BioOne COMPLETE

Variation of the Outer Circumferential Layer in the Limb Bones of Birds

Authors: Ponton, Fleur, Elżanowski, Andrzej, Castanet, Jacques, Chinsamy, Anusuya, Margerie, Emmanuel De, et al.

Source: Acta Ornithologica, 39(2) : 137-140

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/068.039.0210

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

ACTA ORNITHOLOGICA
Vol. 39 (2004) No. 2

Variation of the outer circumferential layer in the limb bones of birds

Fleur Ponton[1], Andrzej Elżanowski[2], Jacques Castanet[1], Anusuya Chinsamy[3], Emmanuel de Margerie[1], Armand de Ricqlès[1] & Jorge Cubo[1,*]

[1]P. & M. Curie University, FRE CNRS 2696, 2 Pl. Jussieu, Case 7077, 75005 Paris, FRANCE
[2]Institute of Zoology, University of Wrocław, Sienkiewicza 21, 50–335 Wrocław, POLAND
[3]Zoology Department, University of Cape Town, Private Bag, Rondebosch 7700, SOUTH AFRICA
* Corresponding author: cubo@ccr.jussieu.fr

Ponton F., Elżanowski A., Castanet J., Chinsamy A., de Margerie E., de Ricqlès A., Cubo J. 2004. Variation of the outer circumferential layer in the limb bones of birds. Acta Ornithol. 39: 137–140.

Abstract. The core of the limb bone cortex of mammals and birds is made of rapidly deposited, fibro-lamellar bone tissue (also present in non-avian theropods), which is usually surrounded by an avascular outer circumferential layer (OCL) of slowly deposited parallel-fibered bone. We present the first comparative allometric study of the relative OCL thickness (expressed as a fraction of the diaphyseal radius) in modern birds. Body size explains 79% of the OCL variation in thickness, which is inversely correlated with size, that is, shows negative allometry (slope -0.799). This may explain the apparent absence of OCL in the ratites. Since the OCL is deposited at the end of growth, we propose that its relative thickness probably correlates with the amount of slow, residual growth, which our results suggest to be on the average larger in small birds.

Key words: bone histology, postnatal growth, ossification, skeleton, periosteal bone, phylogenetically independent contrasts

Received — July 2004, accepted — Sept. 2004

INTRODUCTION

In mammals, birds and some non-avian archosaurs, the bulk of the limb bone cortex is made of highly vascularized, fibro-lamellar bone tissue, which is deposited at higher rate than parallel-fibered or lamellar bone. In mammals and birds, the fibro-lamellar core is often surrounded by avascular outer circumferential layer (OCL) of slowly deposited parallel-fibered bone, which has also been referred to as the outer circumferential lamellae (Ham 1953), outer layers of circumferential lamellae (Enlow & Brown 1957), periosteal zone (Klevezal et al. 1972, van Soest & van Utrecht 1978), periosteal layers (Lewis 1979, Nelson & Bookhout 1980), and external fundamental system (Cormack 1987). The presence of outer circumferential layer in birds and mammals is most probably another homoplasy of these two taxa since their respective lineages split in the Carboniferous soon after the beginning of amniote evolution and the OCL is not differentiated in any other tetrapods.

The OCL has been found in the majority of hitherto studied neognathous birds (Amprino & Godina 1947, Klevezal et al. 1972, van Soest & van Utrecht 1978, Koubek & Hrabe 1984, Chinsamy et al. 1995, Castanet et al. 1996, Chinsamy et al. 1998, Zhang et al. 1998), although it seems poorly if at all developed in the ratites studied to date including *Struthio, Rhea,* and *Casuarius* (Amprino & Godina 1947, Chinsamy 1995, Chinsamy et al. 1995). The OCL is well developed in the basal bird *Confuciusornis* (de Ricqlès et al. 2003), but absent in the studied specimens of odontognathous birds, *Ichthyornis* and *Hesperornis*, which was taken as evidence of their immature age (Chinsamy et al. 1998), as well as in the Mesozoic flightless bird *Patagopteryx* (Chinsamy et al. 1995). In the Enantiornithes, which branched off after *Confuciusornis* but before the odontognaths, the entire cortex is made of poorly vascularized par-

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

allel-fibered tissue (Chinsamy et al. 1995) which must have completely replaced the fibrolamellar bone found in the enantiornithine perinatal skeletons (Chinsamy & Elzanowski 2001).

