and Gahagan, 2003; Scher et al., 2006). Although the formation of the Current

probably caused the large drop in sea surface temperature observed throughout the Oligocene (Zachos et al., 2001), it seems to have had no adverse effect on penguins. In fact, penguin diversity only dropped, via the extinction of most palaeodyptid and paraptodytid species, after climate warmed, about 26 mya. In the Miocene, penguins drastically declined in diversity for about ten million years, a period encompassing the mid-Miocene climatic optimum (Zachos et al., 2001). Finally, penguin diversity increased again only when ice sheets initially formed in the west of Antarctica. This Late Miocene radiation resulted in the high diversity of penguin species seen today, which exist in a currently comparably cold climate.

Taken together, these patterns suggest that although penguins originated in a warm climate, they did not diversify until they were exposed to the new environmental conditions associated with climatic cooling. This accords well with the hypothesis that fluctuating Eocene climates caused corresponding taxon pulses in penguins (Jadwiszczak, 2003). These birds may thus be favored by cold climatic regimes, possibly owing to increased nutrient availability and hence food production, and adversely affected by climatic warming. Previous, contradictory suggestions that penguin diversity, especially in the Oligocene, correlates with warm climatic regimes (Fordyce and Jones, 1990) predate more recent knowledge of the high diversity of Eocene Seymour Island taxa, which drastically changes the patterns of observed penguin diversity and supports the climatic hypothesis proposed here.

## Conclusions

The penguin record is largely complete, especially considering that it is the record of a vertebrate and an avian taxon. Large gaps do exist in the Early Eocene and the middle of the Miocene, and the vast majority of the record comprises point, not range estimates, but measures of SCI and GER also show that the stratigraphic record is half congruent with penguin phylogeny and that nearly all the ghost lineages present in the record exist because of the cladogram topology. This may, in part, reflect incorrectly resolved phylogenetic relationships, particularly those involving the oldest, Miocene fossils assigned to crown-clade taxa, because cladogram topology determines the calculated SCI and GER values. However, assignment of these taxa, particularly *Chubutodyptes* and *Eretiscus*, to the crown-clade is what causes the majority of long ghost lineages within the penguin fossil record. This suggests that potential incorrect phylogenetic placement of these taxa would only artificially inflate the incompleteness of the record, and therefore that not much more than 25% of the record is absent. This missing portion probably includes unknown fossils from the Early Eocene and Middle Miocene gaps, as well as representatives of the ancestral penguin and the ancestral spheniscid.

Penguins probably originated in the latest Cretaceous, prior to the K/T extinction. Although this date is based on an interval, not an absolute value, it was estimated by three independent methods: confidence intervals based on the fossil record, molecular clock dating based on extant penguin phylogeny (Baker et al., 2006; Slack et al., 2006), and minimum age node dating, or a literal reading of the fossil record and the age of penguin

sister taxa. This fact lends much more support to the Cretaceous origin of penguins than if only one method had suggested the date. There is less confidence about the age of the crown-group, Spheniscidae, because these three methods do not agree as closely and because confidence intervals for this group are larger. While molecular methods suggest that the group may have originated in the Late Eocene (Baker et al., 2006), that date is nearly sixteen million years before crown-penguins appear in the stratigraphic record. Long confidence intervals placed on the beginning of the sphenisciform range also extend the record back to the Late Eocene, nearly exactly to the suggested molecular date, and thus at least confirm that a Late Eocene origination is possible. Because these intervals encompass both the minimum node age (earliest Miocene), and the molecular date (Late Eocene), it is not yet possible to determine which is correct, and both dates remain valid extrapolations.

If penguins are in fact Cretaceous, this suggests that numerous other bird lineages also date to the Mesozoic and survived the K/T extinction. The phylogenetic position of penguins within Aves is derived. No matter exactly which bird is their sister taxon, penguins are certainly neoavian (e.g., Livezey and Zusi, 2007) and thus their date of origin would constrain that of their closest relative and hence of Neoaves, to the Cretaceous. If seabirds, including penguins, are even more derived within Neoaves (e.g., Mayr and Clarke, 2003), numerous additional neoavian lineages would also be dated as Cretaceous in origin. This has wide-ranging implications for the patterns of diversity and origination of living birds.

As expected, the biogeographic history of penguins includes both vicariance and dispersal. This is important because, until recently, most biogeographic analyses excluded the possibility of dispersal under the assumption that it is not a testable process and generally used only as an *ad hoc* explanation (Zink et al., 2000; de Quieroz, 2005). Upon realization of the fact that dispersal is in fact testable, numerous studies subsequently showed this process to be important and sometimes even dominant in biogeographic history (e.g., Lieberman and Eldredge, 1996; Beu et al., 1997; Yoder and Nowak, 2006). In particular, a group such as penguins that is oceanic, widely distributed, and currently inhabits young, volcanic islands of the Southern Ocean, is nearly certain to have undergone episodes of dispersal (Cowie and Holland, 2006). Future biogeographic work, especially on penguins, that ignores dispersal in favor of vicariance will fail to recover the true historic pattern. Similarly, biogeographic analyses that do not explicitly incorporate a temporal element will lack any sort of context for patterns that changed throughout the history of a group. Analyzing biogeography without accounting for time will blur any reconstructed events by amalgamating them and will confuse the history of vicariance and dispersal by obscuring the relative order of geologic events with resulting biological responses. If vicariant patterns are recognized as always postdating tectonic breakup of areas, for example, then temporal constraints are integral to the determination of whether various area relationships could reflect such vicariant events. It is important in biogeography, as in all evolutionary research, to include all relevant data, not just phylogenetic patterns and area relationships, but also the possibility of dispersal and temporal incongruence.

The reconstruction of penguin biogeography, including analysis of time-slices, indicates that the group originated in either New Zealand or a widespread area including New Zealand and West Antarctica. The basic biogeographic pattern is one of major clades vicariating in synchronicity with tectonic splitting events, following by numerous, repeated dispersals by members of these clades throughout the entire Southern Ocean. The two extinct penguin clades, Palaeudyptidae and Paraptenodytidae, are both West Antarctic in origin, although the former evolved from vicariation with New Zealand, while the latter arrived via New Zealand dispersal. The crown-clade is probably also West Antarctic in origin, although it was certainly widespread in distribution, and includes numerous and repeated dispersals. In particular, areas such as South Africa and Australia never underwent vicariant speciation, only dispersal, which probably reflects their geographic separation from the centers of penguin diversity: New Zealand and Western Antarctica. Area relationships indicated by penguins generally align with geography, although Antarctica and the sub-Antarctic islands probably group together because they share similar climatic and biotic elements, not geographic proximity. When compared with other southern hemisphere taxa, the area relationships indicated by penguins are mainly congruent, although the separation of New Zealand and Antarctica disagrees with tectonic data, probably owing to the restricted distribution of penguins within the Antarctic continent.

The penguin record, when correlated with Gondwanan climatic and tectonic history, reflects the intimate relationship between evolutionary events and these large-scale processes. Just as penguin history was long shaped by geological process, the fossil

penguin record reflects the tectonic and climatic history of the Southern Ocean. Penguin radiations and extinctions correlate well with events such as the Paleocene-Eocene Thermal Maximum, the opening of the Drake Passage and initiation of the Antarctic Circumpolar Current, and the commencement of Antarctic glaciation. Interestingly, penguins originated not in the cold environments for which they are popularly known, but in the warm, shallow seas of Late Cretaceous New Zealand. The group only radiated significantly when climate cooled, and undergoes periodic extinction events whenever climate warms. It seems that although penguins originated because of the creation of new, tectonically induced environments, their diversity is mediated not by tectonics, but by climate. In particular, the first, Late Eocene, Antarctic cooling resulted in a proliferation of penguin species, known from Seymour Island, while Late Oligocene climatic warming caused a large extinction among extinct taxa, including nearly all palaeodyptid species.

The current, widespread diversity of penguin species probably owes its origin to the initiation of the Quaternary ice ages. Future global warming will undoubtedly affect most, if not all, living penguin species, although whether warming of such scale and tempo will have a positive or negative effect on penguin diversity remains to be seen (e.g., Emslie, 1995; Emslie and McDaniel, 2002; Emslie et al., 2007). It is important to keep in mind the fact that although correlations shown here predict future declines in penguin diversity and abundance related to global warming and related decreases in cold-water nutrients and food sources, these predictions are also preliminary because they

depend on a number of independent assumptions about phylogeny, geologic dating, and climatic and tectonic data.

The relationship between climate change and penguin evolution is probably not as straightforward as it may appear, however. Recent work shows, for example, that giant penguin species invaded the low-latitudes of Peru at least twice, in the Middle and even Early Eocene, before any significant cooling occurred in global climate (Clarke et al., 2007). Those species were probably supported by food sources provided by cold water currents, as are tropical penguins today, but what mechanism allowed tropical species to achieve and maintain such large size (*Ichthyophaga*, for example, could have stood around 1.6 m in height; Clarke et al., 2007) remains unknown. Problems such as this indicate that conclusions drawn here about the links between climate and organismal evolution remain preliminary. Although the major pattern of relationship between penguins and climate may consist of a connection between diversity and cooling climates, it is obvious that further work is needed to determine more precisely what and how historical factors drive penguin evolution.

Combining estimates of the timing and of the location of various events within the history of an organism, such as its origin, radiations, and extinctions, results in a more complete picture of the evolutionary history of a group than examination of, for example, biogeographic patterns alone. For example, if climate change caused penguins to radiate, but also caused dispersal to occur, what is the relationship between this adaptive radiation and simultaneous dispersal? Does dispersal from an ancestral area cause organisms to diversify taxonomically or does the radiation of taxa cause them to disperse from their

center or origin? Is this even a question that can be answered considering the order of magnitude difference between ecological events and evolution in deep time?

What is certain is that such synthetic questions cannot be answered without examining the entire taxonomic complement of a group. Neontological studies, while indispensable to evolutionary analyses, owing to their use of immense quantities of morphological, molecular, and other non-preserved data missing from most paleontological specimens, are not adequate to answer questions of a historical nature without also incorporating fossil, and hence temporal, data. Obviously, examining the historical pattern of penguin radiations and extinctions is impossible without use of the presence and absence, distributional, and temporal data associated with extinct penguins. This inclusion is particularly important in a group such as penguins, that possess an excellent stratigraphic record, and in consideration of numerous objections to and complications resulting from the use of molecular clocks in dating lineages (e.g., Smith and Peterson, 2002; van Tuinen and Hedges, 2004; Brochu et al., 2004; Peterson, 2006). Lack of fossils altogether or even inclusion of particular fossils but lack of important temporal, morphological, or geographic characters, can result in different and probably incorrect dating of lineages and in the incorrect reconstruction of patterns of diversity. For example, a recent study claimed that waterbird lineages are evolutionarily younger than other avians based, in part, on the young age of the clade Sphenisciformes (van Tuinen et al., 2006). This result is questionable not only because penguins and crown-penguins are probably much older, but also because it ignores the immense diversity and evolutionary radiations that penguins achieved long before the crown-group originated.

Future work on penguin evolution should include biogeographic analyses comparing patterns reconstructed for penguins with those of other southern hemisphere taxa. This will allow analysis using paleobiogeographical tests that require multiple, independent taxa (e.g., Lieberman and Eldredge, 1996), and the recovery of patterns broader than those suggested by penguins alone. Numerous other patterns within penguins also remain to be explored, for example, the question of why penguins never expanded into the northern hemisphere. Various hypotheses for this restriction include the presence of an equatorial climate barrier caused either by ambient water temperature or lack of prey associated with cold ocean currents; the presence of numerous, terrestrial, northern hemisphere predators that are absent in the south, combined with the lack of suitable, predator-free, offshore islands in the north; and the historical artifact that penguin species only recently arrived at the equator and have not had sufficient time to disperse further (Simpson, 1946; Cracraft, 1973; Baker et al., 2006). The equatorial barrier hypothesis may be the most useful for further exploration, as there are certainly numerous aquatic predators in the Southern Hemisphere and as penguins had at least the entire Cenozoic to disperse past the equator.

Numerous evolutionary patterns are also noted within penguins that deserve further consideration. These include, for example, the cause of Bergmann's Rule, or the correlation of increasing latitude with increasing size (Simpson, 1946) and the reasons for the evolution of gigantism in a number of extinct, palaeodyptid species (Jadwiszczak, 2001), both of which may relate to the effect of cold climates on body size. Additional questions include the cause for the original loss of flight in penguins and the evolution of

swimming adaptations, as well as why this transition occurred when and where it did. Finally, the prediction that undiscovered, Cretaceous penguins exist, probably in New Zealand, may be corroborated in time, allowing further analysis of the biogeographic history and pattern of origination of penguins.

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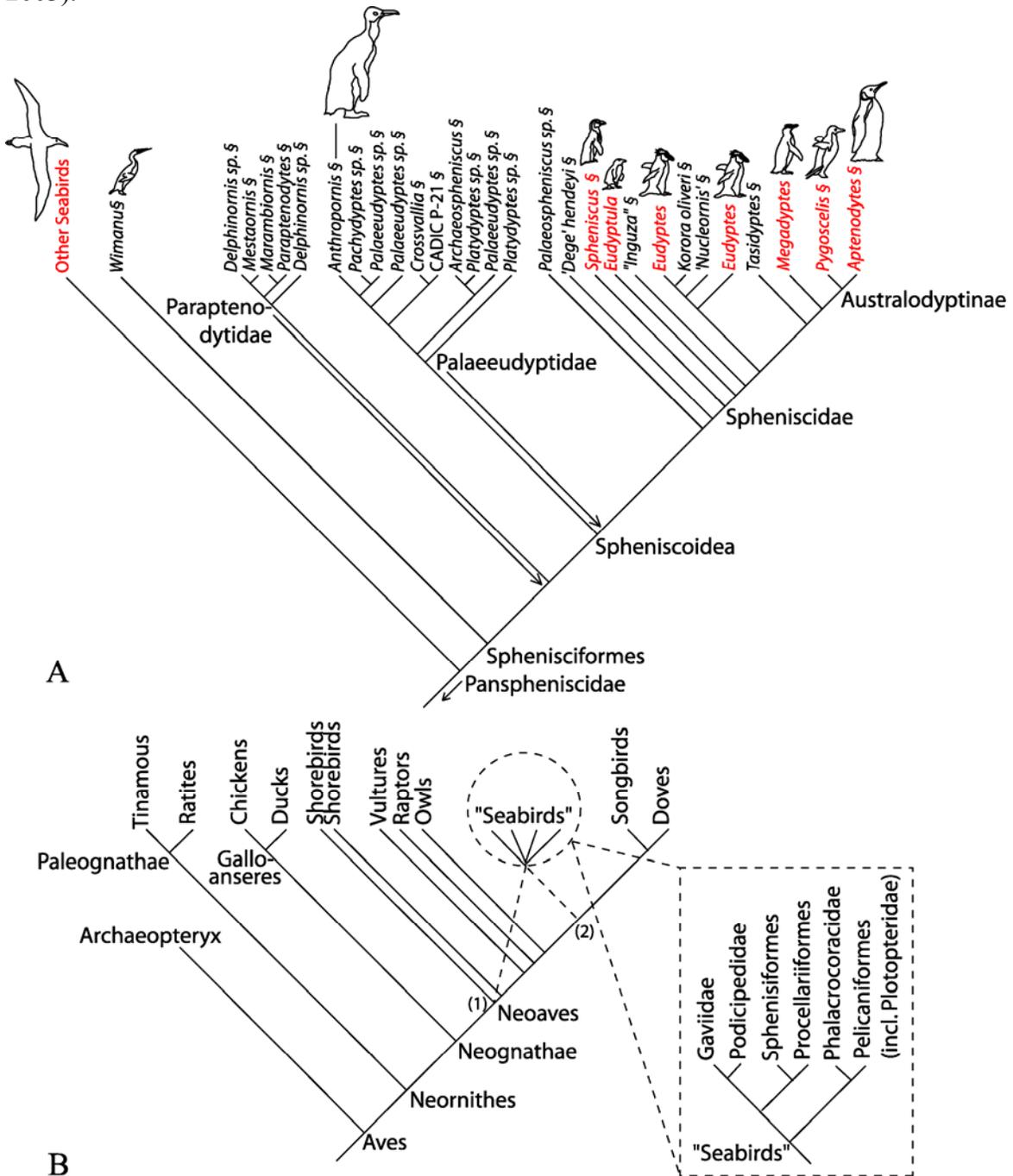
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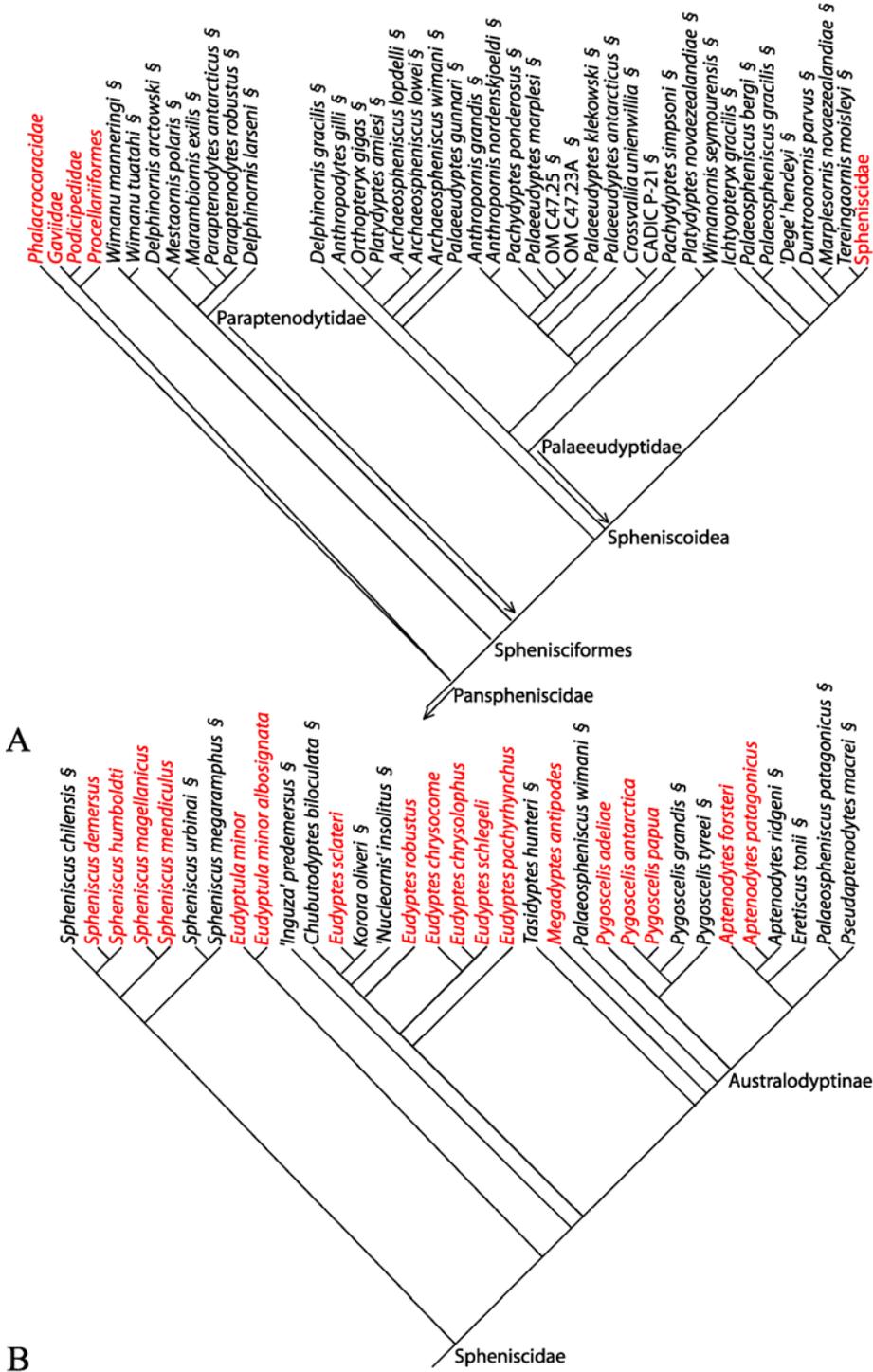
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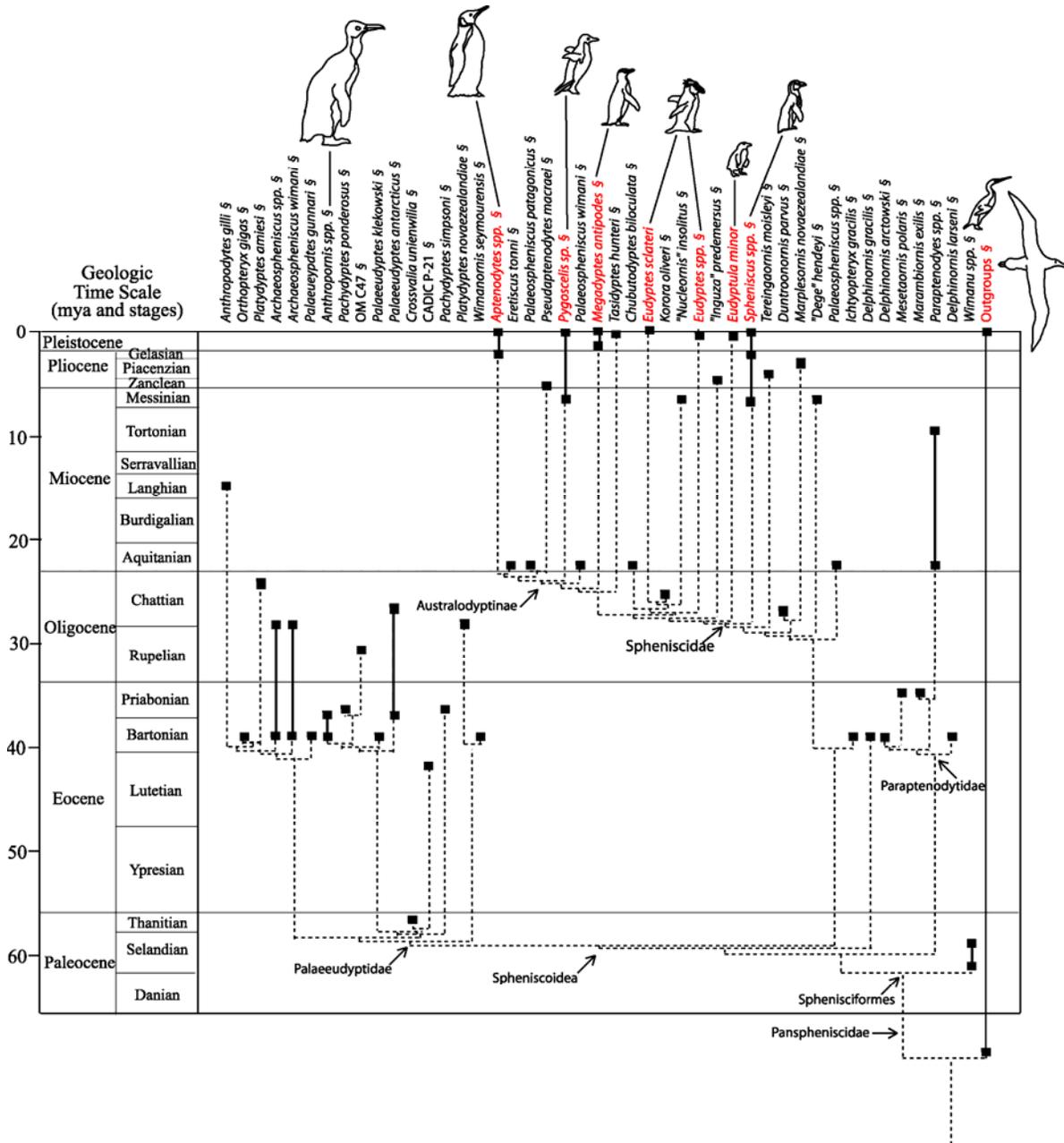
**Figure 4.1. Phylogenetic Relationships of Penguins.** A. Relationships within Panspheniscidae. Simplified from Triche, Chapter 3. Extinct taxa indicated by §, extant taxa in red. Arrows indicate stem-based names, all others node-based. A. Relationships within Aves. Simplified from Mayr and Clarke, 2003. Dashes indicate potential placement of 'seabird' clade (Livezey and Zusi, 2007 (1); Mayr and Clarke, 2003 (2); inset depicts most commonly recovered topology among seabirds (Mayr and Clarke, 2003).



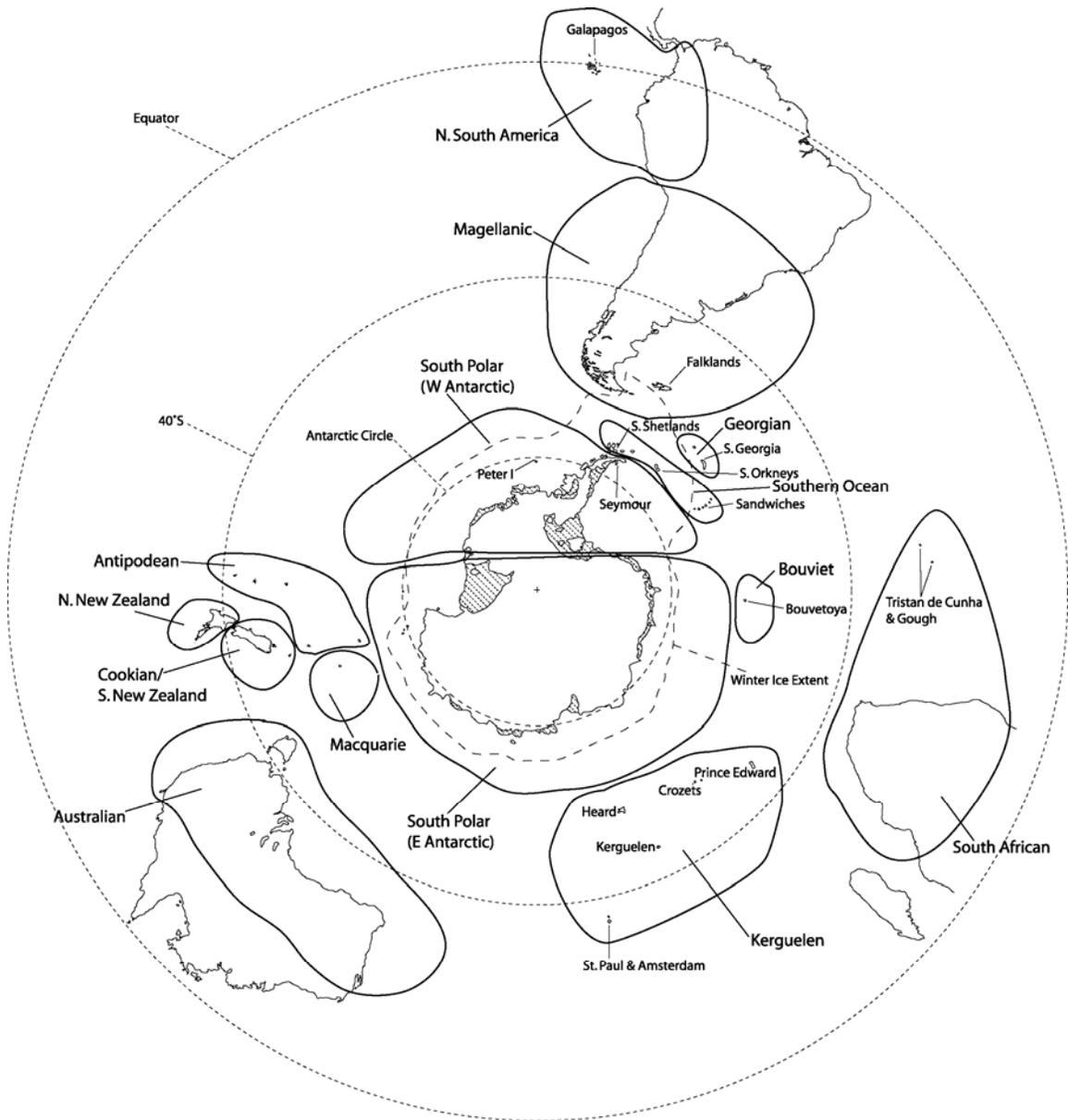
**Figure 4.2. Phylogenetic Hypothesis for Penguins.** From Triche, Chapter 3. Symbols as in Figure 4.1. A. Relationships of Panspheniscidae. B. Relationships of the crown-clade, Spheniscidae.



