OSTEOSCLEROSIS IN THE EXTINCT *CAYAOA BRUNETI* (AVES, ANSERIFORMES): INSIGHTS ON BEHAVIOR AND FLIGHTLESSNESS

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Abstract. Many studies on avian microanatomy have established a relationship between high bone compactness (*i.e.*, considerable degree of osteosclerosis) and diving behavior. Greatest degrees of compactness have been observed in the femora and humeri of fossil and extant penguins, femora of *Hesperornis* Marsh, and *Polarornis gregorii* Chatterjee, and to a somewhat lesser degree, in the humeri of flightless Pan-Alcidae. Within Anatidae, humeral and femoral compactness among diving species is greater than among non-diving ones, whereas flightless diving species have a greater degree of compactness than their volant close relatives. In *Cayaoa bruneti* Tonni, an extinct flightless foot-propelled, diving anatid with extreme forelimb reduction, femoral osteosclerosis is as great as that of penguins. Osteosclerosis in the femur of both foot- and wing-propelled divers could be part of the consequences of flightlessness and a result of selection to counter buoyancy.

Key words. Microanatomy. Bone compactness. Diving birds. *Cayaoa bruneti*.

Resumen. OSTEOSCLEROSIS EN EL EXTINTO *CAYAOA BRUNETI* (AVES, ANSERIFORMES): PERSPECTIVAS SOBRE EL COMPORTAMIENTO Y LA PÉRDIDA DE VUELO. Múltiples estudios en microanatomía aviana han establecido una relación entre una alta compactación ósea (es decir, un grado considerable de osteosclerosis) y el comportamiento buceador. Los mayores grados de compactación han sido observados en fémures y húmeros de pingüinos actuales y fósiles, fémures de *Hesperornis* Marsh, y de *Polarornis gregorii* Chaterjee, y en un grado algo menor, en húmeros de Pan-Alcidae no voladores. Dentro de los Anatidae, la compactación humeral y femoral es mayor entre las especies buceadoras que entre las no buceadoras, mientras que las especies buceadoras no-voladoras presentan un grado de compactación mayor que sus parientes cercanos voladores. En *Cayaoa bruneti* Tonni, un anatido extinto no volador, buceador propulsado por las patas, con una reducción extrema de los miembros anteriores, la osteosclerosis en el fémur es tan alta como la de pingüinos. La osteosclerosis en el fémur de los buceadores propulsados por las patas y los propulsados por las alas puede ser parte de las consecuencias de la pérdida de vuelo, seleccionada positivamente para contrarrestar la flotabilidad.

Palabras clave. Microanatomía. Compactación ósea. Aves buceadoras. *Cayaoa bruneti*.

Birds have various mechanisms of aquatic locomotion. Diving involves total immersion and underwater propulsion to feed on nectic or benthic fauna or to avoid predators. Two styles of propulsion are used by divers, and involve using either legs or wings. Most diving ducks (all Anatidae with diving behavior) are foot-propelled divers (*i.e.*, these species use their legs for underwater propulsion) (Ibañez and Tambussi, 2012), although some of them use their wings for the initial strokes and even for underwater strokes (Humphrey and Livezey, 1982). Underwater propulsion using wings is typical of penguins, the extinct plotopterids, dippers and auks.

Many birds can fly as much as dive. Very few have lost their ability to fly and this has happened both in foot- and wing- propelled divers. The overall relationship between flightlessness and foot-propelled diving received little attention compared with the relationship between flightlessness and wing-propelled diving (Livezey and Humphrey, 1986; Livezey, 1989). This may be in part because flightless foot-propelled divers, both extant and recently extinct species, are evolutionary oddities. Among these few examples are the Galapagos Cormorant (*Phalacrocorax harrisi* Rothschild, 1898; Livezey, 1992), three species of grebes