The slowly formed OCL is deposited in grown-up individuals and smooths off the rough periosteal surface of juvenile bones, hence their presence is commonly taken as an indication of the termination of growth. Accordingly, the only detailed study of timing of the OCL deposition showed that parallel-fibered bone appears in the major limb bones and coracoid of immature but already adult-sized Mallards *Anas platyrhynchos* at the age of about 5 months (Castanet et al. 1996). However, the termination of growth seems to vary in its temporal extent between avian taxa, e.g. the fast growth phase ends early on and growth continues at a slow rate in Crowned Cranes *Balearica pavonina*, whereas Sandhill Cranes *Grus canadensis* maintain their initial growth rate until almost fully grown (Pomeroy 1980). Variation in the terminal growth phases may in fact be reflected in bone histology. In most of the studied neognathous species, the OCL is sharply set off from the remaining cortex by a "subperiosteal resorption line" (de Ricqlès et al. 2001), but in some of them, including large passerines such as *Corvus* (Enlow & Brown 1957: fig. 27/5) and large accipitrids such as *Aquila* and *Gyps* (Amprino & Godina 1947) and *Buteo* (Enlow & Brown 1957), the outer avascular tissue is poorly defined from the remaining fibro-lamellar cortex. The OCL of birds is commonly layered itself, showing what appears to be growth rings separated by lines of arrested growth (LAGs), although their deposition does not seem to occur in an annual cycle (Lewis 1979, Nelson & Bookhout 1980).

We present the first comparative and allometric study of the relative OCL thickness in birds.

MATERIAL AND METHODS

We measured the cross-sectional parameters of the femoral shafts in 17 neognathous species from 14 families representing the entire spectrum of developmental modes (Table 1). All specimens were adults. Thin sections (14 to 16 μm thick) at the mid-shaft of decalcified femora were prepared using a freezing microtome and stained with Ehrlich's haematoxylin.

Using a reticule, we measured (in μm^2) the OCL area and the total cross-sectional area (including the medullary cavity). The relative thickness of the femoral OCL at the diaphysis of each section was determined as the ratio of the OCL area to the total cross-sectional area. The mean diaphyseal radius was calculated from total cross-sectional area and used as a proxy of body size. The cross-sectional measurements (diameter or cirumference) of the femur can be treated as approximate measures of body size in birds (e.g. Campbell & Marcus 1992). The obtained figures were multiplied by 100 to avoid negative values after a log transformation.

In order to determine a size dependence of the relative OCL thickness, we used both a standard regression on raw data and the method of Phylogenetically Independent Contrasts (PIC), which addresses the non-independence of data

Table 1. The studied specimens with the calculated values of femoral radius (in mm) and taxon-specific developmental modes.

Family	Species	Femoral radius	Developmental mode
Megapodiidae	*Alectura lathami*	5.207	precocial
	Megapodius nicobariensis	2.934	precocial
Phasianidae	*Phasianus colchicus*	3.342	precocial
	Perdix perdix	1.715	precocial
Anatidae	*Anas platyrhynchos*	2.306	precocial
Scolopacidae	*Scolopax rusticola*	2.050	precocial
Laridae	*Larus ridibundus*	2.424	semiprecocial
Ardeidae	*Bubulcus ibis*	2.429	semialtricial
Accipitridae	*Accipiter nisus*	2.209	semialtricial
	Buteo buteo	3.373	semialtricial
Falconidae	*Falco tinnunculus*	1.915	semialtricial
Columbidae	*Streptopelia decaocto*	1.547	semialtricial
Strigidae	*Asio flammeus*	2.126	semialtricial
Procellariidae	*Macronectes giganteus*	4.122	altricial
Corvidae	*Corvus corone*	2.089	altricial
Turdidae	*Erithacus rubecula*	0.604	altricial
Sturnidae	*Sturnus vulgaris*	1.291	altricial

