THESIS

TAKING THE PLUNGE: POUCH MORPHOLOGY AND FUNCTION IN BROWN PELICANS

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY RENÉ P. MYERS ENTITLED "TAKING THE PLUNGE: POUCH MORPHOLOGY AND FUNCTION IN BROWN PELICANS" BE ACCEPTED AS FULFILLING PARTIAL REQUIREMENTS FOR THE THESIS IN ZOOLOGY.

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Abstract

Brown Pelicans (*Pelecanus occidentalis*) plunge-dive for food, and can attain speeds of 18 m/s before impact with the water. After immersion, their mandibles bow from a resting position of about 5 cm apart to over 15 cm apart and their pouches distend with water (and fish) to hold a volume of about 11 liters. In order to determine how this is accomplished, many techniques were used including gross dissection, histology, and bone ashing. I found that the pouch is composed of several layers: an oral epithelium, a muscular layer, a layer of elastin bundles, and skin. The oral epithelium and the skin both have longitudinal folds for pouch expansion. The fibers of the M. mylohyoideus and the elastin layer are arranged perpendicularly to each other, providing the necessary support and elastic recoil for the pouch to function. The keratin that overlays the rostral bending zone is quite different from typical rhamphothecal keratin in that it is more skin-like. Bending occurs along the rostral two-thirds of the mandible. This area contains the caudal bending zone that is made up of several bones joined by connective tissue. Evidence suggests that these syndesmotic joints act as leaf springs and combine with the rostral bending zone adjacent to the mandibular symphysis that is highly demineralized in forming the correct curves for jaw bowing to take place. The pterygoid muscles function in mandibular bowing by rotating the mandible outwards on its articulation with the quadrate. Due to the attachment at the symphysis and the presence of the bending zones, the mandible bows. It has been suggested that pouch filling, and possibly even mandibular bowing, could be accomplished passively. I propose that when a Brown Pelican dives into the water it sets up a situation that can be described by Bernoulli's Principle in which the water outside of the pelican moves faster than that within the

pelican's mouth. Therefore, the pressure within the mouth would exceed that on the outside. This pressure difference could account for passive pouch filling and possibly jaw bowing. Pouch filling could also be simply explained by drag, similar to the mechanism that allows a parachute to open.

Introduction

Brown Pelicans (*Pelecanus occidentalis*) are distributed extensively along the coasts of North and South America. They can be found breeding along the Atlantic from Maryland to Florida and along the Gulf of Mexico to Texas. Near the Pacific they can be found from the southern coastal regions of California to Baja California and down along the Pacific and Caribbean coasts of Mexico, Central America, and South America. They also reside in the West Indies and on the Galapagos islands. There are six subspecies of Brown Pelicans whose common names include the Eastern Brown Pelican (*carolinensis*), California Brown Pelican (*californicus*), Chilean Brown Pelican (*thagus*), Molina's Pelican (*thagus*), Peruvian Pelican (*thagus*), the West Indian Brown Pelican (*carolinensis*) as well as *occidentalis, murphyi,* and *urinator*. They can all be identified by their predominantly brown to brownish-black plumage and, of approximately seven different pelican species in the world, are the only ones that consistently plunge-dive for food (Johnsgard, 1993).

Brown Pelicans dive into water after fish from altitudes of between 9 and 16 meters (Allen, 1923), often attaining speeds of up to 18 m/s before water impact (Johnsgard, 1993). Richardson (1939) observed that pelicans quickly resurface following a dive and noted that this is probably due to their pneumatic skin. Their skin's pneumaticity has also been implicated in cushioning their impact with the water as an adaptation for plunge diving (Richardson, 1939).

Schreiber et al. (1975) did an in-depth photographic study of Brown Pelican diving. Though several factors were suggested to influence variation between dives

(such as individual experience of the birds, subspecies, size of the birds, the activities of their prey, and aspects of their physical environment (wind, light, water clarity, etc.)), they still concluded that some aspects of every dive are the same. One is that a successful dive means a filled pouch.

The pouch is a very thin structure comprised of an inner mouth lining, a muscular layer, an elastic layer, and skin (Kühnau, 1932). Both the skin and the oral cavity lining exhibit longitudinal folds that provide redundant surface area for expansion. Indeed, the gular pouch is highly distensible, holding up to 11 liters of water (Schreiber et al., 1975). In addition to the pouch filling, the mandibles bow from a resting position of about 5 cm apart to over 15 cm apart. Schreiber et al. (1975) estimated that the opening created when the mandibles bow is approximately 500 cm^2. When bowed, the mandible has two distinct curves: a pronounced convex curve occupying approximately the rostral two-thirds of the mandible and a smaller concave curve near the mandibular symphysis (Figure 1). They proposed that it was the direct forceful interaction between the water and the flexible mandibles that causes the mandibular rami to bow. This suggestion is similar to what is seen in rorqual whales. Lambertsen (1983) described how rorquals (Balaenopteryidae) passively fill their oral sacs with no muscular activity except that needed for locomotion. However, there are arguments for muscular activity in pelican pouch filling.

Böker (1938) originally thought that the tongue and its muscles were associated with mandibular bowing, but rejected this in favor of pterygoid muscle activity as playing a significant role in jaw bowing. He described seeing Brown Pelicans flying low over the water and then opening *and* widening their bills before dipping them into the water.

Burton (1977) discussed how an object moving through the water is subject to compressive forces, especially the side of the object that is leading it through the water. In the case of the pelican, this side would be the rostral tip of the bill. However, the area of the bill from its rostral aspect is quite small and so large compressive forces would never develop; hence the water wouldn't be forceful enough to push the bill into the bowed position (Burton, 1977). Furthermore, Burton (1977) states that there would be an increase in the forces acting on the lateral aspects of the jaws while the pelican continues to move through the water. These forces would actually tend to counteract bowing and so Burton (1977) rejected Schreiber et al.'s (1975) hypothesis of direct interaction with the water causing mandibular bowing. Another of the hypotheses that he discounted was that the mandibles could be bowed by the water weight that was contained within the distended pouch. An outward force component would exist when the pouch was filled, but this doesn't explain how the mandibles can bow when the pouch is not full of water. Furthermore, the photographs of Schreiber et al. (1975) show that the mandibles can move back into place without the pouch being emptied. Burton (1977), like Böker (1938), also suggested that the mandibular bowing could be caused by the contraction of the pterygoid muscles, but fails to cite Böker's earlier paper. Lastly, Johnsgard (1993) suggests that a pouch muscle could bow the mandibles pulling the chin posteriorly and causing the rami to bow outwards.