–the Titicaca Grebe (*Rollandia microptera* Gould, 1868; Livezey, 1989), the Junin Grebe (*Podiceps taczanowskii* Berlepsch and Stolzmann, 1894; Livezey, 1989) and the Atitlán Grebe (*Podylimbus gigas* Griscom, 1929; Livezey, 1989)– and the steamer ducks (genus *Tachyeres* Owen, 1875; Livezey and Humphrey 1986). Steamer ducks include the completely flightless Fuegian Steamer Duck (*Tachyeres pteneres* Forster, 1844; Livezey and Humphrey, 1986); the Chubut Steamer Duck (*T. leucocephalus* Humphrey and Thompson, 1981) in which only some females fly (Livezey and Humphrey, 1986); the Flying Steamer Duck (*T. patachonicus* King, 1831) in which only 25% of males are flightless (Humphrey and Livezey, 1982; Livezey and Humphrey, 1986); and the Falkland Steamer Duck (*T. brachypterus* Latham, 1790) for which there is a flying population that breeds in inland freshwater and a flightless population that breeds on the coast (Fulton *et al.*, 2012). Loss of flight capacity in all extant foot-propelled divers occurred in Recent or post glacial times (Livezey, 1986; Fulton *et al.*, 2012); for that reason they are collectively known as “neoflightless” birds in the sense of Habib and Ruff (2008).

There is a strong association between bone microanatomy and lifestyle (Wall, 1983; de Ricqlès and de Buffrènil, 2001; Germain and Laurin, 2005; Meier *et al.*, 2013). In general terms, divers have skeletons with greater bone density due to a thickening of the cortex by higher deposition of periosteal bone which is known as pachyostosis (Fracillon-Vieillot *et al.*, 1990). There may be also a reduction in the medullary resorption, a process called osteosclerosis. Both of these processes may occur in combination (de Ricqlès and de Buffrènil, 2001; Kriloff *et al.*, 2008).

Among wing-propelled divers, several studies showed that penguins have highly osteosclerotic limbs (Ksepka, 2007; Meister, 1962; Cerda *et al.*, 2014). Such high osteosclerosis levels were also verified in foot-propelled divers such as the Cretaceous flightless bird *Hesperornis* Marsh, 1872, and the Antarctic Cretaceous loon *Polarornis gregorii* Chatterjee, 2002 (Chinsamy *et al.*, 1998).

Habib and Ruff (2008) compared the cortical area in both femur and humerus of many species, including diving birds such as penguins and cormorants, and found that osteosclerosis was greater among divers than among non-diving birds. They showed that, while humeral thickness of flying and flightless cormorants was very similar, femoral thickness in the Galapagos Cormorant was significantly greater. The most plausible explanation for the increased thickness of bone cortices is the progressive replacement of trabeculae by compact bone during ontogeny (Ksepka, 2007).

Cayaoa bruneti is an extinct Anatidae from the Gaiman Formation (early Miocene) of Chubut, Argentina (Tonni, 1979; Noriega *et al.*, 2008). Because it shows the characters of a short curved femur with deep *fossa poplitea*, long tibiotarsus with flat *facies cranialis*, large *crista cnemialis cranialis*, and tarsometatarsus with narrow *trochlea metatarsi* II it was undoubtedly regarded as a diving duck (Noriega *et*

Figure 1. ***Cayaoa bruneti***, fore- and hindlimb bones. **1,** MPEF-PV-3104, carpometacarpus in internal view; **2,** MPEF-PV-3105, carpometacarpus in internal view; **3,** MPEF-PV-3100, humerus in palmar view; **4,** MPEF-PV-3115, tibiotarsus in anterior view; **5,** MLP 69-II-29-15, femur in anterior view; **6,** MLP 69-II-29-13, femur in anterior view; **7,** MPEF-PV-3116, tibiotarsus in anterior view; **8,** MLP 69-II-29-15, transversal section of femur; **9,** MLP 77-XII-22-1, tarsometatarsus in anterior view. Scale bars= 1cm.

al., 2008). *Cayaoa* had very small forelimbs so it would have been also a flightless bird (Fig.1; Noriega *et al.*, 2008). In fact, the ratio of forelimbs/hindlimbs length is smaller than any other flightless foot-propelled diver within Ornithurae (De Mendoza and Tambussi, 2014), with the exception of the late Pleistocene–Holocene *Chendytes lawi* (Anatidae, Merginae; Miller, 1925; Livezey, 1993), and Cretaceous Hesperornithiformes (Cracraft, 1982). In this paper, we are especially interested in the characteristics of leg bone microanatomy of *Cayaoa bruneti* and explore potential relationships with this species' way of life.

