ORNITOLOGIA NEOTROPICAL 15 (Suppl.): 73–81, 2004

RECENT ANATOMICAL STUDIES ON NEOTROPICAL BIRDS

Elizabeth Höfling

Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 101, CEP 05508-900, São Paulo, Brazil. *E-mails*: ehofling@usp.br & ehofling@ib.usp.br

Resumo. – Estudos anatômicos recentes de aves Neotropicais. – O conhecimento anatômico é um pré-requisito fundamental para entender as séries de transformações nos caracteres e a história evolutiva dos organismos. Os métodos tradicionais, utilizados no estudo anatômico, foram sendo gradualmente substituídos por uma abordagem dinâmica e funcional, em que são empregadas técnicas cada vez mais sofisticadas. Além disso, o estudo das relações de parentesco entre os organismos, como proposto pelo entomologista alemão Willi Hennig, tem motivado os biólogos a reviver a anatomia por ser ela indicativa das relações entre os táxons. Assim, as novas idéias e os conceitos da sistemática filogenética foram, também, incorporados à ornitologia. Na década de 1980 iniciamos, na Universidade de São Paulo, um programa de pesquisa com vários projetos em ornitologia que não haviam sido, até então, explorados no Brasil, voltados, principalmente, para a avifauna Neotropical. O novo grupo de pesquisa em anatomia conta, atualmente, com 18 pesquisadores e estudantes que trabalham nos seguintes temas: a) anatomia osteológica e miológica, que fornece subsídios para entender a mecânica dos movimentos, além de ser uma importante fonte de caracteres para sustentar hipóteses filogenéticas; b) anatomia da siringe, que tem possibilitado a caracterização dos padrões morfológicos de vários grupos de aves; e c) pesquisa sobre aves fósseis da América do Sul. Os táxons estudados nesses projetos pertencem principalmente às seguintes ordens: Tinamiformes, Ciconiiformes, Falconiformes, Galliformes, Opisthocomiformes, Gruiformes, Psittaciformes, Cuculiformes, Strigiformes, Trogoniformes, Coraciiformes, Piciformes e Passeriformes (i.e., Furnariidae e Dendrocolaptidae).

Abstract. – The knowledge of anatomy is a necessary prerequisite for understanding changes in characters, and the evolutionary history of organisms. Traditional methods of anatomical study have been gradually replaced by functional and dynamic approaches, using techniques that have become increasingly sophisticated over time. Moreover, the study of the relationships among organisms, as proposed by the German entomologist Willi Hennig, has motivated biologists to revive anatomy as the basic indicator of biological relationships among taxa. Ornithology has kept pace with these new ideas and concepts. In the early '80s, at the Universidade de São Paulo, we began a research program with various ornithology projects on aspects that had not been previously explored in Brazil, and that focused on the Neotropical avifauna. This anatomical research group currently consists of 18 scientists and students working on the following topics: a) osteological and myological anatomy, which enables us to understand the mechanics of movement and provides with a series of important characters to support phylogenetic hypotheses; b) the anatomy of the syrinx, which is important for the characterization of morphological patterns of various bird groups; c) research on the fossil avifauna of South America. The taxa studied in all these projects belong mainly to the following orders: Tinamiformes, Ciconiiformes, Falconiformes, Galliformes, Opisthocomiformes, Gruiformes, Psittaciformes, Cuculiformes, Strigiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes (i.e., Furnariidae and Dendrocolaptidae). *Accepted 9 December 2003.*

Key words: Anatomy, systematics, Brazil, phylogenetic hypotheses, fossil birds.

In Latin America there are relatively few avian anatomists. In Brazil, I have the privilege of belonging to this select group, together with my current and former students of the last two decades. We worked mainly with extant birds, but more recently we included some fossil taxa. In Argentina, avian anatomists are represented mainly by paleontologists with at least five active researchers working on fossil birds.