The purpose of this study was to determine the anatomical construction of the pouch and how this anatomy is related to the mechanisms of pouch filling and jaw bowing.

Methods

Specimens

Four fresh specimens of Brown Pelicans (*Pelecanus occidentalis carolinensis*) were obtained from the North Carolina State Museum of Natural History. These specimens, which consisted of the head and most of the neck, were prepared as follows: one was cut into serial coronal sections (approximately 1 cm in width) with a saw, two were fixed in 10% formalin and were used for dissection, and one was skeletonized to provide information regarding muscle attachments.

An additional four specimens were obtained from Pelican Harbor Seabird Station in Florida. They were euthanized on site and shipped to Weber State University overnight. I received the fresh specimens the following day and processed them. Two (one adult, one juvenile) were immediately frozen. These two were used for fresh manipulations of the pouch. The other two juveniles were fixed in 10% buffered formalin. One of these was fixed with its jaws in a bowed position (approximately 15 cm across) and the other in a natural, resting position.

Three mandibles were removed, skeletonized, and dried for use in determination of mineral content.

Histology

Fresh tissue squares approximately 1 cm to a side were excised from various sites on the pouch and embedded in 5% gum tragacanth on cork blocks. These were then frozen in isopentane (2-methylbutane) cooled to approximately –150°C with liquid nitrogen. The tissue was kept at -80°C in an ultra cold freezer until sectioned. A cryostat

cooled to -20°C was used to cut the tissue into sections 10-12 μm thick that were then mounted on glass slides. The tissue was then immediately stained with an iodine solution (Bock and Shear, 1972) and viewed using an Olympus BH-4 compound microscope. Photographs were taken with a Nikon Coolpix 995 Digital Camera with an MMCool Microscope adapter attached to an Olympus BH-4 compound microscope. Color corrections were accomplished with Adobe Photoshop v. 6.0.

Bone Ashing

Mineral content of mandibular bones was determined by ashing fragments of dried bone from areas along the length of the lower jaw of three Brown Pelican specimens. Small pieces of bone (Mean mass = 0.120g +/- 0.097g) were weighed using a Mettler PE 360 milligram balance to determine initial mass (m_o) and then placed in a ceramic crucible. The samples were heated with a bunsen burner to over 600°C for single periods of twenty minutes, similar to the method of Papadmitriou et al. (1996). The crucible was weighed after it was cool enough to handle. The crucible's mass was then subtracted out to obtain the bone fragment's end mass (m). After the period of burning all of the organic material in the bone should have burned away, leaving only the mineral behind. The percent mineral content can be determined by using the following simple equation (Papadimitriou et al., 1996):

(1) Mineral content (%) = $(m/m_o) * 100$

Second Moment of Area

A CT scan of a Brown Pelican's mandible was obtained at McKay Dee Hospital's Department of Radiology in Ogden, Utah. These cross-sectional images were then used to determine the mandible's second moment of area, a measurement of how well

structures resist bending (Vogel, 1988). The cross sections were first estimated as ellipses and then measured (Figure 2). The following equation was used to determine the degree to which different portions of the mandible could resist bending:

(2) $J = [(\pi^3 a_2^3 b_2^3)/(a_2^2 + b_2^2)][1 - k^4]$ where $k = (a_1/a_2) = (b_1/b_2)$ and

a_1/a_2 = Ratio between the inner width and outer width of a hollow ellipse measured through the center of the ellipse

b_1/b_2 = Ratio between the inner length and outer length of a hollow ellipse measured through the center of the ellipse

Results

Pouch Morphology

Characteristics that are immediately noticed upon examination of the pouch are its extremely thin nature and its elasticity. Though it is thin, the pouch has very distinctive layers including an oral mucosa, a layer of muscle, a distinct layer of elastic ligaments, and an outermost layer of skin (Figure 3).

The oral mucosa is folded longitudinally. In contrast to other birds, there are no salivary glands present (Homberger and Meyers, 1989).

The muscular layer of the pouch is composed of three different muscles, from rostral to caudal: M. mylohyoideus, M. constrictor colli intermedius, and M. constrictor colli cervicalis (Figure 4). The fascicles of the M. mylohyoideus originate at the mandible and insert on the midventral raphe whereas the fascicles of the M. constrictor colli intermedius originate from the connective tissue of the head and insert on the midventral raphe (Figure 5a). The fascicles of the M. constrictor colli cervicalis extend around the neck (Figure 5a). Another major component of the pouch musculature is the

midventral M genioglossus. This muscle extends the full length of the pouch from the tongue to the tip of the lower jaw (Figure 5a). The tongue itself is vestigial and lacks direct attachment of the hyoid horns to the skull as is present in other birds (Homberger and Meyers, 1989). Instead, it is completely supported by, and is integrated into, the pouch.

Superficial to the muscular layer is a layer of elastic ligaments. These ligamentous bands are oriented almost perpendicular to the direction of the muscle fascicles (Figure 5b). They are approximately 500 μm in width and are spaced about 300-500 μm apart in the relaxed state. This layer of the pouch is very complex. The individual ligamentous bands form a plexus with many anastomoses between adjacent bands (Figure 6).

The skin is folded much like the oral mucosa and also has many small, typical elastin fibers present in the dermis (Figure 3).