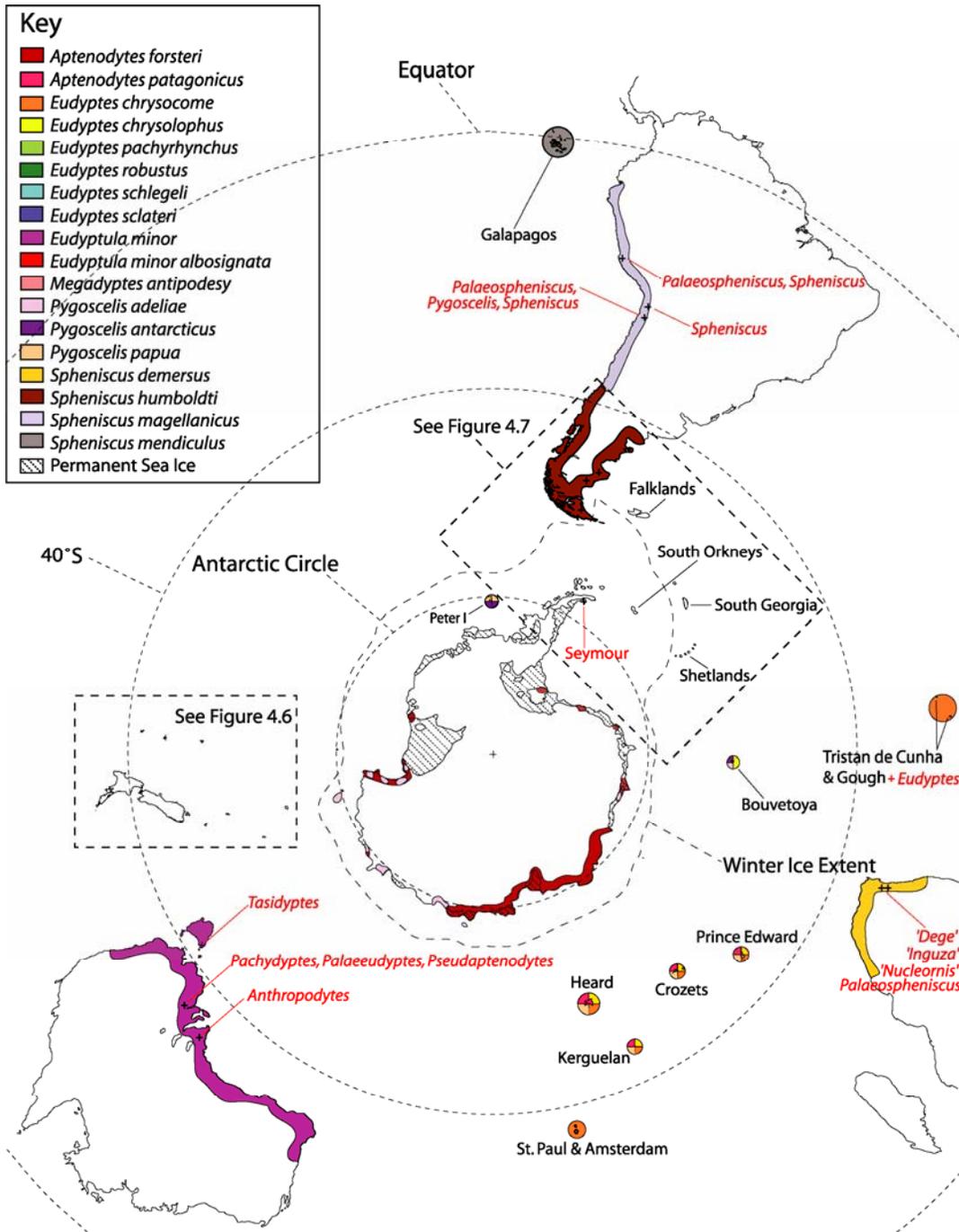
**Figure 4.3. Time-calibrated Penguin Phylogeny.** Phylogeny simplified by collapsing only terminal taxa that comprise monophyletic genera with identical geographic ranges.



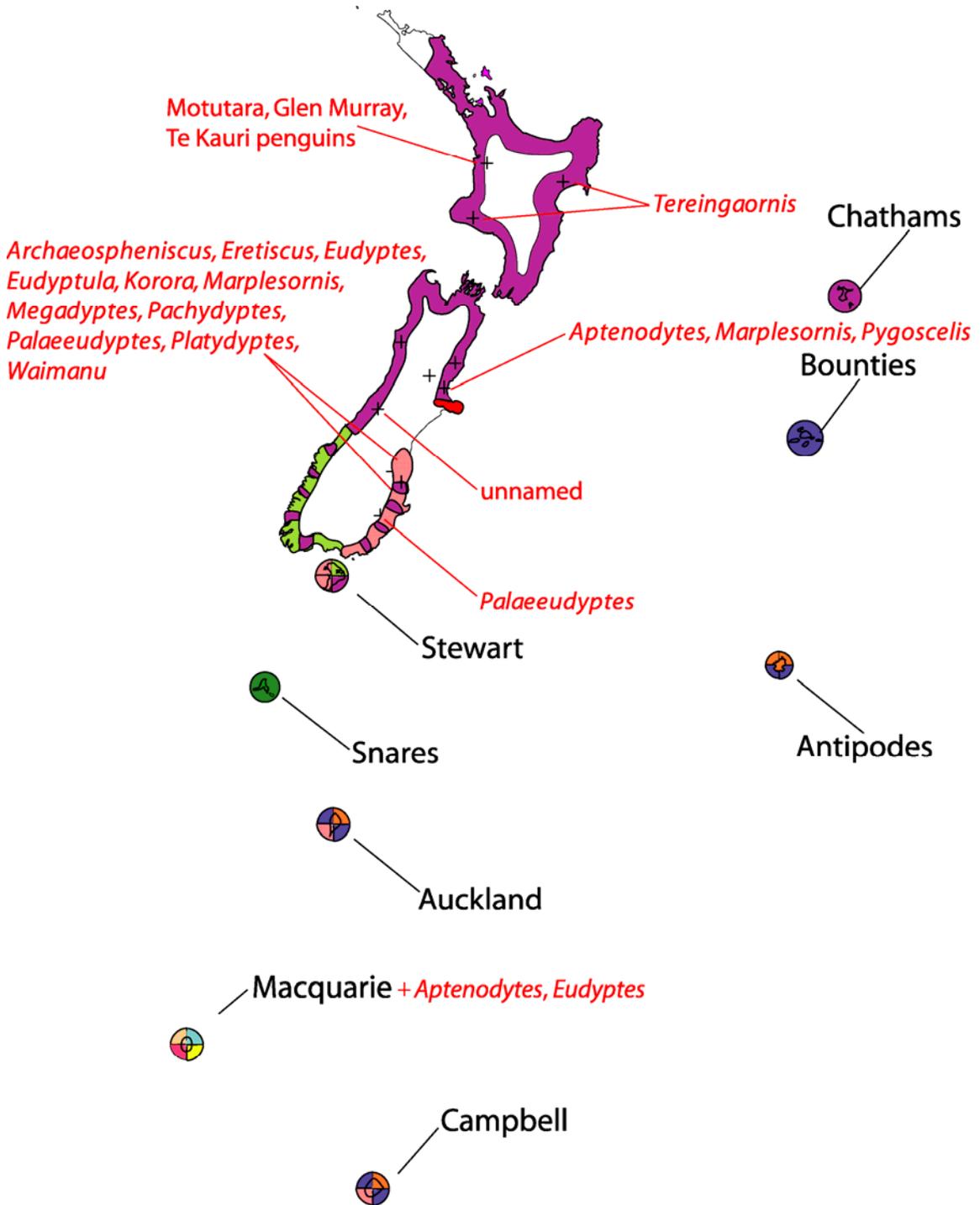
**Figure 4.4. Biogeographic Areas Used in Analysis.** See text for discussion of sources.



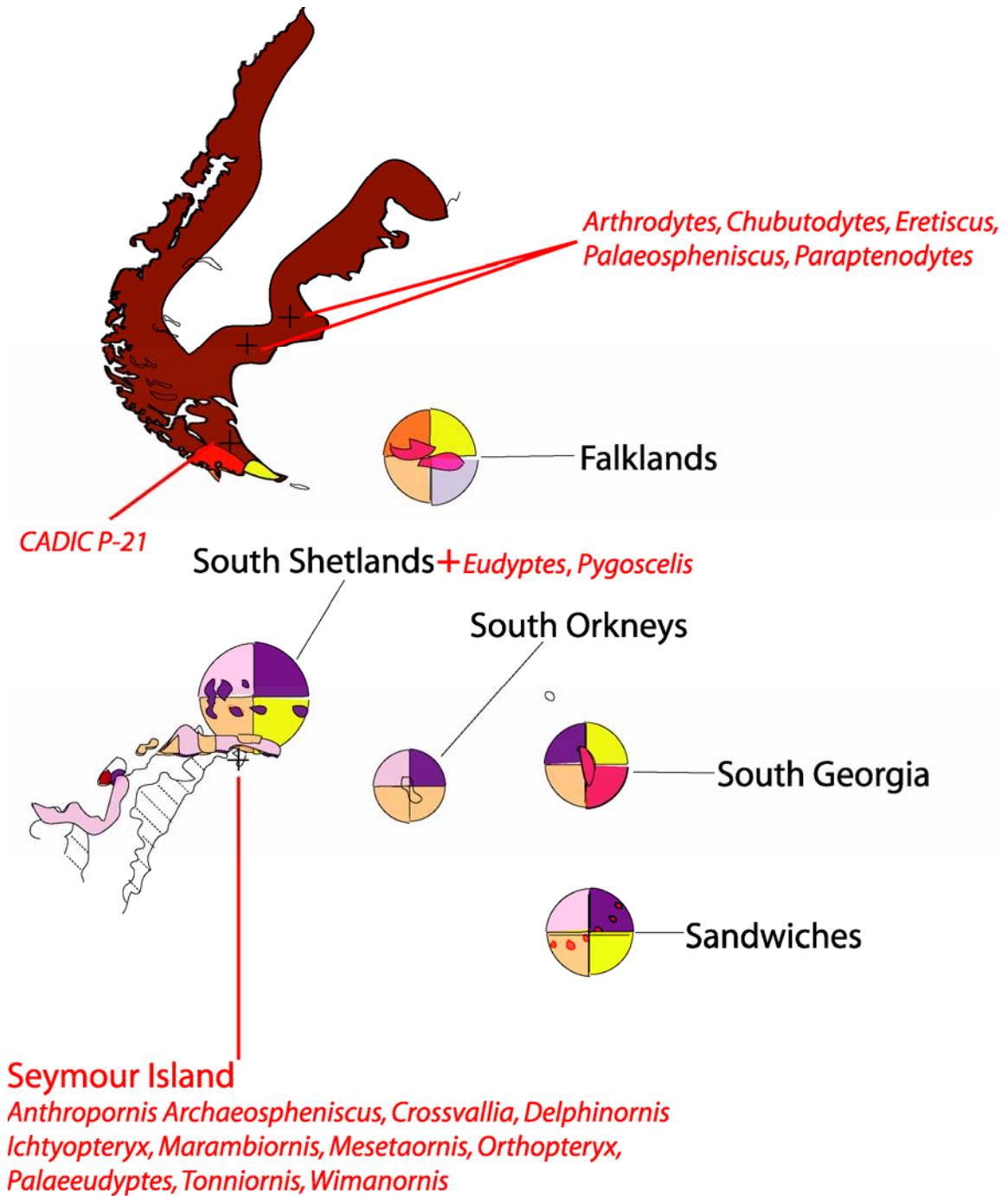
**Figure 4.5. Distribution of Extinct and Living Penguins in Southern Hemisphere Biogeographic Areas.** Fossil localities marked with red X and list of genera present. Breeding ranges of extant species circled in color (Wilson, 1983; Harrison, 1985). Overlapping distributions indicated with pie diagrams (islands) and banded colors (continents).



**Figure 4.6. Geographic Distribution of Penguin Species in New Zealand.** Continued from the inset in Figure 4.7. Key and symbols are as in Figure 4.5.



**Figure 4.7. Geographic Distribution of Penguin Species in South America.** Continued from the inset in Figure 4.5. Key and symbols are as in Figure 4.7.



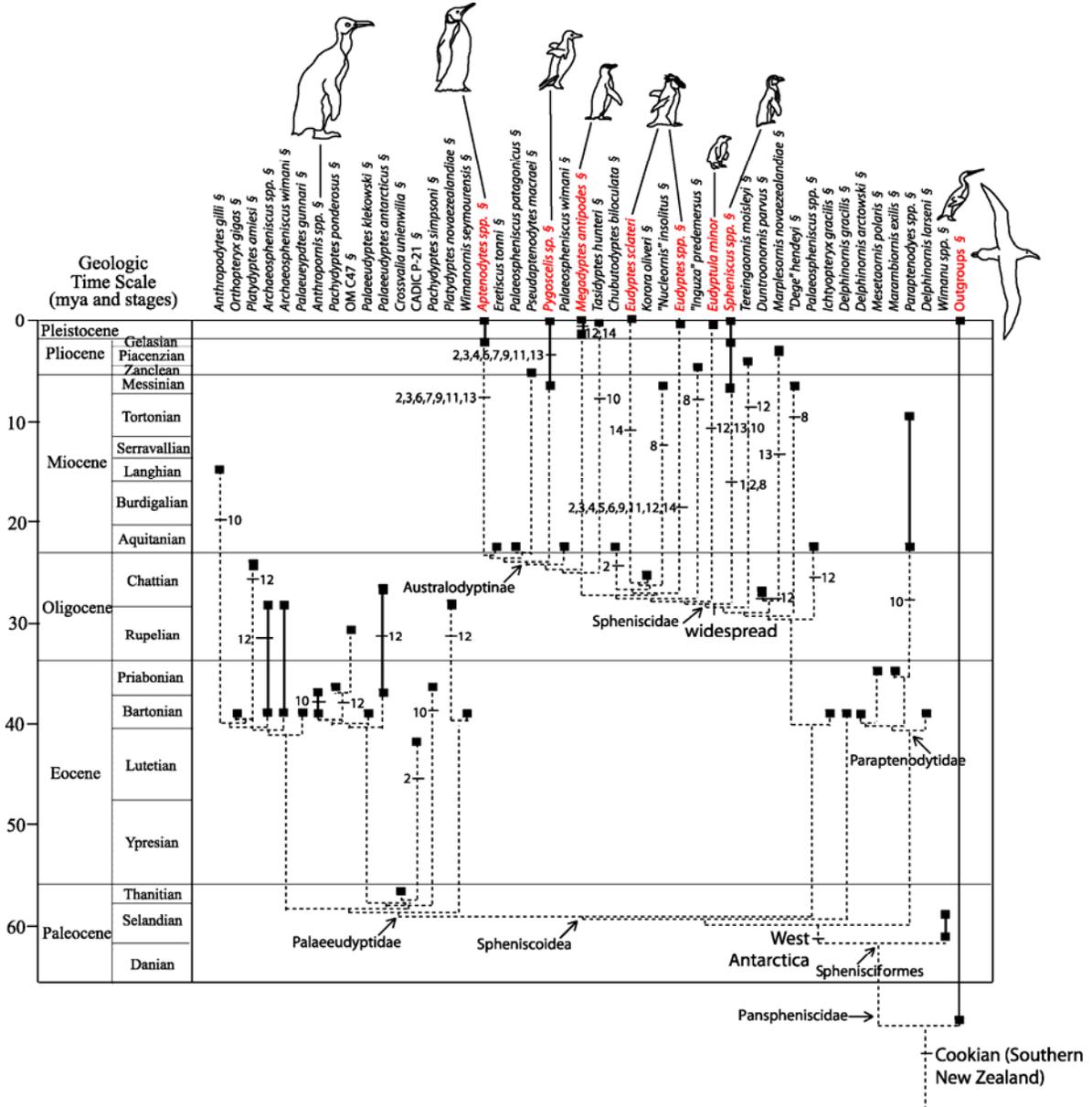
**Figure 4.8. Biogeographic Matrix.** A. MacClade. Biogeographic areas as follows: Northern South America (1), Magellanic (2), Georgian (3), Southern Ocean (4), Bouvet (5), Western Antarctica (6), Eastern Antarctica (7), South Africa (8), Kerguelan (9), Australian/Tasmanian (10), Macquarie (11), Cookian (12), Northern New Zealand (13), Antipodean (14), Northern Hemisphere (15). B. PAUP. Taxa numbered as for 5a.

A	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	<i>A. gilli</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>A. grandis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>A. nordenskjoeldi</i>	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
	<i>A. forsteri</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
	<i>A. patagonicus</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0
	<i>A. ridgeni</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>A. lopdelli</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>A. lowei</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>A. wimani</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>C. biloculata</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. unienwillia</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	"D." <i>hendeyi</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>D. arctowski</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>D. gracilis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>D. larseni</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>D. parvus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>E. tonnii</i>	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>E. chrysocome</i>	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0
	<i>E. chrysolophus</i>	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0
	<i>E. pachyrhynchus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>E. robustus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>E. schlegeli</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	<i>E. sclateri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>E. minor</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
	<i>E. m. albosignata</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>I. gracilis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	"I." <i>predemersus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>K. oliveri</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>M. exilis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>M. novaezealandiae</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>M. antipodes</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
	<i>M. polaris</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	"N." <i>insolitus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>O. gigas</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>P. ponderosus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>P. simpsoni</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>P. antarcticus</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
	<i>P. gunnari</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>P. klekowski</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>P. marplei</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>P. bergsi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. gracilis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. patagonicus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. wimani</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. antarcticus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. robustus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. amiesi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>P. novaezealandiae</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>P. macaei</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	<i>P. addiae</i>	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
	<i>P. antarcticus</i>	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0
	<i>P. grandis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. papua</i>	0	1	1	1	0	1	0	0	1	0	1	0	0	0	0
	<i>P. tyreei</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>S. chilensis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. demersus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>S. humboldti</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. magellanicus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. megaramphus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. mendiculus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. urbinai</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. hunteri</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>T. moisleyi</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	<i>W. seymourensis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>W. manningi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>W. tuatahi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	CADIC P-21	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	OM C47.23A	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	OM C47.25	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	Gaviidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Phalacrocoracidae	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1
	Procellariiformes	1	1	0	0	0	0	0	1	0	1	0	1	1	0	1
	Podicipedidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

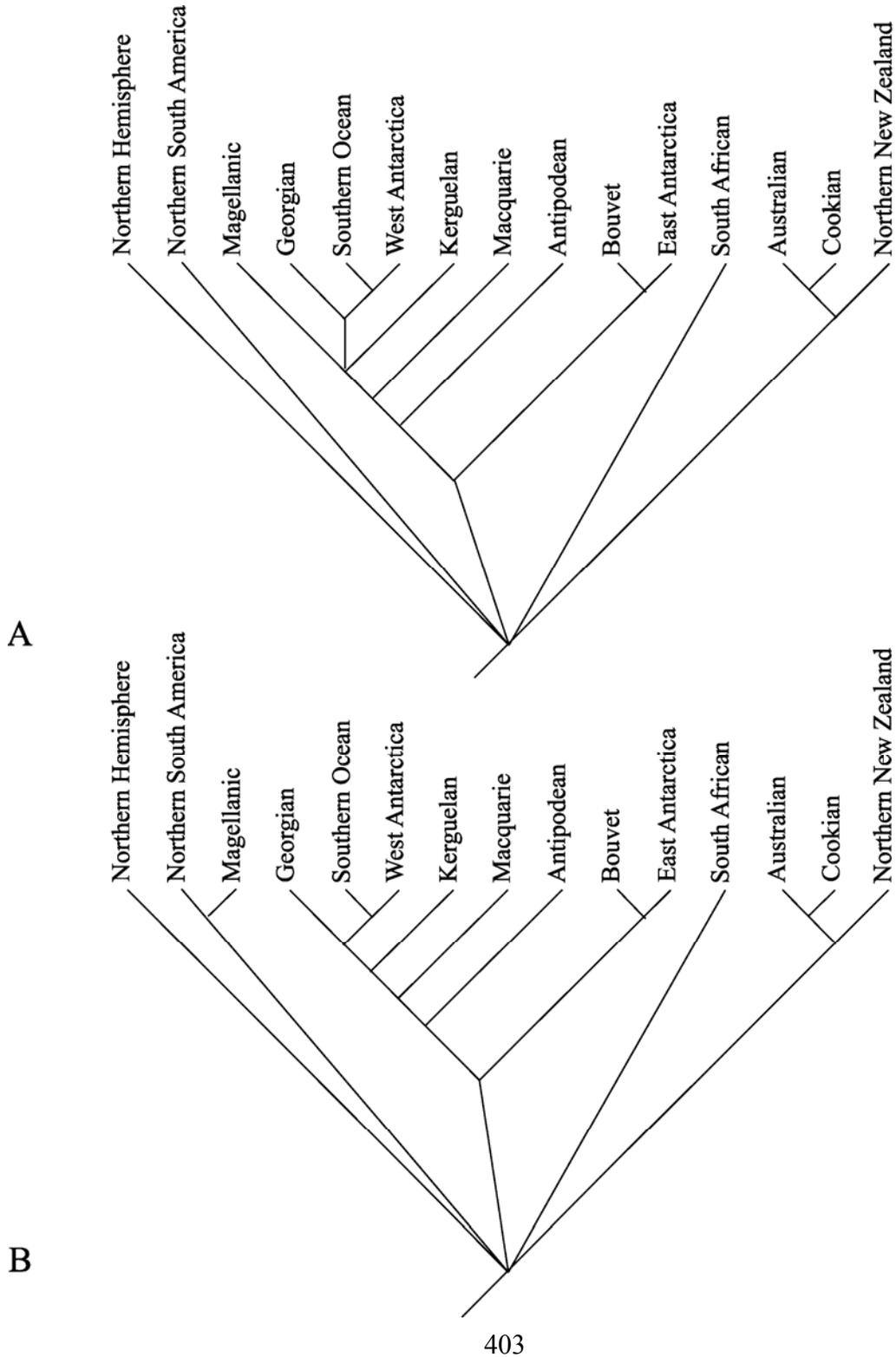
**B**

Area	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37		
Northern South America	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Magellanic	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Georgian	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Southern Ocean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Bouvet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Western Antarctica	0	1	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	
Eastern Antarctica	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
South Africa	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kerguelan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Australian	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Macquarie	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cookian	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0
Northern New Zealand	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Antipodean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Hemisphere	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Area	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74		
Northern South America	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	
Magellanic	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	
Georgian	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Southern Ocean	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bouvet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Western Antarctica	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1
Eastern Antarctica	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
South Africa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kerguelan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Australian	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macquarie	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cookian	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern New Zealand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antipodean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Hemisphere	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

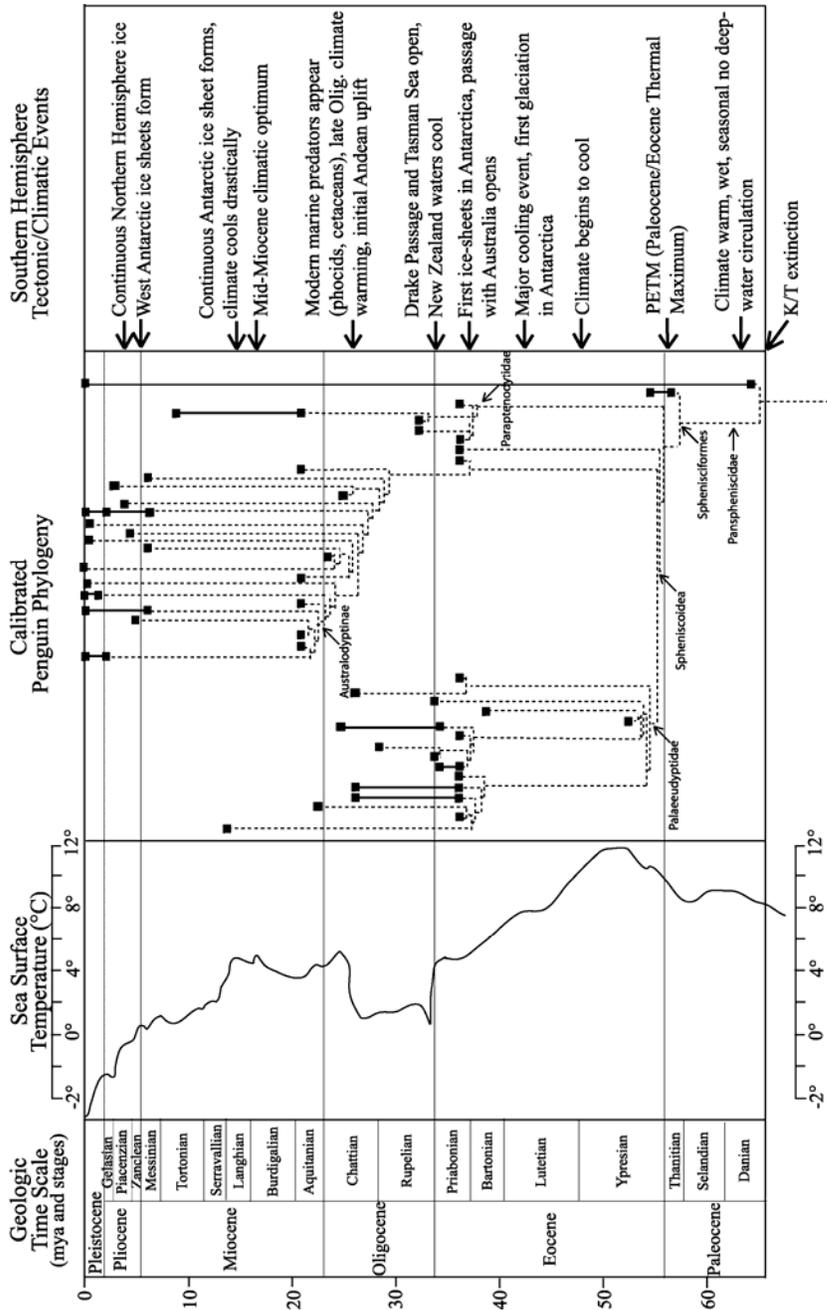
**Figure 4.9. Reconstruction of Historical Biogeography of Panspheniscidae.** Reconstructed areas listed at hatch marks. Areas of major vicariant and dispersal events listed, other areas numbered as in Figure 4.5.