HISTORIC OVERVIEW OF AVIAN MORPHOLOGY

One cannot talk about anatomical studies without acknowledging the pioneer contributions made in this area especially during the second half of the 19th century, which was an extremely important and fertile period for bird anatomy. At that time, classical studies were produced e.g., by Blanchard (1859), Garrod (1873a, 1873b, 1874), Fürbringer (1888), Seebohm (1888, 1895), Gadow (1889, 1892), and Beddard (1898). The first proposals for avian classifications were established by grouping birds based on total similiarities within a precladistic philosophy. The classical work of Beddard (1898), entitled "The structure and classification of birds", assumed an important role in ornithology, not only because of the quality of anatomical descriptions, but also because of its taxonomic scope.

Stresemann (1959) considered that the relationships among the large groups of birds were so well established that any newly discovered species could simply be assigned to one of these groups. This statement contributed to the belief, which has predominated in ornithology until very recently, that little remains to be done in bird anatomy and systematics. Partly as a consequence of this view, suprageneric systematics advanced only slowly during a time in which birds were considered a morphologically uniform group of vertebrates.

Whereas the ecology, behavior and reproductive biology of birds received increasing attention, particularly during the second half of the 20th century, the anatomy of birds was neglected and little effort was made to absorb modern concepts of comparative biology therein. Perhaps this was partly because ornithology began to adopt the concepts of phylogenetic reconstruction, notably the cladistic approach, only relatively late among zoological disciplines. In addition, the power of the evolutionary school in ornithology is seen in the frequent use of trinomials (i.e., subspecies). This concept was much used by ornithologists, despite its conceptual inconsistencies (de Pinna 1999), and Cracraft (1974, 1981, 1988) was the one who pioneered the use of cladistic methods in ornithology.

Birds are frequently considered to be a morphologically homogeneous group, at least in comparison to other vertebrates. Nevertheless, this homogeneity is only relative and should not be considered as an impediment of attempts to identify characters with phylogenetic information. On the contrary, we should increase research in this area, and several studies show that morphological characters exist and are informative (Livezey & Zusi 2001).

With the advance of molecular biology since 1990, a new discipline started in ornithology. Several molecular studies have provided new phylogenetic hypotheses for avian taxa. Works based on molecular data have assumed a dominant role in systematics due to the large amount of information derived from DNA, and due to technical advances in the extraction, sequencing, and analysis of the DNA molecule. However, the large amount of base-pair does not necessarily represent data that contain phylogenetic information. Thus, analyses of molecular data should be integrated together with anatomical and other source of taxonomic data. A coherent matrix of such data may help to eliminate the noise generated by enormous quantities of molecular data, thereby permitting more trustworthy phylogenetic hypotheses using the total evidence of characters (e.g., Kluge 1989).

NEOTROPICAL BIRDS

François Vuilleumier (2003) published an important review entitled "Neotropical Ornithology: then and now". The reading of this paper is recommended for anyone who wants to learn something about the historical development of our knowledge of Neotropical birds, and to receive suggestions for future studies. Vuilleumier (2003) particularly emphasizes the fundamental role of systematics in ornithology, and, in this context, I would like to stress that anatomy is a basic tool for such studies. Livezey & Zusi (2001) have noted that there is a large amount of under-utilized anatomical information at our disposal in the literature, which implies that a potentially important source of characters with phylogenetic information has been neglected for decades and should be reclaimed.

Various researchers (e.g., Olson 1983, Raikow & Cracraft 1983, Burton 1984, Prum 1988, Cracraft & Prum 1988) have used Neotropical avian taxa in their surveys, thus enriching the base for systematics and evolutionary studies of birds. But anatomy also has an important role in clarifying our understanding of the function of structures, in the area of biomechanics and functional anatomy, which applies the principles of classical mechanics to living animals, including birds.