Mandibular Morphology and Bending Zones

The mandible itself is a long, thin structure that is flattened along its rostral two-thirds in the medio-lateral direction. The rostral two-thirds of the mandible is solid in cross section. As seen in CT scans the pneumaticity of the bones increases until the most proximal area of the mandible is a hollow, robust piece of bone (Figure 2).

Two distinct bending zones were found in the pelican mandible. The rostral bending zone ("anterior intramandibular joint" of Bühler, 1970) is directly adjacent to the symphysis. Ash analysis determined that this is an area of decreased mineralization (Mean % Mineral = 20.5 +/- 5.73%) (Figure 7). It is solid in cross section. Occupying

the rostral two-thirds of the mandible are the lateral bending zones ("posterior intramandibular joint" of Bühler, 1970) which are composed of syndesmoses between the dentary and splenial, rostrally, and the prearticular and surangular, caudally (Figure 8). These areas have a mean mineral content of 49.95 +/- 3.25% (Figure 7). The posterior one-thirds of the mandible had a mineral content similar to that of the lateral bending zone (Mean % Mineral = 48.5 +/- 5.69%).

Discussion

The mechanism of pouch expansion and mandibular bowing of the Brown Pelican is a subject that has been studied very little and with conflicting results. It has been suggested that the jaws expand due to contraction of the pterygoid muscles by both Böker (1938) and Burton (1977). Schreiber et al. (1975) suggested that the likely way that the pouch expands is largely passive and is due to the interaction of the jaws with the water. Lastly, Johnsgard (1993) explains how it may be possible for a pouch muscle to bow the jaws by pulling the chin posteriorly.

The pouch is an extremely specialized structure that allows for significant stretching, but is still clearly derived from the throat region of typical birds (Homberger and Meyers, 1989). The folds in both the oral mucosa and the skin are essential to the functioning of the pouch. Although the tissue itself has some degree of extensibility, it is greatly enhanced by the presence of these folds. As the pouch stretches, these folds straighten out, ultimately attaining a completely smooth outer profile. The elastin layer allows for passive recoil in the pouch to occur. This is remarkably similar to what was described by Lambertsen (1983) in rorqual whales that also have a very elastic connective fiber matrix and epithelial corrugations useful for engulfing massive amounts

of water. Recoil to the unexpanded position might also be assisted actively by the pouch muscles, the M. mylohyoideus, M. constrictor colli intermedius and M. constrictor colli cervicalis.

After examination of the pterygoid musculature, it was determined that they do, in fact, play a large role in mandibular bowing as suggested by Böker (1938) (Figure 1). The M. pterygoidei are very large and prominent muscles within the mouth of the Brown Pelican; they are readily visible as dorsal "swellings" when looking into a living pelican's mouth. Böker (1938) determined that when these muscles were to contract and shorten, that they would pull on the medial process of the mandible. When this process is pulled forward the mandible would rotate on its articulation with the skull causing the lateral surface of the mandible to swing outwards (Figure 1). This action, coupled with the bending zones, allows the mandible to bow.

Equally integral to the function of the Brown Pelican feeding apparatus are the mandibular bending zones. Bühler (1970) described the mechanism for lower jaw bowing in Nightjars (Caprimulgidae; a group of non-pelicaniform birds) in which there are two bending zones: an anterior intramandibular joint and a posterior intramandibular joint. Bühler (1970) describes the anterior intramandibular joint as a "kinetic synostosis" caudal to the symphysis and the posterior intramandibular joint as a "well-known hinge joint". The anatomical arrangement of bending zones in the Brown Pelican is quite similar to that of Nightjars. The decreased mineralization and solid cross-section of the rostral bending zone make for an extremely bendable structure. This area of the mandible is slightly concave during mandibular bowing. The lateral bending zone's syndesmotic joints allow for these bones to move relative to one another, much like a

leaf-spring functions, allowing for a very convex structure during bowing (Figure 1). Judin (1961) describes how this separation of bones "increases space" within the Pelican's zone of flexibility allows this area of the mandible to bow. Movement of these bony elements relative to one another was directly observed in a gull jaw as well as Brown Pelican mandibles and a wooden model constructed in the same way as Figure 8B.

In addition to the bony elements of the bending zones, one must consider the overlying keratin. Brush and Wyld (1988) showed how the chemical structure of keratin is fundamental to functional as well as morphological changes. A softer keratin would be more amenable to flexion than a very stiff keratin. Homberger and Brush (1986) described four different categories of keratin based on mechanical properties and molecular weight of the keratin monomers. The differences in the molecular weights of keratin monomers are due to the presence of an insoluble tryptic peptide that has abundant glycine, phenylalanine, leucine, and tyrosine residues (Brush and Wyld, 1982). A keratin monomer in the 10,500 Dalton range would be stiff and flexible as in feathers and the 15,500 Dalton keratin is the harder keratin that can either be rigid (e.g. claws, rhamphotheca) or somewhat pliable (e.g. scales, lingual nail) depending on the thickness of the keratin layers. Keratin with a molecular weight in the 25,000 Dalton range is found in softer tissues such as oral linings and the soft lingual epithelia. The keratin monomers with the highest molecular weights (between 46,000 and 66,000 Daltons) are found in the avian interfollicular epidermis and are quite similar in size and configuration to mammalian keratin (Homberger and Brush, 1986). I propose that the keratin overlying the rostral bending zone will be of this last type in contrast to the rest of the

rhamphotheca which should consist of the usual form of rhamphothecal keratin. Further work needs to be done to evaluate the biochemistry of the keratin contributing to the rostral bending zone.

Johnsgard (1993) states that "a thin band of muscles extends forward from the hyoid to the anterior tip of the lower mandible." He suggests that this is responsible for pulling the jaw into a bowed position. I identified this unspecified muscle as the M. genioglossus. Johnsgard's suggestion that this muscle bows the lower jaw is unlikely since the force required to bow the lower jaw rami by pushing on the tip of the lower jaw is quite large and the genioglossus is a rather thin muscle in cross-sectional area. Moreover, pushing on the bill in this manner tends to bow the jaws inward, not outward. This muscle is clearly too small to be able to pull the anterior tip of the mandible with sufficient force to bow the lower jaws. The more likely role of this muscle is to pull the vestigial tongue toward the chin rather than vice versa. However, the genioglossus does have interesting morphology in that there are blood vessels running down the center of the muscle itself. Further study of this muscle and its blood vessels are needed to assess its role in the function of the pouch.