**Figure 4.10. Most Parsimonious Reconstruction of Southern Hemisphere Area Relationships. A. MPT number 1. B. MPT number 2.**



**Figure 4.11. Correlation of Southern Hemisphere and Penguin Evolutionary Events.** Temperature curve from average carbon and oxygen isotope values (Zachos et al., 2001). Data on right from Fordyce and Jones, 1990; Lawver et al., 1992; Buening et al., 1998; Dingle et al., 1998; Dingle and Lavelle, 2000; Dutton et al., 2002; Zachos et al., 2001; Bocheński and Bocheński, 2002; Tambussi et al., 2002; Tyrberg 2002; Lawvery and Gahagan 2003, 2003; Birkenmajer et al., 2005; Holbourn et al., 2005; Lourens et al., 2005, Tripathi et al., 2005; Slack et al., 2006.



**Appendix 1.1. Accepted Extinct Penguin Species.** Named species only are listed by geographic provenance.

Abbreviations: E (early), Eo (Eocene), L (late), M (middle), Mio (Miocene), Olig (Oligocene), Pleisto (Pleistocene), ‘/’ (range denoting stratigraphic uncertainty). Institution abbreviations: AMNH (American Museum of Natural History, New York, USA), ANWC (Australian National Wildlife Collections, Canberra, Australia), CADIC (Centro Austral de Investigaciones Cientificas, Tierra del Fuego, Argentina), CM (Canterbury Museum, Christchurch, New Zealand), DM (Dominion Museum, now Museum of New Zealand Te Papa, Wellington, New Zealand), FLMNH (Florida Museum of Natural History, Gainesville, USA), MACN (Museo de Ciencias Naturales, Buenos Aires, Argentina), MDLP (Museo de La Plata, La Plata, Argentina), MEF (Museo Paleontológico Egidio Feruglio, Trelew, Argentina), MUSM (Museo de Historia Natural, Universidad de San Marcos, Lima, Peru), NHM (Natural History Museum, London, UK), NMV (National Museum of Victoria, Melbourne, Australia), NZGS (New Zealand Geographic Survey, Lower Hutt, New Zealand), OM (Otago Museum, Dunedin, New Zealand), RM (Riksmuseet, Stockholm, Sweden) SAfM (South African Museum, Cape Town, South Africa), UO (University of Otago, Geology Department Museum, Dunedin, New Zealand), WU (Warsaw Museum, Institute of Biology, Białystok Branch, Warsaw, Poland).

<u>Locality</u>	<u>Species</u>	<u>Age</u>	<u>Repository</u>	<u>References</u>
Argentina	<i>Arthrodytes grandis</i>	L Olig/E. Miocene	MACN	Ameghino 1905, Simpson 1946, Tonni 1980
Argentina	<i>Chubutodyptes biloculata</i>	L Olig/E Miocene	AMNH	Simpson 1972, Tonni 1980
Argentina	<i>Eretiscus tonii</i>	M Miocene	MDLP	Simpson 1981, Olson 1986
Argentina	<i>Madrynornis mirandus</i>	L Miocene	MEF	Acosta Hospitaleche et al., 2007
Argentina	<i>Palaeospheniscus bergi</i>	L Olig/E Miocene	MDLP,NHM, MACN	Moreno & Mercerat 1891, Simpson 1946, 1972, Tonni 1980
Argentina	<i>Palaeospheniscus gracilis</i>	L Olig/E Miocene	AMNH, MDLP, MACN	Ameghino 1899, Simpson 1946, 1972, Tonni 1980
Argentina	<i>Palaeospheniscus patagonicus</i>	L Olig/E Miocene	AMNH, MDLP	Ameghino 1899, Simpson 1946, 1972, Tonni 1980
Argentina	<i>Palaeospheniscus wimani</i>	L Olig/E Miocene	AMNH, MDLP, MACN	Moreno & Mercerat 1891, Simpson 1946, 1972, Tonni 1980
Argentina	<i>Paraptenodytes antarcticus</i>	L Olig/E Miocene	AMNH, MDLP	Moreno & Mercerat 1891, Simpson 1946, 1972, Tonni 1980, Bertelli et al. 2006
Argentina	<i>Paraptenodytes robustus</i>	L Olig/E Miocene	MACN, NHM	Ameghino 1899, Simpson 1946, 1972, Tonni 1980
Australia	<i>Anthropodytes gilli</i>	L Miocene	NMV	Simpson 1959
Australia	<i>Anthropornis nordenskjoldi</i>	L Eocene	SAM	Glaessner 1955, Jenkins 1985
Australia	<i>Pachydyptes simpsoni</i>	L Eocene	SAM,AMNH	Jenkins 1974
Australia	<i>Palaeodyptes antarcticus</i>	L Eocene	NMV	Simpson 1970

Australia	<i>Pseudaptodytes macraei</i>	L Miocene	NMV	Simpson 1970
Australia	<i>Tasidyptes hunteri</i>	Holocene	ANWC	van Tets & O'Connor 1983
Chile	<i>Pygoscelis grandis</i>	?E Pliocene	MNHN	Walsh and Suarez 2006
Chile	<i>Spheniscus chilensis</i>	L Pliocene	FLMNH	Emslie & Guerra Correa 2003
Macquarie I.	<i>Aptenodytes patagonicus</i>	Holocene	NMV	McEvey & Vestjens 1974
Macquarie I.	<i>Eudyptes schlegeli</i>	Holocene	NMV	McEvey & Vestjens 1974
New Zealand	<i>Aptenodytes ridgeni</i>	L Pliocene	CM	Simpson 1972b
New Zealand	<i>Archaeospheniscus lowei</i>	E/M Oligocene	OM	Marples 1952, Simpson 1971c
New Zealand	<i>Archaeospheniscus lopdelli</i>	E/M Oligocene	OM	Marples 1952, Simpson 1971c
New Zealand	<i>Dunroonornis parvus</i>	E/M Oligocene	OM	Marples 1952, Simpson 1971c
New Zealand	<i>Eretiscus tonii</i>	M Miocene	MDLP	Simpson 1981, Olson 1986
New Zealand	<i>Eudyptes pachyrhynchus</i>	Holocene	CM	Scarlett 1973
New Zealand	<i>Eudyptula minor</i>	Pleisto-Holocene	CM	Grant-Mackie & Simpson 1973, Scarlett 1983
New Zealand	<i>Korora oliveri</i>	L Oligocene	OM, NZGS	Marples 1952, Simpson 1971c
New Zealand	<i>Marplesornis novaezealandiae</i>	L Pliocene	CM	Marples 1952, 1960, Simpson 1972b
New Zealand	<i>Megadyptes antipodes</i>	E Pleist-Holocene	CM	Scarlett 1983
New Zealand	<i>Pachydyptes ponderosus</i>	L Eocene	DM, OM	Hector 1873, Oliver 1930, Simpson 1971c
New Zealand	<i>Palaeudyptes antarcticus</i>	E/L Oligocene	NZGS, OM, NHM	Huxley 1859, Marples 1952, Simpson 1971c
New Zealand	<i>Palaeudyptes marplei</i>	L Eocene	OM	Brodkorb 1963, Simpson 1971c
New Zealand	<i>Platydyptes amiesi</i>	L Oligocene	OM, UO	Marples 1952, Simpson 1971a
New Zealand	<i>Platydyptes novaezealandiae</i>	Oligocene	OM, DM	Oliver 1930
New Zealand	<i>Pygoscelis tyreei</i>	L Pliocene	CM	Simpson 1972b
New Zealand	<i>Tereingaornis moisleyi</i>	Pliocene	CM	Scarlett 1983, McKee 1987, 1988
New Zealand	<i>Wimanu manningi</i>	Late E Paleocene	CM	Fordyce & Jones 1990, Slack et al. 2006
New Zealand	<i>Wimanu tuatahi</i>	Early L Paleocene	CM, OM	Fordyce & Jones 1990, Slack et al. 2006
Peru	<i>Icadyptes salasi</i>	M-L Eocene	MUSM	Clarket et al., 2007
Peru	<i>Perudyptes devriesi</i>	M-L Eocene	MUSM	Clarke et al., 2007
Peru	<i>Spheniscus megaramphus</i>	L Olig/E. Miocene	MUSM	Stucchi 2003
Peru	<i>Spheniscus urbinai</i>	L Olig/E Miocene	MUSM	Stucchi 2002

Seymour I.	<i>Anthropornis grandis</i>	M/L Eocene	RM	Wiman 1905, Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
Seymour I.	<i>Anthropornis nordenskjoldi</i>	M/L Eocene	RM, NHM	Wiman 1905, Marples 1953, Simpson 1971a, Cione et al. 1977, Olson 985b, Millener 1988, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
Seymour I.	<i>Archaeospheniscus wimani</i>	M/L Eocene	NHM	Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a
Seymour I.	<i>Crossvallia unienwillia</i>	L Paleocene	MDLP	Tambussi et al. 2005
Seymour I.	<i>Delphinornis arctowskii</i>	M/L Eocene	WU, MDLP	Myrcha et al. 2002, Jadwiszczak 2006a
Seymour I.	<i>Delphinornis gracilis</i>	M/L Eocene	WU	Myrcha et al. 2002, Jadwiszczak 2006a
Seymour I.	<i>Delphinornis larseni</i>	M/L Eocene	RM, NHM	Wiman 1905, Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
Seymour I.	<i>Ichtyopteryx gracilis</i>	M/L Eocene	RM	Wiman 1905, Simpson 1971a, Jadwiszczak 2006a
Seymour I.	<i>Marambiornis exilis</i>	L Eo-?E Oligo	WU, MDLP	Myrcha et al. 2002, Jadwiszczak 2006a
Seymour I.	<i>Mesetaornis polaris</i>	L Eo-?E Oligo	WU	Myrcha et al. 2002, Jadwiszczak 2006a
Seymour I.	<i>Orthopteryx gigas</i>	M/L Eocene	RM	Wiman 1905, Marples 1953, Simpson 1971a, Jadwiszczak 2006a
Seymour I.	<i>Palaeudyptes gunnari</i>	M/L Eocene	RM, NHM	Wiman 1905, Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
Seymour I.	<i>Palaeudyptes klekowskii</i>	M/L Eocene	WU	Myrcha et al. 1990, Jadwiszczak 2006a, Tambussi et al. 2006
Seymour I.	<i>Wimanornis seymourensis</i>	M/L Eocene	NHM	Simpson 1971a, Jadwiszczak 2006a
Seymour I.	<i>Tonniornis mesetaensis</i>	M/L Eocene	MDLP	Tambussi et al., 2006; Jadwiszczak 2006b
Seymour I.	<i>Tonniornis minimum</i>	M/L Eocene	MDLP	Tambussi et al., 2006; Jadwiszczak 2006b
South Africa	<i>'Dege' hendeyi</i>	L Mio-E Pliocene	SAfM	Simpson 1971b, 1973, 1979a, 1979b, Olson 1983, Hendey 1975, Vickers-Rich 1980
South Africa	<i>'Inguza' predemersus</i>	L Pliocene	SAfM	Simpson 1971b, Olson 1983
South Africa	<i>'Nucleornis' hendeyi</i>	L Pliocene	SAfM	Simpson 1971b, Olson 1983
South Africa	<i>?Palaeospheniscus huxleyorum</i>	L Pliocene	SAfM	Simpson 1971b, Olson 1983

## Appendix 2.1. CT Scanning Parameters.

Taxon	Specimen Number	Scan Date	Slice Thickness and Interslice Spacing (mm)	Image field of Reconstruction (mm)	Total Slices
<i>Aptenodytes forsteri</i>	UF 22281	July 19, 2005	0.199	95	916
<i>Aptenodytes forsteri</i>	AMNH 11125	Sept. 8, 2005	0.103	98	1300
<i>Eudyptula minor</i>	UF 31924	Sept. 14, 2005	0.113	50	810
<i>Phalacrocorax penicillatus</i>	TMM M-1180	Oct. 31, 2006	0.1149	50	1652
<i>Podilymbus podiceps</i>	TMM M-7139	Nov. 3, 2006	0.05573	26.4	1110
<i>Pygoscelis adeliae</i>	UF 36633	Sept. 14, 2005	0.14	66.8	900
<i>Pygoscelis antarctica</i>	UF 36657	July 5, 2005	0.1341	56	900
<i>Spheniscus demersus</i>	UF 21341	July 11, 2005	0.119	56	954

## Appendix 2.2. Extant, Extinct, and Outgroup Specimens Examined.

Institutional abbreviations: AMNH (American Museum of Natural History, New York, U.S.A.), ANWC (Australian National Wildlife Collections, Canberra, Australia), CM (Canterbury Museum, Christchurch, New Zealand), DM (Dominion Museum, Wellington, New Zealand), MDLP (Museum de la La Plata, La Plata, Argentina), NHM (Natural History Museum, London, U.K.), NMV (National Museum of Victoria, Melbourne, Australia), OM (Otago Museum, Dunedin, New Zealand), SAfM (South African Museum, Cape Town, South Africa), TMM (Texas Memorial Museum, Austin, U.S.A.), UF (University of Florida, Gainesville, U.S.A.), UO (University of Otago, Dunedin, New Zealand), WU (Warsaw Museum, Institute of Biology, Bialystok Branch, Poland).

Specimens examined directly: *Aechmorphus occidentalis* (AMNH 18782), *?Anthropornis grandis* (NHM A2022), *Anthropornis grandis* (NHM A2002, A2007, A2018, A2025), *Anthropornis nordenskjoeldi* or *Palaeudyptes antarcticus* (NHM A3328-30, A3338, A3348-56, A3363), *Anthropornis nordenskjoeldi* (NHM A2000, A2005, A2006, A2011-4, A2019, A2021, A2023-4, A3327, A3343, A3357-9, A3362, A3369B, A5574), *Aptenodytes forsteri* (AMNH 11125; UF 22280-1), *Aptenodytes patagonicus* (AMNH 1623-4, 2611, 4382-3, 25471-2, 27330; TMM ??), *Archaeospheniscus lopdelli* (OM C47.21), *Archaeospheniscus lowei* (OM C47.20, C47.27), *?Archaeospheniscus wimani* (NHM A2017, A2026), *Archaeospheniscus wimani* (NHM A3331), *Chubutodytes biloculata* (AMNH 3341, 3346), *?Delphinornis sp.* (NHM A5579), *Delphinornis gracilis* (NHM A5578), *Delphinornis c.f. larseni* (NHM A5577), *Delphinornis larseni* (NHM A2003, A5580), *Diomedea bulleri* (OM AV585), *Diomedea epomophora sanfordi* (OM AV9502), *Diomedea immutabilis* (FLMNH 313780), *Diomedea melamophris* (AMNH 23564), *Dunroonornis parvus* (OM C47.31), *Eudyptes chrysocome* (AMNH 3854, 5398, 5972; OM AV829), *Eudyptes chrysolophus*

(TMM ??; AMNH 26478, 27338), *Eudyptes ?pachyrhynchus* (NHM 3272), *Eudyptes pachyrhynchus* (AMNH 14824, 26509; NHM A948, A3268, A3270-1, A3273, 32116; OM 309, AV965), *Eudyptes robustus* (AMNH 27678; OM AV1909, AV1178), *Eudyptes schlegeli* (AMNH 5399; UF 22277), *Eudyptes sclateri* (OM 764, AV1331, AV7861), *Eudyptes sp.* (CM 1051; OM AV712948), *Eudyptula minor* (TMM M2931, M2943-5, M2948, M951-2; NHM A714, A4205; OM AV7081, AV7104), *Eudyptula minor albosignata* (NHM A32112; UF 22283), *Eudyptula minor novaehollandiae* (UF 22285-6), *Eudyptula sp.* (NHM A953, A982, A2998, A3273, A3275-7, A3831, A3839, A3849, A3861-4, 3868-83, A3885-968, 3970-89, A3992-7, A3999-4003, 32120), *Fulmar glacialis* (OM AV10251), *Gavia immer* (digimorph.org), *Gavia stellata* (AMNH 4974, 27341), *Ichthyopteryx gracilis* (AMNH 2004, A5573), *Isotremornis nordenskjoldi* (AMNH 3310), *Korora oliveri* (OM C50.63), *Megadyptes antipodes* (AMNH 5615; NHM 32167; OM AV832, AV948, AV954, AV962), *?Notodyptes sp.* or *Wimanornis seymourensis* (NHM A3326), 'Nucleornis' *insolitus* (SAfM 4), *Orthopteryx ?gigas* (NHM A2028-9), *Orthopteryx gigas* (NHM A2027), *Pachydyptes ponderosus* (DM 1450; OM C47.16), *Pachydyptes simpsoni* (NHM A3361), *Palaeodyptes ?antarcticus ?gunnari* (NHM A3332-3, A3364-5), *Palaeodyptes antarcticus* (DM 1449; NHM A1048, A3334-6, A4077-9; OM C47.17, C47.22-5, C47.34, C48.73-81, C50.25-47), *Palaeodyptes gunnari* or *Wimanornis seymourensis* (NHM A3368), *Palaeodyptes ?gunnari* (NHM A3342), *Palaeodyptes c.f. gunnari* (NHM A5581), *Palaeodyptes gunnari* (NHM A2001, A2008-10, A2015, A2020, A2030, A3341, A5572), *Palaeodyptes c.f. marplei* (NHM A5571), *Palaeodyptes marplei* (NHM A6118; OM C50.25-47), *?Palaeodyptes sp.* (NHM A3372), *Palaeodyptes sp.* (NHM A3340, A3369, A6117, A6120; OM 22232, C47.17-8, C48.73-81), *Palaeospheniscus bergi* (NHM A590, A684, A688-91, A693-4), *Palaeospheniscus gracilis* (AMNH 3284, 3288, 3313, 3322, 3326, 3333-4, 3345, 3355, 3362-3, 3367), *Palaeospheniscus patagonicus* (AMNH 3214-5, 3273-7, 3280-2, 3286-7, 3289-91, 3293, 3295-9, 3306, 3307-9, 3311-2, 3317-8, 3320-1, 3323-4, 3330-2, 3335, 3340, 3343-4, 3348-51, 3353, 3358, 3368, 3372-3, 3383), *?Palaeospheniscus sp.* (NHM A484, A687), *Palaeospheniscus sp.* (AMNH 3304-5, 3319, 3325, 3327, 3342, 3347, 3356-7, 3359, 3375-7; NHM A684, A688, A695), *?Paraptenodytes antarcticus* (NHM A592), *Paraptenodytes antarcticus* (AMNH 3338; NHM A592, A686), *Paraptenodytes robustus* (NHM A591), *Perispheniscus robustus* (AMNH unnumbered), *Phalacrocorax carbo* (OM AV881), *Platydyptes amiesi* (OM C50.61-2, C47.35), *Platydyptes novaezealandiae* (DM 1451; OM C47.15, C50.51-2), *Podiceps major* (AMNH 5044), *Pygoscelis adeliae* (TMM ??; UF 22288, 36633), *Pygoscelis antarctica* (UF 36655, 36657), *Pygoscelis papua* (UF 36660-1; OM 40), *Pygoscelis sp.* (NHM A945, A32168), *Spheniscus demersus* (NHM unnumbered; UF 21341), *Spheniscus humboldti* (TMM ??; UF 22270, 22274; CM 2129, 2138), *Spheniscus magellanicus* (AMNH 26480-1; TMM M1930), *Spheniscus mendiculus* (AMNH 2624, 3648, 3650, 3741; NHM unnumbered), *?Wimanornis seymourensis* (NHM A2016), *Wimanornis ?seymourensis* (NHM A5575), *Wimanornis seymourensis* (NHM A3325, A3339, A3346, A3367, A3370, A5570, A5576), Spheniscidae indet. (AMNH 3273, 3379, 3382, 3451), Spheniscidae gen. et sp. nov. (OM C47.25, OM C47.23A).

Specimens examined from the literature: *Anthropodytes gilli* (NMV P17167), *Anthropornis grandis* (WU 0483; MDLP83-V-20-84, 95-I-10-142, 94-III-15-178; RM A22), *Anthropornis nordenskjoeldi* (WU 0070, 0085a-b, 0287; MDLP 84-II-1-7, 83-V-20-50, 83-II-1-19; NHM A3330; RM A45, A8), *Aptenodytes ridgeni* (CM AV22632), *Archaeospheniscus wimani* (WU 0284, 0289, 0491; MDLP 90-I-20-24, 91-II-4-173), *Crossvallia unienwillia* (MDLP 00-I-10-1), '*Dege*' *hendeyi* (SAfM L28455, L5503, L5505, L5510, L28217), *Delphinornis arctowskii* (WU 0484; MDLP 93-X-1-92), *Delphinornis gracilis* (WU 0279a, 0492), *Delphinornis larseni* (WU 0062, 0280, 0299, 0547-8; MDLP 83-V-20-5, 91-II-4-174, 84-II-1-79), *Eretiscus tonii* (MDLP 81-VI-26-1, 69-III-29-25), '*Inguza predemersus*' (SAfM L6510, L6507, L3656, L13154), *Marambiornis exilis* (WU 0490; MDLP 93-X-1-111), *Marplesornis novaezealandiae* (CM AV16527), *Mesetaornis polaris* (WU 0278), *Palaeudyptes gunnari* (MDLP 92-II-4-222; WU 0072, 0112, 277, 0487; NHM A3340, A3368), *Palaeudyptes klekowski* (WU 0061, 0065, 0081, 0093, 0101, 0142, 0), *Pseudaptenodytes macraei* (MV P26668), *Pygoscelis grandis* (SGOPV 1104-8), *Pygoscelis tyreei* (CM AV22631), *Spheniscus chilensis* (UF 1-130697), *Spheniscus megaramphus* (MUSM 362-5485; MDLP 93-X-1-142, 84-II-1-78, 84-II-1-124, 94-III-15-20), *Spheniscus urbinai* (MUSM 401-5, 269), *Tasidyptes hunteri* (ANWC BS2667-70), *Tereingaornis moisleyi* (CM zfa11; NZGS unnumbered), *Wimanornis seymourensis* (NHM A3325, A3367), *Wimanu manningi* (CM zfa35), *Wimanu tuatahi* (OU 12651; CM zfa33-4), Spheniscidae gen. et sp. nov. (Tierra del Fuego species, CADIC P-21).

**Appendix 3.1. Extant, Extinct, and Outgroup Specimens Utilized in Phylogenetic Analysis.** Institutional abbreviations: AMNH (American Museum of Natural History, New York), ANWC (Australian National Wildlife Collections, Canberra), CM (Canterbury Museum, Christchurch), DM (Dominion Museum, Wellington), MDLP (Museum de la Plata, La Plata), MNHM (Museo Nacional de Historia Natural, Santiago), NHM (Natural History Museum, London), NMV (National Museum of Victoria, Melbourne, Australia), OM (Otago Museum, Dunedin), SAfM (South African Museum, Cape Town), TCWC (Texas Cooperative Wildlife Collection, Austin), TMM (Texas Memorial Museum, Austin), UF (University of Florida, Gainesville), UO (University of Otago, Dunedin), WU (Warsaw Museum, Institute of Biology, Białystok Branch).

Specimens examined directly: *Aechmorphismus occidentalis* (AMNH 18782), *Anthropornis grandis* (NHM A2002, A2007, A2018, A2022, A2025), *Anthropornis nordenskjoldi* (NHM A2000, A2005, A2006, A2011-4, A2019, A2021, A2023-4, A3327, A3343, A3357-9, A3362, A3369B, A5574), *Aptenodytes forsteri* (AMNH 11125; UF 22280-1), *Aptenodytes patagonicus* (AMNH 1623-4, 2611, 4382-3, 25471-2, 27330; TMM ??), *Archaeospheniscus lopdelli* (OM C47.21), *Archaeospheniscus lowei* (OM C47.20, C47.27), *Archaeospheniscus wimani* (NHM A2017, A2026, A3331), *Chubutodytes biloculata* (AMNH 3341, 3346), *Delphinornis gracilis* (NHM A5578), *Delphinornis larseni* (NHM A2003, A5577, A5580), *Diomedea bulleri* (OM AV585), *Diomedea epomophora sanfordi* (OM AV9502), *Diomedea immutabilis* (FLMNH 313780), *Diomedea melamophris* (AMNH 23564), *Dunroonornis parvus* (OM C47.31), *Eudyptes chrysocome* (AMNH 3854, 5398, 5972; OM AV829), *Eudyptes chrysolophus* (TMM ??; AMNH 26478, 27338), *Eudyptes pachyrhynchus* (AMNH 14824, 26509; NHM A948, A3268, A3270-3, 32116; OM 309, AV965), *Eudyptes robustus* (AMNH 27678; OM AV1178, AV1909), *Eudyptes schlegeli* (AMNH 5399; UF 22277), *Eudyptes sclateri* (OM 764, AV1331, AV7861), *Eudyptula minor* (TMM M M931, 2943-5, M2948, M2951-2; NHM A714, A4205; OM AV7104, AV7081), *Eudyptula minor albosignata* (NHM A32112; UF 22283), *Eudyptula minor novaehollandiae* (UF 22285-6), *Fulmarus glacialis* (OM AV10251), *Gavia immer* (TCWC 13300), *Gavia stellata* (AMNH 4974, 27341), *Ichthyopteryx gracilis* (AMNH 2004, A5573), *Korora oliveri* (OM C50.63), *Megadyptes antipodes* (AMNH 5615; NHM 32167; OM AV954, AV962, AV832, AV948), *'Nucleornis' insolitus* (SAfM 4), *Orthopteryx gigas* (NHM A2027-9), *Pachydyptes ponderosus* (DM 1450; OM C47.16), *Pachydyptes simpsoni* (NHM A3361), *Palaeodyptes antarcticus* (DM 1449; NHM A1048, A3334-6, A4077-9; OM C47.17, C47.22-5, C47.34, C48.73-81, C50.25-47), *Palaeodyptes gunnari* (NHM A2001, A2008-10, A2015, A2020, A2030, A3341-2, A5572, A5581), *Palaeodyptes marplei* (NHM A5571, A6118; OM C50.25-47), *Palaeospheniscus bergi* (NHM A590, A684, A688-91, A693-4), *Palaeospheniscus gracilis* (AMNH 3284, 3288, 3313, 3322, 3326, 3333-4, 3345, 3355, 3367, 3362-3), *Palaeospheniscus patagonicus* (AMNH 3214-5, 3273-7, 3280-2, 3286-7, 3289-91, 3293, 3295-9, 3306, 3307-9, 3311-2, 3317-8, 3320-1, 3323-4, 3330-2, 3335, 3340, 3343-4, 3348-51, 3353, 3358, 3368, 3372-3, 3383), *Paraptenodytes antarcticus* (AMNH 3310, 3338; NHM A592, A686), *Paraptenodytes robustus* (NHM A591), *Phalacrocorax carbo* (OM AV881), *Platydyptes amiesi* (OM C50.61-2, C47.35), *Platydyptes novaezealandiae* (DM 1451; OM C47.15, C50.51-2),

*Podiceps major* (AMNH 5044), *Pygoscelis adeliae* (TMM ??; UF 22288, 36633), *Pygoscelis antarctica* (UF 36655, 36657), *Pygoscelis papua* (UF 36660-1; OM 40), *Spheniscus demersus* (NHM unnumbered; UF 21341), *Spheniscus humboldti* (TMM ??; UF 22270, 22274; CM 2129; 2138), *Spheniscus magellanicus* (AMNH 26480-1; TMM M1930), *Spheniscus mendiculus* (AMNH 2624, 3648, 3650, 3741; NHM unnumbered), *Wimanornis seymourensis* (NHM A2016, A3325, A3339, A3346, A3367, A3370, A5570, A5575-6), Spheniscidae gen. et sp. nov. (OM C47.25; C47.23A).