METHODS

Taxa selection and nomenclature

Femora and humeri from a number of species were studied. Species included flightless and flying foot-propelled diving and non-diving anseriforms as well as non-anatids. We examined material from the collections of the Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN): *Cayaoa bruneti* MLP 69-III-29-13 and MLP 69-III-29-15, Chubut Steamer Duck (*Tachyeres leucocephalus*) MACN 68554, Fuegian Steamer Duck (*T. pteneres*) MACN 68541, Flying Steamer Duck (*T. patachonicus*) MACN 54416*,* Red-breasted Merganser (*Mergus serrator* Linneaeus, 1758) MACN 54477, Lesser Scaup (*Aythya affinis* Eyton, 1838) MACN 54788, Rosy-billed Pochard (*Netta peposaca* Vieillot, 1816) MACN 68424, Andean Ruddy Duck (*Oxyura jamaicensis* Gmelin, 1789) MACN 68400, Black-necked Swan (*Cygnus melanocoryphus* Molina, 1782) MLP 565, Rock Shag (*Phalacrocorax magellanicus* Gmelin, 1789) MLP 15, Great Grebe (*Podiceps major* Boddaert, 1783) MLP 657, Gull (*Larus* sp. Linnaeus, 1758) MLP 948, Gentoo Penguin (*Pygoscelis papua* Forster, 1781) MLP 927 and Paleocene Stem-penguin *Crossvallia unienwillia* Tambussi *et.al.*, 2005 MLP 00-I-10-1. The humeri of *Cayaoa bruneti* MPEF-PV-3100 to 3103 (Museo de Paleontología Egidio Feruglio) were not available for comparisons.

Osteological nomenclature follows Baumel and Witmer (1993).

CT-Scanning

All bones were CT-Scanned using axial computer tomography with a General Electric Bright Speed High Speed CT scanner at 140 kv and 300 mA with 0.62 mm slice thickness at the San Juan de Dios Hospital in La Plata, Argentina. In all cases we used a cotton bed to better separate the specimen from the platform during image processing. All CT-Scan images were saved in DICOM format and analyzed with 3D Slicer 4.1.1 r20318 (Fedorov *et al.*, 2012).

CT-Scans cross section analysis and measures taken

All CT-Scanned femora and humeri were measured at mid-shaft using Bone Profiler (Girondot and Laurin, 2003) and Relative Bone Thickness (RBT) was calculated following the method of Smith and Clarke (2014) with the assumption that the mid-shaft represents a region morphologically equivalent in different taxa. In brief, Bone Profiler creates a dimensionless parameter, ranging from an impossible zero to one, called Observed Compactness (C) which is a measure of a bone surface in a given section. RBT is presented as percentage of thickness and is calculated by applying the formula:

$$RBT = [Cv+Cd/(D/100)]/2$$

Where Cv represents the thickness in mm of the ventral cortex, Cd the thickness in mm of dorsal cortex, and D the dorsoventral diameter in mm. Linear measures were taken using the ruler tool of the 3D Slicer software. RBT and C of a natural (non virtual) bone section of *Cayaoa bruneti* was also measured. Both C and RBT are methods for quantifying osteosclerosis.

RESULTS

Wall Compactness

Wall compactness (ratio between the surface occupied by bone tissues and total bone surface) of all humeri studied was almost homogeneous along the whole shaft. Wall compactness in the femur was low at distal and proximal extremes and highest at mid-shaft.