Although it was seen previously that the pterygoid muscles could bow the jaw, the water through which the Brown Pelican is diving could play a significant role. Indeed, Schreiber (1975) proposed that the mandibles bow and pouch fills completely passively due to interaction with water. There are a few different possibilities how this could happen. First, when a bird enters the water traveling at a given velocity (v_1), the water will be moving past the bird at the same relative velocity. However, the water in the bird's mouth will be moving much more slowly ($v_2 = 0$ for the most part) than the water

outside the bird's mouth (v_1). According to Bernoulli's Principle, velocity and pressure are inversely proportional. Thus, the pressure within the pouch would be greater than that on the outside. Theoretically, the pressure difference can be calculated using the equation

$$(3) \quad p_2 - p_1 = (dv_1^2)/2$$

where d is the density of freshwater (1000 kg/m^3) and v_2 has been assumed to be 0 m/s (Table 1).

Another possibility is that the pouch fills in a drag-based fashion. An analogy would be to think of how a parachute opens. The fabric of the parachute opens by virtue of the air that is trapped within it. This functions passively with only gravity and air resistance being a factor. Lambertsen (1983) described how whales open their oral sacs by opening their mouths and then moving forward. In this case, gravity has been replaced with locomotory forces and air resistance has been replaced with water resistance. The same mechanism may account for pouch filling in the pelican.

In summary, the Brown Pelican's pouch has highly derived characteristics that allow it to function as a "fishing net". The pouch itself has folds in both the oral epithelium and the skin. These folds provide the extra material that allows the pouch's surface to flatten out as it expands. The pouch also has a thin layer of muscle that is homologous to that of other birds'. When contracted, this muscular layer could possibly function to return the pouch to its resting position. However, superficial to the muscle is a layer of elastin that forms a complex network of ligamentous bands that form complex anastomoses between adjacent bands. This layer of elastin functions in returning the pouch to its resting position passively simply by elastic recoil. Though I had expected to

also find a layer of collagen fibers in the pouch that would limit expansion, it appears not to be necessary. As some materials are stretched, they become increasingly resistant to stretching (Vogel, 1998). Thus, when the elastin is fully extended, it acts as an expansion-limiting network, negating the need for an additional tensile component in the pouch (i.e. collagen). The mandible itself bows in two different areas, referred to in this paper as the rostral bending zone and the caudal bending zone. The caudal bending zone is made up of several bones connected via syndesmoses. This arrangement allows these bones to move past one another as in the metal plates of a bending leaf spring. This imparts a high degree of bendability to this area of the mandible. The rostral bending zone is morphologically dissimilar to the caudal bending zone in that it is represented by a single area adjacent to the mandibular symphysis that is highly demineralized. Decreased mineralization is correlated to a high degree of bendability as observed by Papadmitriou et al. (1996) in the distal portions of bat digits. Furthermore, this rostral bending zone has a solid cross section which incurs a low second moment of area. Since higher second moments of areas are indicative of resistance to torsional forces, this implies that this structure is very bendable relative to other portions of the mandible (Figure 2). Bending is also certainly not hindered by the presence of overlying keratin as the keratin that overlies the rostral bending zone is much more skin-like and not at all similar to typical rhamphothecal keratin.

Further work must be done to evaluate the forces acting on and within the Brown Pelican's feeding apparatus. Also, further inquiry into the biochemical makeup of the keratin overlying various portions of the mandible will be of great use in determining the biomechanical properties of these structures. An inquiry into the muscle fibers present in

the pouch would help elucidate how these muscles are stretching. Lastly, it would be interesting to study the function of the M. genioglossus (Figure 5a) and the blood vessels that run through the center of this thin muscle and to determine what, if any, function they serve in the process of Brown Pelican feeding.

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I would like to thank Dr. Adam Johnston and Dr. John Cavitt for serving on my thesis committee and for providing insight during the preparation of this thesis. Harry Kelton and Wendy Fox of Pelican Harbor Seabird Station as well as John Gerwin of The North Carolina State Museum of Natural History provided anatomical specimens. I am indebted to Angie Martinez of McKay Dee Hospital for allowing us access to her skills with a CT scanner. This research was funded by a Thompson Research Fellowship and a Hemingway Faculty Vitality Award in support of undergraduate research. The Ogden Nature Center was very helpful when I needed to observe living pelicans. Lastly, I am indebted to Dr. Ron Meyers, without whom this research would have been impossible and for his mentoring skills over the years.