Specimens coded from the literature: *Anthropodytes gilli* (NMV P17167), *Anthropornis grandis* (WU 0483; MDLP83-V-20-84, 95-I-10-142, 94-III-15-178; RM A22), *Anthropornis nordenskjoeldi* (WU 0070, 0085a-b, 0287; MDLP 84-II-1-7, 83-V-20-50, 83-II-1-19; NHM A3330; RM A45, A8), *Aptenodytes ridgeni* (CM AV22632), *Archaeospheniscus wimani* (WU 0284, 0289, 0491; MDLP 90-I-20-24, 91-II-4-173), *Crossvallia unienwillia* (MDLP 00-I-10-1), 'Dege' *hendeyi* (SAfM L28455, L5503, L5505, L5510, L28217), *Delphinornis arctowskii* (WU 0484; MDLP 93-X-1-92), *Delphinornis gracilis* (WU 0279a, 0492), *Delphinornis larseni* (WU 0062, 0280, 0299, 0547-8; MDLP 83-V-20-5, 91-II-4-174, 84-II-1-79), *Eretiscus tonii* (MDLP 81-VI-26-1, 69-III-29-25), 'Inguza' *predemersus* (SAfM L6510, L6507, L3656, L13154), *Marambiornis exilis* (WU 0490; MDLP 93-X-1-111), *Marplesornis novaezealandiae* (CM AV16527), *Mesetaornis polaris* (WU 0278), *Palaeedyptes gunnari* (DMLP 92-II-4-222; WU 0072, 0112, 277, 0487; NHM A3340, A3368), *Palaeedyptes klekowski* (WU 0061, 0065, 0081, 0093, 0101, 0142, 0), *Pseudaptenodytes macraei* (MV P26668), *Pygoscelis grandis* (SGOPV 1104-8), *Pygoscelis tyreei* (CM AV22631), *Spheniscus chilensis* (UF 1-130697), *Spheniscus megaramphus* (MUSM 362-5485; MDLP 93-X-1-142, 84-II-1-78, 84-II-1-124, 94-III-15-20), *Spheniscus urbinai* (MUSM 401-5, 269), *Tasidyptes hunteri* (ANWC BS2667-70), *Tereingaornis moisleyi* (CM zfa11; NZGS unnumbered), *Wimanornis seymourensis* (NHM A3325, A3367), *Wimanu manneringi* (CM zfa35), *Wimanu tuatahi* (OU 12651; CM zfa33-4), Spheniscidae gen. et sp. nov. (CADIC P-21).

**Appendix 3.2. Percentage of Data Scored for Analyzed Taxa.** Generic names abbreviated, as in character matrix.

Taxon	% scored	% osteology scored	Taxon	% scored	% osteology scored	Taxon	% scored	% osteology scored
<i>A. gilli</i>	4.3	6.5	<i>I. gracilis</i>	7.2	11.2	<i>P. antarcticus</i>	90.4	---
<i>A. grandis</i>	10.1	15.0	" <i>I. predemersus</i> "	14.5	21.8	<i>P. grandis</i>	19.1	28.5
<i>A. nordenskjoldi</i>	17.1	25.6	<i>K. oliveri</i>	7.5	11.2	<i>P. papua</i>	91.9	---
<i>A. forsteri</i>	91.9	---	<i>M. exilis</i>	6.7	10.0	<i>P. tyreei</i>	7.5	11.2
<i>A. patagonicus</i>	92.7	---	<i>M. novaezealandiae</i>	3.7	5.6	<i>S. chilensis</i>	11.4	17.1
<i>A. ridgeni</i>	10.4	15.6	<i>M. antipodes</i>	98.2	---	<i>S. demersus</i>	91.6	---
<i>A. lopdelli</i>	18.5	27.7	<i>M. polaris</i>	6.9	10.3	<i>S. humboldti</i>	91.4	---
<i>A. lowei</i>	16.7	26.0	" <i>N. insolitus</i> "	6.7	10.0	<i>S. magellanicus</i>	91.9	---
<i>A. wimani</i>	13.9	20.9	<i>O. gigas</i>	3.9	5.9	<i>S. megaramphus</i>	6.1	9.1
<i>C. biloculata</i>	5.9	8.8	<i>P. ponderosus</i>	12.0	17.9	<i>S. mendiculus</i>	88.8	---
<i>C. unienwillia</i>	6.7	10.0	<i>P. simpsoni</i>	11.8	17.7	<i>S. urbinai</i>	19.3	28.9
<i>D. hendeyi</i>	11.2	16.8	<i>P. antarcticus</i>	22.6	33.8	<i>T. hunteri</i>	12.2	18.2
<i>D. arctowski</i>	7.3	10.9	<i>P. gumari</i>	16.7	25.0	<i>T. moisleyi</i>	8.6	12.9
<i>D. gracilis</i>	7.5	11.2	<i>P. klekowski</i>	6.9	10.3	<i>W. seymourensis</i>	14.7	22.1
<i>D. larseni</i>	9.6	14.4	<i>P. marplei</i>	20.2	30.3	<i>W. manningi</i>	12.6	18.8
<i>D. parvus</i>	6.9	10.3	<i>P. bergi</i>	25.6	38.2	<i>W. tuatahi</i>	26.5	10.3
<i>E. tonii</i>	7.1	10.6	<i>P. gracilis</i>	2.0	3.0	CADIC P-21	4.9	7.4
<i>E. chrysocome</i>	92.9	---	<i>P. patagonicus</i>	25.5	38.2	OM C47.25	12.2	18.2
<i>E. chrysolophus</i>	94.1	---	<i>P. wimani</i>	7.7	11.5	OM C47.23A	12.4	18.5
<i>E. pachyrhynchus</i>	97.4	---	<i>P. antarcticus</i>	32.2	48.2	Gaviidae	80.4	---
<i>E. robustus</i>	89.2	---	<i>P. robustus</i>	20.8	31.2	Phalacrocoracidae	67.2	---
<i>E. schlegeli</i>	90.6	---	<i>P. amiesi</i>	8.1	12.1	Podicipedidae	64.8	---
<i>E. sclateri</i>	89.4	---	<i>P. novaezealandiae</i>	16.9	25.3	Procellariiformes	92.3	---
<i>Eu. minor</i>	98.2	---	<i>P. macreei</i>	3.5	5.3			
<i>Eu. minor albognata</i>	90.0	---	<i>P. adeliae</i>	98.2	---			

**Appendix 3.3. Character Definitions.** Previous authors are listed only for characters used in systematic analyses. Character numbers from Giannini and Bertelli 2004, Bertelli et al. 2006, and Ksepka et al. 2006 are listed only if they are not included in Bertelli and Giannini 2005. Characters analyzed in O'Hara 1989 are numbered here, while those discussed but not analyzed are unnumbered. Characters not previously pictured in other systematic works are illustrated here in text figures (referenced by final parenthetical item).

General:

1. Skull and post-cranial pneumaticity. State 0: absent. State 1: present, in both skull and postcrania, as in all outgroups (Figure 13).
2. Temporal fossae. State 0: deeply excavated, nearly to midline, and narrow. State 1: far apart, at least the width of the cerebellar prominence, only weakly hollowed, and narrow. State 2: deeply excavated, nearly to the midline, and extremely wide. Modified from Zusi 1975, Cracraft 1982 (char. 2, Fig. 2), Mayr 2005 (char. 17), Bertelli and Giannini 2005 (char.76, Fig. 9), Walsh and Suarez 2006 (char. 4).
3. Orbit. State 0: small, as in Gaviidae. State 1: large, as in *Aptenodytes* (Figure 8).
4. Foramen magnum. State 0: taller than broad, as in *Megadyptes*. State 1: broader than tall, as in *Eudyptes* State 2: equally tall and broad, as in *Spheniscus* (Figure 10).
5. Foramen magnum, slight lateral indentations. State 0: absent, as in Procellariiformes. State 1: present, small, as in *Spheniscus*. State 2: present, large, as in Gaviidae (Figure 10). Ordered.
6. Skull length, measured from tip of beak to posteriormost section of braincase in a horizontal plane. State 0: 115 mm or less. State 1: 116 mm-130 mm. State 2: 131 mm-170 mm. State 3: 171 mm or more Ordered.
7. Cranial height. State 0: flattened dorsoventrally, as in *Spheniscus*. State 1: unflattened, as in *Eudyptula* (Figure 8).
8. Length of beak compared with length of remainder of skull. Beak measured from anterior tip to break in slope for orbit. Remainder of skull measured to posteriormost section of braincase in a horizontal plane. State 0: beak shorter. State 1: equal in length. State 2: beak longer. Ordered.
9. Shape of beak. State 0: gracile and long, expands somewhat distally, as in *Aptenodytes*. State 1: short and robust, triangular, owing to laterally expanded premaxilla, as in *Spheniscus* (Figure 9).
10. Jaw compared with basitemporal plate. State 0: both lie horizontally, as in *Aptenodytes*. State 1: jaw depressed, as in *Pygoscelis*. State 2: jaw upturned, as in Gaviidae (Figure 8).
11. Wing bones, degree of flattening. State 0: extreme. State 1: less extreme. State 2: absent. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 121), Mayr 2005 (char. 41) (Figure 14). Ordered.
12. Angle of humerus with radius/ulna. Measured at point of intersection between two bones. State 0: 140°-150°. State 1: 110°. State 2: 160° (Figure 14).
13. Radius width compared with ulna width. State 0: equal. State 1: radius wider. State 2: ulna wider (Figure 14).
14. Limb bones. State 0: heavily pachyostotic and rigid (little elbow movement), as in *Paraptenodytes*. State 1: not pachyostotic or rigid, as in extant Spheniscidae. Modified from Mayr 2005 (char. 50).

Premaxilla:

15. Tip. State 0: deflected downward and laterally compressed. State 1: deflected downward, uncompressed. State 2: neither deflected nor compressed. Modified from Mayr 2005 (char. 1, Fig. 6).
16. End, distal to nostril. State 0: smooth. State 1: marked furrow present. State 2: marked furrow present, extremely elongated. Modified from Mayr and Clarke 2003 (char. 4, Fig. 4a), Mayr 2005 (char. 5).

17. Nostrils. State 0: small, holorhinal (with rounded posterior border ending anterior to nasal process of premaxilla). State 1: reduced. State 2: large, holorhinal. Modified from Mayr 2005 (char. 3, Fig. 6).
18. Nostrils. State 0: extend caudally beyond the antorbital fenestra, which is elongated anteriorly. State 1: extend caudal to antorbital fenestra, which is triangular. State 2: do not extend caudally beyond antorbital fenestra, which is triangular. State 3: do not extend caudally beyond antorbital fenestra, which is elongated anteriorly. Modified from O'Hara 1989 (char. 5, Fig. 2), Bertelli and Giannini 2005 (char. 84, Fig. 11).
19. Nasal process (pila supranasalis). State 0: long, narrow, slightly constricted laterally. State 1: short, narrow, slightly constricted laterally. State 2: short, wide, unconstricted. Modified from O'Hara 1989 (char. 6, Fig. 3), Bertelli and Giannini 2005 (char. 85, Fig. 12).
20. Nasal process sutures (premaxilla-premaxilla). State 0: present and visible in adult, as in *Aptenodytes*. State 1: fused proximally, as in *Spheniscus* (Figure 9).
21. Bony tomial ridge. State 0: lies at level of basitemporal plate. State 1: lies dorsal to level of basitemporal plate. Modified from Zusi 1975, Bertelli and Giannini 2005 (char. 97).
22. Nasopremaxillary suture. State 0: present and visible in adult, as in *Aptenodytes*. State 1: completely fused, as in Podicipedidae. Modified from Bertelli and Giannini 2005 (Figure 9).
- Maxilla:
23. Palatine contact. State 0: sutured. State 1: fused. Modified from Mayr 2005 (char. 6) (Figure 11).
24. Length of maxillopalatine. State 0: short, as in *S. demersus*. State 1: long, as in *Aptenodytes* (Figure 11).
25. Maxillopalatine. State 0: narrow horizontally, as in Spheniscidae. State 1: wide horizontally, extending nearly to midline, as in Procellariiformes (Figure 11).
- Nasal:
26. Fronto-nasal contact. State 0: unhinged, large depression. State 1: unhinged, small depression. State 2: somewhat hinged. State 3: distinctly hinged. Modified from Mayr 2005 (char. 2, Fig. 6).
27. Fronto-nasal contact. State 0: sutured, as in *Aptenodytes forsteri*. State 1: fused, as in remaining Spheniscidae (Figure 9).
28. Frontal process. State 0: short, as in *Aptenodytes*. State 1: long, as in *Pygoscelis* (Figure 9).
- Lacrimal:
29. Dorsal surface. State 0: covered by frontal, as in *Spheniscus*. State 1: visible externally, as in *Aptenodytes*. State 2: extensively visible dorsally, as in Procellariiformes. Modified from Bertelli and Giannini 2005 (char. 82) (Figure 9). Ordered.
30. Orbital process. State 0: absent. State 1: prominent. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 82, Fig. 11).
31. Anteroventral process. State 0: absent, as in all outgroups. State 1: present, as in *Aptenodytes* (Figure 8).
32. Jugal contact and lacrimal foramen. State 0: both absent. State 1: contact present, forming flattened boot with small foramen. State 2: contact present, forming flattened boot with large foramen. Modified from O'Hara 1989 (char. 11), Bertelli and Giannini 2005 (char. 81, Fig. 11).
33. Frontal contact. State 0: present. State 1: bones separated by wide split. Modified from Bertelli and Giannini 2005 (char. 83).
34. Width between lacrimals compared with cranial width. Lacrimals measured at widest point, cranial width measured at postorbital process. State 0: lacrimal at least  $\frac{1}{2}$  cranial width. State 1: lacrimal less than  $\frac{1}{2}$  cranial width.
- Ectethmoid:
35. Ectethmoid. State 0: absent. State 1: present, small. State 2: robust, contacting or fused with lacrimal. Modified from Bertelli and Giannini 2005 (char. 80) (Figure 8). Ordered.
36. Ectethmoid, anteroventral emargination. State 0: absent, as in *Aptenodytes*. State 1: present, as in *Spheniscus* (Figure 8).
- Mesethmoid:
37. Interorbital septum. State 0: small, as in *Aptenodytes*. State 1: well-developed, as in *Spheniscus*.

38. Orbitocranial foramen. State 0: small or vestigial. State 1: large and conspicuous. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 79, Fig. 10).

Frontal:

39. Shape, interorbital section (excluding supraorbital shelf). State 0: narrow, as in *Pygoscelis*. State 1: wide, as in *Aptenodytes* (Figure 9).

40. Supraorbital salt gland fossa (fossa glandulae nasalis). State 0: absent, as in Phalacrocoracidae. State 1: very marked, on dorsal surface of supraorbital margin of orbits, as in *Aptenodytes*. State 2: very marked, with lateral supraorbital shelf, as in *Eudyptes chrysocome*. Modified from O'Hara 1989 (char. 10), Mayr and Clarke 2003 (char. 25), Bertelli and Giannini 2005 (char. 75, Fig. 9), Mayr 2005 (char. 18).

41. Posterior, orbital section of bone. State 0: rounded, as in *Spheniscus*. State 1: elongate, as in *Aptenodytes* (Figure 9).

42. Postorbital process. State 0: thin and vertical. State 1: thin and angled. State 2: thick and vertical. State 3: thick and angled (Figure 8).

43. Scleral ossicles, number. State 0: 13 or fewer. State 1: fourteen or more. Modified from Mayr 2005 (char. 21).

Jugal:

44. Curvature in lateral view. State 0: straight. State 1: slightly curved. State 2: ventrally bowed. State 3: strongly curved, sigmoid shape. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 93, Fig. 14), Walsh and Suarez 2006 (char. 1).

45. Zygomatic process. State 0: absent or vestigial, as in Procellariiformes. State 1: present, as in Spheniscidae.

Quadrate:

46. Position of mandibular articulation. State 0: lies directly ventral to otic articulation, as in *Spheniscus*. State 1: lies anterior to otic articulation, owing to quadrate angling anteriorly with its descent, as in *Aptenodytes* (Figure 8).

47. Body, lateral mandibular condyle. State 0: lies in same plane as medial mandibular condyle, as in *Spheniscus*. State 1: lies anterior to medial mandibular condyle, *Aptenodytes*. State 2: lies posterior to medial mandibular condyle, as in Procellariiformes (Figure 13).

48. Body, caudal mandibular condyle. State 0: absent, as in *Pygoscelis*. State 1: present, as in *Aptenodytes* (Figure 10).

49. Quadratojugal cup. State 0: absent. State 1: present and small, as in *Pygoscelis*. State 2: present and deep, as in *Aptenodytes* (Figure 13). Ordered.

50. Pterygoid condyle. State 0: confluent with body. State 1: extended from body. State 2: extended from body to form distinct tubercle. Modified from Mayr 2005 (char. 19) (Figure 13).

51. Pterygoid condyle. State 0: concave articular surface, as in Procellariiformes. State 1: convex articular surface, as in Spheniscidae (Figure 13).

52. Neck. State 0: long and slender, as in Spheniscidae. State 1: short and wider, as in all outgroups (Figure 8).

53. Otic process, rostralateral process for attachment of *M. adductor mandibulae externus, pars profunda*. State 0: absent. State 1: present as ridge. State 2: present as tubercle. Modified from Bertelli and Giannini 2005 (char. 96, Fig. 15).

54. Otic process. State 0: bifurcate, as in Spheniscidae. State 1: single, as in all outgroups (Figure 13).

55. Orbital process. State 0: short. State 1: medium. State 2: very long. Modified from Mayr 2005 (char. 20) (Figure 8). Ordered.

56. Orbital process. State 0: dorsal edge sharp and concave, extends dorsally at 45° angle, as in *Aptenodytes*. State 1: dorsal edge sharp and concave, extends nearly horizontally, as in *Pygoscelis*. State 2: not sharp or concave, as in Procellariiformes (Figure 8).

57. Orbital process. State 0: distal end pointed, as in *S. humboldti*. State 1: distal end with expanded vertical hook as in *Aptenodytes*. State 2: distal end truncated vertically, as in *Pygoscelis* (Figure 8).

58. Lateral surface and orbital process. State 0: somewhat excavated. State 1: sharply excavated. Modified from Cracraft 1982 (char. 1, Fig. 2).

59. Medial surface. State 0: somewhat excavated. State 1: sharply excavated (Figure 10).

Squamosal:

60. Nuchal crest. State 0: semi-circular posteriorly, as in *Aptenodytes*. State 1: square posteriorly, as in *Eudyptula*. State 2: triangular posteriorly, as in *Spheniscus*. State 3: flat, as in Procellariiformes (Figure 10).
61. Zygomatic process. State 0: small, as in *Spheniscus*. State 1: large, as in *Aptenodytes* (Figure 8).
62. Temporal fossa, lateral horizontal platform. State 0: absent. State 1: present, shallow fossa. State 2: present, greatly deepened fossa. Modified from Cracraft 1982 (char.2, Fig. 2), Bertelli and Giannini 2005 (char. 77, Fig. 10). Ordered.
63. Lateral foramen for *rami occipitalis arteriae ophthalmicae externae* in caudoventral area of temporal fossa. State 0: small or vestigial. State 1: large. Modified from Bertelli and Giannini 2005 (char. 78, Fig. 10).
64. Dorsal tympanic recess. State 0: small. State 1: greatly enlarged. Modified from Mayr 2005 (char. 16) (Figure 13).
65. Dorsal tympanic recess. State 0: lies lateral to articular facet of quadrate. State 1: lies barely anterior to articular facet of quadrate. State 2: lies well anterior to articular facet of quadrate, distinctly visible in lateral view of skull. Modified from Mayr 2005 (char. 16) (Figure 8). Ordered.

Columella:

66. Orientation from base at prootic. State 0: extends ventrolaterally. State 1: extends horizontally.
67. Shape throughout length. State 0: curved. State 1: straight.
68. Length of extension. State 0: entirely enclosed within prootic bone. State 1: extends laterally exterior to bone.

Vomer:

69. Vomer. State 0: present. State 1: absent. Modified from Mayr 2005 (char. 12) (Figure 11).
70. Shape. State 0: laterally compressed, with vertical laminae. State 1: Laterally compressed, with vertical laminae and dorsal shelf. State 2: neither lateral compression nor dorsal shelf present. Modified from Mayr and Clarke 2003 (char. 20, Fig. 5a), Bertelli and Giannini 2005 (char. 91, Fig. 13).
71. Vomer. State 0: free from palatines. State 1: ankylosed with palatines. Modified from Bertelli and Giannini 2005 (char.91, Fig. 13).

Palatine:

72. Angle of orientation. State 0: horizontal (flat). State 1: somewhat angled. State 2: strongly angled. Modified from Mayr 2005 (char. 11) (Figure 12). Ordered.
73. Midline fusion. State 0: absent. State 1: present. Modified from Mayr 2005 (char. 10) (Figure 11).
74. Choanae, surrounding lamella. State 0: curved, smooth plate, slightly differentiated from main palatine. State 1: ridged, separated from palatine by low keel. State 2: extended vertically ventrally into the crista ventralis. Modified from Bertelli and Giannini 2005 (char. 90, Fig. 13).

Pterygoid:

75. Size. State 0: small, as in *Aptenodytes*. State 1: large, as in Procellariiformes (Figure 11).
76. Shape. State 0: horizontal plate. State 1: angled (Figure 12).
77. Shape. State 0: dorsally round, as in *Eudyptes*. State 1: medially crested, as in *Aptenodytes*. State 2: medial crest extended as tubercle, as in *Paraptenodytes* (Figure 11).
78. Shape. State 0: elongated. State 1: broadly triangular. State 2: sharply triangular. Modified from Bertelli et al. 2006 (char. 89, Fig. 7). Ordered.
79. Anterior border. State 0: free. State 1: articulates entirely with palatine (Figure 11).
80. Caudal end, enlarged ventromedial flange. State 0: absent, as in Spheniscidae. State 1: present, as in Procellariiformes (Figure 11).

Basioccipital:

81. Basitemporal plate. State 0: hexagonal. State 1: triangular. Modified from Cracraft 1982 (char. 4, Fig. 3).
82. Basitemporal plate, central portion. State 0: flat. State 1: depressed, owing to presence of anterolateral bony walls. Modified from Cracraft 1982 (char. 4, Fig. 3), Mayr 2005 (char.15), Bertelli and Giannini 2005 (char. 86).

83. Basitemporal plate compared with occipital condyle. State 0: ventral to level of condyle. State 1: at level of condyle. State 2: dorsal to level of condyle. Modified from Bertelli and Giannini 2005 (char. 86) (Figure 10).
84. Basitemporal plate, basal tubercles. State 0: weak. State 1: robust. Modified from Mayr 2005 (char. 15) (Figure 10).
85. Parasphenoid rostrum, weak ventral longitudinal groove. State 0: absent, as in *Aptenodytes*. State 1: present, as in *Pygoscelis* (Figure 11).
86. Basipterygoid process. State 0: absent. State 1: weak or vestigial. State 2: well-developed, articulates with pterygoid. Modified from Mayr 2005 (char. 13), Bertelli and Giannini 2005 (char. 87) (Figure 11). Ordered.
87. Subcondylar fossa. State 0: absent or shallow. State 1: deep. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 73, Fig. 7).
88. Eustachian tube. State 0: not ossified. State 1: mostly bony, ossification extends over posterior half of basitemporal platform. State 2: mostly bony, ossification extends to anterior basitemporal platform. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 88, Fig. 7). Ordered.
- Laterosphenoid:
89. Orbitocranial fonticuli, number and position. State 0: one large and one small. State 1: one extremely large and one-three large. State 2: one small. State 3: one dorsal and various others.
90. Cranial Nerves IV and III, foramina positions. State 0: lie close together, as in *Aptenodytes*. State 1: somewhat separated, as in *Pygoscelis* (Figure 12).
- Supraoccipital:
91. Grooves for exit of external occipital veins. State 0: poorly developed. State 1: deeply excavated. Modified from Bertelli and Giannini 2005 (char. 74, Fig. 8).
92. Cerebellar dome. State 0: small. State 1: large. Modified from Bertelli et al. 2006 (char. 76, Fig. 5).
93. Styliiform process. State 0: absent. State 1: present. Modified from Mayr 2005 (char. 22).
94. Ventral portion (dorsal to foramen magnum). State 0: hooked, as in *Aptenodytes*. State 1: smooth, as in *Eudyptula* (Figure 8).
- Exoccipital:
95. Paroccipital process. State 0: small, as in Gaviidae. State 1: large, as in Spheniscidae. State 2: bifid, as in *Paraptentodytes* (Figure 10).
96. Paroccipital process, posterior surface. State 0: lies on posterior surface of braincase only, with lateral, vertical, dividing ridge, as in *Aptenodytes*. State 1: curves onto the lateral surface of the braincase, with no dividing ridge, as in *Eudyptula*. State 2: lateral edge curved posteriorly, exposing an anteromedial surface, as in Podicipedidae (Figure 8).
97. Paroccipital process. State 0: lies vertically. State 1: ventral end extends posteriorly. State 2: ventral end extends laterally. State 3: ventral end extends both posteriorly and laterally. Modified from Mayr 2005 (char. 14) (Figure 8).
98. Vaguglossopharyngeal ganglii fovea (internal opening of cranial nerves IX, X, and the carotid canal). State 0: small, as in *Aptenodytes*. State 1: large, as in *Spheniscus* (Figure 12).
- Prootic:
99. Otic region, lateral, enlarged, bulbous wall. State 0: absent. State 1: small. State 2: large. Modified from Cracraft 1982 (char. 4, Fig. 3). Ordered.
100. XII foramen. State 0: doubled (2 foramina). State 1: combined (2 foramina in 1 confluent groove, bordered by medial crest). Modified from Cracraft 1982 (char. 4, Fig. 3).
101. Fenestra ovalis, position. State 0: opens posterolaterally, narrow opening. State 1: opens laterally, wide opening. Modified from Cracraft 1982 (char. 4, Fig. 3).
102. Fenestra ovalis. State 0: single, as in Gaviidae. State 1: two fossae separated by a vertical, anterolateral ridge, as in *Aptenodytes*. State 2: as in State 1, with accessory foramen lying on the ridge, as in *S. humboldti* (Figure 12).
103. Facial foramen. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 92).