Both C and RBT in femora (Tab.1, Figs. 2, 3) showed similar results. All divers have thicker bone cortices than non-diving species (C is greater by 0.293 on average). Even the Rosy-billed Pochard (C = 0.545, RBT = 19.47%) –which is more reluctant to dive than other diving ducks (Livezey, 1996)– has thick bone cortices. The C and RBT of flightless *Tachyeres* species are greater than in flying species. The highest C and RBT were obtained for *Cayaoa bruneti* (C =

Table 1. Observed Compactness (C) and Relative Bone Thickness (RBT) estimated on the femur of selected species.

Collection number	*Taxa*	*C*	*RBT*
MLP 69-III-29-15	Cayaoa bruneti *-Bone-*	*0,985*	*37,1*
MLP 69-III-29-13	Cayaoa bruneti *-Scan-*	*0,999*	*35,45*
MLP 657	*Great Grebe*	*0,547*	*16,97*
MACN 68424	*Rosy-billed Pochard*	*0,545*	*19,47*
MACN 68400	*Andean Rudy Duck*	*0,636*	*27,81*
MACN 54477	*Red-breasted Merganser*	*0,509*	*16,74*
MACN 54416	*Flying Steamer Duck*	*0,552*	*16,04*
MACN 68554	*Chubut Steamer Duck*	*0,654*	*23,41*
MACN 68541	*Fuegian Steamer Duck*	*0,645*	*23,35*
MACN 54788	*Lesser Scaup*	*0,581*	*21,60*
MLP 15	*Rock Shag*	*0,629*	*21,17*
MLP 00-I-10-1	Crossvallia unienwillia	*0,52*	*19,91*
MLP 927	*Gentoo Penguin*	*0,858*	*32,83*
MLP 948	*Gull*	*0,372*	*12,84*
MLP 565	*Black-necked Swan*	*0,398*	*12,56*

0.99 and RBT = 37% respectively), reaching values as high as a Gentoo Penguin (C = 0.86 and RBT = 33%). The C and RBT value observed in the stem penguin *Crossvallia unienwillia* was lower (C = 0.52 and RBT = 20%). The C and RBT of the humeri of anatids are presented in Table 2 and Figure 4. Humeri and femora behaved differently about these attributes: humeri values were similar while femora values obtained for our entire sample were dissimilar. This is true except for the humerus of the Andean Ruddy Duck whose values were remarkably high (C = 0.79) compared to the rest.

Bone profiler and RBT

Since RBT takes in consideration only the bone cortices, the high amount of trabecula in bone sections of *Cayaoa bruneti* and the Gentoo Penguin could not be measured with this technique, while the Bone Profiler software takes into account all of the area occupied by bone in a section. In the Andean Ruddy Duck, the RBT value is relatively higher than its compactness, perhaps due to a difference in femoral cross sectional shape. As the Bone Profiler software works with overall cross-sectional shape, C may be a better estimator of osteosclerosis in that case.

DISCUSSION

Osteosclerosis, diving and flightlessness

The values of cortical thickness of the femur of *Cayaoa bruneti* obtained here were similar to those of the crown penguins, *Hesperornis* and *Polarornis gregorii*. *Polarornis* had a value for cortical thickness of 37% and *Hesperornis* was similar although the material was too distorted to provide an accurate percentage (Chinsamy *et al.*, 1998). Two alternative hypotheses have been offered to explain the higher femoral thickness of Galapagos Cormorants compared with their volant counterparts (Habib and Ruff, 2008): (1) the higher cortical area was an adaptation of neoflightless forms but ancient flightless forms (such as in *Rhea*) instead have greater hindlimb width but thinner cortical area. A non-