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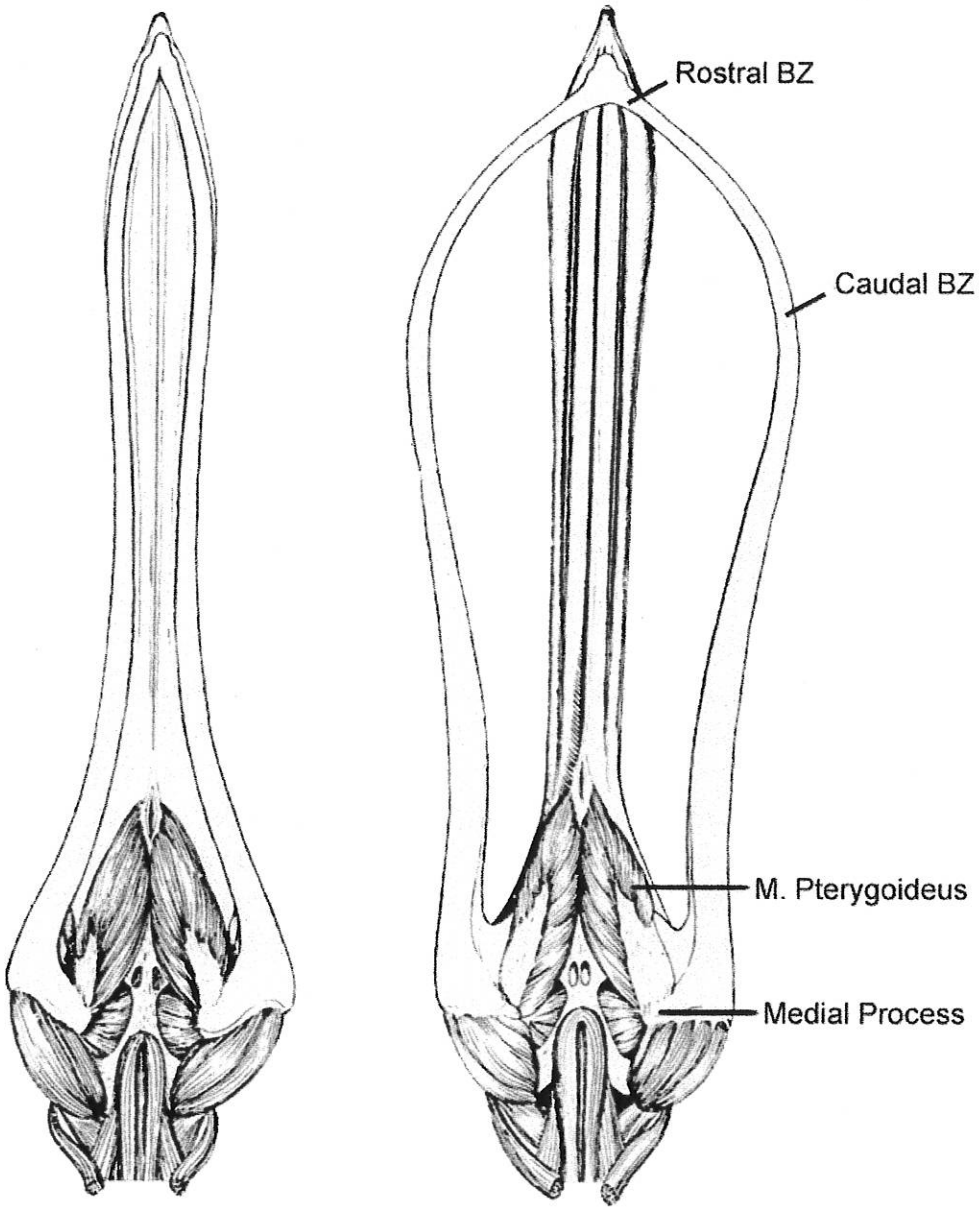

Figure 1: Ventral view of the Brown Pelican's head with the pouch removed. The resting position of the mandible is shown in A and the bowed position is showed in B. Note that for the mandible to bow, two curves must exist in the mandible as shown in B. Jaw bowing can be accomplished via contraction of the pterygoid musculature (Adapted from Böker, 1938).

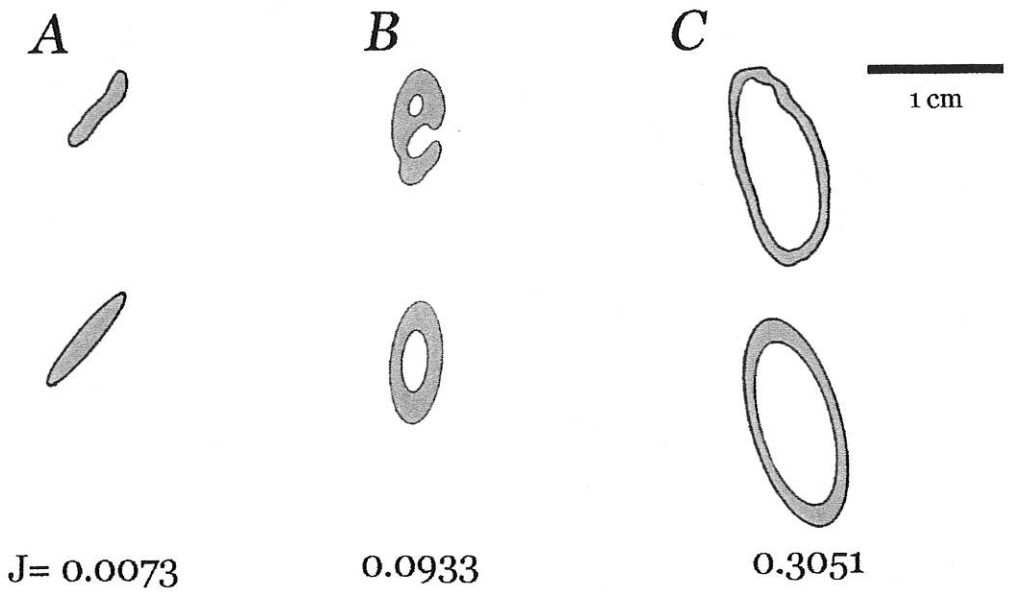

Figure 2: CT scans from three selected regions of the pelican's mandible. The actual cross sections are depicted, with the ovals that were used to approximate their second moment of areas directly below them. The rostral bending zone (A) was found to have a second moment of area of approximately 0.0073. The rostral bending zone (B) was found to have a second moment of area of approximately 0.0933. The rostral mandible (C) was found to have a hollow cross section and concomitant second moment of area of 0.3051.