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

points linked to phylogeny (Felsenstein 1985). For the latter purpose we used a recent avian phylogeny based on morphological characters (Mayr & Clarke 2003) and assumed a gradual model in which branch lengths were computed by using geological divergence times: Galloanserae-Neoaves: 104.2 MYA, Galliformes-Anseriformes: 89.8 MYA and basal Neoaves 89.3 MYA (van Tuinen & Hedges 2001). We used CAIC computer package (Purvis & Rambaut 1995) to calculate PICs: values for both the log relative thickness of the femoral OCL and the log femoral radius at all nodes in the phylogeny were estimated and sister-taxon contrasts for both variables computed.

We checked the validity of statistical and evolutionary assumptions of the PIC analysis for our data. Then, we constructed a scaling equation by using a phylogenetically independent slope (obtained from a regression through the origin of contrasts) and an intercept calculated from the estimate of each variable for the root node (Garland et al. 1993, Weathers & Siegel 1995).

RESULTS AND DISCUSSION

The result obtained from the raw data regression ($y = 3.0779\text{-}0.9263x$, $R^2 = 0.799$, $p = 0.000001$, $n = 17$ species) and by using PIC ($y = 2.74997\text{-}0.7992x$, $R^2 = 0.791$, $p < 0.0001$, $n = 16$ contrasts) is essentially identical: body size explains 79% of the variation of the log relative thickness of the OCL. The relative OCL thickness shows a negative allometry with respect to body size, that is, smaller birds have relatively thicker OCL than bigger birds (Fig. 1), which implies that small birds have a longer period of slow residual growth than do large birds. If real, the apparent absence of OCL in the ratites (Chinsamy 1995) may possibly indicate a complete phasing out of the residual growth phase in largest birds. Thus, all birds of similar size appear to have similar relative thickness of the OCL, apparently regardless of their developmental mode (Table 1).

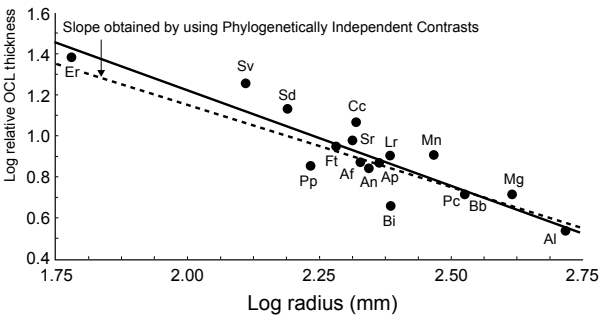


Fig. 1. Logarithmic regression of the relative thickness of the outer circumferential layer (OCL) on the radius of the femoral shaft (solid line). The scaling equation has also been constructed by using Phylogenetically Independent Contrasts (dotted line). Af — *Asio flammeus*, Al — *Alectura lathami*, An — *Accipiter nisus*, Ap — *Anas platyrhynchos*, Bb — *Buteo buteo*, Bi — *Bubulcus ibis*, Cc — *Corvus corone*, Er — *Erithacus rubecula*, Ft — *Falco tinnunculus*, Lr — *Larus ridibundus*, Mg — *Macronectes giganteus*, Mn — *Megapodius nicobariensis*, Pc — *Phasianus colchicus*, Pp — *Perdix perdix*, Sd — *Streptopelia decaocto*, Sr — *Scolopax rusticola*, Sv — *Sturnus vulgaris*.

Size dependence of the OCL thickness seems unlikely to be adaptive in terms of mechanical design because this could not be demonstrated even for the entire cortex of avian tubular bones (Currey 2002). It is more likely to be a side effect of terminal growth dynamics as imposed by the growth rate in the preceding main phase. The overall growth rate is known to be size dependent, with small birds growing faster than large birds (Starck & Ricklefs 1998).