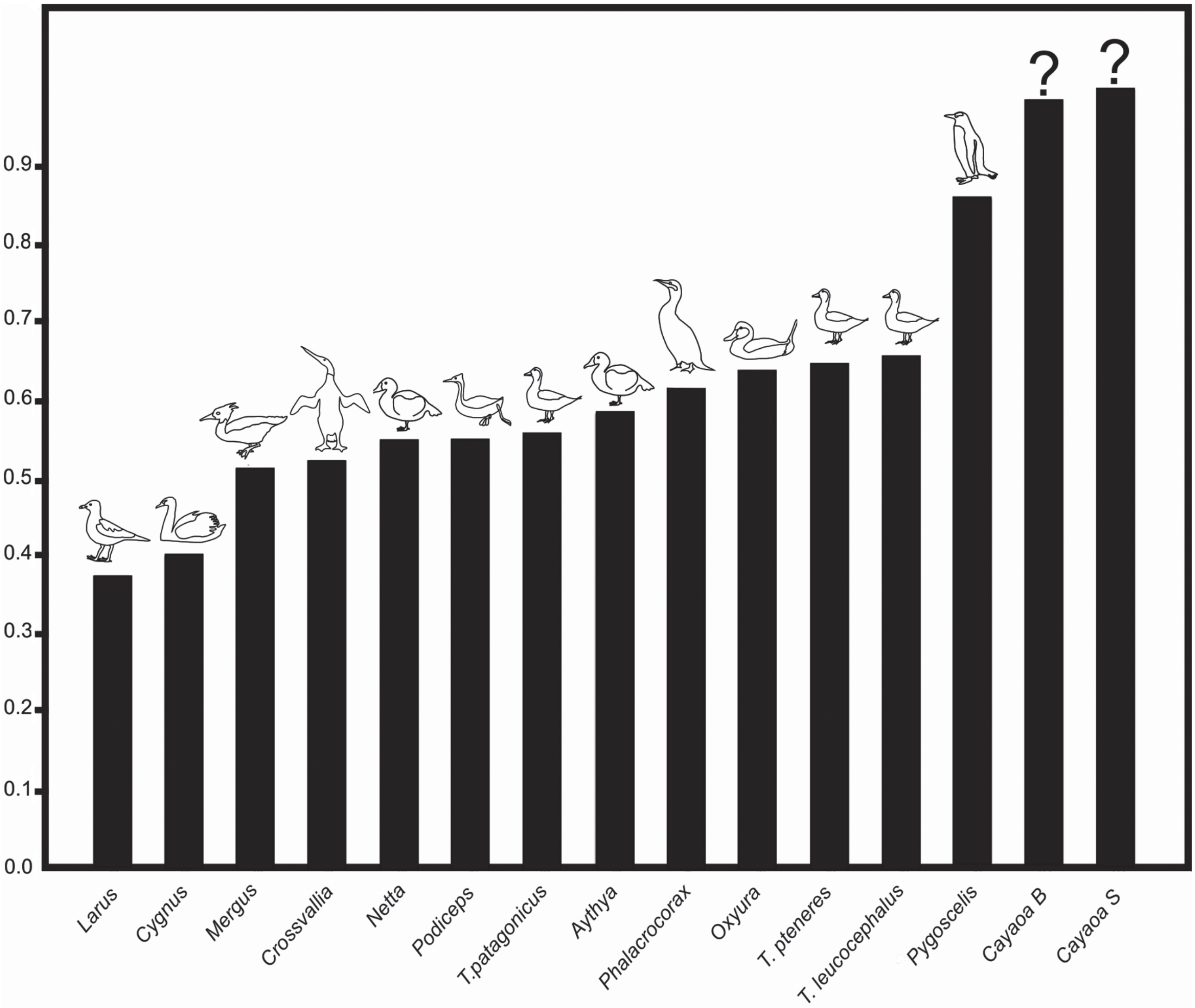

Figure 2. Barplot representing Observed Compactness (C) in the femora of Anatidae and other birds. Bars are organized from lowest (left) to highest values. Values are included in Table 1.

flying terrestrial bird is necessarily a walker, so the mechanical forces acting on its hindlimbs are high; (2) the higher cortical area is a result of the loss of flight capacity in conjunction with diving behavior. In this hypothesis, flightlessness in a diving species removes any constrains for the necessity for hollowness of bones for efficiency in flying, rather bones can be thicker to reduce buoyancy. The high (extant penguin-like) femoral thickness in *Cayaoa bruneti* does not conform to this first hypothesis. Being an ancient flightless species, its femoral thickness is greater than that of Galapagos Cormorant (and also greater than that of flightless steamer ducks), but its hindlimb bones are not wider. Its femoral thickness seems to be more in line with the second hypothesis.