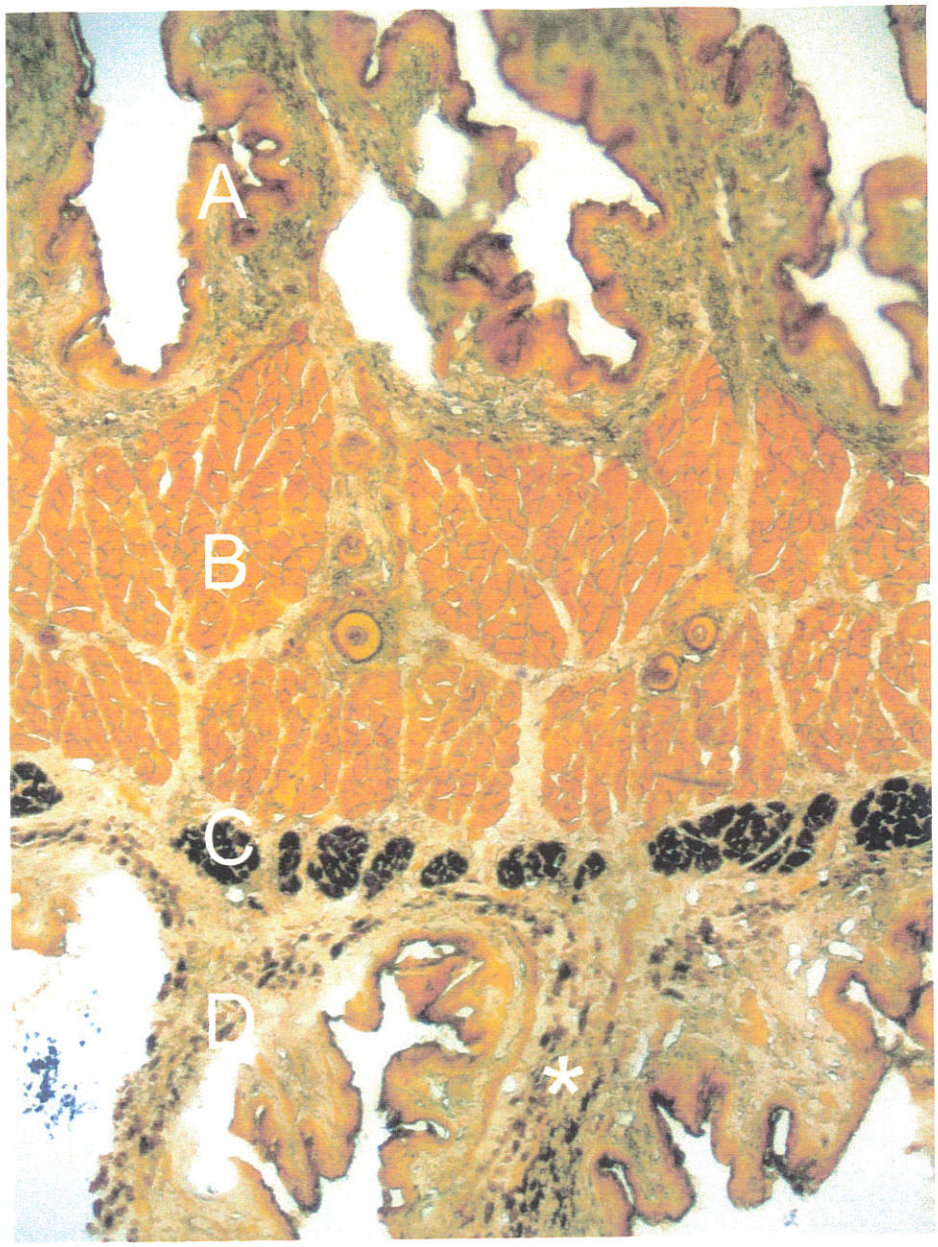

Figure 3: Pouch Histology. The oral mucosa is visible as a region of distinct folds (A) followed by a layer of muscle (B). Superficial to the muscle is a layer of elastin ligaments (C) that are approximately 500μm in diameter. These ligamentous bands are especially important in returning the pouch to its resting state after expansion. The skin (D) also has many smaller elastin bands within its dermis (*) that is typical amongst most types of skin.

