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Feather biomechanics of penguins and other seabirds

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FEATHER BIOMECHANICS OF PENGUINS AND OTHER SEABIRDS

A Thesis

Presented to the

Faculty of

California State University,

San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

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by

Katherine Elizabeth Johnson

June 2012

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ABSTRACT

Penguins are flightless birds that evolved from flying birds at least 60 million years ago. And yet to call a penguin flightless is inaccurate. During their evolution, penguins have become wing-propelled aquatic flyers. This transition resulted in significant modifications to the penguin's anatomy (e.g., flattened bones in the wing). Although many aspects of penguin biology have been studied, the feathers have received less attention except with regard to thermoregulation. The biomechanics of penguin feathers are the focus of this thesis. Penguins are unique, but they are not alone in their ability to fly aquatically. Several other clades, including alcids, dippers, and diving petrels also fly under water. By studying penguins in comparison to other wing-propelled aquatic fliers, it may be possible to understand how penguin feathers evolved. Fourteen species were sampled, including aerial flyers, aerial flyers that are also wing-propelled divers, as well as flightless wing-propelled divers. Two measurements, including aspect ratio (a measure of dorsoventral flattening) and standardized resistance to torsion, reveal that penguin feathers have significantly different shape and biomechanical properties than even closely related or ecologically similar birds. Differences between penguins and their close relatives may have resulted from the long evolutionary time separating these lineages as well as differences in the modes of wing-propelled diving. The results presented here could be used to direct future research efforts in penguin feather structure and evolution.

ACKNOWLEDGEMENTS

This project was my first foray into independent research and while it was independent I could not have accomplished what I did without the help of many individuals. First and foremost I would like to mention my parents. They taught me the importance of education and have been my constant supporters throughout my academic career. I next would like to thank my sister who is a constant source of inspiration. She even took time from writing her dissertation to edit this thesis. There are many individuals from California State University San Bernardino that I would like to thank. Britt Coats aided me in the lab, teaching many of the lab techniques I needed for this project. I would also like to thank my committee members Dr. Stuart Sumida and Dr. Tomasz Owerkowicz for the use of Dr. Sumida's lab and for both of their input. Finally, I would like to thank my advisor Dr. Kevin Middleton. He gave me guidance when I most needed it. Dr. Middleton allowed me to see the exciting nature of research and has inspired me to continue my education and explore experimental evolution.

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CHAPTER ONE

EVOLUTION AND BIOLOGY OF PENGUINS

Introduction

Penguins (Aves: Sphenisciformes) are secondarily flightless birds whose body form and function have been shaped by their ecology. Penguin evolution is intimately tied to their transition from aerial flight to wing-propelled diving. Aquatic flight exerts very different mechanical forces on the structural components of the wing and its feathers compared to aerial flight. This dichotomy results from the significant differences in the physical properties of air and water: water approximately 800 times as dense and 70 times as viscous as air (Denny 1993). Therefore, wing biomechanics during aquatic flight are expected to differ dramatically from those used in aerial flight (Hamilton 2005).

Powered, flapping flight has only evolved four times (insects, pterosaurs, birds, and bats), and in Aves, feathers are essential. However, not all birds retain the ability to fly. The reasons why and how often flightlessness evolved in Aves remains a matter of debate (Roff 1994). In penguins aerial flight appears to have been lost in association with the adoption of aquatic flight. Penguins are one of several clades of extant wing-propelled divers, which also include diving petrels (*Pelecanoides* spp.; Procellariiformes), dippers (Passeriformes), and the Alcidae (including puffins, auks, and murres; Figure 1). Although the extinct Plotopteridae (Pelecaniformes) were a diverse clade of Eocene-Miocene flightless seabirds from the northern Pacific (Mayr 2004), penguins are the only extant group restricted only to aquatic flight.

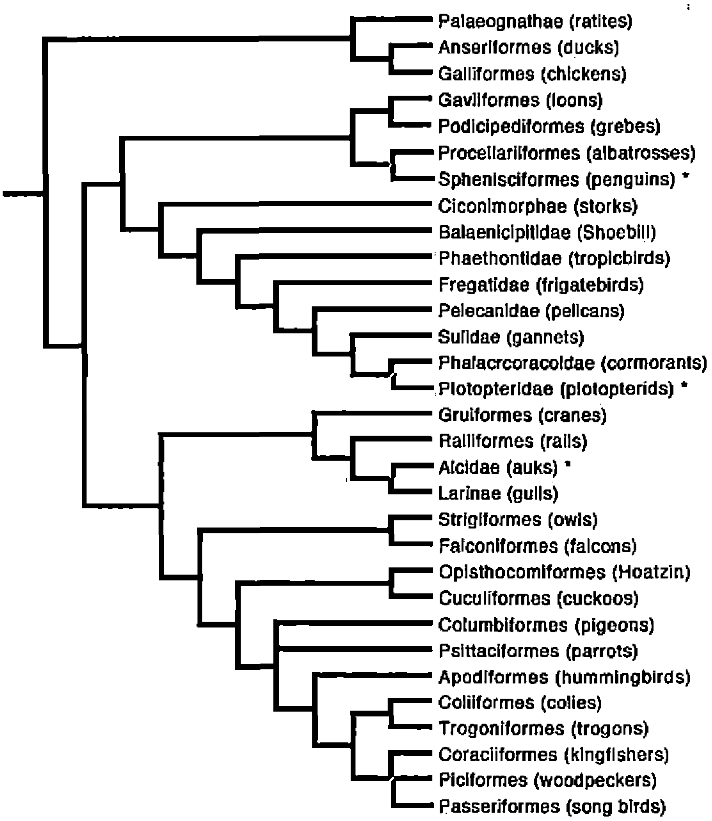

Figure 1. Phylogenetic Relationships Among Aves. Branches colored red represent clades with wing-propelled taxa. Starred clades include flightless wing-propelled diving birds. Tree topology based on Livezey and Zusi (2007), Livezey (2010), and Smith (2011).

Penguin Biology

Based on fossil evidence, penguins and their ancestors have always lived in the Southern hemisphere, and today penguins can only be found in areas that the Antarctic current reaches, including Antarctica, areas of Australia and New Zealand, parts of South America, and South Africa (Sparks and Soper 1987). The complete range penguins have inhabited during geologic time is unknown, however, most fossil penguins have been discovered within the extant penguin range (Sparks and Soper 1987) with the exception of a few fossils, including *Inkayacu paracasensis* (Clarke et al. 2010). Penguins' current range shows that they can be adapted to very cold environments. Thus, during the transition to wing-propelled diving, it is hypothesized that, although feathers were no longer necessary for aerial flight, they were probably necessary for the stresses applicable for aquatic flight as well as thermoregulation. The relative importance of the two in the evolution of penguin feathering remains to be determined.

Penguin ancestry is unsettled, given that the oldest fossil penguin from the Paleocene (*Waimanu* spp.; Slack et al. 2012) already demonstrates most of the recognizable osteological traits of extant penguins. Compared to their volant ancestors, penguin flippers are one of the most highly modified anatomical structures. The bones of the flipper are broad and flattened, giving the flipper a paddle-like quality (Sparks and Soper 1987). To date, no transitional fossils have been found, as stem penguins had likely already branched off by the late Cretaceous. It is believed that the mass extinctions of the Cretaceous-Tertiary era opened up new niches to birds, which, until then, had been occupied by marine reptiles (Ksepka et al. 2006).

Simpson (1946) recognized the similarities between the phylogenetically distant auks and diving petrels as an example of convergent evolution. There are members of both of these groups that are able to both fly aerially and aquatically, a condition that may demonstrate a possible intermediate step through which the ancestors of penguins may have passed.