Smith and Clarke (2014) found that humeral osteosclerosis in flightless Pan-Alcidae (*i.e.*, *Pinguinus* Bonnaterre, 1791, and Mancallinae) was closer to penguins, but femoral compactness was closer to flying species. They attributed the increase in forelimb compactness not to the necessity for countering buoyancy, but as part of the mechanical stiffening of forelimbs in their transformation from wings to flippers. The forelimb transformations that led to flightlessness in Pan-Alcidae also led to greater forelimb bone density. As the hindlimbs of flightless foot-propelled divers are not more rigid than the hindlimbs of other birds, the most probable explanation is positive selection towards

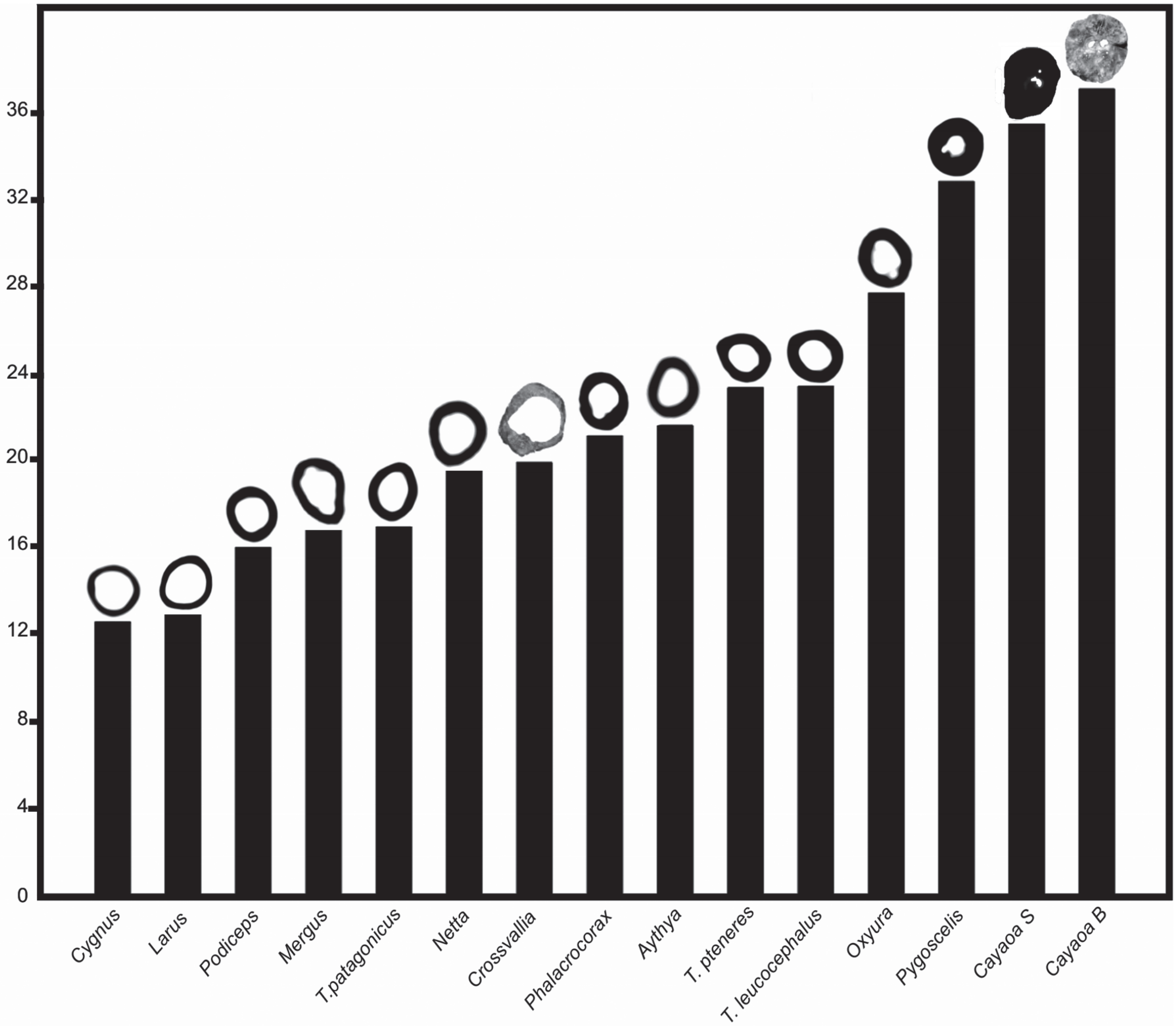

Figure 3. Barplot representing Relative Bone Thickness (RBT) in the femora of Anatidae and other birds. Bars are organized from lowest (left) to highest values. Values are included in Table 1.

countering buoyancy having been released from the constraint imposed by flight. Femoral osteosclerosis in flightless foot-propelled divers and flightless wing-propelled divers is apparently one of the consequences of flightlessness+diving behavior. Both flightless foot-propelled divers and flightless wing-propelled divers may reach a high level of osteosclerosis in their femora as evident in extant penguins, *Hesperornis regalis* (Chinsamy *et al*., 1998) and *Cayaoa bruneti*. We argue that a femoral osteosclerosis level as high as the one found in penguins is a derived condition in flightless divers. Chinsamy and colleagues (1998) found that the osteosclerosis in *Polarornis gregorii* was significantly higher (37%) than in modern foot-propelled diving birds and about the same level found among penguins (31%), and suggested that the cause for this high level of osteosclerosis may have been flightlessness. This work strongly supports that hypothesis. However the other species of *Polarornis,* considered to be a flying bird (Chaterjee *et al*., 2006), is expected to have a lesser degree of osteosclerosis. *Chendytes lawi*, a flightless diving anatid with the same limb proportions of *Cayaoa bruneti*, is also expected to have a measure of osteosclerosis similar to that of *Cayaoa* or penguins, but its microanatomy awaits study.