In Latin America, few people have dedicated themselves to anatomical studies, although there has been considerable development in ornithology in other areas, such as ecology, behavior, reproductive biology, migration, molecular biology and conservation. In Brazil, over the last two decades, anatomical studies focusing mainly on the Neotropical avifauna have been carried out by two research groups: one at the Universidade Federal de Minas Gerais in Belo Horizonte led by Gérman A. B. Mahecha, and the other group at the Universidade de São Paulo. The first group has worked mainly on the reproductive apparatus of the Tinamidae as well as on other anatomical aspects, including histopathology (Oliveira & Mahecha 1996, Mahecha & Oliveira 1998, Oliveira & Mahecha 2000, Mahecha & Oliveira 2001, Mahecha *et al.* 2002). The other group began studies in the early 1980s and has investigated the following topics: (1) osteological and myological anatomy, which enables us to understand the mechanics of movement and provides a series of important characters to test phylogenetic hypotheses; (2) anatomy of the syrinx, which enables the characterization of morphological patterns for various bird groups, even in spite of a low resolving power at the species level; (3) research on the fossil birds of South America.

Comparative anatomy and systematics. Our descriptive osteological and myological study of the skull and jaw apparatus of toucans, including the aponeuroses of each muscular band (Höfling & Gasc 1984a), formed the basis for the kinetic analysis of the skull in this group (Höfling & Gasc 1984b). In species of the genus *Ramphastos*, there is a sheet of connective tissue that is continuous with the postorbital ligament. Burton (1984), in contrast, concluded that there is no postorbital ligament in the Ramphastidae. However, although this is true for species of other ramphastid genera, it is not the case with *Ramphastos*, which does have such a ligament. This example highlights the dangers of generalizing characters for all members of a family. We can consider the presence of the postorbital ligament as an important mechanical trait for the larger species, and as a diagnostic character for the genus *Ramphastos*.

Several groups of Neotropical birds have been studied for cranial and myological characteristics that may be used to interpret systematic relationships. These groups are the following: Galbulidae (Donatelli 1992), Picidae (Donatelli 1996), Opisthocomidae (Marceliano 1996), Psophiidae (Donatelli *et al.* 1997), Dendrocolaptidae (Donatelli 1997), Cuculidae (Posso 1999, Posso & Donatelli 2001), Bucconidae (Alvarenga *et al.* 2002 Ladeira & Höfling in press), Momotidae (Pascotto & Donatelli 2003), Cracidae (Silveira 2003, Silveira & Höfling 2003), Tinamidae (Silveira & Höfling in press), and Alcedinidae (Mendez & Höfling in press).

Silveira & Höfling (2003) analyzed the complete skeletons of 44 out of 50 recognized species of Cracidae and of 25 species from 14 genera as the outgroup. On the basis of this analysis, they established the validity of 151 characters. A phylogenetic analysis generated a very robust cladogram that showed: (a) the existence of two subfamilies, the Cracinae and the Penelopinae, which supports the original classification by Huxley (1868); (b) the subfamily Cracinae is composed of the genera *Nothocrax*, *Pauxi*, and *Crax*, whereas the genera *Oreophasis, Penelopina*, *Aburria*, *Penelope*, *Chamaepetes*, and *Ortalis* belong to the subfamily Penelopinae; (c) there is no support for maintaining the genera *Pipile* Bonaparte, 1856, and *Mitu* Lesson, 1831, but rather the analysis indicates that these genera should be considered synonymous with *Aburria* Reichenbach, 1853, and *Pauxi* Temminck, 1813, respectively, which results in the reduction of the genera from eleven to nine; (d) osteology, in the Cracidae, does not provide characters that can be used unequivocally to define the relationships among species belonging to the same genus. This cladogram based on morphological data is very different from that based on molecular data proposed by Pereira *et al.* (2002). This disagreement indicates the need for further research with a larger sample of characters.

As noted by Zusi (1993), the ontogenetic development of the skull also furnishes important data for identifying homologies, since the adult skeleton alone may offer insufficient data for phylogenetic hypotheses. When there are juveniles available for study, which is rare, such a comparative approach may be productive, as we can see in the Tinamidae (Silveira & Höfling in press).