The close relatives of penguins are also birds that exhibit aquatic flight and a sister-taxon relationship with Procellariiformes is most parsimonious (Smith 2011; Figure 1). Examining other diving sea birds may help tease out the relationships between penguins and their relatives. The fossil record suggests that wing-propelled diving did not appear until the end of the Cretaceous (Feduccia 1996). Again this radiation into the water most likely corresponds with the mass-extinction at the end of the Cretaceous. In the Southern Hemisphere three groups of wing-propelled divers evolved: (1) petrels (Procellariiformes); (2) the diving-petrels (Pelecanoididae); and (3) the penguins (Sphenisciformes), with penguins thought to have evolved from a procellariiform-like ancestor (Feduccia 1996; Smith 2011). The fourth group of wing-propelled divers is the Alcidae. These birds evolved in the Northern Hemisphere and include the auks, puffins, murres, murrelets, and guillemots (Feduccia 1996).

Fossil Penguins

The oldest penguin fossils are two species in the genus *Waimanu*, which is more closely related to extant penguins than any other known bird (Slack et al. 2012). Four representative skeletons are known from Paleocene sediments in New Zealand. *Waimanu* shares many penguin characteristics including being a flightless wing-propelled diver. However, *Waimanu* does not have the widened ulna and radius characteristic of modern penguins (Slack et al. 2012). The *Waimanu* fossils confirm that penguins already separated from other Neornithes by the early Paleocene (Slack et al. 2012).

A recent study describes a more derived but still relatively basal fossil penguin, *Inkayacu paracasensis*, from the Eocene of Peru (~36 Ma) (Clarke et al. 2010). Notably multiple feathers were preserved with *Inkayacu*, providing insight into the evolution of penguin featheration. Penguins, both extinct and extant, have melanic feathers. The melanin granules, or melanosomes, are hypothesized to provide not only color, but also resistance to wear in the penguin feathers (Bonser and Purslow 1995). The melanosomes of *Inkayacu* were examined and compared to the feather melanosomes from extant penguins and of other extant birds (Clarke et al. 2010). These authors found that the size of melanosomes of extinct penguins are more similar to other extant non-penguin birds than to extant penguins. Clarke and coauthors hypothesized that further adaption to wing-propelled diving may be attributable to nanoscale modification in the structure of melanosomes. Thus, melanosome evolution may shed light into penguin feather evolution.

Gross Anatomy of Feathers

Feathers are extremely important to bird biology and are thought to be one of the most derived structures of the integument (Lucas and Stettenheim 1972). The integument system is comprised of the skin and all of its appendages, including, but not limited to, hair, scales, claws, and feathers (Lucas and Stettenheim 1972).

Typical feathers have a shaft and a vane. The shaft is comprised of two main parts, the calamus and the rachis. The proximal end that inserts into the skin is called the calamus, a mostly hollow tube that appears circular in cross section. At the proximal end of the calamus is a hole called the inferior umbilicus. This hole is the site where the nourishing pulp was located during feather growth. At the distal most part of the calamus, the superior umbilicus is the point of transition from the calamus to the rachis.

The rachis, which is the site where the vane is attached, is the second portion of the shaft and is much more solid in structure (Figure 2). In most birds, the rachis has a more rectangular cross-section, usually wider than thick. The vane extends out of the rachis and is composed of barbs that emerge from both sides of the rachis (Figure 2). Barbules branch off of the ramus and barbicels branch off of the barbules, which are different on their proximal and distal sides of the shaft. This organization allows the opposing barbules to attach to each other through their barbicel projections. The vane is the most important feather structure in flight. The barbule projections enables the vane to interlock providing the important feature that allows the feather to act as an airfoil (Lucas and Stettenheim 1972). The afterfeather is one more structure that is found on many feathers but not all. As its name implies, the afterfeather is another feather protruding out of the main feather near the superior umbilicus of the calamus. The afterfeather is thought to be important in insulation (Lucas and Stettenheim 1972; Figure 2).

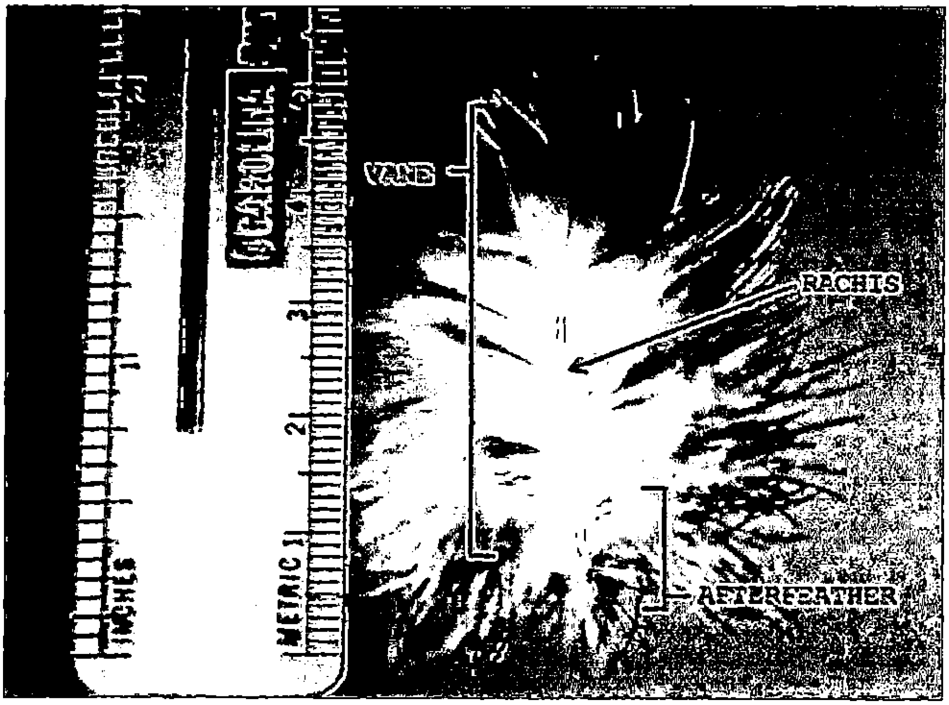

Figure 2. Feather Anatomy.

While many feathers follow the basic feather plan, variations in structure exist that most likely arose from different selective pressures on feather morphology. These selective pressures range from the location on the body to the different functions the feather needs to perform. Feathers are not only important for flight, but also in thermoregulation, protection, display, and, in some cases, can act as a sensory structure (Proctor and Lynch 1993).

Classification of feathers is based on function and location, and there are five major categories of feathers that have been recognized (Proctor and Lynch 1993). The body and flight feathers are categorized as contour feathers. Flight feathers have special barbs that hook to each other that produce the friction that is needed to maintain the aerodynamic surface of the wing. The hook and lock structure of the barbicels ensures that these flight feathers remain stiff and do not allow significant separation during flight (Proctor and Lynch 1993), which would result in the loss of aerodynamic lift. Other feather types include semiplumes, bristles, filoplumes, and powder feathers. These feather types function respectively for insulation, protection, sensation, and grooming (Proctor and Lynch 1993).

Contour Feathers

The contour feathers are especially important for this study because they contain the body feathers, which will be the point of comparison between species. Body feathers are usually smaller than flight feathers, have symmetrical vanes, and sometimes have a more substantial afterfeather (Proctor and Lynch 1993).

Feather Tissue

As part of the integumentary system, feathers are primarily composed of the protein keratin, which is found only in epithelial cells (Bragulla and Homberger 2009). Keratin exhibits several unique properties. Whereas most proteins are vulnerable to degradation by the proteases pepsin and trypsin, keratins are not (Bragulla and Homberger 2009). Keratins are also insoluble in water and organic solvents (Bragulla and Homberger 2009).