The phenomenon of residual growth is evidenced by the lines of arrested growth in the OCL of many birds (Klevezal et al. 1972, van Soest & van Utrecht 1978, Lewis 1979, Nelson & Bookhout 1980, Koubek & Hrabe 1984) but otherwise remains poorly known. Postmaturational residual growth has recently been demonstrated in Pied Flycatchers *Ficedula hypoleuca*, which grow at a very low rate for two years past sexual maturity and so does their tarsal length (Dale et al. 2002). The OCL is deposited at a much slower rate than is the fibro-lamellar core (Castanet et al. 1996, de Margerie et al. 2002), which suggests that its thickness may reflect the amount of residual growth. This conclusion is in general agreement with the proposition that slow growth is conducive to enhanced ossification (Blom & Lilja 2004), but raises a question of why the amount of residual growth would be larger in smaller birds, which grow faster (Starck & Ricklefs 1998). We feel that the answer lies in a more abrupt termination of fast growth. However, since the relationship between the overall growth rate and ossification processes are only beginning to be understood at any developmental stage (Blom & Lilja 2004), more dedicated studies of residual growth with precisely aged individuals are needed in order to test this hypothesis.

ACKNOWLEDGMENTS

We thank Marek Konarzewski (University of Białystok) and Ken Campbell (Los Angeles County Museum) for constructive reviews, Łukasz Paśko

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(University of Wrocław) for discussion of statistical methods and Storrs Olson (Smithsonian Institution) for pointing to us the striking variation in terminal growth stages among the cranes. A. E. and A. C. gratefully acknowledge the support from a Poland-RSA collaboration grant for 2003–2004.

REFERENCES

Amprino R., Godina G. 1947. La struttura delle ossa nei vertebrati. Ricerche comparative negli amfibi e negli amnioti. Comment. Pontif. Acad. Sci. 11: 329–467.

Blom J., Lilja C. 2004. A comparative study of growth, skeletal development and eggshell composition in some species of birds. J. Zool. 262: 361–369.

Campbell K. E., Marcus L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. Science Ser. Nat. Hist. Mus. Los Angeles County 36: 395–412.

Castanet J., Grandin A., Abourachid A., de Ricqlès A. 1996. [Expression of growth dynamics in the structure of periosteal bone in the Mallard *Anas platyrhynchos*]. C. R. Acad. Sci. Paris Life Sci. 319: 301–308.

Chinsamy A. 1995. Histological pespectives on growth in the birds *Struthio camelus* and *Sagittarius serpentarius*. Courier Forschungsinst. Senckenberg 181: 317–323.

Chinsamy A., Chiappe L. M., Dodson P. 1995. Mesozoic avian bone microstructure: physiological implications. Paleobiology 21: 561–574.

Chinsamy A., Elzanowski A. 2001. Evolution of growth pattern in birds. Nature 412: 402–403.

Chinsamy A., Martin L. D., Dodson P. 1998. Bone microstructure of the diving *Hesperonis* and the volant *Ichthyornis* from the Niobrara Chalk of western Kansas. Cretaceous Research 19: 225–235.

Cormack D. 1987. Ham's histology. Lippincott, New York.

Currey J. D. 2002. Bones/Structure and Mechanics. Princeton Univ. Press, Princeton & Oxford.

Dale S., Slagsvold T., Lampe H. M., Lifjeld J. T. 2002. Age-related changes in morphological characters in the pied flycatcher *Ficedula hypoleuca*. Avian Science 2: 153–166.

Enlow D., Brown S.O. 1957. A comparative histological study of fossil and Recent bone tissues. Part II. Texas J. Sci. 9: 185–214.

Felsenstein J. 1985. Phylogenies and the comparative method. Am. Nat. 125: 1–15.

Garland T. Jr., Dickerman A. W., Janis C. M., Jones J. A. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42: 265–292.

Ham A. W. 1953. Histology. 2nd ed. Lippincott, Philadelphia.

Klevezal G. A., Kaller Salas A. V., Kirpichev S. P. 1972. Determination of age in birds by layers in the periosteal zone. Zool. Zhurnal 51: 1726–1730.