A comparative study of the morphometric characteristics of the skull (Höfling 1991, 1995), analyzed 33 skull measurements of 19 species of Ramphastidae, and showed that certain measurements, such as the length and caudal width of the skull, have a low coefficient of variation, whereas others, such as the upper maxilla, have a high one. Morphometric analysis of the braincase shows that ramphastid species are very conservative with regard to these measuments. Another aspect observed in a sample of 84 specimens of these 19 species was the intraspecific morphological variation of the fronto-nasal suture.

In general, the skull does not provide significant interspecific anatomical differences. Nevertheless, we were able to validate *Notharchus swainsoni* (Gray, 1846), a puffbird from southeastern Brazil, Paraguay, and northeastern Argentina, by craniological differences in addition to the characteristics of plumage color, size, and geographical distribution (Alvarenga *et al.* 2002). In osteology, the main differences are in the width and shape of the temporal fossae, in the opening between the palatines, and in the thickness and height of the maxillary processes of the nasals.

An osteological study of the shoulder girdle of the Piciformes, Coraciiformes, Passeriformes and other related groups, such as the Trogoniformes, Coliiformes, Apodiformes, Strigiformes and Caprimulgiformes (Höfling & Alvarenga 2001), permitted a re-evaluation of their systematic relationships. A number of observed characters justify the inclusion of the families Indicatoridae, Picidae, Capitonidae, and Ramphastidae in the Piciformes. Furthermore, the characters indicate that (a) the Piciformes and Passeriformes have a monophyletic origin; (b) the Galbuloidea, including the Galbulidae and Bucconidae, should not be placed in the Piciformes because they are closer to the Coraciiformes, both groups possessing a developed procoracoid process; and (c) the Trogonidae and Coraciiformes are not related.

Some undergraduate and graduate students are currently studying the syringeal anatomy for phylogenetic purposes, although it is necessary to use a large series of specimens, because this organ presents enormous intraspecific variation. The first study, dealing with 25 species (105 specimens) of New World parrots (Gaban-Lima 2001, Gaban-Lima & Höfling 2002), showed that we can identify three patterns of variation in the syringeal anatomy of Arini: chaotic intraspecific variation, intraspecific variation with a discernible pattern among taxa, and interspecific variation (fixed characters). However, in the genus *Xiphorhynchus* (Raposo 2001), as in some dendrocolaptid genera (Raposo *et al.* in prep.), the syringeal anatomy does not help in species characterization.

Biomechanics and functional anatomy. With regard to functional anatomy, the cranial kinesis and the locomotion of Neotropical birds have been studied. Höfling & Gasc (1984b) discussed several aspects of such functional analyses in the genus *Ramphastos.* With the particular specimens studied and the particular type of analysis employed at that time we could not verify the prokinesis of the skull. Subsequently, with additional specimens and different analytical techniques (Höfling & Gasc 1994), it was possible to verify, that depending on the extent of the mandibular depression (between 22° and 25.8°), the upper jaw is elevated relative to the braincase between 5.5° and 6.7° in *Ramphastos toco* and 3.8° in *R. vitellinus*, but that such a movement is practically absent in *R. dicolorus.*

Currently, we are working on the terrestrial locomotion of Neotropical birds based on film analyses of Tinamidae and Cariamidae (Abourachid *et al.* 2003), comparing walking kinematic parameters between paleognathous and neognathous birds.

South American fossil birds. A knowledge of anatomy is a fundamental tool for fossil bird studies, and we can deduce several characteristics for an individual that lived some millions of years ago from one or a few fossilized bones. For example, the first bird from the Tertiary of Chile, *Meganhinga chilensis*, was a large and probably flightless anhinga, whose holotype was designated by its tarsometatarsus, even though there were several other bones from at least two individuals available (Alvarenga 1995). The South American, in particular Brazilian, fossil birds were reviewed by Alvarenga & Höfling (2000), but several additional South American fossil birds have been described since that publication (Olson & Alvarenga 2002, Alvarenga & Guilherme 2003, Alvarenga & Olson 2004).