The types of keratin differ mainly in the amino acid sequences. The primary structure of the protein confers a particular secondary structure, which is how most keratins are classified. The most prevalent form of keratin is α-keratin, named for the presence of α-helices in the secondary structure of the protein (Bragulla and Homberger 2009). In birds, α-keratin is the main component of the skin (Stettenheim 2000). However an additional keratin is present as well, β-keratin, named for the β-sheets in its secondary structure (Bragulla and Homberger 2009). β-keratin is a novel keratin that has only been found in Sauropsida, the clade that includes reptiles and birds (Bragulla and Homberger 2009). β-keratin is the major structural component of feathers (Sawyer et al. 2000) comprising up to 90% of the feather rachis (Bonser & Purslow 1995) and is also found in the claws and beak (Bragulla and Homberger 2009).

β-keratin differs from α-keratin in the length of its amino acid chain (Bragulla and Homberger 2009) and sequences of feather β-keratin show a high degree of homology between species (Cameron et al. 2003). The central domain of β-keratin is 32 amino acids long, arranged in four anti-parallel β-sheets (Bragulla and Homberger 2009). The central area of the protein is highly hydrophobic containing large amounts of the amino acids serine, proline, valine, leucine, glutamate, and aspartate (Bragulla and Homberger 2009).

Feathers are composed of two keratinous materials that together provide a strong yet light material. The first keratin type is in the form of filaments, and the second is an amorphous keratinous matrix that surrounds the filaments (Gill 1990). The structure created by these two materials enables the feather to withstand the stresses involved in flight while remaining light. Bragulla and Homberger (2009, p. 534), explain how keratin is able to provide the mechanical functions that are needed of it: "The best-known function of keratins and keratin filaments is to provide a scaffold (through self-bundling and by forming thicker strands) for epithelial cells and tissues to sustain mechanical stress, maintain their structural integrity, and ensure mechanical resilience."

Feather Colors

Feathers come in a spectrum of colors and many studies have examined the causes and consequences of feather coloration. Three main pigments are involved in feather coloration. The first and most widespread pigment is melanin (Gill 1990). The second two are carotenoids and porphyrins. Carotenoids are responsible for creating bright reds, oranges, and yellows, and porphyrins produce red and brown feathers (Gill 1990). Carotenoids and porphyrins are very important in bird biology. However, due to the biomechanical focus of this project only melanins will be discussed because it is believed that melanin imparts important biomechanical properties to the feather.

Melanin is found in almost all birds (Gill 1990). This pigment also has a variety of functions making melanin a highly studied subject. Melanin is critical because it seems to strengthen the feather. The melanin pigment is contained within granules, called melanosomes. Melanoblasts are cells that produce melanosomes from the amino acid tyrosine (Vinther et al. 2010). This pigment produces blacks, browns, and grays colors that are separated into two categories based on the appearance of the granules. Eumelanians have large regularly shaped granules and produce colors ranging from dark brown to black and gray (Gill 1990). Phaeomelanins have smaller more irregularly shaped granules and produce tans, reddish browns, and some shades of yellow (Gill 1990).

Penguin Feathers and Thermoregulation

Penguin feather morphology is very different from that of other birds. This unique morphology is usually understood in the context of thermoregulation. Penguins have body feathers with flattened rachises and scale-like feathers on the wings (Giannini and Bertelli 2004). Their feathers are also smaller, measuring around 30-40 mm with a substantial afterfeather measuring 20-30 mm (Dawson et al. 1999).

Extant penguins live from the frigid Antarctic to the temperate conditions of South America and South Africa and as far north as the Galapagos Islands. This wide range of habitats presents a wide variety of thermoregulatory challenges for the different species of penguins.

In extremely cold temperatures, penguins need to be well insulated and protected from snow, ice, and high winds. A thick coat of feathers traps air and reduces heat loss (Dawson et al. 1999). Penguins also require protection from frigid water when they are diving. Feathering that would work on land would be problematic in the water. Having too much air trapped in the feathers would lead to buoyancy issues for the penguin when diving and the best coat of feathers for a diving penguin would be streamlined and waterproof.

Penguins are able to accomplish insulation on land and in the water. The shaft of the feather is attached to muscles (Dawson et al. 1999). While diving these muscles contract to create a "water-tight barrier" (Dawson et al. 1999). The flattened feathers of the body can also mold to the body and withstand increases in water pressure (Dawson et al. 1999). When a penguin gets back on land, the same muscles move the feather shaft to allow for an air-filled coat (Dawson et al. 1999).

Most birds only have feathers in certain areas of the skin called tracts. In most birds there are eight tracts of feathers separated by featherless skin called apteria (Gill 1990). Penguins lack apteria and have feathers covering their whole body. This covering provides increased insulation, which is essential for the penguin species that live in the Antarctic and other very cold habitats. However, this increase in insulation leads to thermoregulatory challenges for penguins in warmer climates.

Penguins have several mechanisms to avoid overheating, including ruffling their feathers to disturb the insulation layer of air around their body (Sparks and Soper 1987). In temperate areas, ruffling feathers is not enough and therefore additional methods of cooling are essential. Penguins have highly vascularized blubber and, if high temperatures occur, blood circulation through the blubber is increased allowing for heat dissipation (Sparks and Soper 1987).

Feather Biomechanics

Feathers have a diverse range of functions and in order to function properly, must possess certain mechanical qualities. Whether that function is flight, insulation, or waterproofing, each feather needs to be adapted to withstand the stresses involved in their function. Understanding these stresses and the capacity for feathers to withstand these stresses is important for understanding the biomechanics of feathers. By examining the feather materials and the three-dimensional arrangement of the materials, it may be possible to understand how the penguin feather evolved.

Beam Theory

A feather can be modeled as a cantilevered beam, fixed at one end and loaded at the other. Elucidating the biomechanical properties of diving bird feathers involves classic mechanics. Beam theory predicts the amount of deflection that a beam will exhibit when subjected to a load.

Flexural stiffness, a central measure in beam theory, determines how much a beam resists bending (Vogel 1988). There are two important factors that determine a beam's flexural stiffness: (1) the material of which the beam is composed and (2) the arrangement of the material (Vogel 1988). The stiffness of the material is measured by Young's modulus (E). Young's modulus is a function of stress and the corresponding strain (stretch; Vogel 1988). The mechanical properties of a beam with certain cross-sectional arrangement may be found by calculating the second moment of area (I; Vogel 1988) The second moment of area relates to the cross-section of a beam and can be determined by measuring the area in discrete units and multiplying that by the square of the distance that unit is from the neutral plane (Vogel 1988).

Forces on Biological Materials

Biological materials experience three main stresses—compression, tension, and shear—and are usually classified based on their mechanical properties, (tensile, pliant, or rigid; Vogel 1988). Materials that are tensile, including silk, cellulose, and collagen, resist being pulled (i.e., loaded in tension) and can be considered biological ropes. Pliant materials deform when a stress is applied but are able to return to their original state (Vogel 1988). The deformation is important for their function. The most common example of a pliant material is rubber. Restilin, abductin, and elastin are all examples of rubber-like proteins (Vogel 1988). Rigid materials, including bone, arthropod cuticle, and keratin, are able to withstand stress without allowing too much deformation (Vogel 1988). Rigid biological materials are usually a composite of protein fibers surrounded by a proteinaceous matrix (Vogel 1988). Feathers are particularly interesting in that they combine features of pliant and rigid materials. Although they are nominally rigid, flexibility is often a critical aspect of their function in terms of aerodynamics.

Mechanics of Biological Materials

Biological materials that function during animal locomotion must be able to withstand stresses. Four types of loading result in stress: axial tension, axial compression, bending, and torsion (Biewener 2003). The cross-sectional area of the structure determines the response to both axial tension and compression (Biewener 2003); however, the responses to bending and torsion are dependent on the cross-section as well as the length of the beam.

