

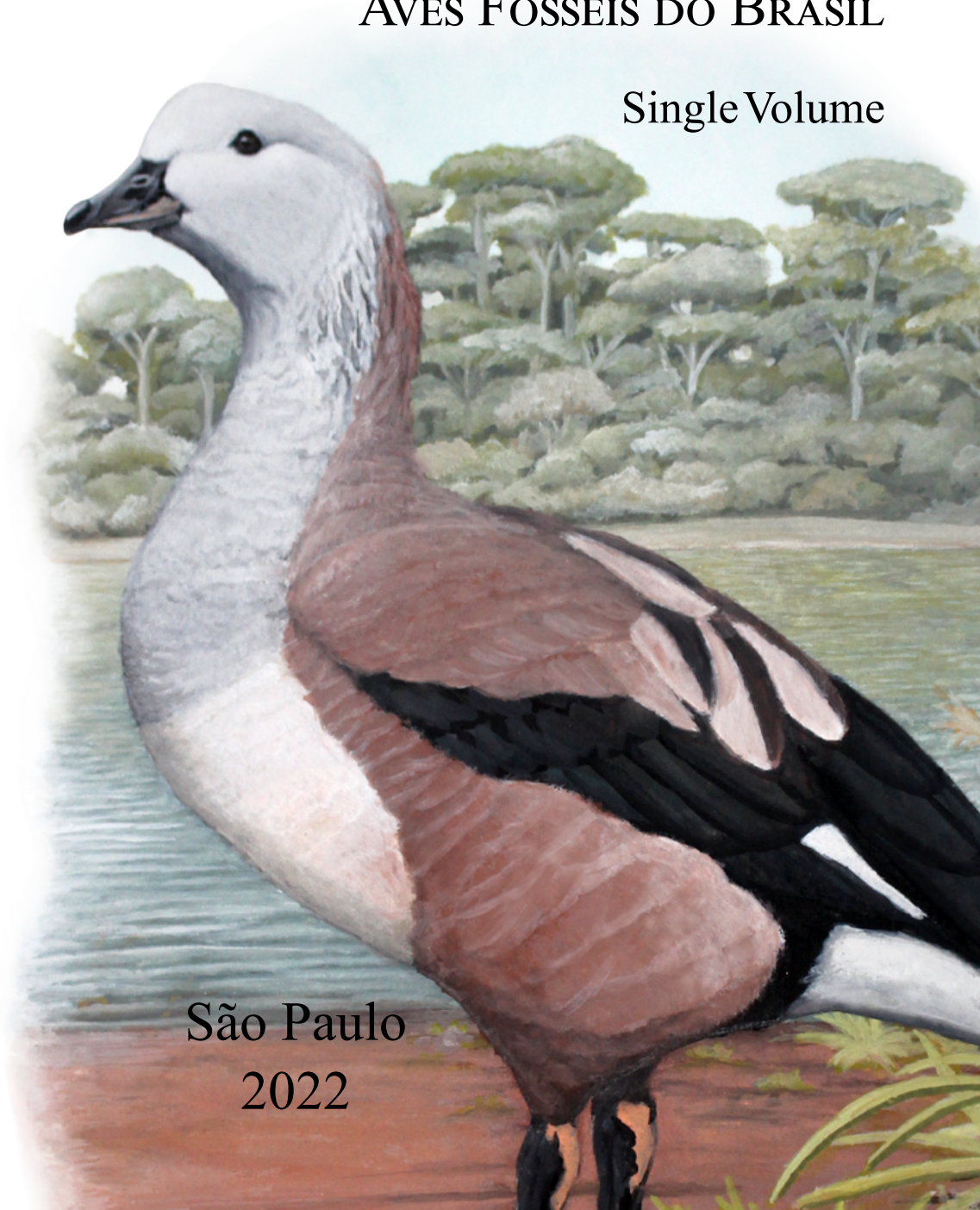


Rafael Silva do Nascimento

# FOSSIL BIRDS *of* BRAZIL

AVES FÓSSEIS DO BRASIL

Single Volume



São Paulo  
2022



**Rafael Silva do Nascimento**

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## **Aves Fósseis do Brasil**

**Single Volume**

**Original Version**

Dissertation submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Master of Science (Systematics, Animal Taxonomy and Biodiversity).

Advisor: Prof. Dr. Luís Fábio Silveira

São Paulo  
2022

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## PROLOGUE

The enigmatic image of a dodo (*Raphus cucullatus*), a bird from the Mauritius Islands that became extinct in historical times, seen in a book during my childhood, cemented my interest on animals that no longer live among us, previously established by unending hours of reading about dinosaurs and other prehistoric creatures. Knowing what circumstances brought these animals to no longer exist, their historical context, where their physical remains and testimonies lie, and with what all of this can help us in retrieving information about these creatures—and what this can aid preventing future extinctions, is a detective's work that fills me with great fascination. In the same mold of the attention and value that humanity usually gives to what is rare. Birds are animals that suffered severely from anthropic actions, particularly the insular species, and countless others, even entire families and orders, were decimated in a relatively short period of time. In Brazil, fortunately, few are the species that are extinct for sure, although many are endangered. The existence of some extinct species in prehistoric times caught my attention, and the equally scarce data available about these long and poorly-explored chapters of the history of these animals immersed me into a fascinating and hidden world that I had no idea existed when I first saw the dodo illustration on that book. It is with the hope of maintaining the memory of these long-gone animals, and to alert of the preservation of the forms that live with us, that this work was made.