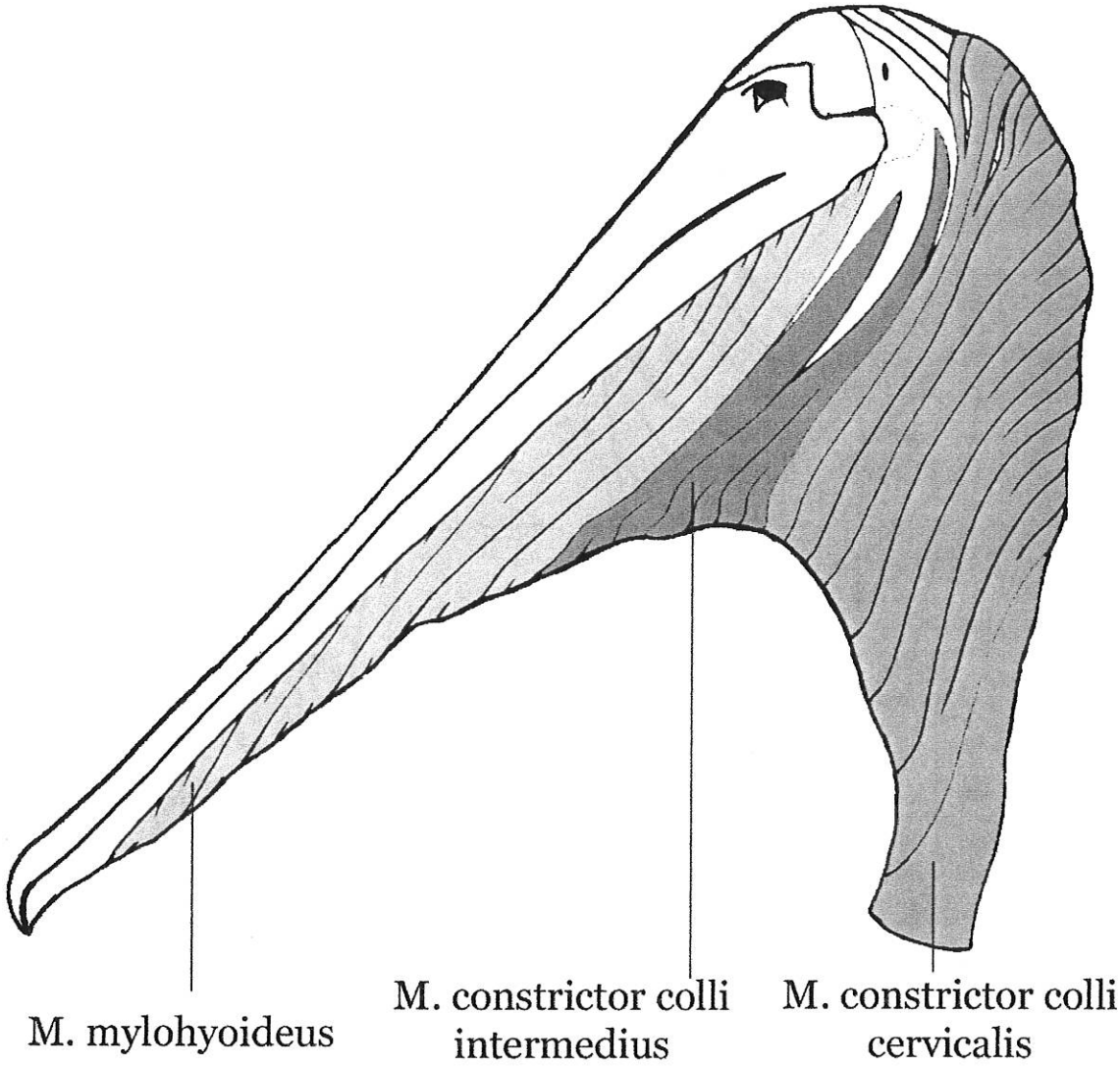

Figure 4: Pouch musculature; lateral view. The musculature of the Brown Pelican's pouch is derived from that of a typical bird ancestor.

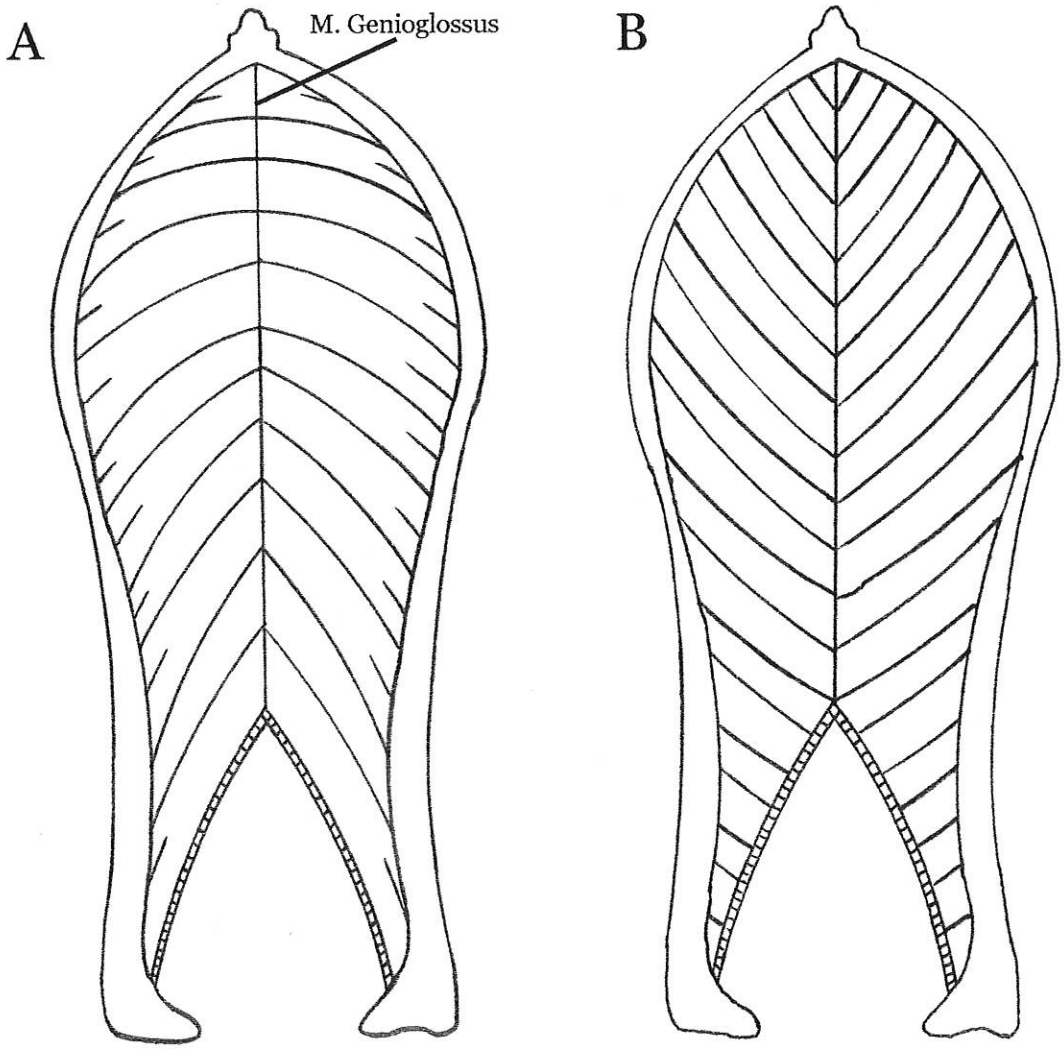

Figure 5: Schematic of muscle fascicle and elastin ligament orientations. The muscle fascicles (A) originate on the mandible and insert on the midventral raphe. Along the midventral raphe is the genioglossus muscle. Superficial to the muscle layer is the layer of elastin ligaments (B). These ligamentous bands are oriented nearly perpendicular to the muscle fascicles.

Figure 6: Gross appearance of elastin anastomoses. The midventral raphe is directly left of center, with elastin ligaments branching from this line in a caudo-rostral direction as shown in Figure 5. These ligaments form a very complex matrix of elastin with many anastomoses between adjacent bands. Magnification is approximately 25x.