When stress is applied to a cantilevered beam, tension and compression occur on opposite sides of the beam. The top of the beam experiences tension, meaning the top surface lengthens, whereas the bottom of the beam experiences compression and shortening (Biewener, 2003). In the presence of these two opposing stresses, an area located somewhere in the center of the beam experiences neither compression nor tension. This area is called the neutral plane (Biewener 2003). The area around the neutral plane also experiences less stress. Because of this principle, a hollow beam, which has more of its material further away from the neutral plane, is able to withstand a greater stress without bending than a solid beam of the same size (Biewener 2003).

Biomechanical Studies on Feathers

Purslow and Vincent (1978) examined the mechanical properties of primary feathers as cantilever beams. In order for a feather to be effective in flight, it must be rigid to provide aerodynamic lift but also flexible enough to resist catastrophic failure. Purslow and Vincent described three factors that affect the bending of a beam. The first depends on the amount of material in the cross-section and how much of the material can withstand a loading stress. The second is the arrangement of the material in the cross section. The last pertains to the location of the material and its distance from the neutral axis. They note that the first and third factor can be determined by calculating the second moment of area (*I*). In order to find the deflections caused by a particular load, Young's Modulus and the second moment of area can be inserted into the beam bending equation.

The feather cross-section shows a cortex of keratin with a spongy keratin matrix or medulla within (Figure 3). Purslow and Vincent (1978) predicted the cortex would be the determining factor in the feather's ability to resist stresses and not the inner spongy material. They first calculated Young's modulus and the second moment of area (*I*), which was used in the Euler-Bernoulli bending equation, which can predict the deflections that would be produced by certain loads. With predicted values, actual feathers could be used to see how much they deflect given an actual load. Purslow and Vincent loaded feathers using different weights and measured the deflection. In order to determine whether the inner medulla had a significant effect on the feather's mechanics, in some of the tests the medullary foam was scraped out leaving only the outer cortex. This would allow for a comparison of the intact feather with the medulla-removed feather.

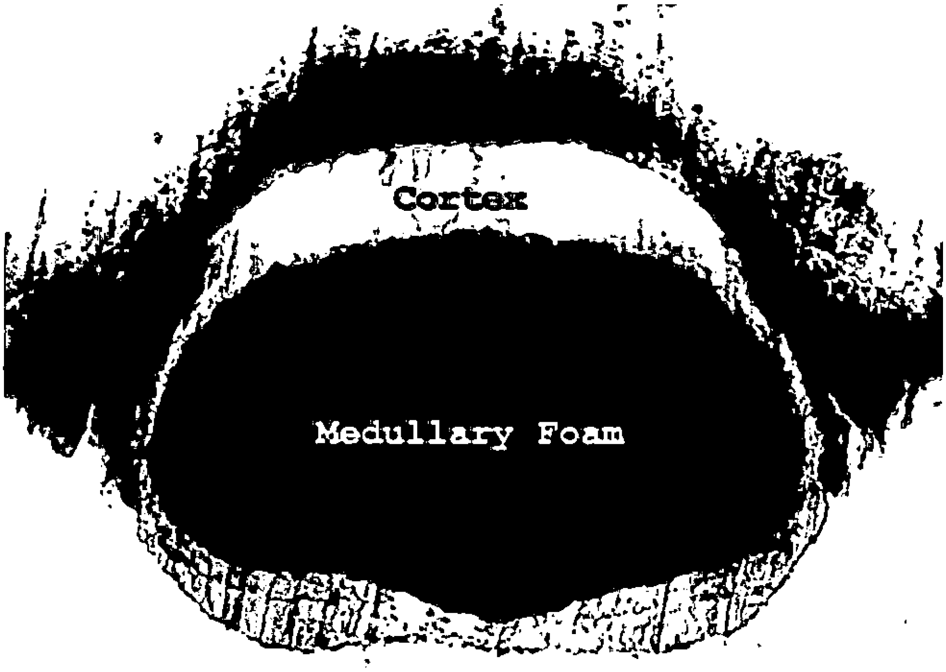

Figure 3.Cross Section of Feather. Outer cortex and inner medullary foam labeled.

Purslow and Vincent (1978) found that the second moment of area varies along the length of the shaft; with the highest *I* near the insertion point of the feather. *I* decreases distally along the shaft, which is consistent with beam theory predictions. Theoretical predictions were found to give good estimates for bending; predicted and observed bending behavior was highly correlated, although not exact. The shape of the cross-section was more important than material propertied, as evidenced by differences between some of the primary feathers. The authors found that the outermost primary feather (P10) was able to resist bending better than those feathers next to it. This finding also correlates with its slightly different cross-section. Purslow and Vincent observed that the outermost primary feather was wider than the other inner feathers. Therefore, they suggested that the cross-sectional shape is a more important determining factor in bending resistance than the material of which it is composed.

Whereas Purslow and Vincent (1978) focused on cross-sectional anatomy of the feather rachis, Bonser and Purslow (1995) examined the stiffness of feather keratin. In previous studies, variations in Young's modulus have been seen in contour feathers of some species. Biochemically, β-keratin is highly conserved (Bonser and Purslow 1995), which is theoretically predicted because flight should constrain variation. Too much variation in the material of feathers might cause them to be non-functional (Bonser and Purslow 1995).

Bonser and Purslow (1995) found that, in the eight bird species they tested, all species had relatively similar Young's moduli, and they concluded that β-keratin is most likely conservative. If this is true, then variation in flexural stiffness will result from differences in cross-sectional area (Bonser and Purslow 1995). They also found that Young's modulus increased distally along the length of the rachis.

Young's Modulus and Feather Orientation

Many biomechanical studies focus on the cross-sectional area of the feather, as it is very important to the mechanical properties of the feather. However the material and its orientation of the feather are also important. Keratin makes up 90% of the rachis and therefore should be considered in the biomechanics of feathers (Cameron et al. 2003). Cameron, Wess, and Bonser (2003) used x-ray diffraction to study the orientation of feather keratin and showed that keratin orientation is important to the stiffness of the feather. Pauling and Corey (1951) used X-ray diffraction, but did not consider the biomechanics of feathers.

Cameron, et al. (2003) measured Young's modulus of the feather at three locations along the rachis to determine if correlation exists between keratin orientation and stiffness. Three species of birds were used for this study: goose, swan, and ostrich. Cameron et al. included ostriches to determine if there is a difference between volant and non-volant birds in their keratin orientation.

Cameron et al. (2003) found that in the goose and swan there is a trend of increasing Young's modulus distally along the rachis. This corresponds with an increase in organization in keratin orientation from the calamus along the rachis length, ending with mis-orientation at the end of the feather. However, the ostrich feather did not follow this trend, and Young's modulus did not increase along the rachis. This corresponded with a lack of organization of keratin along the rachis. The authors hypothesized that the difference between the volant feathers and the non-volant feathers might result from lack of selection for the ostrich feather to be "aero-dynamically competent." For the volant birds, the increase in organization may reduce the costs of flight, allowing the feathers to be stiffer but also thinner moving along the feather (Cameron et al. 2003).

Only a few studies have addressed the biomechanics of penguin feathers. One study deals with the mechanical properties of down feathers of Gentoo penguins, *Pygoscelis papua* (Bonser and Dawson 2000). The down feathers of penguins are essential for insulation and substantial afterfeathers on the down feathers of penguins increase the insulating capabilities of the down. The feathers must be compressible during diving while retaining the capacity to return to their original state on land and must also withstand wind-related stress while on land (Bonser and Dawson 2000).

Bonser and Dawson's measure of Young's modulus of the afterfeather was substantially lower than the average modulus for primary flight feathers; however, it did fall within the range of previously reported moduli for feather keratin (Bonser and Dawson 2000). These results suggest that down feathers are not significantly different from primary flight feathers. On the other hand, the materials that make-up flight feathers and down feathers seem to be conserved.