Koubek P., Hrabe V. 1984. Estimating the age of male *Phasianus colchicus* by bone histology and spur length. Folia Zool. 33: 301–313.

Lewis J. C. 1979. Periosteal layers do not indicate ages of Sandhill cranes. J. Wild. Manage. 43: 269–271.

de Margerie E., Cubo J., Castanet J. 2002. Bone typology and growth rate: testing and quantifying "Amprino's rule" in the mallard (*Anas platyrhynchos*). C. R. Biologies 325: 221–230.

Mayr G., Clarke J. 2003. The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. Cladistics 19: 527–533.

Nelson R. C., Bookhout T. A. 1980. Counts of periosteal layers invalid for aging Canada geese. J. Wild. Manage. 44: 518–521.

Pomeroy D. E. 1980. Growth and plumage changes of the Grey Crowned Crane *Balearica regulorum gibbericeps*. Bull. Brit. Ornith. Club 100: 219–223.

Purvis A., Rambaut A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. Computer Appl. Biosci. 11: 247–251.

de Ricqlès A., Padian K., Horner J. R. 2001. The bone histology of basal birds in phylogenetic and ontogenetic perspective. In: Gauthier J., Gall L. F. (eds). New perspectives on the origin and early evolution of birds. Peabody Mus. Nat. Hist./Yale Univ., New Haven, pp. 411–426.

de Ricqlès A., Padian K., Horner J. R., Lamm E. T., Myhrvold N. 2003. Osteology of *Confuciusornis sanctus* (Theropoda: Aves). J. Vert. Pal. 23: 373–386.

Starck J. M., Ricklefs R. E. 1998. Variation, constraint, and phylogeny. Comparative analysis of variation of growth. In: Starck J. M., Ricklefs R. E. (eds). Avian growth and development. Evolution within the altricial-precocial spectrum. Oxford Univ. Press, New York, pp. 247–265.

van Soest R. W. M., van Utrecht W. L. 1978. The layered structures of bones of birds as a possible indication of age. Bijdragen tot de Dierkunde 41: 61–66.

van Tuinen M., Hedges S. B. 2001. Calibration of avian molecular clocks. Mol. Biol. Evol. 18: 206–213.

Weathers W. W., Siegel R. B. 1995. Body size establishes the scaling of avian postnatal metabolic rate: an interspecific analysis using phylogenetically independent contrasts. Ibis 137: 532–542.

Zhang F., Hou L., Ouyang L. 1998. Osteological microstructure of *Confuciusornis*: preliminary report. Vertebrata Palasiatica 36: 126–135.

STRESZCZENIE

[Zmienność grubości blaszki okalającej zewnętrznej w kościach kończyn ptaków]

Rdzenne części kości ssaków, ptaków i teropodów zbudowane są z szybko odkładanej kości włóknisto-blaszkowatej (fibrolamellar bone) i otoczone są beznaczyniową warstwą (blaszką) okalającą zewnętrzną (OCL), w której u ptaków często znajdują się gęsto upakowane pierścienie przyrostowe. Obecna praca jest pierwszą analizą względnej grubości OCL u ptaków, tzn. stosunku jej grubości bezwzględnej do promienia trzonu (diafyzy). Stwierdzono, że względna grubość OCL zależna jest w 79% od wielkości ciała ptaka i wykazuje ujemną allometrię (-0.799), tzn. jest mniejsza u większych ptaków, co może wyjaśnić dotychczasowy brak jednoznacznego stwierdzenia OCL u Ratitae. OCL odkładana jest pod koniec wzrostu, stąd Autorzy wysuwają hipotezę, że jej grubość skorelowana jest z długością okresu resztkowego wzrostu, który zachodzi przynajmniej u niektórych ptaków po osiągnięciu w przybliżeniu ostatecznych rozmiarów ciała, a nawet po osiągnięciu dojrzałości płciowej. Uzyskane wyniki sugerują, że resztkowy wzrost wyrażony jest mocniej u mniejszych ptaków.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use