The systematic revision of the Phorusrhacidae (Alvarenga & Höfling 2003) is an example of such studies. Throughout the Tertiary, South America was inhabited by these ralliform birds. The Phorusrhacidae are amongst the largest birds that have ever existed, and *Brontornis burmeisteri* is the largest phorusrhacid and the largest known bird of the American continent, reaching more than 250 cm in height and weighing more than 400 kg. The limited number of known specimens of *Brontornis burmeisteri* does not allow for more precise calculations. The skeleton of the only known specimen of *Paraphysornis brasiliensis* Alvarenga, 1982, was re-constructed and considered to have been around 240cm high. The femora and tibiotarsi of this bird have much larger diameters and circumferences than those of a large male specimen of an ostrich (*Struthio camelus*) with a live body-mass of 130 kg. This indicates that the weight of *Paraphysornis brasiliensis* may have been around 180 kg. The smallest phorusrhacid, *Psilopterus bachmanni*, was had approximately the same height (i.e., about 80 cm) as the present-day Seriema (*Cariama cristata*), and weighed nearly 5 kg.

ANATOMICAL COLLECTIONS

In Latin America, anatomical collections of birds have been neglected as a whole, and there were no criteria or incentives to build some. Skeleton collections were established mainly in those places where paleontologists were working, as the Museo de La Plata in Argentina, and at the Museu de História Natural de Taubaté in Brazil. Alvarenga (1992) has drawn attention to the role of osteological collections for Brazilian ornithology. Few institutions in South America possess a representative anatomical collection. The Museu Paraense Emilio Goeldi (MPEG) has a good anatomical collection of Amazonian species preserved in alcohol (around 8400 specimens) and also a skeleton collection composed mainly of skulls (around 4000 specimens). In the Museu Nacional do Rio de Janeiro (MNRJ), there is a small anatomical collection with few prepared skeletons. Around a thousand of anatomical specimens (some 400 skeletons and 600 specimens in alcohol) are available at the Museu de Zoologia da Universidade de São Paulo (MZUSP). The Departamento de Zoologia do Instituto de Biociências da Universidade de São Paulo (AZ) has a very specific collection linked to our anatomical research (around 200 skeletons and 550 specimens in alcohol). The Museu de História Natural de Taubaté (MHNT) has the most representative and well prepared collection of skeletons (about 2000) and fossil birds. In Argentina, at the Museo de La Plata, there are two skeleton collections (about 350). The Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" has approximately 200 skeletons, and the Centro de Investigationes Cientificas y Transferencia de Tecnología a la Producción, in Diamante, has about 100 skeletons.

As Zusi (1993) suggested, advances in anatomical research will ultimately depend on the availability of anatomical specimens. Worldwide inventories of anatomical specimens make it possible to be selective and efficient in developing our collections for the maximum benefit to science (Zusi *et al.* 1982, Wood & Schnell 1986). The prospects for anatomical research on Neotropical birds are very promising.

We have a dream: to see anatomical studies established and diffused in Latin America equal to the other areas of ornithology. Unfortunately, some ornithologists have not yet recognized the fundamental value of anatomy for ornithological systematics and phylogenetic hypotheses, as well as for understanding the evolution of present and past avifauna of the Neotropical region.

ACKNOWLEDGMENTS

I dedicate this article to my former and current students who are spreading anatomical research to various Brazilian institutions and universities. They believe that bird anatomy is a rich discipline with interesting problems to be studied, and with many questions to be answered. I thank H. M. F. Alvarenga, L. F. Silveira, P. Gibbs and D. Homberger for critical reading of the manuscript. I also thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for financing much of our research.

REFERENCES

Abourachid, A., E. Höfling, & S. Renous 2003. Walking kinematics parameters: comparison between paleognathous and neognathous birds. Pp. 157 *in* Programme and book of abstracts, VII Neotropical Ornithological Congress, Neotropical Ornithological Society & Unión de Ornitologos de Chile, Termas de Puyehue, Chile.

Alvarenga, H. M. F. 1992. Coleções osteológicas e perspectivas da ornitologia no Brasil. Bol. Mus. Para. Emilio Goeldi 8: 247–257.