However, this study neglected to take into account the shape of the rachis of these feathers. The material of the feathers may be conserved, but the arrangement of the keratin may be very different. The second moment of area should also be measured to truly compare flight feathers with down feathers.

Biomechanical Role of Melanin

The obvious function of melanins is to produce color, however melanins appear to have some other functions that may be just as important. Many studies have looked at the melanin as it pertains to strength and resilience of the feather, suggesting that melanized feathers are more resistant to bacterial degradation (Burtt 1979).

Two experiments have examined the biomechanics of melanized feathers. Bonser (1995) discussed the mechanical basis for the increased resistance of melanized feathers. Prior to this study, it was accepted that melanized feathers were more resistant to wear without actual mechanical tests, although the actual mechanism for increased resistance was unknown. Bonser carried out a Vickers hardness test on melanic and non-melanic feathers of a Willow ptarmigan, *Lagopus lagopus*, to examine the actual mechanism. Vickers hardness tests measure the resistance of a material to deformation under a load. Bonser found that melanic feathers were significantly harder than non-melanic feathers and that the presence of melanin granules in the feather keratin increases hardness by 39%. He suggested that non-melanized feathers would then have to be 39% thicker in order to have the same hardness as the melanized feathers and thus an added metabolic cost. Therefore, melanin may add strength while leaving the metabolic costs lower. However the metabolic costs of producing melanin were not discussed.

Butler and Johnson (2004) analyzed the strength of melanized feather barbs to test whether the results of previous studies may have been confounded by unmeasured variables, including the importance of the location of the barb. Butler and Johnson used the primary feathers of an Osprey, *Pandion haliaetus*, for all of their tests. After performing hardness tests, breaking stress, and strain tests, they found that when position is considered there was not a significant difference in melanized and non-melanized barbs.

CHAPTER TWO

FEATHER BIOMECHANICS

Introduction

Relatively few biomechanical studies have been carried out on feathers (Chapter 1), and the ones that have are often narrow in species range and frequently measure only Young's modulus or second moment of area. The reasons for studying diving birds are twofold. The first is that diving birds encounter two extreme mechanical stresses: aerial flight and aquatic flight. The feathers of these birds must be able to function in two very different fluid environments and therefore might have evolved unique anatomical, material, or biomechanical properties.

The second reason for studying diving birds is to gain insights into penguin evolution. Because penguin ancestors could fly, ancestral penguin feathers were capable of flight and as true penguins evolved, flight was lost. The feathers of penguins no longer had selective pressures from the aerial environment that presumably used to constrain their form and function. Insulation and streamlining the body became important functions of the feathers. Other groups of birds went through similar transitions; however, in these groups the ability to fly was not always lost as they began to fly under water.

By understanding the biomechanics of diving bird feathers it may be possible to understand the evolutionary and functional transition that took place in penguin feathers. This can be examined by looking at feathers from aerial fliers, aerial fliers with diving abilities, and underwater fliers (Table 1). It is possible that differences in morphology might arise due to the diverse stresses involved with these various modes of locomotion. Studies of the feathers from these birds may help shed light on some of the intermediate steps feathers went through during penguin evolution.

Table 1. Specimens Analyzed. Group Other represents non-alcid aerial fliers, Alcidae contains aerial fliers with the ability to wing-propelled dive, and Spheniscidae (penguins) represent flightless wing-propelled divers.

Species	Common name	Group
Sialia mexicana	Western bluebird	Other
Eclectus roratus	Eclectus parrot	Other
Taeniopygia guttata	Zebra finch	Other
Ptychoramphus aleuticus	Cassin's auklet	Alcidae
Cerorhinca monocerata	Rhino auklet	Alcidae
Uria aalge	Common murre	Alcidae
Larus occidentalis	Western gull	Other
Fulmarus glacialis	Northern fulmar	Other
Phalacrocorax pelagicus	Pelagic cormorant	Other
Phalacrocorax penicillatus	Brandt's cormorant	Other
Phalacrocorax auritus	Double-crested cormorant	Other
Aechmophorus occidentalis	Western grebe	Other
Melanitta perspicillata	Surf scoter	Other
Eudyptula minor	Little blue penguin	Spheniscidae

Materials and Methods

Contour feathers, in most cases both dorsal and ventral, were collected from each sample bird (Table 1). The feathers were measured, and then their vanes were cut off. The feathers were embedded into epoxy resin (EpoThin; Buehler, Inc.) along with a scale bar (Figure 3). Three ~1 mm sections were marked out per feather. The sections were cut using a low speed saw (IsoMet; Buehler, Inc.). Sections were marked on their proximal and distal sides to ensure the correct orientation. The sections were affixed to microscope slides with epoxy adhesive. All sections were polished until the medullary foam could be distinguished from the outer cortex (Figure 4). This process allowed for digital removal of the medullary foam during photo post-processing.

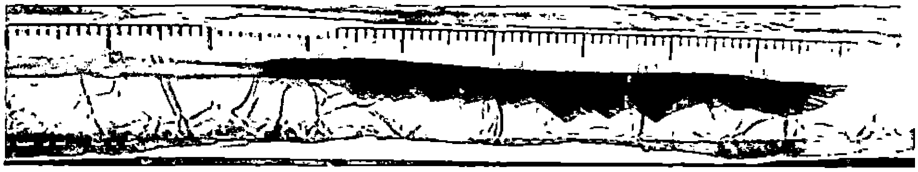

Figure 4. Feather Embedded in Resin with Scale Bar.

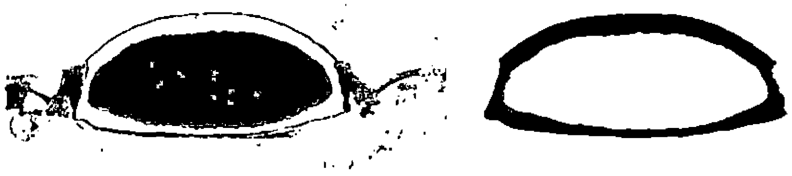

Figure 5. Specimen Preparation. A polished cross-section is shown on the left, and a processed image with medullary foam removed is shown on the right.

Feather sections were photographed using a Nikon petrographic microscope at 10x. All images were post-processed in an imaging program (http://gimp.org) until only the cortex outline remained. The images were then loaded into NIH ImageJ (http://rsbweb.nih.gov/ij/). Cross-sectional geometric properties, including dorsoventral and mediolateral diameters, cross-sectional area, and mediolateral and dorsoventral second moments of area were measured using BoneJ, a set of macros for ImageJ (Doube et al. 2010). Aspect ratio of the rachis was calculated as the mediolateral diameter divided by the dorsoventral diameter (Figure 5).

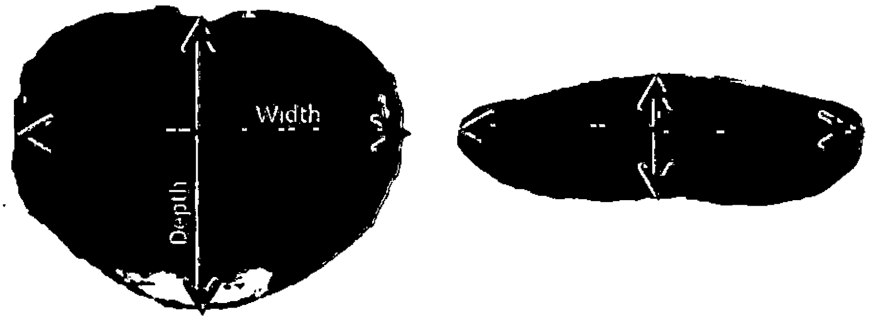

Figure 6. Aspect Ratio. Aspect ratio (AR) is a calculated index of dorsoventral flattening. AR is calculated from the maximum rachis width divided by the maximum rachis depth. Parrot cross-section represented on the left, and penguin on the right.