It is clear that *Cayaoa* was a diver with an increased bone

TABLE 2. Observed Compactness (C) and Relative Bone thickness (RBT) estimated on the humerus of selected anseriforms.

Collection number	*Taxa*	*C*	*RBT*
MLP 565	*Black-necked Swan*	*0,476*	*16,70*
MACN 68424	*Rosy-billed Pochard*	*0,484*	*15,67*
MACN 54416	*Flying Steamer Duck*	*0,539*	*16,31*
MACN 54477	*Red-breasted Merganser*	*0,546*	*16,96*
MACN 68541	*Fuegian Steamer Duck*	*0,594*	*17,32*
MACN 68554	*Chubut Steamer Duck*	*0,628*	*19,52*
MACN 54788	*Lesser Scaup*	*0,689*	*21,49*
MACN 68400	*Andean Rudy Duck*	*0,794*	*31,42*

mass (hyperostosis, osteosclerosis). This increased mass acts as a passive control system (Taylor, 2000; Kriloff *et al.*, 2008) to counteract buoyancy (Cook *et al.*, 2010). This condition characterizes shallow water divers (Taylor, 2000) and *Cayaoa*. Buoyancy also depends on body size and the amount of stored or retained air in the body (Cook *et al.*, 2010). Small animals tend to have proportionately more air than larger animals and thereforehave more difficulty submersing. Many birds counteract this problem by deliberate stone-swallowing (Taylor, 1993; Wings, 2007). Evidence of stone-swallowing in *Cayaoa* is now only speculative and details of its diving habits remain unsettled.

The transition between penguins, hesperornithiforms, *Cayaoa bruneti*, *Chendytes lawi* and their respective volant ancestors, is not documented in the fossil record (Livezey, 1993; but see Howard, 1955). It is assumed that all flightless diving birds are descendants of smaller flying ancestors with thin cortices in their limb bones but these ancestral taxa share a taphonomic bias with their descendants.