104. Pneumatic foramen (posterior to dorsal rim of tympanic cavity, deep to the stapedial artery foramen). State 0: absent, as in *Eudyptes*. State 1: present, as in *Aptenodytes*.

Mandible:

105. Shape. State 0: slender throughout length. State 1: deep/robust throughout length. State 2: markedly deepened at midpoint. Modified from Bertelli and Giannini 2005 (char. 101, Fig. 16), Walsh and Suarez 2006 (char. 2).
106. Anterior mandibular fenestra. State 0: imperforate. State 1: very small. State 2: large. Modified from O'Hara 1989 (char. 8, Fig. 4), Bertelli and Giannini 2005 (char. 99, Fig. 16). Ordered.
107. Anterior mandibular foramen, posterior connecting groove. State 0: absent or vestigial, as in *Spheniscus*. State 1: present and elongate, as in *Aptenodytes* (Figure 12).
108. Posterior mandibular foramen. State 0: visible medially and laterally. State 1: not visible from either side. Modified from O'Hara 1989 (char. 9), Bertelli and Giannini 2005 (char. 100, Fig. 16).
109. Medial mandibular fossa (fossa aditus). State 0: shallow. State 1: deep. Modified from Bertelli and Giannini 2005 (char. 107, Fig. 16).
110. Posterior mandibular foramen, position. State 0: lies within medial mandibular fossa (fossa aditus), as in *Aptenodytes*. State 1: lies extremely posteriorly within fossa, as in Procellariiformes (Figure 12).

Dentary:

111. Mandible tip. State 0: pointed. State 1: slightly truncated. State 2: strongly truncated and squared off. State 3: procellariiform in shape. Modified from O'Hara 1989 (char. 7, Fig. 4), Bertelli and Giannini 2005 (char. 1, Fig. 14).
112. Posterior end. State 0: single. State 1: bifurcate (Figure 8).
113. Ventral process. State 0: long anteriorly and short vertically, as in *Aptenodytes*. State 1: short anteriorly, tall and tapered abruptly posteriorly, as in *Pygoscelis*. State 2: long anteriorly, tall and tapered abruptly posteriorly, as in *S. demersus* (Figure 8).
114. Angle between dorsal and ventral processes. State 0: small. State 1: large.
115. Dorsal edge. State 0: straight, greater than half the length of mandible. State 1: arched, half length of mandible. State 2: straight, half length of mandible. State 3: arched, greater than half length of mandible. Modified from Bertelli and Giannini 2005 (char. 103, Fig. 16).

Splenic:

116. Surangular contact. State 0: absent. State 1: present, short and horizontal, as in *Pygoscelis*. State 2: present, tall and vertical, as in *Eudyptes* (Figure 12).

Angular

117. Surangular. State 0: slender, as in *Aptenodytes*. State 1: robust, as in *Spheniscus* (Figure 12).
118. Coronoid process compared with posterior mandibular fenestra. State 0: process lies anterior to fenestra. State 1: process lies on anterior end of fenestra. State 2: process lies posterior to or on very posterior end of fenestra. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 98, Fig. 16). Ordered.
119. Retroarticular process compared with articular surface. State 0: absent (angular truncated caudally). State 1: equal in size. State 2: process long, narrower than surface. State 3: process extremely long, longer and narrower than surface. Modified from Bertelli and Giannini 2005 (char. 105, Fig. 17), Walsh and Suarez 2006 (char. 8 and 9).
120. Retroarticular process, midline fossa. State 0: absent. State 1: present, as in *Aptenodytes* (Figure 10).
121. Pseudotemporal tubercle. State 0: absent or weak. State 1: distinct knob, as in *Spheniscus*. State 2: elongated tubercle, as in *Aptenodytes* (Figure 12).

Articular:

122. Articulatory surface, lateral border. State 0: longitudinal (straight). State 1: inturned posteriorly. Modified from Bertelli et al. 2006 (char. 108, Fig. 6).
123. Lateral surface. State 0: excavated ventrally, as in *Aptenodytes*. State 1: nearly flat (Figure 8).
124. Medial surface, anteroventral fossa. State 0: absent or very small. State 1: present, large, as in *Aptenodytes* (Figure 12).

125. Medial mandibular process, accessory midline fossa. State 0: absent. State 1: present, as in *Aptenodytes* (Figure 11).
126. Medial mandibular process, hooked projection. State 0: absent. State 1: present, weak, as in *Pygoscelis*. State 2: present, robust, as in *Aptenodytes* (Figure 11). Ordered.
127. Lateral mandibular process, hooked projection. State 0: absent. State 1: present, as in Gaviidae (Figure 13).

Vertebrae:

128. Number of vertebrae. Includes one free vertebra and pygostyle counted as a single element. State 0: 42. State 1: 43. State 2: over 43.
129. Anterior articulatory surface. State 0: slight degree of protrusion, as in outgroups. State 1: robust degree of protrusion, as in Spheniscidae (Figure 15).
130. Number of cervicals whose carotid arches form canals. State 0: 9. State 1: 11. State 2: 10.
131. 3<sup>rd</sup> cervical with bony bridge connecting transverse process to caudal articular process. State 0: absent. State 1: present. Modified from Mayr and Clarke 2003 (char. 52, Fig. 6d), Mayr 2005 (char. 24).
132. Dorsal, crested arch lying longitudinally. State 0: present on 6<sup>th</sup> cervical, with spine. State 1: present on 8<sup>th</sup> cervical. State 2: absent. State 3: present on both 6<sup>th</sup> (with spine) and 8<sup>th</sup> (without spine). Modified from Bertelli and Giannini 2005 (char. 110).
133. 12<sup>th</sup>-13<sup>th</sup> cervicals, transverse process. State 0: neither deflected dorsally nor elongated laterally. State 1: elongated laterally, not deflected dorsally. State 2: elongated laterally and deflected dorsally. Modified from Bertelli and Giannini 2005 (char. 112) (Figure 15).
134. Last thoracic. State 0: opisthocoelous. State 1: weakly opisthocoelous. State 2: heterocoelous. Modified from Mayr 2005 (char. 26, Fig. 5), Bertelli et al. 2006 (char. 114). Ordered.
135. Number of caudals. Includes one free vertebra and pygostyle counted as a single element. State 0: 7. State 1: 8. State 2: 9. Modified from Bertelli and Giannini 2005 (char. 113).
136. Number of caudals with haemal spines. State 0: two present. State 1: three present. State 2: four present.
137. Haemal spines. State 0: large and bifurcate, as in *Aptenodytes*. State 1: small and bifurcate. State 2: small and single, as in Procellariiformes. State 3: large and single (Figure 15).
138. Pygostyle, perforated at caudoventral end. State 0: absent. State 1: present. Modified from Mayr and Clarke 2003 (char. 61, Fig. 6g).

Synsacrum:

139. Number of sacrals in fused synsacrum. State 0: 12. State 1: 13. State 2: 14. Modified from Mayr and Clarke 2003 (char. 91).
140. Shape. State 0: short and broad. State 1: long and narrow. Modified from Cracraft 1982 (character 6).
141. Widest portion visible dorsally. State 0: lies anterior to acetabulum, as in *Aptenodytes*. State 1: lies posterior to acetabulum, as in Procellariiformes. State 2: never widens (Figure 16).
142. Ventral surface. State 0: flat posteriorly. State 1: grooved posteriorly, as in *Pygoscelis*. State 2: columnar, as in *Wimanu* (Figure 16).
143. Sacral process. State 0: short. State 1: medium. State 2: long (Figure 16). Ordered.
144. Ventral spines. State 0: absent. State 1: present (Figure 16).
145. Robust ventral projection on first fused vertebra. State 0: absent. State 1: present (Figure 16).
146. Post-acetabular vertebrae. State 0: Length: Width=1:2 or 1:3. State 1: L:W=2:1 (Figure 16).

Ribs:

147. Number of ribs. State 0: 10. State 1: 8. State 2: 9.
148. Cervical ribs. State 0: long, as in *Aptenodytes*. State 1: short, as in *Spheniscus* (Figure 15).
149. Number of vertebra at which cervical ribs appear. State 0: 13. State 1: 14. State 2: 15. Modified from Bertelli and Giannini 2005 (char. 109).
150. Uncinate processes. State 0: wide and spatulate, sutured with ribs. State 1: narrow, sutured with ribs. State 2: narrow, fused with ribs. State 3: wide and spatulate, fused with ribs. Modified from Mayr and Clarke 2003 (char. 74), Bertelli and Giannini 2005 (char. 114, Fig. 19).

Coracoid:

151. Length. State 0: less than or equal to 80 mm. State 1: 81 mm-120 mm. State 2: 121 mm-170 mm. State 3: 171 mm or greater.
152. Shape. State 0: long and rod-like. State 1: short and broad (Figure 17).
153. Shaft. State 0: tubular, as in Phalacrocoracidae. State 1: flattened, as in Spheniscidae (Figure 17).
154. Shaft. State 0: curved, as in Gaviidae. State 1: straight, as in Spheniscidae (Figure 17).
155. Distal end. State 0: flared, as in Procellariiformes. State 1: not flared, as in Spheniscidae (Figure 17).
156. Acrocoracoid, angle with body of bone. Measured at point of acrocoracoid origin. State 0: forms 90° angle with body. State 1: rests on bent neck (angle <90°) (Figure 17).
157. Acrocoracoid. State 0: absent. State 1: present (Figure 17).
158. Acrocoracoid. State 0: hooks medially, as in Spheniscidae. State 1: hooks anteriorly, as in Procellariiformes (Figure 17).
159. Acrocoracoid. State 0: thin dorsoventrally, as in *Pygoscelis*. State 1: thick dorsoventrally, as in *Spheniscus* (Figure 17).
160. Acrocoracoid, lateral and medial surfaces. State 0: both flat. State 1: lateral flat, medial concave. State 2: lateral concave, medial flat. State 3: lateral flat, medial convex. State 4: lateral concave, medial convex. State 5: both concave. State 6: lateral convex, medial flat.
161. Proximal end. State 0: wide laterally. State 1: medium laterally. State 2: narrow laterally. Modified from Bertelli and Giannini 2005 (char. 120, Fig. 21). Ordered.
162. Sternal articulation. State 0: concave up. State 1: convex up. State 2: flat. Modified from Bertelli et al. 2006 (char. 124, Fig. 7)
163. Proximal end, elongate lateral process. State 0: absent. State 1: present. Modified from Mayr 2005 (char. 30, Fig. 9).
164. Procoracoid. State 0: large and tall, as in *Aptenodytes*. State 1: small and short, as in all outgroups. State 2: large but short, as in *Pygoscelis* (Figure 17).
165. Supracoracoid fenestra. State 0: absent. State 1: notch. State 2: small. State 3: large. Modified from O'Hara 1989 (char. 14, Fig. 6), Bertelli and Giannini 2005 (char. 119, Fig. 21), Walsh and Suarez 2006 (char. 10). Ordered.
166. Scapular facet. State 0: shallow and small, as in *Aptenodytes*. State 1: shallow and big, as in Procellariiformes. State 2: deep and small. State 3: deep and big (Figure 17).
167. Glenoid facet. State 0: deep. State 1: shallow.
168. Sternocoracoidal impression. State 0: deep, as in *Aptenodytes*. State 1: shallow, as in Gaviidae (Figure 17).
169. Dorsal extension of medial angle. State 0: absent, as in *Aptenodytes*. State 1: small, as in *Eudyptes*. State 2: large, as in *S. demersus*. State 3: forms elongate foramen, as in *S. humboldti* (Figure 17). Ordered.

Furcula:

170. Shape in anterior view. State 0: U-shaped. State 1: V-shaped (Figure 18).
171. Acrocoracoid articulation. State 0: small. State 1: large. Modified from Mayr 2005 (char. 27, Fig. 8) (Figure 18).
172. Furcular apophysis. State 0: absent. State 1: projects proximally, as in *Aptenodytes*. State 2: projects posteriorly, as in *Pygoscelis* (Figure 18).
173. Sternal articulation. State 0: abuts sternum with articular facet at apex. State 1: does not abut sternum. Modified from Mayr 2005 (char. 28) (Figure 18).
174. Proximal end. State 0: flattened and broad, rounded, as in *Aptenodytes*. State 1: flattened and broad, sharp, as in *Pygoscelis*. State 2: narrow and sharp, as in Gaviidae. State 3: narrow and rounded, as in Phalacrocoracidae (Figure 18).
175. Scapular articulation, orientation. State 0: horizontal. State 1: angled laterally. State 2: angled medially. State 3: vertical (Figure 18).

Scapula:

176. Shape. State 0: narrowed anteriorly. State 1: narrowed posteriorly. State 2: equally narrow throughout. Modified from Mayr 2005 (char. 32), Bertelli and Giannini 2005 (char.118) (Figure 17).
177. Blade. State 0: torsion of 45° with head, as in *Aptenodytes*. State 1: no torsion, straight, as in *Pygoscelis* (Figure 17).
178. Medial surface. State 0: hollowed for ribs (subscapular fossa present). State 1: not hollowed (Figure 17).
179. Medial surface. State 0: distinct proximodorsal ridge, as in *Aptenodytes*. State 1: distinct proximomedial ridge, as in *Pygoscelis*. State 2: neither present (Figure 17).
180. Proximal edge. State 0: vertical, flat orientation. State 1: medially concave. State 2: horizontal and flat (Figure 17).
181. Proximal edge. State 0: thickened anteriorly. State 1: not thickened (Figure 17).
182. Coracoid articulation compared with humeral articulation. State 0: coracoid articulation larger. State 1: coracoid articulation smaller. State 2: articulations equal in size (Figure 17).
183. Glenoid fossa. State 0: small, as in Podicipedidae. State 1: large, as in *Aptenodytes* (Figure 17).
184. Acromion. State 0: distinctly hooked laterally, doesn't extend anteriorly past coracoid articulation. State 1: not hooked laterally, doesn't extend anteriorly past coracoid articulation. State 2: not hooked, extends anteriorly beyond coracoid articulation. Modified from Mayr 2005 (char. 31) (Figure 17).
185. Posterior end. State 0: round. State 1: truncated and flat, as in *Spheniscus*. State 2: pointed, as in *Aptenodytes* (Figure 17).
186. Foramen at distal tip. State 0: absent. State 1: one present. State 2: two present (Figure 17).

Sternum:

187. Shape. State 0: U-shaped in anterior view (laterally compressed). State 1: not laterally compressed (Figure 18).
188. Shape. State 0: oblong. State 1: short, as in Procellariiformes (Figure 18).
189. Carina. State 0: long and high, as in *Aptenodytes*. State 1: long and low, especially anteriorly. State 2: short and high. State 3: short and low, especially anteriorly, as in *Eudyptula* (Figure 17, 18).
190. Carinate apex. State 0: pointed, extends anteriorly to coracoid sulcus. State 1: does not extend to coracoid sulcus. Modified from Mayr 2005 (char. 33, Fig. 7) (Figure 18).
191. Furcular facet. State 0: absent. State 1: distinct process. Modified from Bertelli and Giannini 2005 (char. 116, Fig. 20) (Figure 18).
192. Rostrum. State 0: absent. State 1: present, no spine. State 2: present, with small spine. State 3: present, with large spine. Modified from Cracraft 1982 (char. 5), O'Hara 1989 (char. 13), Mayr and Clarke 2003 (char. 62), Bertelli and Giannini 2005 (char. 115, Fig. 20) (Figure 17, 18). Ordered.
193. Coracoid sulcus. State 0: not continuous across midline. State 1: continuous across midline. State 2: continuous across midline, interrupted by manubrial spine. Modified from Cracraft 1982 (char. 5) (Figure 17, 18).
194. Coracoid sulcus. State 0: vertical, as in Procellariiformes. State 1: horizontal, as in Spheniscidae (Figure 17, 18).
195. Anterior process. State 0: base broad, as in Gaviidae. State 1: base laterally compressed, as in *Aptenodytes* (Figure 17, 18).
196. Anterior process. State 0: lies completely anterolateral to coracoid sulcus, as in Gaviidae. State 1: lies somewhat dorsal to coracoid sulcus, as in *Aptenodytes* (Figure 18).
197. Anterior process, foramen. State 0: absent. State 1: present (Figure 18).
198. Posterolateral process (lateral wing trabecula). State 0: thin and vertical. State 1: thick and horizontal, as in *Aptenodytes*. State 2: thin and horizontal, as in *Spheniscus* (Figure 18).
199. Posterolateral process (lateral wing trabecula). State 0: extends posterior to body of bone. State 1: does not extend posterior to body of bone. Modified from Cracraft 1982 (char. 5) (Figure 18).
200. Xiphisternum. State 0: one notch present. State 1: two notches present. State 2: both notched and perforated. Modified from O'Hara 1989 (char. 12, Fig. 5) (Figure 18).

201. Xiphisternum. State 0: wide, as in *Spheniscus*. State 1: narrow, as in *Aptenodytes* (Figure 18).
- Humerus:
202. Shape. Taken as ratio of width to height. State 0: long and slender, W:H much less than 1:4. State 1: short and stout, W:H=1:4. State 2: very short and stout, W: H=1:3 (Figure 19).
203. Length. State 0: less than 70cm. State 1: 71-100cm. State 2: 101-140cm. State 3: 141cm or more. Ordered.
204. Head. State 0: large, as in Gaviidae. State 1: small, as in *Aptenodytes*. State 2: medium, as in *E. chrysocome* (Figure 19). Ordered.
205. Head. State 0: round. State 1: square, owing to external tuberosity projected distally and articular surface flattened. State 2: bean-shaped (reniform). Modified from Mayr 2005 (char. 36), Bertelli and Giannini 2005 (char. 122, Fig. 22).
206. Head, articular surface. State 0: located ventrally. State 1: located horizontally. Modified from Mayr 2005 (char. 36) (Figure 19).
207. Shaft. State 0: narrows distally. State 1: same width distally. Modified from Walsh and Suarez 2006 (char. 12), Bertelli et al. 2006 (char. 136, Fig. 10).
208. Shape sigmoidal. State 0: absent. State 1: present. Modified from Walsh and Suarez 2006 (char. 13), Bertelli et al. 2006 (char. 137, Fig. 10).
209. Preaxial border. State 0: straight. State 1: with rounded, angular projection, as in *Pygoscelis*. State 2: with abrupt angular projection, as in *Aptenodytes*. State 3: with abrupt angular projected marked by distinct tubercle, as in *Platydyptes* (Figure 19).
210. Preaxial angle. Measured at break in preaxial border (as in character 209). State 0: about 140° (shaft offset distally), as in *Pygoscelis*. State 1: about 155° (shaft offset distally), as in *Eudyptes*. State 2: about 180° (shaft not offset), as in *Spheniscus* (Figure 19).
211. Distal angle. Measured as angle between distal trochleae and shaft. State 0: about 120°. State 1: about 135°. State 2: about 180°. Modified from Walsh and Suarez 2006 (char. 15), Bertelli et al. 2006 (char. 141, Fig. 10).
212. Distal end. State 0: with three tuberosities and two tendinal grooves. State 1: with two tuberosities and one tendinal groove. State 2: with three tuberosities and two tendinal grooves that are displaced from the shaft. Modified from Mayr 2005 (char. 37) (Figure 19).
213. Distal end, cranial edge. State 0: straight. State 1: bumpy. State 2: greatly extended. Modified from Mayr 2005 (char. 37) (Figure 19).
214. Distal end, extended cranial edge compared with ulnar condyle width. State 0: narrower. State 1: equal. State 2: wider. Modified from Bertelli et al. 2006 (char. 143, Fig. 12).
215. Distal end, caudal border, extended trochlear process. State 0: present, extends past humeral shaft. State 1: present, does not extend past humeral shaft. State 2: absent. State 3: present, separated from other processes by deep fossa. Modified from O'Hara 1989 (char. 15), Mayr 2005 (char. 37), Bertelli and Giannini 2005 (char. 127 and 128, Fig. 23).
216. Proximal end, transverse ligament sulcus. State 0: shallow and short. State 1: deep, long, and rectangular. State 2: deep, short, and round. State 3: deep, short, and round, with distinct pit formed posteriorly. Modified from Mayr 2005 (char. 38), Bertelli et al. 2006 (char.128, Fig. 8).
217. Entepicondylar process, size. State 0: large. State 1: small. Modified from Bertelli and Giannini 2005 (char. 126) (Figure 19).
218. Ectepicondylar attachments, orientation. State 0: oval and dorsal. State 1: oval and lateral. State 2: round and lateral. State 3: round and dorsal (Figure 19).
219. Deltoid crest on proximal cranial margin. State 0: absent. State 1: present, small. State 2: present, large and triangular. Modified from Mayr 2005 (char. 39) (Figure 19). Ordered.
220. Bicipital crest. State 0: wide, lies on proximoventral side of shaft, as in *Aptenodytes*. State 1: wide, lies on proximoanterior side of shaft, as in Procellariiformes. State 2: narrow, lies on proximoventral side of shaft. State 3: rims absent, lies on proximoanterior side of shaft, as in *Pygoscelis* (Figure 19).
221. Radius/ulna articulations. State 0: ulna articulation larger than radius articulation. State 1: articulations equal in size. State 2: ulna articulation smaller than radius articulation. State 3: ulna articulation smaller than radius articulation and separated from it by a groove (Figure 19).

222. Capital groove. State 0: shallow and wide. State 1: shallow and tapered caudally. State 2: deep and wide. State 3: deep and tapered caudally. Modified from Bertelli et al. 2006 (char. 127, Fig. 10).
223. Pneumatic fossa (pneumotricipital fossa). State 0: circular. State 1: flattened anteroposteriorly. State 2: square, as in Procellariiformes (Figure 19).
224. Pneumatic fossa (pneumotricipital fossa). State 0: large and deep, as in *Aptenodytes*. State 1: large and shallow. State 2: small and shallow, as in Procellariiformes. State 3: small and deep (Figure 19).
225. Pneumatic fossa (pneumotricipital fossa), pneumatic foramen. State 0: absent. State 1: present. Modified from Mayr and Clarke 2003 (char. 77, Fig. 7f), Bertelli and Giannini 2005 (char. 123).
226. Pneumatic fossa (pneumotricipital fossa). State 0: lies caudally on shaft, as in all outgroups. State 1: lies ventrally on shaft, as in Spheniscidae (Figure 19).
227. Pneumatic fossa (pneumotricipital fossa). State 0: single. State 1: partially divided. State 2: bipartite. Modified from Bertelli and Giannini 2005 (char. 124, Fig. 22), Walsh and Suarez 2006 (char. 14). Ordered.
228. Pneumatic fossa, partition (pneumotricipital fossa). State 0: nearly transverse, angled lateroanteriorly; divisions of equal size, as in *Aptenodytes*. State 1: nearly longitudinal, angled anterolaterally; divisions of equal size, as in *Spheniscus*. State 2: nearly longitudinal, angled anterolaterally; ventral division excavated into distinct pit (Figure 19).
229. *Latissimus dorsi* insertion. State 0: large and round, as in *Eudyptula*. State 1: large and elongate. State 2: small and elongate, as in *S. humboldti*. State 3: small and round (Figure 19).
230. *Pectoralis primus* insertion (on deltopectoral crest). State 0: shallow groove. State 1: deep, oblong fossa. Modified from Bertelli and Giannini 2005 (char. 125) (Figure 19).
231. *Supracoracoideus* insertion. Lies on dorsal surface of head, from preaxial border of articular surface to postaxial border of shaft. State 0: lies far from *latissimus dorsi* insertion. State 1: lies close to *latissimus dorsi* insertion. Modified from Bertelli et al. 2006 (char. 134, Fig. 9).
232. *Supracoracoideus* insertion. State 0: large and straight. State 1: small and curved. State 2: small and straight. State 3: large and curved. Modified from Bertelli et al. 2006 (char. 133, Fig. 9).
233. Fossa between insertions for *supracoracoideus*, on dorsal margin of pneumatic fossa. State 0: small, closed distally, as in *Eudyptula*. State 1: small, open distally, as in *Spheniscus*. State 2: large, closed distally, as in *Megadyptes*. State 3: large, open distally, as in *E. pachyrhynchus*. State 4: extends distally as sharp ridge to *latissimus dorsi* insertion, as in *Pachydyptes ponderosus* (Figure 19).
234. *Latissimus dorsi anteriori* and *posteriori*. State 0: form separate attachments and separate muscle scars, as in *S. demersus*. State 1: form only 1 attachment, as in *Aptenodytes* (Figure 19).
- Radius:
235. Length. State 0: 50 mm or less. State 1: 51 mm-80 mm. State 2: 81 mm-120 mm. State 3: 121 mm or more. Ordered.
236. *Brachialis internus* insertion (in notch on proximal end of preaxial border). State 0: sharply concave, as in *Eudyptes*. State 1: smooth, as in *Aptenodytes*. State 2: flat and short, as in Phalacrocoracidae (Figure 14).
237. Tendinal grooves and distal oblique grooves for extensor metacarpus radialis brevis. State 0: both deep. State 1: both shallow. State 2: tendinal grooves shallow, oblique grooves deep. State 3: tendinal grooves deep, oblique grooves shallow (Figure 14).
238. Angle of head with body. State 0: nearly straight, as in Spheniscidae. State 1: distinctly offset. State 2: curves entire bone, as in *Anthropornis* (Figure 14). Ordered.
- Ulna:
239. Length. State 0: shorter than humerus. State 1: longer than humerus. State 2: nearly equal in length. Modified from Mayr and Clarke 2003 (char. 82). Ordered.
240. Proximal end. State 0: widened and flattened horizontally, as in *Aptenodytes*. State 1: widened only, as in *Eudyptes*. State 2: extensively widened and flattened. State 3: ridged, as in *Wimanu* (Figure 14).
241. Postaxial edge elongated 'like' an olecranon. State 0: absent. State 1: present. Modified from Bertelli et al. 2006 (char. 144, Fig. 12).