Phylogenetic Comparative Methods

Understanding the relationships between different species has intrigued biologists for a long time and comparative studies have a long history. However, comparative studies are complicated by the shared evolutionary history among species. A set of methods used to disentangle comparative data from its confounding evolutionary history is comparative phylogenetic methods (Felsenstein 1985; Garland et al. 1993, 2005). Species that are related to each other cannot be treated as independent observations in a statistical sense (Garland et al. 2005) because closely related species will tend to be phenotypically similar based on their evolutionary relationships alone. Phylogenetic comparative methods account for the non-independence of species data points and allow the use of standard statistical analysis techniques.

The specimens were analyzed using the phylogenetic comparative method. A tree was constructed in Mesquite based on published phylogenies (Figure 6; Livezey and Zusi 2007; Livezey 2010; Smith 2011). Phylogenetically informed linear regression and ANOVA was used to examine the relationships between cross-sectional parameters (e.g., area, aspect ratio, standardized resistance to torsion) and species or clades, with rachis length included as a covariate where necessary. Analyses were carried out using R (http://r-project.org).

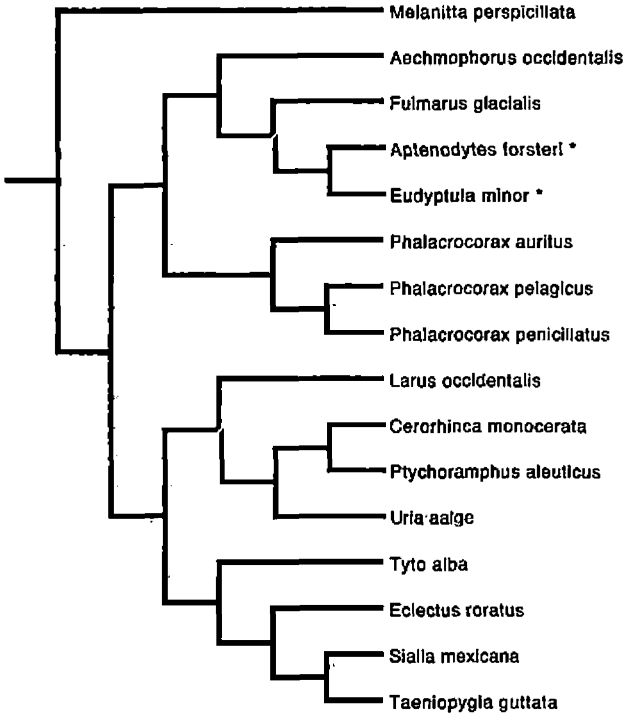

Figure 7. Phylogenetic Sampling of Specimens. Branches in red are wing-propelled divers. Starred species are flightless birds (penguins). Tree topology based on Livezey and Zusi (2007), Livezey (2010), and Smith (2011)

Results

After inserting the cross-sectional images into BoneJ (Doube et al. 2010), the measurements were analyzed in R. Seven variables were examined across the specimens: Dorsoventral Diameter (DDV), Mediolateral Diameter (DML), Aspect Ratio (AR; Figure 7), Cross-sectional Area (CSA), Dorsoventral Second Moment of Area (IDV), Mediolateral Second Moment of Area (IML), and Standardized Resistance to Torsion ($J_{std} = [I_{max} + I_{min}]$/Length; Figure 8). The dorsal and ventral feather cross-sections were examined separately. The dorsal feather measurements were separated into three groups, the Alcidae, the Spheniscidae, and Other (all non-Alcidae/non-Spheniscidae; Table 1). The ventral feather measurements contained only two groups, Alcidae and Other. For statistical analyses, the mean values for all measurements for a feather were used. Although not ideal, this measure provides a useful first approximation for comparisons between species.

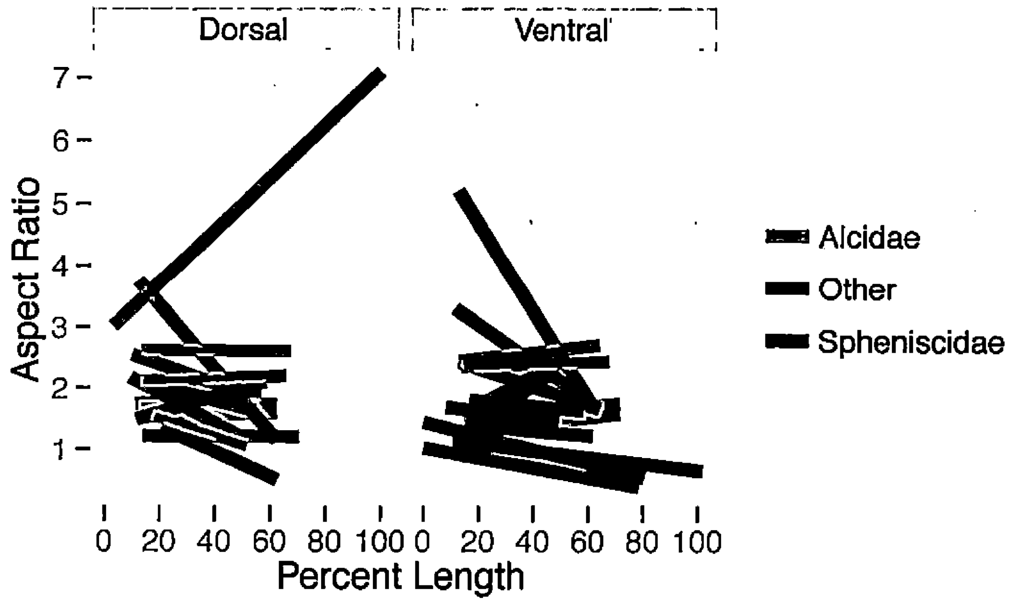

Figure 8. Aspect Ratio of Dorsal and Ventral Contour Feathers. The aspect ratio of the penguin is higher than all of the other birds sampled. The aspect ratio also increases distally along the rachis.

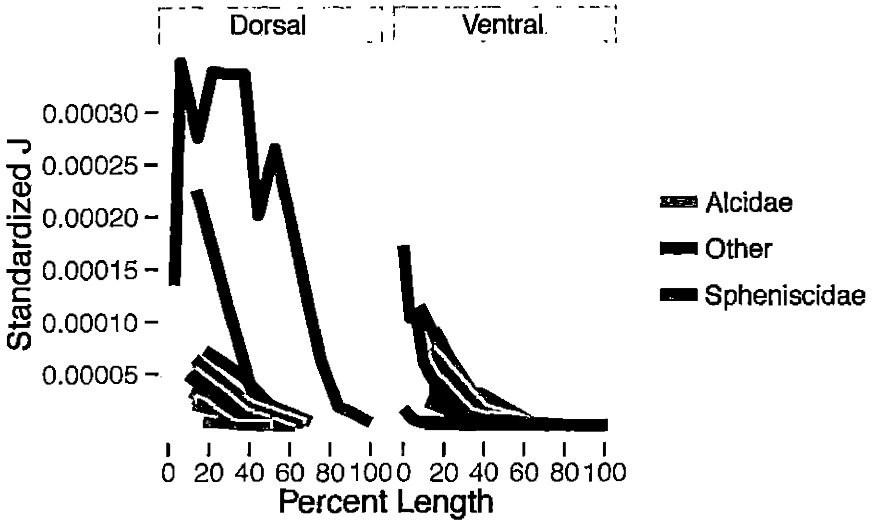

Figure 9. Standardized Resistance to Torsion (J_{std}). For a given position along the rachis, J_{std} is higher in penguins than in non-penguins.