Alvarenga, H. M. F. 1995. A large and probably flightless anhinga from the Miocene of Chile. Cour. Forschungsinst. Senckenb. 181: 149–161.

Alvarenga, H. M. F., & E. Guilherme. 2003. The anhingas (Aves: Anhingidae) from the upper Tertiary (Miocene-Pliocene) of southwestern Amazonia. J. Vertebr. Paleontol. 23: 614–621.

Alvarenga, H. M. F., & E. Höfling. 2000. Aves. Pp. 579–593 *in* Carvalho, I de S. (ed.). Paleontologia. Ed. Interciência, Rio de Janeiro, Brazil.

Alvarenga, H. M. F., & E. Höfling. 2003. Systematic revision of the Phorushacidae (Aves: Ralliformes). Pap. Avulsos Zool. (São Paulo) 43: 55–91.

Alvarenga, H. M. F., E. Höfling, & L. F. Silveira. 2002. *Notharchus swainsoni* (Gray, 1846) Bucconidae é uma espécie válida. Ararajuba 10: 73–77.

Alvarenga, H. M. F., & S. Olson. 2004. A new genus of tiny condor from the Pleistocene of Brazil (Aves: Vulturidae). Proc. Biol. Soc. Wash. 117: 1–9.

Beddard, F. E. 1898. The structure and classification of birds. Longmans, Green and Co., London, UK.

Blanchard, C. E. 1859. Recherches sur les caractères ostéologiques des oiseaux, appliquées à la classification naturelle de ces animaux. Ann. Sci. Nat. 11: 1–141.

Burton, P. J. K. 1984. Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. Bull. Br. Mus. (Nat. Hist.) Zool. 47: 331–443.

Cracraft, J. 1974. Phylogeny and evolution of the ratite birds. Ibis 116: 494–521.

Cracraft, J. 1981. Toward a phylogenetic classification of the recent birds of the world (class Aves). Auk 98: 681–714.

Cracraft, J. 1988. The major clades of birds. Pp. 339–361 *in* Benton, M. J. (ed.). The phylogeny and classification of the tetrapods. Volume 1. Clarendon Press, Oxford, UK.

Cracraft, J., & R. O. Prum. 1988. Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. Evolution 43: 603–620.

Donatelli, R. J. 1992. Cranial osteology and myology of the jaw apparatus in the Galbulidae. Arq. Zool. (São Paulo) 32: 1–32.

Donatelli, R. J. 1996. The jaw apparatus of the Neotropical and Afrotropical woodpeckers (Aves: Piciformes). Arq. Zool. (São Paulo) 33: 1–70.

Donatelli, R. J. 1997. Osteologia e miologia cranianas de Dendrocolaptidae (Passeriformes, Tyranni). Gêneros *Glyphorynchus*, *Campylorhamphus*, *Dendrocincla*, *Xiphorhynchus* e *Dendrocolaptes*. Ararajuba 5: 19–37.

Donatelli, R. J., M. L. V. Marceliano, E. Höfling, & S. R. Posso. 1997. Osteologia e miologia cranianas de Psophiidae (Aves; Gruiformes). Bol. Mus. Para. Emílio Goeldi Ser. Zool. 13: 39–76.

Fürbringer, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz – und Bewegungsorgane. 2 v. J. Van Holkema, Amsterdam, Netherlands.

Gaban-Lima, R. 2001. Anatomia comparada da siringe da tribo Arini (Aves: Psittacidae). Dissertação de Mestrado, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil. 137 p.

Gaban-Lima, R., & E. Höfling. 2002. Comparative anatomy of the syrinx in Arine parrots (Psittacidae: Arini). Pp. 224 *in* Abstract volume. 23rd. International Ornithological Congress, Beijing, China.

Gadow, H. 1889. On the taxonomic value of the intestinal convolutions in birds. Proc. Zool. Soc. Lond. 1889: 303–316.

Gadow, H. 1892. On the classification of birds.