242. Articulatory surface. State 0: hollowed for humerus, as in *Spheniscus*. State 1: undulating surface, as in *Aptenodytes* (Figure 14).
243. Small, proximal foramen located on postaxial edge. State 0: absent. State 1: present (Figure 14).
- Radiale:
244. Shape. State 0: hourglass-shaped and semi-circular, not wedge-shaped, as in *Aptenodytes forsteri*. State 1: rectangular, wedge-shaped, as in *S. magellanicus*. State 2: hourglass-shaped/semi-circular, wedge-shaped, as in *Eudyptula*. State 3: rectangular, not wedge-shaped, as in *E. sclateri* Figure 14.
245. Foramen. State 0: forms indentation only. State 1: present (Figure 14).
246. Radial articulation. State 0: Cup-shaped, as in Gaviidae. State 1: nearly flat, as in *Aptenodytes* (Figure 14).
- Ulnare:
247. Shape. State 0: flattened extensively. State 1: round, not flattened. Modified from Mayr 2005 (char. 42) (Figure 14).
248. Ulnar articulation. State 0: displaced only a large ventrocaudal process, rest of bone free from contact. State 1: not displaced, most of bone contacts ulna. Modified from Mayr 2005 (char. 42) (Figure 14).
249. Distinct knob distal to ulnar articulation. State 0: absent, as in Gaviidae. State 1: present, as in *Aptenodytes* (Figure 14).
- Carpometacarpus:
250. Length. State 0: 40 mm or less. State 1: 41 mm-90 mm. State 2: 91 mm or more. Ordered.
251. Proximal end with convex articulations in a semicircle. State 0: absent, as in Procellariiformes. State 1: present, as in *Aptenodytes* (Figure 14).
252. Preaxial edge. State 0: notched distally, as in *E. chrysolophus*. State 1: straight, as in *Aptenodytes* (Figure 14).
253. Metacarpal 1. State 0: slants distally into metacarpal 2, as in *Aptenodytes*. State 1: ends abruptly, as in Gaviidae. State 2: completely fused, as in *Paraptenodytes* (Figure 20).
254. Metacarpal 3. State 0: extends distal to metacarpal 2. State 1: does not extend distally (Figure 20).
255. Facets for digits 2 and 3. State 0: deep, with a separating notch, as in *Aptenodytes*. State 1: shallow, with a very shallow notch, as in *Pygoscelis* (Figure 20).
256. Distal fusion between metacarpal 1/2 and metacarpal 3. State 0: deeply grooved, as in *Aptenodytes*. State 1: shallowly grooved, as in Gaviidae (Figure 20).
257. Metacarpal 3 with widened flange/wing distally. State 0: absent, as in *Aptenodytes*. State 1: present, as in *Megadyptes* (Figure 20).
- Manual Phalanges:
258. Digits 4, 5, and allular. State 0: absent, as in Spheniscidae. State 1: present, as in all outgroups. Modified from O'Hara 1989, Bertelli and Giannini 2005 (char. 129) (Figure 14).
259. Digits. State 0: short. State 1: long. Modified from Bertelli and Giannini 2005 (char.131) (Figure 14).
260. Digit 3, proximal process. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 130) (Figure 14).
- Pedal Phalanges:
261. Hallux. State 0: greatly reduced, proximal phalanx greater than 1/2 length of proximal phalanx of toe 3 or absent. State 1: present. Modified from Mayr and Clarke 2003 (char. 110).
- Ox Coxae:
262. Shape, elongated and mediolaterally compressed, dorsal ilial crests reduced. State 0: absent. State 1: present. Modified from Mayr and Clarke 2003 (char. 90) (Figure 16).
263. Keel. State 0: robust, as in Spheniscidae. State 1: weak, as in all outgroups (Figure 16).
264. Acetabulum compared with ilioischadic fenestra in lateral view. State 0: acetabulum larger. State 1: acetabulum smaller. Modified from O'Hara 1989 (char. 16, Fig. 7), Bertelli and Giannini 2005 (char. 132, Fig. 24), Walsh and Suarez 2006 (char. 18).
265. Ilioischadic fenestra. State 0: occluded by dorsolateral ilial crest in dorsal view. State 1: not occluded, visible in dorsal view. Modified from Walsh and Suarez 2006 (char. 19) (Figure 16).

266. Ischiopubic fenestra. State 0: very wide, closed caudally, as in Gaviidae. State 1: slit-like, open caudally, as in *Aptenodytes*. State 2: very short and open, as in Phalacrocoracidae. Modified from Bertelli and Giannini 2005 (char. 133, Fig. 24).
267. Ilium. State 0: one anterior notch, shallow, as in *Aptenodytes*. State 1: one anterior notch, deep, as in *S. demersus*. State 2: two anterior notches, shallow. State 3: two anterior notches, deep. State 4: fenestrate (Figure 16).
268. Ilium, allae. State 0: flat, lateral edge straight, as in *Pygoscelis*. State 1: ventrally concave, lateral edge straight, as in Gaviidae. State 2: ventrally concave, laterally edge curved, as in *Eudyptula*. State 3: flat, lateral edge straight, as in Procellariiformes (Figure 16).
269. Ilium, allae. State 0: expanded, far separated. State 1: expanded, nearly meet at midline. State 2: not expanded, nearly meet at midline. Modified from Walsh and Suarez 2006 (char. 17) (Figure 16).
270. Ilium. State 0: notched posterodorsally, as in Gaviidae. State 1: V-shaped posterodorsally, as in Phalacrocoracidae. State 2: U-shaped posterodorsally, as in *Spheniscus* (Figure 16).
271. Ilium-sacral fusion. State 0: fused. State 1: sutured. Modified from Walsh and Suarez 2006 (char. 16), Bertelli et al. 2006 (char. 149, Fig. 13).
272. Ischium compared with postacetabular ilium. State 0: ischium shorter. State 1: ischium slightly longer. State 2: ischium far longer. Modified from Bertelli and Giannini 2005 (char. 134, Fig. 24). Ordered.
273. Pubis. State 0: deepened and decurved posteriorly, as in Gaviidae. State 1: decurved posteriorly, equal depth throughout, as in *Aptenodytes patagonicus*. State 2: straight, deepened posteriorly, as in *Spheniscus*. State 3: straight, equal depth throughout, as in *Megadyptes* (Figure 16).
- Femur:
274. Length compared with width in midsection. Length measured at longest point, width measured perpendicular to shaft. State 0: L:W<9 mm. State 1: L:W>9 mm. Modified from Mayr and Clarke 2003 (char. 96) (Figure 22).
275. Length compared with tarsometatarsus. State 0: tarsometatarsus less than one half length of femur. State 1: tarsometatarsus greater than one half length of femur. State 2: tarsometatarsus greater than length of femur (Figure 22). Ordered.
276. Proximal portion in lateral view, as measured perpendicular to shaft. State 0: composed of head. State 1: composed of trochanter. State 2: both equally proximal. Modified from O'Hara 1989 (char. 17) (Figure 22).
277. Head. State 0: large, with prominent ventral rugosity, as in *Pygoscelis*. State 1: small, with prominent ventral rugosity, as in *Aptenodytes*. State 2: small, no rugosity present, as in Gaviidae (Figure 22).
278. Capital ligament impression on head. State 0: broad and deep, as in *Pygoscelis*. State 1: narrow and shallow, as in *Aptenodytes* (Figure 22).
279. Articular surface. State 0: U-shaped (concave anteriorly), as in *Pygoscelis*. State 1: V-shaped, as in *Aptenodytes*. State 2: straight, as in Procellariiformes (Figure 22).
280. Shaft. State 0: sigmoidal, bowed. State 1: straight. Modified from Walsh and Suarez 2006 (char. 20) (Figure 22).
281. Angle of head with shaft. Measured at point where head attached, perpendicular to shaft. State 0: about 90°. State 1: >90° (Figure 22).
282. Trochanter. State 0: sharp crest, projected far proximally, as in *Aptenodytes*. State 1: bumpy process, projected slightly or not projected at all, as in Gaviidae. State 2: bumpy process, projected far anteriorly, as in Podicipedidae. State 3: sharp crest, projected slightly or not projected at all, as in *Pygoscelis*. State 4: sharp crest, projected far anteriorly, as in *Eudyptes* (Figure 22).
283. Supracondylar crests, lateral and medial. State 0: medial crest strongly projected medially, lateral crest absent, as in *Aptenodytes*. State 1: medial crest strongly projected medially, lateral crest present, as in *P. papua*. State 2: medially crest not projected, lateral crest absent, as in *Spheniscus*. State 3: medial crest not projected, lateral crest present, as in *Megadyptes* (Figure 22).
284. Condyles (lateral and medial). State 0: far separated, as in Gaviidae. State 1: close together, as in Spheniscidae (Figure 22).

285. Anterior patellar groove. State 0: wide and shallow, as in *Aptenodytes*. State 1: narrow and deep, as in *Spheniscus* (Figure 22).
286. Fibular groove. State 0: small, as in Gaviidae. State 1: large, as in *Aptenodytes*. State 2: ends in proximal pit, as in *Megadyptes* (Figure 22).
287. Popliteal fossa. State 0: deep and discrete, as in *Aptenodytes*. State 1: shallow and not discrete, as in *Eudyptula* (Figure 22).
288. Fibular trochlea. State 0: smaller than tibiofibular crest, as in *Spheniscus*. State 1: equal in size, as in *Aptenodytes* (Figure 22).
- Patella:
289. Shape. State 0: perforate. State 1: shallowly grooved for tendon of musculus ambiens. State 2: deeply grooved. Modified from O'Hara 1989 (char. 18, Fig. 8), Mayr 2005 (char. 43, Fig. 5), Bertelli and Giannini 2005 (char. 135, Fig. 25), Walsh and Suarez 2006 (char. 22).
290. Shape. State 0: large, acute wedge shape, as in *Eudyptula*. State 1: large, rounded, as in *Aptenodytes*. State 2: small, rounded, as in Gaviidae. Modified from Mayr 2005 (char. 43) (Figure 20).
- Tibiotarsus:
291. Dorsoventral flattening. State 0: absent. State 1: present. Modified from Walsh and Suarez 2006 (char. 24).
292. Shaft, size. State 0: small, as in Gaviidae. State 1: large, as in Spheniscidae. State 2: extra large, as in *Wimanu* (Figure 21). Ordered.
293. Cnemial crests (cranial and lateral). State 0: project only to femur articulation (externally everted). State 1: project just further than articulation. State 2: project well past articulation. Modified from Mayr and Clarke 2003 (char. 99), Mayr 2005 (char. 44) (Figure 21). Ordered.
294. Patellar crest (rotular crest). State 0: small, overhangs proximal tibiotarsus. State 1: robust, overhangs proximal tibiotarsus. State 2: small, doesn't overhang proximal tibiotarsus. State 3: robust, doesn't overhang proximal tibiotarsus. Modified from Mayr 2005 (char. 46), Bertelli and Giannini 2005 (char. 136) (Figure 21).
295. Popliteal tuberosity. State 0: extends to medial cotyles. State 1: doesn't extend to medial cotyle. Modified from Bertelli and Giannini 2005 (char. 137) (Figure 21).
296. Medial condyle. State 0: medial condyle deflected medially, projects further distally than lateral condyle. State 1: medial condyle not deflected, does not project further than lateral condyle. State 2: medial condyle not deflected, projects further distally than lateral condyle. State 3: medial condyle deflected medially, does not project further than lateral condyle. Modified from Mayr 2005 (char. 45), Walsh and Suarez 2006 (char. 30) (Figure 21).
297. Extensor sulcus (tendinal groove). State 0: broad and lateral, large. State 1: broad and lateral, small. State 2: narrow and medial, large. State 3: narrow and medial, small. Modified from Walsh and Suarez 2006 (char. 25 and 26) (Figure 21).
298. Supratendinal bridge. State 0: tall, as in *Spheniscus*. State 1: short, as in *Aptenodytes*. State 2: short and diagonal, as in *Wimanu*. (Figure 21).
299. Sulcus for m. fibularis. State 0: absent/small. State 1: enlarged. Modified from Walsh and Suarez 2006 (char. 29) (Figure 21).
300. Internal ligamental prominence (medial epicondyle). State 0: projects medially past condyle, as in *Aptenodytes*. State 1: flat, doesn't project, as in *Spheniscus* (Figure 21).
- Fibula:
301. Size. State 0: robust, as in *Aptenodytes*. State 1: small, as in Procellariiformes. State 2: robust and untapered ventrally, as in CADIC P-21 (Figure 21).
302. Proximal femur articulation. State 0: concave dorsally, as in *Aptenodytes*. State 1: concave medially. State 2: flat, as in Procellariiformes (Figure 21).
- Tarsometatarsus:
303. Size. State 0: width is greater than or equal to 1/2 height. Height measured at longest point, width measured at exact midpoint. State 1: width is less than 1/2 height. Modified from Bertelli and Giannini 2005 (char. 138), Walsh and Suarez 2006 (char. 32) (Figure 23).
304. Length. State 0: less than 1/4 that of tibiotarsus. State 1: more than 1/4 that of tibiotarsus. Modified from Mayr 2005 (char. 46).

305. Length (articulation to articular surface of trochlea 3. State 0: 34 mm and below. State 1: 35-50 mm. State 2: 51-69 mm. State 3: 70 mm and above. Ordered.
306. Body. State 0: waisted throughout midlength, as in *Wimanu*. State 1: equally thickened throughout length, as in *Aptenodytes* (Figure 23).
307. Articular surface. State 0: large and rectangular, as in *Aptenodytes*. State 1: medium and rectangular, as in *Spheniscus*. State 2: large and round, as in Procellariiformes. State 3: small and round, as in Gaviidae. State 4: small and rectangular, as in *Palaeospheniscus bergi*. State 5: medium and round, as in *Palaeudyptes klekowskii* (Figure 23).
308. Sulcus ligamentosus. State 0: absent, as in Phalacrocoracidae. State 1: present, as in *Aptenodytes* (Figure 23).
309. Intercotylar eminence. State 0: large, wide, raised. State 1: small, narrow, not raised. Modified from Bertelli and Giannini 2005 (char. 142) (Figure 23).
310. Intercotylar depression (intercotylar area). State 0: absent, as in *Aptenodytes*. State 1: small, as in *Spheniscus*. State 2: deep, as in *Anthropornis* (Figure 23). Ordered.
311. Tibiotarsus articulation. State 0: flat, as in *Aptenodytes*. State 1: medial cotyle depressed, as in *Spheniscus* (Figure 23).
312. Metatarsal 2, shaft. State 0: straight. State 1: curved (Figure 23).
313. Medial edge. State 0: neither proximal V-shaped groove nor convexity. State 1: proximal V-shaped groove present. State 2: pronounced proximal convexity present. Modified from Bertelli et al. 2006 (char. 157, Fig. 14).
314. Metatarsal 3, shaft. State 0: straight. State 1: curved (Figure 23).
315. Metatarsal 4, shaft. State 0: straight. State 1: curved (Figure 23).
316. Tibialis cranialis tubercle (tibialis anticus). State 0: absent. State 1: small and elongate, as in *Aptenodytes*. State 2: prominent and round, as in *Pygoscelis*. Modified from Walsh and Suarez 2006 (char. 33) (Figure 23).
317. Tibialis cranialis tubercle (tibialis anticus). State 0: raised onto metatarsal 3, lies somewhat distally. State 1: raised onto metatarsal 3, lies very distally. State 2: raised onto metatarsal 3, lies proximally. State 3: lies between metatarsal 2 and 3, lies somewhat distally. State 4: lies between metatarsal 2 and 3, lies very distally. Modified from Walsh and Suarez 2006 (char. 33) (Figure 23).
318. Metatarsal 2, distal end. State 0: inflected medially, as in *Aptenodytes*. State 1: straight, as in Gaviidae. State 2: inflected medially, with a strongly concave medial border, as in *Anthropornis* (Figure 23).
319. Trochleae. Measured along axis of bone as a whole. State 0: metatarsal 2 is shorter than 3 and longer than four. State 1: metatarsal 2 is shorter than three and equal to 4. State 2: metatarsal 2 is as long as 3 and longer than 4. State 3: metatarsal 2 is shorter than both 3 and 4. State 4: metatarsal 2 is equal in length to both 3 and 4 (Figure 23).
320. Trochleae. State 0: small, metatarsal three enlarged, as in Procellariiformes. State 1: all small, as in *Spheniscus*. State 2: massive, metatarsal three enlarged, as in *Aptenodytes*. State 3: all massive, as in *Delphinornis arctowskii* (Figure 23).
321. Metatarsal 4, trochlea. State 0: lies in same vertical plane as other trochleae, as in *Aptenodytes*. State 1: posteriorly deflected, as in *Wimanu* (Figure 23).
322. Lateral compared with medial intertrochlear incision. State 0: lateral smaller than medial. State 1: lateral and medial equal in size. State 2: lateral larger than medial (Figure 23). Ordered.
323. Collateral ligament foveae. State 0: pronounced, as in *Spheniscus*. State 1: metatarsal 2 small or absent, metatarsal four pronounced, as in Gaviidae. State 2: small or absent. State 3: metatarsal 2 pronounced, metatarsal four small or absent, as in *Aptenodytes* (Figure 23).
324. Lateral intermetatarsal groove. State 0: deep (absent in Bertelli and Giannini 2005). State 1: shallow. State 2: absent. Modified from Walsh and Suarez 2006 (char. 31) (Figure 23). Ordered.
325. Lateral intermetatarsal groove. State 0: shallows distally, as in *Delphinornis*. State 1: does not shallow distally (remains deep throughout), as in Spheniscidae (Figure 23).
326. Medial intermetatarsal groove. State 0: absent. State 1: shallow. State 2: deep. Modified from Walsh and Suarez 2006 (char. 31), Bertelli et al. 2006 (char. 159, Fig. 15). Ordered.

327. Lateral intermetatarsal foramen. State 0: absent. State 1: pit only (no plantar opening). State 2: small (about 3.3 mm by 5.1 mm). State 3: large (about 4.2-6.3 mm). Modified from O'Hara 1989 (char. 20, Fig. 9), Bertelli et al. 2006 (char. 162, Figs. 14 and 15). Ordered.
328. Lateral intermetatarsal foramen. State 0: distal and oval, as in *Aptenodytes*. State 1: proximal and oval, as in *Spheniscus*. State 2: medially proximodistal and oval, as in *Archaeospheniscus lopdelli*. State 3: proximal and circular, as in *Mesetaornis*. State 4: medially proximo-distal and circular, as in *Anthropornis nordenskjöldi* (Figure 23).
329. Lateral intermetatarsal foramen. State 0: lies in deeply excavated pit, as in Spheniscidae. State 1: does not, as in *Anthropornis* (Figure 23).
330. Medial intermetatarsal foramen. State 0: absent. State 1: pit only (no plantar opening). State 2: small. State 3: large. Modified from O'Hara 1989 (char. 19, Fig. 9), Bertelli and Giannini 2005 (char. 139, Fig. 26). Ordered.
331. Medial intermetatarsal foramen, medially bordering crista. State 0: absent, as in *Eudyptes*. State 1: present, as in *Spheniscus* (Figure 23).
332. Medial compared with lateral intermetatarsal foramina. State 0: medial smaller than lateral. State 1: equal in size. State 2: lateral smaller. Modified from Walsh and Suarez 2006 (char. 35) (Figure 23).
333. Medial and lateral intermetatarsal foramina. State 0: widely separated, as in *Anthropornis*. State 1: widely separated, as in *Aptenodytes*. State 2: close together, as in Phalacrocoracidae (Figure 23).
334. Medial intermetatarsal foramen, plantar opening. State 0: lies lateral to medial hypotarsal crest. State 1: lies medial to medial hypotarsal crest. State 2: lies ventral to medial hypotarsal crest. Modified from O'Hara 1989 (char. 19), Bertelli and Giannini 2005 (char. 140, Fig. 27), Walsh and Suarez 2006 (char. 34).
335. Distal intermetatarsal foramen and external adductor groove. State 0: foramen absent, groove open. State 1: foramen present, groove closed. Modified from Mayr 2005 (char. 48, Fig. 4), Bertelli et al. 2006 (char. 163, Fig. 15).
336. Lateral and medial hypotarsal (calcaneal) crests. State 0: slender. State 1: robust. State 2: very robust, forming marked sulcus for passage of all flexor tendons. State 3: flexor digitorum longus enclosed in separate bony canal. Modified from Mayr and Clarke 2003 (char. 106, Fig. 9d).
337. Hypotarsal (calcaneal) crests, lateral pit. State 0: absent, as in Spheniscidae. State 1: present on lateral ridge, as in *Korora*. State 2: present ventral to ridge, as in *Marambiornis* and *Mesetaornis* (Figure 23).
338. Hypotarsal (calcaneal) crests. State 0: Parallel, as in *Aptenodytes*. State 1: converge to a V, as in *Spheniscus*. State 2: broad and continuous, as in *Archaeospheniscus lopdelli*. State 3: medial crest slants towards medial margin, as in *Delphinornis* (Figure 23).
339. Hypotarsal (calcaneal) crests. State 0: large, three. State 1: small, three. State 2: large, two. State 3: small, two. Modified from Walsh and Suarez 2006 (char. 36), Bertelli et al. 2006 (char. 158, Figs. 14 and 15).
340. Medial compared with lateral hypotarsal (calcaneal) crests. State 0: inner more prominent. State 1: outer more prominent (Figure 23).

Myology:

341. *Ambiens*. State 0: absent or vestigial. State 1: present. Modified from McKittrick 1991 (character 29), Mayr and Clark 2003 (char. 125), Mayr 2005 (char. 51).
342. *Ambiens*, extent of origin. State 0: on preacetabular tuberculum only. State 1: from preacetabular tuberculum to pubis. State 2: two origins, on preacetabular tuberculum and on pubis. Modified from McKittrick 1991 (char. 30), Mayr and Clarke 2003 (char. 236).
343. *Biceps brachii*. State 0: absent. State 1: present vestigially.
344. *Brachialis*, small slip inserting on ulna. State 0: absent. State 1: present.
345. *Caudofemoralis, pars pelvica* ('B' muscle) State 0: absent. State 1: present. Modified from McKittrick (char. 15), Mayr 2005 (char. 120).
346. *Deltoideus, propatagialis*, superficial and deep layers. State 0: undivided. State 1: divided. Modified from Bertelli and Giannini 2005 (char. 147).

347. *Deltoideus, major*. State 0: triangular or fan-shaped. State 1: strap-shaped. Modified from Bertelli and Giannini 2005 (char. 148).
348. *Deltoideus, major, caput caudal*. State 0: short. State 1: intermediate. State 2: long. Modified from Bertelli and Giannini 2005 (char. 149). Ordered.
349. *Deltoideus, minor*, origin on clavicular articulation of coracoid. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 150).
350. *Extensor hallucis longus*. State 0: absent or vestigial. State 1: present. Modified from McKittrick 1991 (char. 60), Mayr and Clarke 2003 (char. 138).
351. *Extensor longus alulae*, radial head. State 0: absent. State 1: present.
352. *Femorotibialis externus*. State 0: separate. State 1: partially fused. State 2: absent or not distinguishable.
353. *Fibularis longus*, branch to flexor perforatus digiti III. State 0: absent. State 1: present. Modified from McKittrick 1991 (char. 42), Mayr and Clarke 2003 (char. 130).
354. *Flexor hallucis brevis*. State 0: absent. State 1: present, but minute.
355. *Flexor hallucis longus*, hallux tendon. State 0: absent. State 1: present. Modified from McKittrick 1991 (char. 51), Mayr and Clarke 2003 (char. 134).
356. *Flexor hallucis longus* and *flexor digitorum longus*, arrangement. State 0: type 1. State 1: type 2.
357. *Flexor perforatus digitis 4*, insertion of tendon. State 0: condition 1. State 1: condition 2. State 2: condition 3. State 3: condition 4.
358. *Flexor perforatus digitis 4*, insertion of middle rami. State 0: on phalanx 3. State 1: on phalanx 4. Modified from Bertelli and Giannini 2005 (char. 156).
359. *Flexor perforatus digitis 4*, rami 2-3. State 0: free. State 1: fused. Modified from Bertelli and Giannini 2005 (char. 154).
360. *Flexor perforatus digitis 4*, rami 1-4. State 0: free. State 1: fused. Modified from Bertelli and Giannini 2005 (char. 155).
361. *Gastrocnemius*, number of heads. State 0: 1. State 1: 2. Modified from McKittrick 1991 (char. 34), Mayr and Clarke 2003 (char. 127).
362. *Iliofemoralis*, origin. State 0: tendinous. State 1: mostly tendinous. State 2: mostly fleshy. State 3: completely fleshy. Modified from Bertelli and Giannini 2005 (char. 153).
363. *Iliotrochantericus caudalis*. State 0: narrow. State 1: wide. Modified from Bertelli and Giannini 2005 (char. 152).
364. *Latissimus dorsi (cranialis and caudalis)*. State 0: narrow. State 1: wide. Modified from Bertelli and Giannini 2005 (char. 144).
365. *Latissimus dorsi (cranialis and caudalis)*. State 0: separate. State 1: fused. Modified from Bertelli and Giannini 2005 (char. 144).
366. *Latissimus dorsi caudalis*, additional origin from dorsal vertebral processes. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 157).
367. *Latissimus dorsi cranialis*, accessory slip from cranial edge of *triceps scapularis*. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 143).
368. Middle ear muscle. State 0: small. State 1: large.
369. *Serratus profundus*, cranial fascicle. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 146).
370. *Ulnometacarpalis ventralis*. State 0: absent. State 1: present vestigially. Modified from Bertelli and Giannini 2005 (char. 151).
- Soft Characters:
371. Sex. State 0: monomorphic. State 1: sexually dimorphic.
372. Bill, grooves. State 0: absent. State 1: deeply grooved.
373. Salt gland. State 0: single-lobed, single efferent duct. State 1: not. Modified from Mayr 2005 (char. 61).
374. Tympanum. State 0: elongate. State 1: round.
375. Cartilaginous attachment to tympanum. State 0: one articulation. State 1: two articulations.
376. Flippers. State 0: long and narrow. State 1: stout and short.

377. Three anterior toes, webbing. State 0: absent. State 1: present. Modified from Mayr and Clarke 2003 (char. 111), Mayr 2005 (char. 57).
378. Third toe, claw, strongly pectinated medially. State 0: absent. State 1: present. Modified from Mayr 2005 (char. 60).
379. Mouth, oral mucosa. Papillae on the medial surface of the lower jaw at the level of the rictus. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 158).

#### Integument

380. Eggshell. State 0: not covered with amorphous calcium carbonate. State 1: covered with amorphous calcium carbonate. Modified from Mayr 2005 (char. 62).
381. Maxillary and mandibular unguis and culminicorn, color. State 0: both black. State 1: both red. State 2: unguis various colors, culminicorn black or red. Modified from Bertelli and Giannini 2005 (char. 13).
382. Longitudinal grooves on culmen base and latericorn and ramicorn base. State 0: both absent. State 1: both present. State 2: grooves present on culmen only. Modified from Bertelli and Giannini 2005 (char. 2).
383. Feathering of maxilla, extent. State 0: unfeathered. State 1: less than half its length feathered. State 2: half its length feathered. State 3: more than half its length feathered. Modified from Bertelli and Giannini 2005 (char. 4).
384. External nares. State 0: tubular. State 1: greatly reduced. State 2: absent. Modified from O'Hara 1989 (char. 2), Bertelli and Giannini 2005 (char. 17).
385. Nostril tubes. State 0: absent. State 1: present in chick. State 2: present in adult. Modified from Bertelli and Giannini 2005 (char. 16).
386. Ramicorn color. State 0: black. State 1: reddish. State 2: pink. State 3: yellowish. State 4: orange. Modified from Bertelli and Giannini 2005 (char. 9).
387. Ramicorn, inner groove at tip. State 0: absent. State 1: present, single. State 2: present, doubled. Modified from Bertelli and Giannini 2005 (char. 5).
388. Ramicorn, orange or pink plate. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 6).
389. Latericorn color. State 0: black. State 1: reddish. State 2: orange. State 3: yellowish. State 4: green. Modified from Bertelli and Giannini 2005 (char. 11). Ordered.
390. Latericorn and ramicorn, light distal mark. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 10).
391. Rhamphotheca, plates inflated. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 7).
392. Gape, aspect. State 0: not fleshy. State 1: margin narrowly fleshy. State 2: margin markedly fleshy. Modified from Bertelli and Giannini 2005 (char. 8).
393. Bill of immature, color. State 0: dark. State 1: red and black. State 2: red. State 3: yellowish. State 4: grayish. Modified from Bertelli and Giannini 2005 (char. 15).
394. Bill of downy chick, color. State 0: dark. State 1: reddish. State 2: pale, variably horn to yellowish. State 3: bluish gray. Modified from Bertelli and Giannini 2005 (char. 14).
395. Iris color. State 0: dark. State 1: reddish-brown. State 2: claret red. State 3: yellowish. State 4: white. Modified from Bertelli and Giannini 2005 (char. 18).
396. White eyebrow. State 0: absent. State 1: narrow, from postocular area. State 2: narrow, from preocular area. State 3: wide, from preocular area. Modified from Bertelli and Giannini 2005 (char. 35).
397. White eye-ring. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 34).
398. Fleshy eye-ring. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 33). Ordered.
399. Periocular area color. State 0: black. State 1: white. State 2: yellowish. State 3: bluish gray. Modified from Bertelli and Giannini 2005 (char. 32).
400. Collar. State 0: absent. State 1: slight notch present. State 2: present, diffusely demarcated. State 3: black, strongly demarcated. Modified from Bertelli and Giannini 2005 (char. 39).