For each variable, the amount of phylogenetic signal (K; Blomberg et al. 2003) was calculated. This calculation utilizes the phylogenetic tree and a Brownian motion evolutionary model. Phylogenetic signal for dorsal values ranged from 0.20-0.94, and ventral values ranged from 0.24-1.25 (Table 2). K = 1 would imply that the Brownian motion model could account for the amount of variation among the specimens (i.e., about as much variation in phenotypic traits as expected under a Brownian motion model of evolution). Values less than one show less variation than expected and values greater than one show more variation between species than would be expected under a Brownian motion model of evolution (Blomberg et al. 2003).

Table 2. Phylogenetic signal (K) and ANOVA Results. Degrees of freedom (*d.f.*), *F*-statistics, and $P_{non\text{-}phy}$ relate to traditional, non-phylogenetic ANOVA. P_{phy} is the result from phylogenetic ANOVA, in which *P*-values were determined by randomization. Side indicates whether the feather was from the dorsal or ventral side of the bird. Variables: Dorsoventral Diameter (DDV), Mediolateral Diameter (DML), Aspect Ratio (AR), Cross-sectional Area (CSA), Dorsoventral Second Moment of Area (IDV), Mediolateral Second Moment of Area (IML), and the Resistance to Torsion (J).

Side	Variable	K	*d.f.*	*F*	$P_{non\text{-}phy}$	P_{phy}
Dorsal	DDV	0.75	2, 11	1.62	0.24	0.20
Dorsal	DML	0.2	2, 11	0.64	0.54	0.52
Dorsal	AR	0.47	2, 11	18.67	< 0.001	< 0.001
Dorsal	CSA	0.29	2, 11	0.10	0.90	0.91
Dorsal	IDV	0.11	2, 11	1.80	0.21	0.19
Dorsal	IML	0.94	2, 11	0.56	0.59	0.57
Dorsal	J_{std}	0.56	2, 11	28.12	< 0.001	< 0.001
Ventral	DDV	0.91	1, 14	1.58	0.23	0.28
Ventral	DML	1.25	1, 14	0.19	0.67	0.72
Ventral	AR	0.77	1, 14	0.18	0.68	0.68
Ventral	CSA	0.54	1, 14	0.05	0.83	0.85
Ventral	IDL	1.15	1, 14	0.15	0.71	0.71
Ventral	IML	0.83	1, 14	0.014	0.91	0.93
Ventral	J_{std}	0.24	1, 14	0.014	0.90	0.91

Cross-sectional measurements were analyzed via ANOVA, both with and without a phylogenetic tree. Two trees, both a dorsal and ventral, were produced to account for certain species only having dorsal feathers (Figure 10) and others only ventral (Figure 11). Branch lengths were scaled using the method described by Pagel (1994).

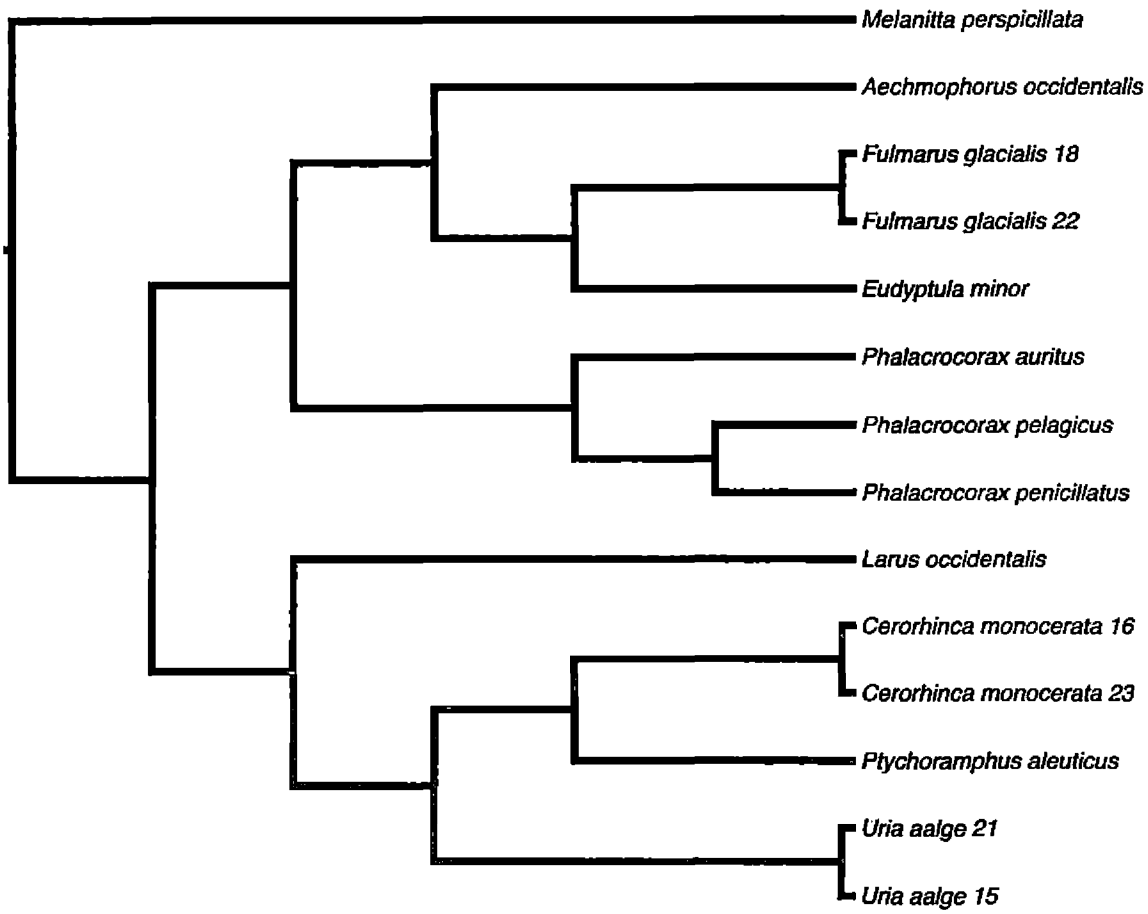

Figure 10. Dorsal Phylogenetic Tree. Color of branches represent the three different groups species where separated into. Group Spheniscidae is in blue, group Alcidae is in coral, and group other is represented in green. Species with more than one sample represented. Branch length was corrected using methods described by Pagel (1994). Tree topology based on Livezey and Zusi (2007), Livezey (2010), and Smith (2011).