Proc. Zool. Soc. Lond. 1892: 229–256.

Garrod, A. H. 1873a. On the value in classification of a peculiarity in the anterior margin of the nasal bones of certain birds. Proc. Zool. Soc. Lond. 1873: 33–38.

Garrod, A. H. 1873b. On certain muscles of the thigh of birds and on their value in classification. Part I. Proc. Zool. Soc. Lond. 1873: 626–644.

Garrod, A. H. 1874. On certain muscles of birds and on their value in classification. Part II. Proc. Zool. Soc. Lond. 1874: 111–124.

Höfling, E. 1991. Etude comparative du crâne chez des Ramphastidae (Aves, Piciformes). Bonn. Zool. Beitr. 42: 55–65.

Höfling, E. 1995. Anatomia do crânio e da cintura escapular dos Ramphastidae (Aves: Piciformes) e de alguns grupos próximos, com implicações sistemáticas. Tese de Livre-docência, Instituto de Biociências, Univ. de São Paulo, São Paulo, Brazil.

Höfling, E., & H. M. F. Alvarenga. 2001. Osteology of the shoulder girdle in Piciformes, Passeriformes and related groups of birds. Zool. Anz. 240: 196–208.

Höfling, E., & J.-P. Gasc. 1984a. Biomécanique du crâne et du bec chez *Ramphastos* (Ramphastidae, Aves). I Description des éléments anatomiques. Gegenbaurs Morphol. Jahrb. 130: 125–147.

Höfling, E., & J.-P. Gasc. 1984b. Biomécanique du crâne et du bec chez *Ramphastos* (Ramphastidae, Aves). II Analyses des conditions du mouvement du bec. Gegenbaurs Morphol. Jahrb. 130: 235–262.

Höfling, E., & J.-P. Gasc. 1994. Cranial kinesis in Ramphastidae (Piciformes). J. Ornithol. 135 (suppl): 52.

Huxley, T. H. 1868. On the classification of and distribution of the Alectoromorphae and Heteromorphae. Proc. Zool. Soc. Lond. 1868: 294–318.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 30: 351–370.

Ladeira, L. M. E., & E. Höfling in press. Osteologia craniana de Bucconidae. Bol. Mus. Para. Emílio Goeldi, Ser. Zool..

Livezey, B. C, & R. L. Zusi. 2001. Higher-order phylogenetics of modern aves based on comparative anatomy. Neth. J. Zool. 51: 179–205.

Mahecha, G. A. B., & C. A. Oliveira. 1998. An additional bone in the sclera of the eyes of owls and the Common Potoo (*Nictybius griseus*) and its role in the contraction of the nictitating membrane. Acta Anat. 163: 201–211.

Mahecha, G. A. B., & C. A.. Oliveira. 2001. Quantitative estimation of intraepithelial plasma cells in the copulatory organ of two tinamous avian species during the breeding and non-breeding seasons. Microsc. Acta 3: 149–151.

Mahecha, G. A. B., C. A. Oliveira, K. Balzuweit, & R. A. Hess. 2002. Epididymal lithiasis in roosters and efferent ductile and testicular damage. Reproduction 124: 821–834.

Marceliano, M. L. V. 1996. Estudo osteológico e miológico do crânio de *Opisthocomus hoazin* (Muller, 1776) (Aves: Opisthocomidae), comparado com algumas espécies de Cracidae, Musophagidae e Cuculidae. Bol. Mus. Para. Emílio Goeldi, Ser. Zool. 12: 95–246.

Mendez, A. C., & E. Höfling in press. Osteologia craniana de Cerylinae (Coraciiformes: Alcedinidae). Bol. Mus. Para. Emílio Goeldi, Ser. Zool.

Oliveira, C. A., & G. A. B. Mahecha. 1996. Cloacal morphology of *Nothura maculosa* (Temminck, 1815) Aves, Tinamiformes. Ann. Anat. 178: 471–476.

Oliveira, C. A., & G. A. B. Mahecha. 2000. Morphology of the copulatory apparatus of the Spotted Tinamou *Nothura maculosa* (Aves, Tinamiformes). Ann. Anat. 182: 161–169.