CONCLUDING REMARKS

One of the characteristics shared among diving birds is a greater degree of osteosclerosis than that among non-diving species. A bird with greater density will sink better in water; so a diving bird would benefit from a greater degree of osteosclerosis but this would be detrimental for flight. Femoral osteosclerosis in flying foot-propelled diving birds here ranged between C= 0.5 and C = 0.6, and that value may be a compromise solution between the benefits from osteosclerosis for diving while still being capable for flight. In flightless foot-propelled diving birds the degree of femoral osteosclerosis is particularly high, as seen in the flightless steamer ducks. Although flightless steamer ducks have a

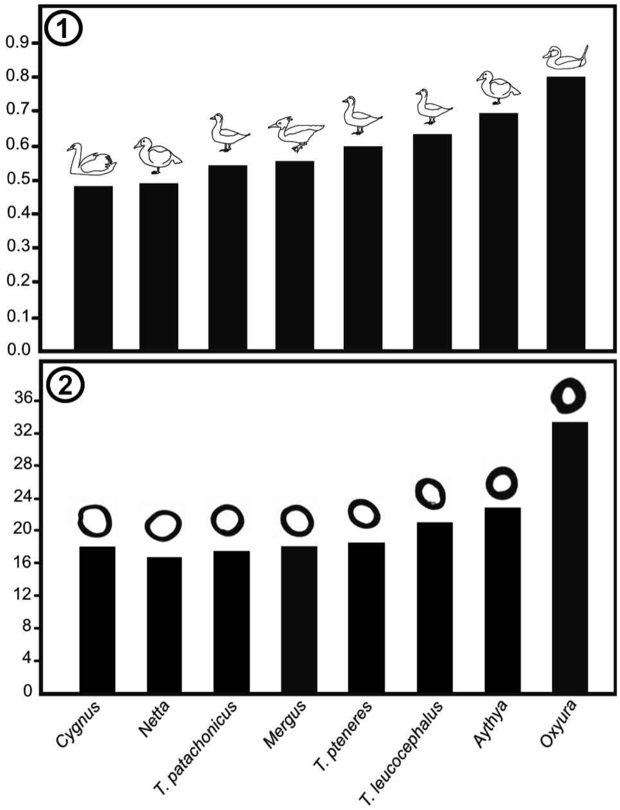

Figure 4. 1, Barplot representing Observed Compactness (C) in the humeri of Anatidae. **2,** barplot representing Relative Bone Thickness (RBT) in the humeri of Anatidae.

higher femoral osteosclerosis degree than Flying Steamer Duck (C = 0.552 in Flying Steamer Duck vs C = 0.645 in Fuegian Steamer Duck and C = 0.654 in Chubut Steamer Duck) these values are far closer to those of flying species than to *Cayaoa bruneti* or to penguins. The release from constraints associated with flying may have allowed an increase in the degree of bone compactness in the evolutionary history of *Cayaoa bruneti*. Perhaps further fossil evidence may shed light on the evolution of flightlessness and osteosclerosis in *Cayaoa bruneti*. An understanding of the phylogenetic position of *Cayaoa bruneti* may allow a better evaluation of the evolution of these characters.

ACKNOWLEDGMENTS

We wish to thank three anonymous reviewers and editor R. Coria for constructive comments that greatly improved the manuscript. We thank D. Ksepka who shared literature with us, the curators of Museo de La Plata and Museo Argentino de Ciencias Naturales Bernardino Rivadavia for allowing access to the material. For assistance with CT scanning and data management, we thank G. Alcuaz and J. I. Cuesta (Hospital San Juan de Dios, La Plata, Argentina). We thank E. Ruigomez and B. Pianzola for the photographs of the fossil material. We appreciate the improvements in English usage made by P. Lowther through the Association of Field Ornithologists' program of editorial assistance. We are very thankful to CONICET for their constant support.

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doi: 10.5710/AMGH.28.02.2015.2843

Submitted: November 1st, 2014

Accepted: February 28th, 2015