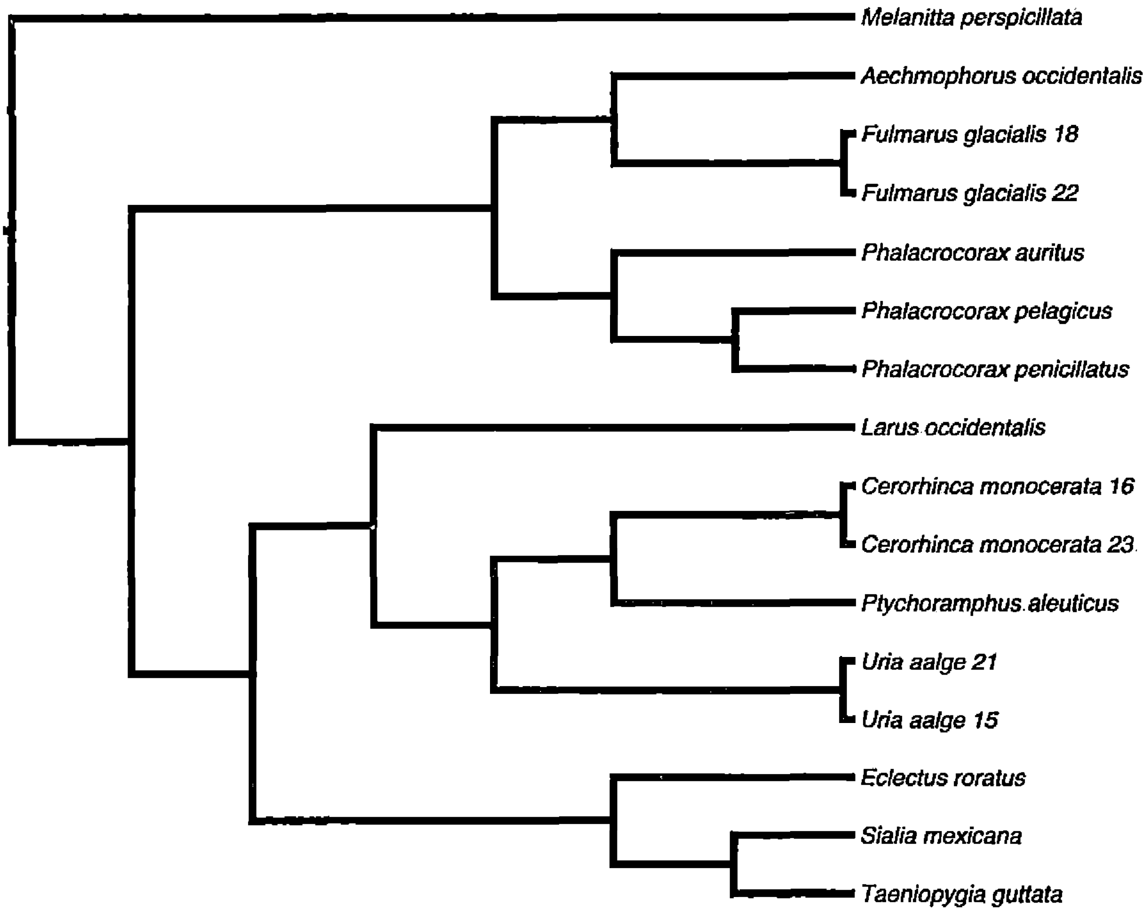

Figure 11. Ventral Phylogenetic Tree. Color scheme same as in figure 10.

A summary of the ANOVA results, including *F*-statistics and their associated *P*-values, is presented in Table 2. Two notable results were found for the dorsal sections. Aspect ratio (AR) and standardized resistance to torsion (J_{std}) were highly significant in both non-phylogenetic and phylogenetic analyses ($P < 0.001$ in all cases).

Discussion

Seven morphometric variables were measured among the penguins and their relatives, including both aerial fliers and those that fly in both air and water. Species were separated into groups by clade: Spheniscidae, Alcidae, and a group including all other birds in the sample (Table 1). Given that penguin feathers are known to have flattened rachises (Bertelli and Giannini 2005) it was hypothesized that alcids might occupy an intermediate morphological position between penguins and other, non-wing-propelled diving birds.

Aspect Ratio

The aspect ratio is a measure of dorsoventral flattening, the mediolateral width divided by the dorsoventral depth. There was no significant difference between the three groups for the diameters both for dorsal and ventral feathers (Table 2). However, when the diameters were used to calculate the aspect ratio, a significant result was found; the penguin has a significantly higher aspect ratio (Figure 7).

It is interesting to note that while the penguin AR is significantly different from other birds, the two diameters that determine the AR as well as the cross-sectional area are not. This seemingly paradoxical finding could be due to the fact that the AR is a ratio and therefore more sensitive to small differences in diameter. AR also gives information about the shape of the cross-section. The cross-sectional area only measures area while ignoring the shape.

Standardized Resistance to Torsion

The aspect ratio is an important measurement and provides a good approximation of the shape of the rachis but tells little about the theoretical biomechanical performance of the feather. In order to understand the biomechanics of the feathers, the second moments of area must be analyzed. Both the dorsoventral and mediolateral second moments of area were calculated (IDV and IML, respectively). For both dorsal and ventral contour feathers the second moments of areas did not differ significantly among groups (Table 2). But like AR, J_{std} (the standardized resistance to torsion incorporating IML, IDV, and the length of the rachis), was significantly different among groups (Table 2; Figure 8). J was standardized to rachis length in order to correct differences in total length of the feathers. The penguin had a significantly higher resistance to torsion than all the other birds, including the Alcidae.

These results present interesting questions. Why do Alcidae, which live in a very similar niche, not have similar feathers to the penguin? One hypothesis for why the penguins have such different feathers is because of the mechanical and environmental stresses the feather must confront.

Behavior may be one of the most important differences between penguins and auks. While both are wing-propelled divers, they differ in their swimming speed and diving ability (Watanuki et al. 2006). When comparing alcids (e.g., *Uria aalge*, *Uria lomvia*, *Alca torda*, and *Cerorhinca moncerata*) with the little blue penguin (*Eudyptula minor*), Watanuki et al. observed differences in diving angle as well as stroke patterns. Slight differences in wing-propelled diving may cause slight changes in feather morphology. More comparative feather studies must be done focusing on the modes of locomotion used by each bird.

Another possible explanation for the difference between penguin and alcid feathers may be their disparate evolutionary histories. To date the oldest recognizable alcid fossil is from around 35 million years ago (Pereira and Baker 2008), whereas the oldest penguin-like fossil is almost twice as old as that (Slack et al. 2012). The difference in penguin feathers could be due to the fact that penguins have had such a long time to adapt to aquatic flight.

Most alcids retain the ability to fly, and therefore their feathers may be constrained for aerial performance. However, this study is concerned only with body feathers, which are not under the same biomechanical constraints as flight feathers. The hydrodynamics of the feathers of both alcids and penguins must be studied in order to understand this discrepancy. Studying feathering of the Great auk (*Pinguinus impennis*), an extinct flightless alcid, may be a good source of information. Great auk feathers might be predicted to be more similar to penguin feathers because Great auks were no longer constrained by flight.

Limitations

Several limitations are associated with the study as carried out. One aspect is the small sample size, which is especially a problem when detecting phylogenetic signal. Blomberg et al. (2003) showed that the power to detect phylogenetic signal is dependent of the size of the tree. Because the sample size was smaller, the predictive power was minimized. Also only one penguin feather was analyzed. In future studies, a wider range of penguin species should be examined. It is possible that different species of penguins may have different feather morphologies.

Another limitation concerns the statistical approach used to analyze the data. The mean value was used for each feather, which reduces the linear association between measurements and distance along the feather rachis (Figures 8 and 9) to a single value. Methods to incorporate the full range of values for each feather rachis could be explored in the future. For example, the slope of the line could be used in statistical analysis or ANCOVA approaches. Nonetheless, the results still give a good first approximation and add evidence to the morphological uniqueness of penguin feathers.

Conclusions

While certain aspects of penguin biology have been explored in depth, the feather has received little attention. This biomechanical study is one of the first of its kind to focus on the feathers of penguins and other seabirds. While limited in sample size, this study has shown that penguin feathers have unique cross-sectional biomechanical properties compared to both phylogenetically closely related (Northern fulmar) and ecologically similar (Alcidae) species. The penguin feather analyzed is significantly flatter dorsoventrally than any of the other birds examined, and this difference in morphology produces a significant increase in resistance to torsion. Therefore, not only are penguin feathers statistically distinct morphologically, but their biomechanical properties also differ.

Many unexplored areas of study remain with regards to penguin feathers. While alcids were originally hypothesized to have intermediate feather morphology between penguins and other non-penguin birds, the results of this study show that, although similar in ecology, they do not represent a transitional stage. Evolutionary history, behavioral, and biomechanical differences between alcids and penguins may account for the morphological distinctness in feather morphology. In order to effectively test this hypothesis, it would be necessary to have a significantly larger sample size, including all penguin species and feathers from all locations of the body. And clearly, this type of larger examination would both be interesting and greatly expand our understanding of penguins.

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