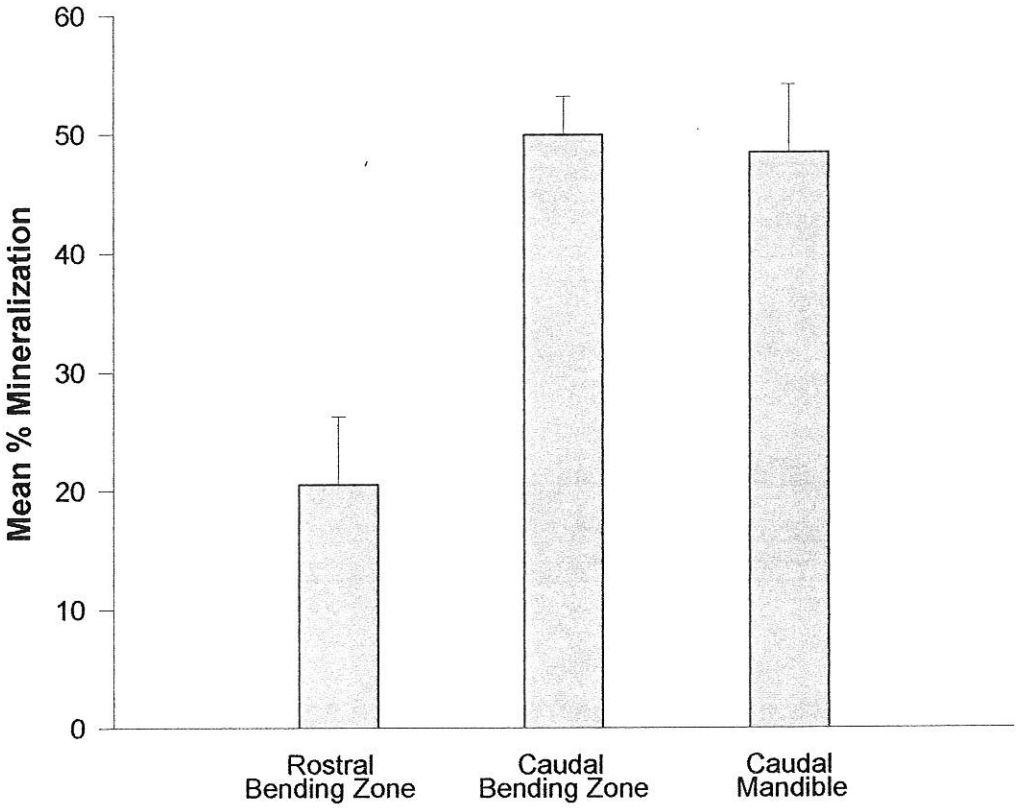

Figure 7: Mean percent mineralization of three selected sites in a Brown Pelican's mandible. The rostral bending zone is dramatically demineralized compared to both the caudal bending zone and the remaining portion of the mandible caudal to the bending zones (caudal mandible). Decreased mineralization is often associated with a high degree of flexibility.

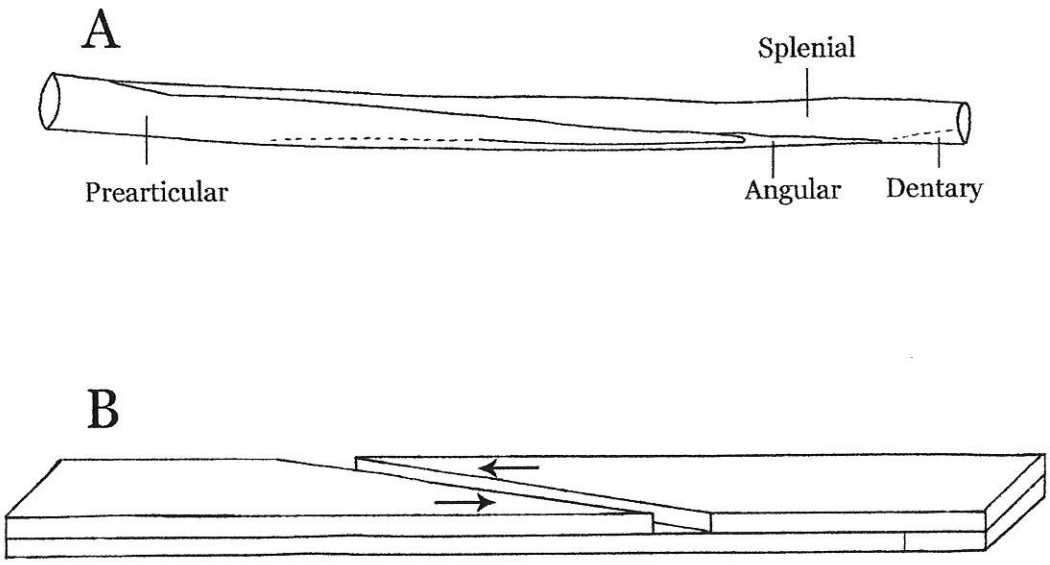

Figure 8: The leaf-spring nature of the caudal bending zone. A medial view of the Brown Pelican's caudal bending zone (A) shows the multiple bones that make up this particular portion of the lower jaw. These bones are interconnected via syndesmoses which are comprised of dense connective tissue in between adjacent bones. This allows these bones to move past one another quite readily when flexed, as in (B). This is somewhat analogous to how the metal plates of a leaf-spring move past one another when the spring is loaded with weight.

Table 1: Theoretical pressure differences based upon a simplified dive into water with the assumption that $v_2 = 0$ (See equation 3). This table uses a number of theoretical water velocities to estimate the pressures that develop within a Brown Pelican's mouth assuming that the water within the oral cavity is stationary.

V_1 (meters/sec)	Pressure Difference (Pa)
1	500
2	2000
3	4500
4	8000
5	12500
6	18000
7	24500
8	32000
9	40500
10	50000
11	60500
12	72000
13	84500
14	98000
15	112500
16	128000
17	144500
18	162000