Olson, S. L. 1983. Evidency for a polyphyletic origin of Piciformes. Auk 100: 126–133.

Olson, S. L., & H. M. F. Alvarenga. 2002. A new genus of small teratorn from the Middle Tertiary of the Taubaté Basin, Brazil (Aves Teratornithidae). Proc. Biol. Soc. Wash. 115: 701–705.

Pascotto, M. C., & R. J. Donatelli. 2003. Cranial osteology in Momotidae (Aves: Coraciiformes). J. Morphol. 258: 32–48.

Pereira, S. L., A. Baker, & A. Wajntal. 2002. Combined nuclear and mitochondrial DNA sequences resolve generic relationships within the Cracidae (Aves, Galliformes). Syst. Biol. 51: 946–958.

Pinna, M. C. C. de. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics 7: 367–394.

Posso, S. R. 1999. Osteologia craniana de Cuculiformes do Novo Mundo, com implicações sistemáticas. Dissertação de Mestrado, Instituto de Biociências, Universidade Estadual Paulista. Botucatu, Brazil..

Posso, S. R., & R. J. Donatelli. 2001. Cranial osteology and systematics implications in Crotophaginae (Aves, Cuculidae). J. Zool. Syst. Evol. Res. 39: 247–256.

Prum, R. O. 1988. Phylogenetic interrelantionships of the barbets (Aves: Capitonidae) and toucans (Aves: Ramphastids) based on morphology with comparisons to DNA-DNA hybridization. Zool. J. Linn. Soc. 92: 313–343.

Raikow, R. J., & J. Cracraft. 1983. Monophyly of Piciformes: a reply to Olson. Auk 100: 134–138.

Raposo, M. A. 2001. Taxonomia, evolução e anatomia da siringe do gênero *Xiphorhynchus* Swainson, 1827 (Aves: Dendrocolaptidae). Tese de Doutorado, Instituto de Biociências, Univ. de São Paulo, São Paulo, Brazil.

Seebohm, H. 1888. An attempt to diagnose the suborders of the great Gallino-Gralline group of birds by the aid of osteological characters alone. Ibis: 415–435.

Seebohm, H. 1895. An attempt to diagnose the suborders of the ancient Ardeino-Anserine assemblage of birds by the aid of osteological characters alone. Ibis: 92–104.

Silveira, L. F. 2003. Filogenia dos Cracidae (Aves: Galliformes), com base em caracteres osteológicos. Tese de Doutorado, Instituto de Biociências, Univ. de São Paulo, São Paulo, Brazil.

Silveira, L. F., & E. Höfling. 1993. The phylogeny of Cracidae (Galliformes) as inferred from the study of osteological characters. Pp. 211 *in* Programme and book of abstracts, VII Neotropical Ornithological Congress, Neotropical Ornithological Society & Unión de Ornitologos de Chile, Termas de Puyehue, Chile.

Silveira, L. F., & E. Höfling in press. Osteologia craniana dos Tinamidae (Aves: Tinamiformes), com implicações sistemáticas. Bol. Mus. Para. Emílio Goeldi, Ser. Zool.

Stresemann, E. 1959. The status of avian systematics and it unsolved problems. Auk 76: 269–280.

Vuilleumier, F. 2003. Neotropical ornithology: then and now. Auk 120: 577–590.

Wood, D. S., & G. D. Schnell. 1986. Revised world inventory of avian skeletal specimens. American Ornithologists' Union and Oklahoma Biological Survey, Norman, Oklahoma.

Zusi, R. L. 1993. Patterns of diversity in the avian skull. Pp. 391–437 *in* Hanken, J., & B. K. Hall (eds.). The skull. Volume 2. Chicago Univ. of Press, Chicago, Illinois.

Zusi, R. L., D. S. Wood, & M. A. Jenkinson. 1982. Remarks on a world-wide inventory of avian anatomical specimens. Auk 99: 740–757.