401. Throat pattern. State 0: black. State 1: white. State 2: yellowish. State 3: irregularly streaked. State 4: with chinstrap. Modified from Bertelli and Giannini 2005 (char. 38).
402. Gular pouch. State 0: absent. State 1: present. Modified from Mayr 2005 (char. 56).
403. Auricular patch. State 0: absent. State 1: inconspicuous and feathered. State 2: large and naked. Modified from Bertelli and Giannini 2005 (char. 37).
404. Loreal area, aspect. State 0: feathered. State 1: with spot of bare skin in recess between latericorn and culminicorn. State 2: with spot of bare skin contacting eye. State 3: bare skin extending to the base of the bill. Modified from Bertelli and Giannini 2005 (char. 36).
405. Nape, crest development. State 0: absent. State 1: slightly distinct. State 2: distinct. Modified from Bertelli and Giannini 2005 (char. 31).
406. Head plumes. State 0: absent. State 1: present, at base of bill close to gape. State 2: present, on recess between latericorn and culminicorn. State 3: present, on forehead. Modified from O'Hara 1989 (char. 1), Bertelli and Giannini 2005 (char. 26).
407. Head plumes, aspect. State 0: heading upward, compact. State 1: heading backward, not drooping, compact. State 2: heading backward, drooping, sparse. Modified from Bertelli and Giannini 2005 (char. 27).
408. Head plumes, color. State 0: yellowish. State 1: orange. Modified from Bertelli and Giannini 2005 (char. 29).
409. Yellow pigmentation in crown feathers. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 30).
410. Feathers. State 0: apteria present, scale-like feathers absent. State 1: apteria absent, scale-like feathers present. Modified from Bertelli and Giannini 2005 (char. 19 and 23).
411. Remiges. State 0: differentiated from contours and specialized for flight. State 1: indistinct from contours. Modified from Bertelli and Giannini 2005 (char. 22). Ordered.
412. Retrices. State 0: forming fan functional for steering. State 1: not. Modified from Bertelli and Giannini 2005 (char. 21).
413. Natal plumage. State 0: none. State 1: some. Modified from Bertelli and Giannini 2005 (char. 59).
414. First and second down color. State 0: pale grey. State 1: brown. State 2: dark above, whitish below. State 3: blackish grey. Modified from Bertelli and Giannini 2005 (char. 60 and 61).
415. Second down, collar. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 62).
416. Immature plumage, white eyebrow. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 56).
417. Immature plumage, throat pattern. State 0: black. State 1: mottled. State 2: L white. State 3: brown. Modified from Bertelli and Giannini 2005 (char. 57).
418. Immature plumage, flanks, dark lateral band. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 58).
419. Molt of contour feathers. State 0: gradual. State 1: simultaneous. Modified from Bertelli and Giannini 2005 (char. 24).
420. Rachis of contour feathers. State 0: cylindrical. State 1: flat and broad. Modified from Bertelli and Giannini 2005 (char. 20).
421. Breast, golden in color. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 40).
422. Flipper, underside, tip pattern. State 0: immaculate. State 1: patchy, variable extent. State 2: small circular dot. Modified from Bertelli and Giannini 2005 (char. 55).
423. Flipper, underside, dark elbow patch. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 54).
424. Leading edge of flipper, underside. State 0: white. State 1: incompletely dark. State 2: completely dark and wide. Modified from Bertelli and Giannini 2005 (char. 53).
425. Leading edge of flipper, upperside. State 0: black. State 1: black, light notch at base. State 2: white. Modified from Bertelli and Giannini 2005 (char. 52).
426. White line connecting leading edge of flipper with white belly. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 50).

427. Black marginal edge of dorsum between lateral collar and axillary patch, contrasting with dorsum. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 42).
428. Black dots irregularly distributed over white belly. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 43).
429. Dorsum color. State 0: black. State 1: dark bluish grey. State 2: light bluish grey. Modified from Bertelli and Giannini 2005 (char. 41).
430. Outer retrices, color. State 0: same as inners. State 1: lighter than inners. Modified from Bertelli and Giannini 2005 (char. 49).
431. Flanks, dark lateral band reaching the breast. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 44).
432. Distinct dark axillary patch of triangular shape. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 45).
433. Flanks, extension of dorsal dark cover. State 0: incomplete, not reaching tarsus. State 1: complete, reaching tarsus. Modified from Bertelli and Giannini 2005 (char. 46).
434. Rump. State 0: indistinct from back. State 1: distinctly whitish. Modified from O'Hara 1989 (char. 3), Bertelli and Giannini 2005 (char. 47).
435. Feet, dorsal color. State 0: dark. State 1: pinkish. State 2: orange. State 3: white-flesh. State 4: blue. Modified from O'Hara 1989 (char. 4), Bertelli and Giannini 2005 (char. 63).
436. Feet, dark soles. State 0: absent. State 1: present. Modified from O'Hara 1989 (char. 4), Bertelli and Giannini 2005 (char. 64).
437. Feet, unguis digiti. State 0: flat. State 1: compressed. Modified from Bertelli and Giannini 2005 (char. 65).
438. Tail length. State 0: short, quills barely emerging from rump. State 1: medium, quills distinctly developed but not surpassing feet as extended caudally. State 2: long, quills surpassing feet as extended caudally. Modified from Bertelli and Giannini 2005 (char. 48).
439. Tail stiff. State 0: absent. State 1: present.

#### Behavior

440. Clutch size. State 0: more than one egg, survival equal for all. State 1: one egg. State 2: two eggs, survival of 1<sup>st</sup> egg better. State 3: two eggs, survival of 2<sup>nd</sup> egg better. Modified from O'Hara 1989 (char. 21), Paterson et al. 1995 (char. 56), Bertelli and Giannini 2005 (char. 66).
441. Incubatory sac. State 0: absent. State 1: present. Modified from Bertelli and Giannini 2005 (char. 67).
442. Nest. State 0: nest. State 1: burrow. State 2: either. State 3: none, on feet. Modified from O'Hara 1989 (char. 22), Paterson et al. 1995 (char. 50), Mayr 2005 (char. 65), Bertelli and Giannini 2005 (char. 68).
443. First egg compared with second egg. State 0: sub-equal in size. State 1: first smaller. State 2: second smaller. Modified from Bertelli and Giannini 2005 (char. 69).
444. Crèche. State 0: absent. State 1: small (3-6 birds). State 2: large (dozens to hundreds of birds). Modified from Paterson et al. 1995 (char. 61), Bertelli and Giannini 2005 (char. 70).
445. Egg, shape. State 0: oval. State 1: conical. State 2: spherical. Modified from Bertelli and Giannini 2005 (char. 71).
446. Chicks feed every day during first weeks. State 0: absent. State 1: present. Modified from Paterson et al. 1995 (char. 1).
447. Predominant food. State 0: crustaceans. State 1: cephalopods. State 2: fish. State 3: mollusks or scavengers. Modified from Paterson et al. 1995 (char. 2).
448. Food capture. State 0: pursuit diving, not solitary. State 1: other method. Modified from Paterson et al. 1995 (char. 3).
449. Time of foraging. State 0: diurnal. State 1: nocturnal. Modified from Paterson et al. 1995 (char. 5).
450. Time of return from foraging. State 0: any. State 1: dusk. State 2: after dark. Modified from Paterson et al. 1995 (char. 6).
451. Land directly at nest-site. State 0: no. State 1: yes. Modified from Paterson et al. 1995 (char. 7).

452. Adults leave after mating and return before laying. State 0: no. State 1: yes. Modified from Paterson et al. 1995 (char. 8).
453. Vocalizations at sea while foraging. State 0: absent. State 1: present. Modified from Paterson et al. 1995 (char. 9).
454. Average weight of chick's meal / average weight of adult. State 0: less than 0.1. State 1: more than 0.1. Modified from Paterson et al. 1995 (char. 10).
455. Adults forage inshore during breeding. State 0: no. State 1: yes. Modified from Paterson et al. 1995 (char. 11).
456. Territory defended. State 0: in the nest or burrow. State 1: in area around the nest or burrow. Modified from Paterson et al. 1995 (char. 14).
457. Predawn chorus. State 0: absent. State 1: present. Modified from Paterson et al. 1995 (char. 15).
458. Gaping and open yell. State 0: absent. State 1: neck stretched horizontally, gape, carpal joints raised. Modified from Paterson et al. 1995 (char. 16).
459. Shoulder hunching. State 0: absent. State 1: body and bill horizontal, neck stretched, bill opened or closed, carpal joints raised, call. State 2: neck lowered, head and bill forward, shoulders raised, body forward, wings slightly forward. Modified from Paterson et al. 1995 (char. 17).
460. Jabbing. State 0: fast thrusts with open bill at another bird, usually not touching other bird, calling. State 1: thrust clapping mandibles toward other bird, calling. Modified from Paterson et al. 1995 (char. 18).
461. Trumpeting. State 0: call, bird leans forward, raises wings, steps towards other bird. State 1: absent. Modified from Paterson et al. 1995 (char. 19).
462. Bills interlocked. State 0: absent. State 1: birds lock bills together and wrestle. Modified from Paterson et al. 1995 (char. 20).
463. Stare, charge, and bite nape fight. State 0: all absent. State 1: all present (bird in upright posture, turns body and bill towards opponent, feathers sometimes erected; defending bird moves towards opponent with short run, upright head forward, crown erect, wings raised; bill strikes or nips feathers and skin of opponents head and neck, swatting of opponent with wing). Modified from Paterson et al. 1995 (char. 21, 22, and 23).
464. Chicks spit oil. State 0: absent. State 1: ejection of oil from stomach at intruder. Modified from Paterson et al. 1995 (char. 24).
465. Hunched submissive. State 0: absent. State 1: body and head low, wings close to sides, steps. State 2: body and head low, wings extended, feathers sleeked, steps. State 3: body stretched up, neck elongated, wings out from body, feathers sleeked. Modified from Paterson et al. 1995 (char. 25).
466. Face away. State 0: absent. State 1: bird looks obliquely at owners of other territories, wings forward, bill upwards and to one side. State 2: body and neck upright, wings forward, bill hung down parallel to neck, head may turn to one side. Modified from Paterson et al. 1995 (char. 26).
467. Shivering. State 0: absent. State 1: wings and sometimes head vibrate rapidly in agonistic situations. Modified from Paterson et al. 1995 (char. 27).
468. Squeal. State 0: absent. State 1: bird utters high pitched squeal in response to sudden danger. Modified from Paterson et al. 1995 (char. 28).
469. Nest or burrow site chosen by. State 0: male. State 1: either. Modified from Paterson et al. 1995 (char. 29).
470. Length of incubating shifts. State 0: equal. State 1: male longer. Modified from Paterson et al. 1995 (char. 30).
471. Males present during egg laying. State 0: no. State 1: yes. Modified from Paterson et al. 1995 (char. 31).
472. Nest burrow construction. State 0: interwoven plant material. State 1: dug using bill and feet. State 2: adult lying in nest kicks out of bowl, shifting material to rim. State 3: adult squats with wings out, pressing back with feet and rotates. State 4: plant and earth material patted onto nest wall. Modified from Paterson et al. 1995 (char. 32).
473. Mock preening. State 0: absent. State 1: bird makes one emphatic sweep under carpal joints or in scapulars. Modified from Paterson et al. 1995 (char. 33).

474. Ecstatic display. State 0: absent. State 1: bird stands on toes, wings stiffly forward, head and open bill vertical, loud trilling call. State 2: bird on toes, wings stiffly forward, head and open bill vertical, loud trilling call, head swung in arcs. Modified from Paterson et al. 1995 (char. 34), Bertelli and Giannini 2005 (char. 72).
475. Allopreening. State 0: absent. State 1: neck, throat and head of mate preened. Modified from Paterson et al. 1995 (char. 35).
476. Mutual bowing. State 0: absent. State 1: members of pair direct open bills into nest bowls and call. Modified from Paterson et al. 1995 (char. 36).
477. Beating wings and treading. State 0: both absent. State 1: both present (male wings vibrated gently on female's sides prior to copulation; male treads on back of female prior to copulation). Modified from Paterson et al. 1995 (char. 37 and 38).
478. Aerial display. State 0: absent. State 1: present (birds land and take off in groups, calling or high speed dives over colony). Modified from Paterson et al. 1995 (char. 39).
479. Gawky look, yapping, parties, head shake and whine. State 0: all absent. State 1: all present (push head forward, neck stretched, head and bill forming obtuse angle, eyes glazed and staring, gape obvious; open mandibles fully, neck at 45° from body, head moving up and down, calling; head rapidly waved from side to side with bill closed, pointing at other bird, stands on toes with erect fanned tail, whining call, wings stretched or no movement of head with bill closed, pointing at other bird, stands on toes with erect fanned tail, whining call, wings stretched or rub heads together, calling; groups of birds congregate and perform all agonistic and sexual behaviors, including flights, in response to arrival of new female or trios fly just above ground in twisting flight calling). Modified from Paterson et al. 1995 (char. 40, 41, 42, and 43).
480. Sky-pointing and wing-waving display, hop display, and kink-throating display. State 0: all absent. State 1: all present. Modified from Mayr 2005 (char. 66).
481. Advertising. State 0: absent. State 1: present (unmated birds call outside burrow or wander around colony calling). Modified from Paterson et al. 1995 (char. 44).
482. Copulation outside nest or burrow. State 0: absent. State 1: present. Modified from Paterson et al. 1995 (char. 45).
483. Stone carrying. State 0: absent. State 1: stones, grass or earth collected and placed around nest. Modified from Paterson et al. 1995 (char. 46).
484. Quivering. State 0: absent. State 1: nesting bird vibrates bill in very small arcs as it bows over nest-bowl to deposit nest material. Modified from Paterson et al. 1995 (char. 47).
485. Type of migration. State 0: coastal or none. State 1: circumpolar. State 2: tropical. State 3: north of Antarctic convergence. State 4: pack ice region. Modified from Paterson et al. 1995 (char. 49).
486. Nest or burrow terrain. State 0: other. State 1: hillside. Modified from Paterson et al. 1995 (char. 51).
487. Vegetation present at nest or burrow. State 0: none. State 1: tussock or grassland. State 2: forest. Modified from Paterson et al. 1995 (char. 52).
488. Pair-bond duration. State 0: several breeding seasons. State 1: lifelong. Modified from Paterson et al. 1995 (char. 53).
489. Sex ratio in adults. State 0: equal. State 1: more males. Modified from Paterson et al. 1995 (char. 54).
490. Chicks abandoned by parents. State 0: no. State 1: yes, after fledging. State 2: yes, before fledging. Modified from Paterson et al. 1995 (character 55).
491. Replacement laying. State 0: absent. State 1: present. Modified from Paterson et al. 1995 (char. 57).
492. Sexual difference in voice. State 0: absent. State 1: present. Modified from Paterson et al. 1995 (char. 58).
493. Nestling state of development. State 0: altricial. State 1: semi-altricial. State 2: precocial. Modified from Paterson et al. 1995 (char. 59).
494. Nestling behavior. State 0: nudifuguous. State 1: semi-nidicolous. State 2: nidicolous. Modified from Paterson et al. 1995 (char. 60).

495. Fledging weight compared with adult weight. State 0: not equal. State 1: equal. Modified from Paterson et al. 1995 (char. 62).
496. General foraging habitat. State 0: marine. State 1: pelagic. State 2: intertidal. Modified from Paterson et al. 1995 (char. 64).
497. Breeding season. State 0: spring. State 1: summer or winter. State 2: autumn. Modified from Paterson et al. 1995 (char. 67).
498. Molt season. State 0: November or February. State 1: December. State 2: March. Modified from Paterson et al. 1995 (char. 68).
499. Nest construction season. State 0: winter. State 1: spring or autumn. State 2: summer. Modified from Paterson et al. 1995 (char. 69).
500. Age of first breeding and first return to colony. State 0: less than one or more than two years. State 1: between one and two years. Modified from Paterson et al. 1995 (char. 70).
501. Nest preparation period / incubation length. State 0: greater than 0.66. State 1: less than 0.66. Modified from Paterson et al. 1995 (char. 71).
502. Nestling period compared with incubation length. State 0: equal. State 1: incubation shorter than nestling. Modified from Paterson et al. 1995 (char. 72).
503. Young feeding mechanism. State 0: down the gullets of adults. State 1: other. Modified from Mayr 2005 (char. 64).

















1	1	11	1	1	11	1	1	11	1	1111	1	1111	1	1111	11	111	11112
6	6	66	6	6	66	6	7	7777	77778	8888	8	88889	99	999	99990	99990	
1	2	34	5	6	78	9	0	12345	67890	1234	5	67890	12	345	67890	67890	
?	?	??	?	?	??	?	?	???	???	???	?	???	??	???	???	???	
A. gilli																	
A. grandis																	
A. nordenskjoldi	1	0	10	2	1	01	0/1	?	???	1/2	?	???	??	???	???	???	
A. forsteri	2	0	00	1	0	10	0	0	00001	0110	1	10001	00	111	10100	10100	
A. patagonicus	2	0	00	1	0	10	0	0	00100	0110	1	10001	00	111	10100	10100	
A. ridgeni	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
A. lopdelli	1	0	? 0?	1/2	?	10	?	?	???	???	?	???	??	???	???	???	
A. lowei	1	0	00?	1/2	0	10	0	?	???	00?	?	???	??	???	???	???	
A. wimani	1	?	??	?	0	1?	?	?	???	???	?	???	??	???	???	???	
C. biloculata	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
C. unienwillia	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
"D." hendeyi	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
D. arctowski	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
D. gracilis	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
D. larseni	?	0	??	2/3	0	01	?	?	???	???	?	???	??	???	???	???	
D. parvus	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
E. tonni	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
E. chrysocome	1	0	00	3	0	00	1	0	00120	0101	1	00011	01	111	10100	10100	
E. chrysolophus	1	0	00	2	0	10	1	0	00102	1011	1	11031	01	111	10100	10100	
E. pachyrhynchus	1	0	00	2	0	10	1	0	01100	0111	0	11011	01	111	10100	10100	
E. robustus	1	0	00	2	0	10	1	0	00100	0111	0	00021	01	110	10100	10100	
E. schlegeli	1	0	02	2	0	10	1	0	00010	0110	1	00021	02/3	111	10102	10102	
E. sclateri	1	0	00	2	2	10	1	1	00110	0101	2	01031	01	110	10100	10100	
E. minor	1	0	02	1	0	10	1	0	01011	1111	1	00031	03	111	10102	10102	
E. m. albognata	1/2	0	02	1	1	10	1	0	01000	1111	1	00031	03	111	10102	10102	
I. gracilis	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
"I." predemersus	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
K. oliveri	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
M. exilis	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
M. novaezealandiae	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
M. antipodes	1	0	00	3	0	10	0	0	00120	0111	1	00011	01	110	10100	10100	
M. polaris	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
"N." insolitus	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
O. gigas	?	?	??	?	?	??	?	?	???	???	?	???	??	???	???	???	
P. ponderosus	1	0	10	2/3	1	01	?	?	???	???	?	???	??	???	???	???	











22	2	22	2222	2	2	223	333	33	3	3	333	333	33	33333
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12	3	45	67890	1234	5	6	7	890	123	45	6	7	890	67890
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A. gilli														
A. grandis	?	?	???	?	?	???	???	??	?	?	???	???	??	???
A. nordenskjöldi	?	?	???	?	?	???	???	??	?	?	???	???	??	???
A. forsteri	0	0	1000	0	0	110	021	23	1	2	001	121	0	202?2
A. patagonicus	0	0	1012	1	0	100	000	01	1	0	110	010	0	14013
A. ridgeni	0?	0	1012	1	0	100	000	01	1	0	111	010	0	14011
A. lopdelli	0	0/3/4	???	?	?	???	???	??	?	?	???	???	??	???
A. lowei	0	2/4	???	?	?	???	???	??	?	?	???	???	??	???
A. wimani	??	?	???	?	?	???	???	??	?	?	???	???	??	???
C. biloculata	??	?	???	?	?	???	???	??	?	?	???	???	??	???
C. unienwillia	??	0/1	???	?	?	2/3	???	??	?	?	???	???	??	???
"D." hendeyi	1?	1	10	10?	?	?	???	??	?	?	???	???	?	???
D. arctowski	??	?	???	?	?	???	???	??	?	?	???	???	?	???
D. gracilis	??	?	???	?	?	???	???	??	?	?	???	???	?	???
D. larseni	??	?	???	?	?	???	???	??	?	?	???	???	?	???
D. parvus	??	?	???	?	?	???	???	??	?	?	???	???	?	???
E. tonni	??	?	???	?	?	???	???	??	?	?	???	???	?	???
E. chrysocome	14	0	10	1002	0	0	100	000	10	1	0	100	0	23201
E. chrysolophus	04	0	10	1102	0	0	110	000	10	1	0	101	0	0-001
E. pachyrhynchus	04	0	10	1002	0	0	110	000	10	1	0	112	0	20001
E. robustus	14	0	00	0101	0	0	1001	000	10	1	0	101	0	20000
E. schlegeli	03	3	11	1002	0	0	111	???	10	1	0	101	0	20000
E. sclateri	14	3	11	2102	0	0	000	000	10	1	1	111	0	10001
E. minor	04	1	10	1101	1	0	111	000	10	1	1	112	0	10101
E. m. albosignata	03	3	10	1101	1	0	111	000	10	1	1	112	0	10101
I. gracilis	??	?	??	???	?	?	???	???	??	?	???	???	??	???
"I." predemersus	04	1	10	100?	?	?	???	???	??	?	???	???	??	???
K. oliveri	??	?	??	???	?	?	???	???	??	?	???	???	??	???
M. exilis	??	?	??	???	?	?	???	???	??	?	???	???	??	???
M. novaezealandiae	??	?	??	???	?	?	???	???	??	?	???	???	??	???
M. antipodes	03	3	10	2102	1	0	1101	000	10	1	1	000	0	22011
M. polaris	??	?	??	???	?	?	???	???	??	?	???	???	??	???
"N." insolitus	??	?	??	???	?	?	???	???	??	?	???	???	??	???
O. gigas	??	?	??	???	?	?	???	???	??	?	???	???	??	???
P. ponderosus	??	?	??	???	?	?	???	???	??	?	???	???	??	???

22	2	22	2222	2	2222	2	2	223	333	33	3	3	333	333	33	333333	
88	8	88	8888	9	9999	9	9	990	000	00	0	0	001	111	11	11112	
12	3	45	6789	0	1234	5	6	7	890	123	45	6	7	890	123	45	67890
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02	0	10	210?	?	11??	?	0	0	111	???	???	1	4	???	000	00	10000
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14	1	00	000?	?	0100	0	0	0	101	???	???	0	1	111	110	00	10011
??	?	??	???	?	???	?	?	???	???	0/1	02	0/1	101	100	00	21212	
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04?	3	00	200?	?	1111	?	0	1	120	???	???	1	0	???	???	00	121??
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13	0	10	10001	1	0101	1	2	1	001	000	00	1	1	111	010	00	20002
13	0	10	1001	1	0100	1	3	1	001	100	00	1	1	111	110	00	21013
12	1	10	1001	1	0100	1	3	1	021	???	???	1	?	111	110	00	20013
13	1	10	1001	1	0100	1	3	1	001	000	00	1	1	111	110	00	02101
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02	1	??	???	?	0???	1	3	0	021	???	10	?	?	???	???	??	???
03	2	11	1001	1	0100	1	3	3	001	000	10	1	1	101	110	00	10001
03	2	11	1001	1	0100	1	3	3	001	000	10	1	1	101	110	00	10001
04	2	11	1002	0	0100	1	3	3	001	100	10	1	1	101	110	00	10001
??	?	??	???	?	???	?	?	???	???	???	???	?	?	???	???	??	???
04	1	10	0001	1	0100	1	3	2	021	000	10	1	1	101	110	00	10001
??	?	??	???	?	???	?	?	???	???	???	???	1	1	10?	110	00	10001
??	?	??	???	?	???	?	?	???	???	???	???	1	1	101	010	00	20010
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W. seymourensis	??	?	???	?	???	?	?	???	???	???	???	1	5	???	000	1	10210/1
W. manningi	??	?	???	?	0212	?	0	3	2??	021	23	0	0/2	10?	110	01	20012
W. tuatahi	03	1	11	???	???	?	?	2/3	???	???	???	0	0/2	???	110	01	22012
CADIC P-21	0 1/3	0	1?	???	???	?	0/3	0/1	???	22?	??	?	?	???	???	??	???
OM C47.25	??	?	???	?	???	?	?	???	???	???	???	?	?	???	???	??	???
OM C47.23A	??	?	???	?	???	?	?	???	???	???	???	?	?	???	???	??	???
Gaviidae	11	2	00	0103	2	0023	0	0	2	101	001	2?	0	3	???	00	0-1? 1/3
Phalacrocoracidae	13	2	10	0112	0	0111	0	0	200	001	22	0	0	10	100	00	0-041
Podicipedidae	12	2	00	0103	2	0013	0	1	0	101	001	23	0	3	???	00	0-111
Procellariiformes	11	3	00	0013	2	0013	0	1	0	001	121	23	0	2	100	00	0-130











P. simpsoni	44444	44444	4444	4	44444	44444	44444	44444	44444	44444	44444	4444	4
P. antarcticus	00000	00001	1111	1	11112	22222	22223	22223	22223	22223	33333	33	33
P. gunnari	12345	67890	1234	5	67890	12345	67890	67890	67890	67890	12345	67	89
P. klekowski	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. marplei	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. bergi	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. gracilis	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. patagonicus	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. wimani	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. antarcticus	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. robustus	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. amiesi	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. novaezealandiae	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. macraei	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. adeliae	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. antarctica	00001	0--01	11101	0	02011	01010	00000	00000	00000	01001	01001	10	11
P. grandis	40000	0--01	1110	0	01011	01110	00001	00001	00001	01001	01001	00	11
P. papua	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
P. tyreei	00000	0--01	11102	0	00011	01012	00001	00001	00001	01002	01002	00	11
S. chilensis	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
S. demersus	00020	0--01	1112	1	11011	01110	00100	00100	00100	10100	10100	01	00
S. humboldti	30030	0--01	1112	1	03011	01111	00100	00100	00100	10100	10100	01	00
S. magellanicus	00010	0--01	1112	1	11111	01101	00100	00100	00100	10100	10100	01	00
S. megaramphus	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
S. mendiculus	30030	0--01	111?	?	03111	01110	01001	01001	01001	01000	01000	10	00/2
S. urbinai	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
T. hunteri	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
T. moisleyi	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
W. seymourensis	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
W. manningi	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
W. tuatahi	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
CADIC P-21	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
OM C47.25	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
OM C47.23A	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	??
Gaviidae	-0---	0----	0011	0	---00	-----	-----	-----	-----	-----	-----	00	-0
Phalacrocoracidae	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	0?
Podicipedidae	?????	?????	????	?	?????	?????	?????	?????	?????	?????	?????	??	0?
Procellariiformes	-?---	0----	001013	0	-----	-----	-----	-----	-----	-----	-----	001	-0









### Appendix 3.5. Autapomorphy List for All Terminal Taxa.

- Anthropodytes gigas*: 207 (1 → 2).  
*Orthopteryx gigas*: no apomorphies.  
*Platydyptes amiesi*: no apomorphies.  
*Anthropornis grandis*: 310 (1 → 2), 325 (0 → 1), 326 (1 → 2), 339 (3 → 2).  
*Anthropornis nordenskjoldi*: 307 (0 → 2), 308 (1 → 0), 327 (2 → 3), 328 (3 → 4).  
*Pachydyptes ponderosus*: 204 (1 → 0), 207 (1 → 0), 211 (0 → 1), 218 (1 → 0), 221 (1 → 0),  
222 (2 → 3), 229 (3 → 1).  
*Palaeodyptes antarcticus*: 158 (0 → 1), 161 (1 → 2), 202 (1 → 0), 208 (1 → 0), 215 (1 → 0),  
232 (0 → 1), 241 (0 → 1), 303 (1 → 0), 319 (1 → 2).  
OM C47.25: no apomorphies.  
OM C47.23a: 151 (2 → 2).  
*Platydyptes novaezealandiae*: 162 (0 → 1), 205 (1 → 2), 209 (2 → 3), 215 (1 → 0), 221 (1 → 3),  
223 (0 → 2), 232 (0 → 1), 253 (1 → 4).  
*Pachydyptes simpsoni*: 202 (1 → 2), 210 (2 → 0), 222 (2 → 3), 229 (2 → 1), 235 (2 → 3), 238 (1 → 0),  
254 (1 → 0).  
*Palaeodyptes marplei*: 213 (1 → 2), 220 (0 → 1), 243 (1 → 0).  
*Crossvallia unienwillia*: 297 (0 → (23)).  
CADIC P-21: 292 (1 → 0).  
*Archaeospheniscus lopdelli*: 203 (2 → 1).  
*Archaeospheniscus lowei*: 151 (3 → 2).  
*Archaeospheniscus wimani*: 203 (2 → 0), 214 (2 → 0), 305 (2 → 1), 320 (2 → 0).  
*Palaeodyptes gunnari*: 229 (2 → 1), 307 (1 → 2), 319 (1 → 0), 329 (0 → 1).  
*Wimanornis seymourensis*: 202 (1 → 0), 229 (2 → 3).  
336 (1 → 0).  
*Palaeodyptes klekowski*: 315 (0 → 1), 317 (0 → 4), 319 (1 → 4), 338 (0 → 1), 339 (3 → 0).  
*Palaeospheniscus wimani*: 305 (0 → 2), 312 (1 → 0), 317 (0 → 1), 318 (0 → 2).  
*Aptenodytes forsteri*: 27 (1 → 0), 65 (1 → 2), 116 (1 → 0), 156 (0 → 1), 159 (0 → 1), 178 (1 → 0),  
180 (0 → 1), 219 (1 → 0), 229 (1 → 0), 244 (2 → 0), 274 (0 → 1), 310 (1 → 0), 405 (0 → 3),  
428 (1 → 0), 430 (1 → 0), 476 (0 → 1), 494 (0 → 1), 507 (1 → 0), 508 (1 → 0).  
*Aptenodytes patagonicus*: no apomorphies.  
*Aptenodytes ridgeni*: 289 (2 → 1), 294 (0 → 1), 305 (1 → 2), 309 (1 → 0), 319 (1 → 0), 332 (1 → 0).  
*Eretiscus tonnii*: 314 (0 → 1), 325 (1 → 0), 330 (2 → 0).  
*Palaeospheniscus patagonicus*: 229 (1 → 2).  
*Pseudaptenodytes macraei*: 224 (0 → 3), 232 (0 → 1).  
*Pygoscelis adeliae*: 8 (1 → 0), 13 (2 → 0), 42 (2 → 3), 77 (1 → 0), 100 (0 → 1), 105 (1 → 2),  
114 (0 → 1), 128 (0 → 1), 178 (1 → 0), 216 (3 → 2), 219 (1 → 2), 233 (0 → 2), 250 (1 → 0),  
267 (0 → 1), 271 (1 → 0), 283 (1 → 0), 294 (0 → 1), 319 (1 → 0), 325 (1 → 0), 333 (1 → 0),  
403 (0 → 1), 411 (0 → 1), 442 (0 → 1), 446 (0 → 2), 449 (0 → 2), 464 (1 → 0), 505 (1 → 2).  
*Pygoscelis antarcticus*: 134 (2 → 0), 160 (3 → 4), 169 (1 → 2), 184 (0 → 1), 198 (0 → 2),  
232 (0 → 2), 271 (1 → 0), 273 (0 → (13)), 283 (1 → 0), 301 (0 → 1), 395 (1 → 0),  
405 (0 → 1), 407 (0 → 4).  
*Pygoscelis papua*: 50 (1 → 0), 91 (1 → 0), 132 (3 → 0), 151 (0 → 1), 209 (1 → 2), 228 (0 → 1),  
229 (1 → 0), 371 (0 → 1), 431 (0 → 2), 441 (1 → 2), 492 (1 → 0), 494 (0 → 1), 496 (1 → 0),  
507 (1 → 0).  
*Pygoscelis grandis*: 227 (2 → 1), 235 (0 → 2), 305 (0 → 1), 332 (1 → 0).  
*Pygoscelis tyreei*: 165 (1 → 2).

*Megadyptes antipodes*: 4 (2 → 0), 12 (0 → 1), 47 (0 → 2), 89 (2 → 0), 91 (1 → 0), 108 (0 → 1),  
 130 (0 → 2), 132 (3 → 1), 169 (1 → 0), 195 (1 → 0), 216 (3 → 1), 233 (0 → 2), 241 (0 → 1),  
 256 (1 → 0), 257 (0 → 1), 267 (0 → 2), 283 (1 → 3), 286 (1 → 2), 287 (0 → 1), 308 (1 → 0),  
 310 (1 → 0), 317 (0 → 2), 369 (1 → 0), 387 (0 → 1), 392 (0 → 2), 401 (2 → 3), 403 (0 → 1),  
 404 (0 → 1), 405 (0 → 2), 407 (0 → 2), 428 (1 → 0), 430 (1 → 0), 431 (0 → 2), 432 (0 → 1),  
 459 (1 → 0), 465 (0 → 2), 476 (0 → 1), 477 (1 → 0), 482 (1 → 0), 490 (0 → 1), 496 (1 → 0),  
 506 (0 → 1).  
*Tasidyptes hunteri*: 320 (1 → 0).  
*Chubutodyptes biloculata*: 209 (1 → 2), 224 (0 → 1), 226 (1 → 0).  
*Eudyptes sclateri*: 323 (1 → 0), 328 (1 → 2).  
*'Nucleornis' insolitus*: 315 (0 → 1), 327 (2 → 0), 334 (1 → 0).  
*Eudyptes robustus*: 12 (0 → 1), 15 (0 → 2), 17 (2 → 0), 18 (1 → 0), 48 (1 → 0), 55 (1 → 0), 57 (1 → 2),  
 132 (3 → 1), 189 (3 → 2), 233 (0 → 2), 246 (1 → 0), 256 (1 → 0), 268 (2 → 3), 278 (1 → 0), 284 (1 → 0),  
 289 (2 → 1), 320 (1 → 0), 446 (3 → 2), 505 (0 → 1).  
*Eudyptes chrysocome*: 8 (0 → 1), 42 (2 → 0), 47 (0 → 1), 57 (1 → 2), 60 (1 → 0), 114 (0 → 1), 165 (2 → 3),  
 167 (1 → 0), 175 (0 → 2), 179 (0 → 2), 183 (1 → 0), 202 (1 → 2), 209 (1 → 2), 210 (1 → 2),  
 232 (0 → 3), 249 (1 → 0), 253 (0 → 2), 280 (0 → 1), 281 (0 → 1), 310 (1 → 0), 312 (1 → 0), 317 (0 → 3),  
 318 (0 → 2), 411 (0 → 2).  
*Eudyptes chrysolophus*: 5 (1 → 0), 20 (0 → 1), 27 (1 → 0), 52 (0 → 1), 66 (1 → 0), 97 (0 → 2), 113 (1 → 2),  
 117 (1 → 0), 128 (0 → 1), 136 (1 → 2), 175 (0 → 1), 180 (0 → 2), 181 (0 → 1), 182 (1 → 0),  
 186 (0 → 1), 187 (0 → 1), 219 (1 → 2), 237 (0 → 2), 252 (1 → 0), 270 (2 → 1), 273 (3 → 2), 278 (1 → 0),  
 287 (0 → 1), 297 (1 → 0), 316 (2 → 0), 452 (1 → 0).  
*Eudyptes schlegeli*: 18 (1 → 0), 37 (0 → 1), 40 (2 → 1), 41 (0 → 1), 46 (0 → 1), 61 (0 → 1),  
 75 (0 → 1), 78 (2 → 1), 115 (1 → 2), 125 (1 → 0), 132 (2 → 1), 135 (1 → 2), 137 (1 → 0),  
 142 (0 → 1), 148 (1 → 0), 164 (0 → 2), 178 (1 → 0), 179 (0 → 1), 184 (1 → 0),  
 192 (1 → (23)), 200 (0 → 2), 211 (0 → 1), 229 (1 → 0), 231 (1 → 0), 241 (0 → 1),  
 268 (2 → 1), 276 (1 → 0), 282 (4 → 3), 285 (0 → 1), 293 (0 → 1), 315 (0 → 1), 320 (1 → 0),  
 340 (0 → 1), 405 (0 → 1), 508 (1 → 0).  
*Eudyptes pachyrhynchus*: 135 (1 → 0), 151 (0 → 1), 186 (0 → 1), 187 (0 → 1), 218 (1 → 3),  
 233 (0 → 3), 250 (1 → 0), 252 (1 → 0), 276 (1 → 2), 278 (1 → 0), 279 (0 → 1), 297 (1 → 2),  
 310 (1 → 2), 331 (0 → 1), 339 (2 → 3), 496 (1 → 0), 506 (0 → 1).  
*Eudyptula minor*: 218 (1 → 0), 480 (1 → 2), 506 (0 → 1), 507 (1 → 0).  
*Eudyptula minor albosignata*: 160 (0 → 3), 166 (0 → 1), 330 (2 → 1).  
*'Inguza' predemersus*: 211 (0 → 1), 277 (1 → 2), 330 (2 → 3), 334 (1 → (02)).  
*Spheniscus chilensis*: 161 (2 → 1), 213 (1 → 2), 231 (1 → 0).  
*Spheniscus demersus*: 17 (0 → 2), 31 (1 → 0), 215 (1 → 0), 229 (3 → 2), 233 (1 → 0), 268 (2 → 1),  
 402 (2 → 3), 406 (0 → 1), 410 (3 → 2), 422 (0 → 1), 450 (0 → 1), 492 (1 → 0).  
*Spheniscus humboldti*: 18 (2 → 3), 50 (1 → 0), 55 (1 → 2), 89 (2 → 1), 102 (1 → 2), 115 (0 → 3),  
 203 (0 → 1), 267 (1 → 3), 407 (0 → 3), 431 (0 → 1), 491 (0 → 2), 494 (0 → 1).  
*Spheniscus magellanicus*: 67 (0 → 1), 147 (0 → 1), 203 (0 → 1), 229 (1 → 0), 231 (1 → 0),  
 237 (0 → 1), 267 (1 → 2), 268 (2 → 3), 283 (1 → 2), 290 (1 → 0), 301 (0 → 1), 410 (3 → 1),  
 422 (0 → 1), 430 (1 → 0), 431 (0 → 1), 489 (0 → 1).  
*Spheniscus mendiculus*: 94 (0 → 1), 175 (0 → 1), 177 (1 → 0), 252 (1 → 0), 265 (0 → 1), 276 (0 → 1),  
 279 (0 → 1), 280 (1 → 0), 286 (1 → 0), 392 (0 → 3), 402 (2 → 1), 407 (0 → 3), 492 (1 → 0),  
 508 (1 → 0).  
*Spheniscus megaramphus*: 92 (1 → 0).  
*Spheniscus urbinai*: no apomorphies.  
*Dunroonornis parvus*: no apomorphies.  
*'Dege' hendeyi*: 222 (1 → 3), 232 (0 → 3), 280 (1 → 0), 281 (0 → 1).  
*Tereingaornis moisleyi*: 215 (1 → 3), 231 (1 → 0).  
*Marplesornis novaezealandiae*: no apomorphies.  
*Palaeospheniscus bergi*: 203 (0 → 1).  
*Korora oliveri*: 303 (0 → 1), 319 (0 → 1), 320 (1 → 0), 329 (0 → 1), 330 (2 → 1).

*Ichtyopteryx gracilis*: 313 (0 → 2), 316 (1 → 2), 322 (1 → 0), 332 (0 → 2).  
*Delphinornis arctowski*: 331 (0 → 1), 333 (2 → 0), 339 (3 → 1).  
*Mesetaornis polaris*: 309 (1 → 0), 316 (1 → 0), 330 (2 → 3), 334 (1 → 0).  
*Marambiornis exilis*: 314 (0 → 1).  
*Paraptenodytes antarcticus*: 209 (0 → 1), 216 (0 → 1), 223 (0 → 2), 229 (2 → 1), 232 (0 → 1),  
277 (2 → 0), 296 (0 → 3), 303 (1 → 0), 338 (0 → 1).  
*Paraptenodytes robustus*: 153 (1 → 0), 203 (2 → 1), 204 (1 → 2), 220 (0 → 1), 254 (1 → 0),  
291 (0 → 1).  
*Delphinornis larseni*: 309 (1 → 0), 330 (2 → 3), 331 (0 → 1), 338 (0 → 3), 339 (3 → 2).  
*Delphinornis gracilis*: 310 (0 → 2), 319 (1 → 3), 338 (0 → 3).  
*Wimanu manningi*: 240 (0 → 3), 309 (1 → 0).  
*Wimanu tuatahi*: 317 (0 → 2).  
Gaviidae: 10 (0 → 2), 20 (1 → 0), 29 (0 → 1), 38 (1 → 0), 59 (1 → 0), 60 (3 → 0), 68 (0 → 1),  
70 (0 → 1), 127 (0 → 1), 136 (1 → 2), 137 (3 → 0), 141 (1 → 2), 179 (2 → 1), 188 (1 → 0),  
198 (1 → 2), 199 (0 → 1), 200 (0 → 2), 218 (1 → (23)), 237 (1 → 2), 273 (3 → 0),  
293 (1 → 2), 297 (0 → 2), 323 (2 → 1).  
Podicipedidae: 6 (0 → 2), 18 (1 → 0), 22 (0 → 1), 23 (0 → 1), 53 (0 → 1), 62 (1 → 2), 67 (0 → 1),  
80 (1 → 0), 96 (0 → 2), 115 (0 → (12)), 128 (0 → 2), 183 (1 → 0), 184 (2 → 1), 192 (1 → 0),  
217 (2 → 1), 221 (0 → 1), 282 (1 → 2).  
Procellariiformes: 7 (0 → 1), 18 (1 → 2), 25 (0 → 1), 29 (0 → 2), 37 (0 → 1), 48 (1 → 0), 51 (1 → 0),  
57 (0 → 2), 70 (0 → 2), 83 (2 → 1), 86 (0 → 1), 92 (0 → 1), 97 (3 → 0), 101 (1 → 0),  
115 (0 → 3), 117 (1 → 0), 122 (1 → 0), 125 (0 → 1), 136 (1 → 3), 137 (3 → 2), 139 (3 → 1),  
145 (1 → 0), 168 (1 → 0), 189 (0 → 2), 194 (1 → 0), 200 (0 → 1), 207 (0 → 1), 223 (0 → 2),  
241 (0 → 1), 251 (1 → 0), 269 (0 → 2), 277 (2 → 1), 301 (0 → 1), 315 (0 → 1), 319 (1 → 3),  
320 (1 → 0), 328 (1 → 0), 387 (0 → 2), 391 (0 → 2), 446 (0 → 1).  
Phalacrocoracidae: 10 (0 → 2), 16 (1 → 2), 22 (0 → 1), 23 (0 → 1), 40 (1 → 0), 55 (1 → 0),  
59 (1 → 0), 69 (1 → 0), 83 (2 → 0), 93 (0 → 1), 97 (3 → 1), 108 (0 → 1), 128 (0 → 2),  
131 (0 → 1), 135 (1 → 0), 144 (0 → 1), 153 (1 → 0), 173 (1 → 0), 183 (1 → 0), 189 (0 → 1),  
192 (1 → 2), 193 (1 → 0), 199 (0 → 1), 201 (0 → 1), 216 (0 → 1), 225 (0 → 1), 236 (1 → 2),  
254 (1 → 0), 261 (0 → 1), 276 (1 → 0), 308 (1 → 0), 319 (1 → 4), 323 (2 → 0), 327 (2 → 1),  
336 (0 → 2), 342 (1 → 0), 350 (0 → 1), 356 (0 → 1), 384 (0 → 1), 408 (0 → 1), 486 (0 → 1).

**Appendix 4.1. Penguin Taxa Included in Analysis.** Dates based on associated literature. Extant species listed only if known from fossil remains.

Taxon	Age	Literature
<i>Anthropodytes gilli</i>	L Miocene	Simpson 1959
<i>Anthropornis grandis</i>	M/L Eocene	Wiman 1905, Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
<i>Anthropornis nordenskjoldi</i>	M/L Eocene	Wiman 1905, Marples 1953, Glaessner 1955, Simpson 1971a, Cione et al. 1977, Jenkins 1985, Olson 1985, Millener 1988, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
<i>Aptenodytes patagonicus</i>	Holocene	McEvey & Vestjens 1974
<i>Aptenodytes ridgeni</i>	L Pliocene	Simpson 1972b
<i>Archaeospheniscus lowei</i>	E/M Oligocene	Marples 1952, Simpson 1971c
<i>Archaeospheniscus lopdelli</i>	E/M Oligocene	Marples 1952, Simpson 1971c
<i>Archaeospheniscus wimani</i>	M/L Eocene	Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a
CADIC P-21	M Eocene	Clarke et al. 2003
<i>Chubutodyptes biloculata</i>	L Olig/E Miocene	Simpson 1972a, Tonni 1980
<i>Crossvallia unienwillia</i>	L Paleocene	Tambussi et al. 2005
'Dege' hendeyi	L Mio-E Pliocene	Simpson 1971b, 1973, 1979a, 1979b, Olson 1983, Hendey 1975, Vickers-Rich 1980
<i>Delphinornis arctowski</i>	M/L Eocene	Myrcha et al. 2002, Jadwiszczak 2006a
<i>Delphinornis gracilis</i>	M/L Eocene	Myrcha et al. 2002, Jadwiszczak 2006a
<i>Delphinornis larseni</i>	M/L Eocene	Wiman 1905, Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
<i>Dunroonornis parvus</i>	E/M Oligocene	Marples 1952, Simpson 1971c
<i>Eretiscus tonii</i>	M Miocene	Simpson 1981, Olson 1986
<i>Eudyptes schlegeli</i>	Holocene	McEvey & Vestjens 1974
<i>Eudyptes pachyrhynchus</i>	Holocene	Scarlett 1983
<i>Eudyptula minor</i>	Pleist-Holocene	Grant-Mackie & Simpson 1973, Scarlett 1983
'Inguza' predemersus	L Pliocene	Simpson 1971b, Olson 1983
<i>Ichtyopteryx gracilis</i>	M/L Eocene	Wiman 1905, Simpson 1971a, Jadwiszczak 2006a
<i>Korora oliveri</i>	L Oligocene	Marples 1952, Simpson 1971c
<i>Marambiornis exilis</i>	L Eo-?E Oligo	Myrcha et al. 2002, Jadwiszczak 2006a
<i>Marplesornis novaezealandiae</i>	L Pliocene	Marples 1952, 1960, Simpson 1972b
<i>Megadyptes antipodes</i>	E Pleist-Holocene	Scarlett 1983
<i>Mesetaornis polaris</i>	L Eo-?E Oligo	Myrcha et al. 2002, Jadwiszczak 2006a
'Nucleornis' hendeyi	L Pliocene	Simpson 1971b, Olson 1983
OM C47.23A	E Oligocene	
OM C47.25	E Oligocene	
<i>Orthopteryx gigas</i>	M/L Eocene	Wiman 1905, Marples 1953, Simpson 1971a, Jadwiszczak 2006a
<i>Pachydyptes ponderosus</i>	L Eocene	Hector 1873, Oliver 1930, Simpson 1971c
<i>Pachydyptes simpsoni</i>	L Eocene	Jenkins 1974
<i>Palaeudyptes antarcticus</i>	L Eocene-E/L Olig.	Huxley 1859, Marples 1952, Simpson 1970, 1971c
<i>Palaeudyptes gunnari</i>	M/L Eocene	Wiman 1905, Marples 1953, Simpson 1971a, Myrcha et al. 2002, Jadwiszczak 2006a, Tambussi et al. 2006
<i>Palaeudyptes klekowskii</i>	M/L Eocene	Myrcha et al. 1990, Jadwiszczak 2006a, Tambussi et al. 2006
<i>Palaeudyptes marplei</i>	L Eocene	Brodkorb 1963, Simpson 1971c
<i>Palaeospheniscus bergi</i>	L Olig/E Miocene	Moreno & Mercerat 1891, Simpson 1946, 1972, Tonni 1980
<i>Palaeospheniscus gracilis</i>	L Olig/E Miocene	Ameghino 1899, Simpson 1946, 1972, Tonni 1980
<i>Palaeospheniscus patagonicus</i>	L Olig/E Miocene	Ameghino 1899, Simpson 1946, 1972, Tonni 1980
<i>Palaeospheniscus wimani</i>	L Olig/E Miocene	Moreno & Mercerat 1891, Simpson 1946, 1972, Tonni 1980
<i>Paraptendytes antarcticus</i>	L Olig/E Miocene	Moreno & Mercerat 1891, Simpson 1946, 1972, Tonni 1980, Bertelli et al. 2006
<i>Paraptendytes robustus</i>	L Olig/E Miocene	Ameghino 1899, Simpson 1946, 1972, Tonni 1980
<i>Platydyptes amiesi</i>	L Oligocene	Marples 1952, Simpson 1971a
<i>Platydyptes novaezealandiae</i>	Oligocene	Oliver 1930
<i>Pseudaptendytes macraei</i>	L Miocene	Simpson 1970
<i>Pygoscelis grandis</i>	?E Pliocene	Walsh and Suarez 2006
<i>Pygoscelis tyreei</i>	L Pliocene	Simpson 1972b
<i>Spheniscus chilensis</i>	L Pliocene	Emslie & Guerra Correa 2003
<i>Spheniscus megaramphus</i>	Miocene	Stucchi 2003
<i>Spheniscus urbinae</i>	L Olig/E Miocene	Stucchi 2002

<i>Tasidyptes hunteri</i>	Holocene	van Tets & O'Connor 1983
<i>Tereingaornis moisleyi</i>	Pliocene	Scarlett 1983, McKee 1987, 1988
<i>Wimanornis seymourensis</i>	M/L Eocene	Simpson 1971a, Jadwiszczak 2006a
<i>Wimanu manningi</i>	Late E Paleocene	Fordyce & Jones 1990, Slack et al. 2006
<i>Wimanu tuatahi</i>	Early L Paleocene	Fordyce & Jones 1990, Slack et al. 2006

**Appendix 4.2. Measures of Completeness and Origination Time for Penguins.** From Strauss and Sadler, 1989; Benton and Storrs, 1994; Huelsenbeck, 1999; Wills, 1999.

	Formula	Abbreviations	Result	
RCI	$= \left(1 - \frac{\Sigma (\text{MIG})}{\Sigma (\text{SRL})}\right) \times 100\%$	MIG = minimum implied gap = 506 SRL = simple range length = 106	= -377%	
SCI	$= \frac{C}{n - 2}$	C = strat. consist. nodes = 20 n = number of taxa = 42	= 48%	
GER	$= 1 - \frac{(\text{MIG} - G_{\min})}{(G_{\max} - G_{\min})}$	$G_{\min}$ = min. possible ghost range = 61.05 $G_{\max}$ = max. possible ghost range = 1735.95	= 74.4%	
Confidence Intervals (CI)	$P = 1 - (1 + \alpha)^{-(n-1)}$  Where: $\alpha$ = CI / oldest taxon (OT) P = confidence level n = fossiliferous horizons	Panspheniscidae	Stages n = 17 OT = 22	P = 0.95 = 65.58mya P = 0.99 = 68.39mya
			Mya n = 33 OT = 62	P = 0.95 = 67.13mya P = 0.99 = 70.65mya
		Spheniscidae n = 9 oldest taxon = 24		P = 0.95 = 34.9mya
				P = 0.99 = 42.7mya

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## Vita

Nina Elise Triche was born in Poughkeepsie, New York, on November 4<sup>th</sup>, 1979. Her parents, Curtis and Marie Stokes, transplanted her to Ohio at a young age, where she remained until graduating from Hudson High School in 1997. They then kindly funded her attendance at Tulane University, where she attained a B.S. in Ecology and Evolutionary Biology, as well as a B.A. in French in May of 2001. She received an Honors Degree for the latter by completing a thesis on the bad composition of a medieval French romance. While at Tulane, Nina worked in various labs cutting up both small fish and mouse lungs, spent three months in London pulling pints, and married Edward J. Triche, Jr. She moved to Texas soon after, in pursuit of a graduate career at The University of Texas at Austin (UT). This venerable institution awarded her an M.S. Geo. Sci. in the fall of 2003 for a thesis on the cranial anatomy of a cute, caiman crocodile. During her tenure at UT, she spent many years teaching numerous labs for biology, geology, and paleontology courses. She also worked to master the Brunton as a geologic field assistant, to accept her students' limited interest in dead things as a Teaching Assistant, and to refine the art of numbering thousands of molluscs without air-conditioning in the Texas summer heat as a Research Assistant at the Non-vertebrate Paleontology Lab. She received a number of external research grants and was awarded the very first Keith and Ann Young Endowment for the Curation of Non-vertebrate Collections for her work with the 7<sup>th</sup> Annual Rudist Congress in June, 2005. This will be her final degree.

Permanent address: 4400 Sinclair Avenue, Austin, Texas 78756

This dissertation was typed by Nina Elise Triche.