## RESUMO

A paleontologia de aves no Brasil é um campo de pesquisa ainda incipiente, a despeito de seu material relativamente abundante. Os vestígios são representados por ossos (fósseis e subfósseis), impressões de penas, ovos, coprólitos e icnofósseis, encontrados em todas as Regiões do país a partir da década de 1830. A revisão e a catalogação do histórico do estudo e de todos esses registros, com atualização de sua nomenclatura taxonômica, incluindo detalhamento do material, sinonímia, dados de deposição e inferências paleobiológicas, são importantes para fornecer um panorama de sua diversidade, além de oferecer subsídios para estudos filogenéticos, taxonômicos e biogeográficos. O levantamento da literatura resultou em 378 registros, representados pelos seguintes grupos: Maniraptora (penas) (70), Aves indet. (23), Columbidae (20), Psittacidae (18), Rallidae (17), Accipitridae (16), Tinamidae (12), Cathartidae (9), Falconidae (9), Passeriformes (9), Strigidae (9), Anhingidae (8), Picidae (8), Anatidae (7), Cracidae (7), Caprimulgidae (6), Ciconiidae (6), Procellariidae (5), Scolopacidae (5), Thamnophilidae (5), Thraupidae (5), Trochilidae (5), Cuculidae (4), Dendrocolaptidae (4), Enantiornithes (4), Icteridae (4), Podicipedidae (4), Tyrannidae (4), Cariamiformes (3), Hirundinidae (3), Laridae (3), Phalacrocoracidae (3), Phorusrhacidae (3), Rheidae (3), Sulidae (3), Ardeidae (2), Bucconidae (2), Charadriidae (2), Diomedidae (2), Formicariidae (2), Furnariidae (2), Momotidae (2), Nyctibiidae (2), Palaeognathae (2), Quercymegapodiidae (2), Ramphastidae (2), Threskiornithidae (2), Troglodytidae (2), Trogonidae (2), Turdidae (2), Vireonidae (2), Alcenididae (1), Anhimidae (1), Apodidae (1), Cardinalidae (1), Cariamidae (1), Corvidae (1), Fregatidae (1), Gracilitarsidae (1), Jacanidae (1), Mimidae (1), Neognathae (1), Odontophoridae (1), Opisthocomidae (1), Ornithuromorpha (1), Palaelodidae (1), Passerellidae (1), Pelagornithidae (1), Phoenicopteridae (1), Spheniscidae (1), Strigiformes (1), Teratornithidae (1) e Tytonidae (1). Dentre esse número, foram descritos 16 gêneros e 21 espécies extintos. A maior parte do material foi encontrada em cavernas calcárias com idade quaternária, quase que exclusivamente representada por neoespécies. No geral, uma grande quantidade de material aguarda análises mais aprofundadas, incluindo elementos não diagnósticos, não acessíveis ou podendo representar neoespécies no caso de material mais recente.

**Palavras-chave:** Ornitologia. Paleontologia. Arqueologia. História da ciência. América do Sul.



## ABSTRACT

Avian paleontology in Brazil is a research field still in its early stages despite its relatively abundant material. The remains are represented by bones, feather impressions, eggs, coprolites, and ichnofossils found in all Regions of Brazil starting in the 1830s. Reviewing and cataloging the history of studies and all records, with updates of their taxonomic nomenclature, including detailed material, synonyms, data on deposition, and paleobiological inference, are important to provide an overview of their diversity and offer subsidies for phylogenetic, taxonomic, and biogeographic studies. The literature survey resulted in 378 records represented by the following groups (number of taxa in brackets) Maniraptora (penas) (70), Aves indet. (23), Columbidae (20), Psittacidae (18), Rallidae (17), Accipitridae (16), Tinamidae (12), Cathartidae (9), Falconidae (9), Passeriformes (9), Strigidae (9), Anhingidae (8), Picidae (8), Anatidae (7), Cracidae (7), Caprimulgidae (6), Ciconiidae (6), Procellaridae (5), Scolopacidae (5), Thamnophilidae (5), Thraupidae (5), Trochilidae (5), Cuculidae (4), Dendrocolaptidae (4), Enantiornithes (4), Icteridae (4), Podicipedidae (4), Tyrannidae (4), Cariamiformes (3), Hirundinidae (3), Laridae (3), Phalacrocoracidae (3), Phorusrhacidae (3), Rheidae (3), Sulidae (3), Ardeidae (2), Bucconidae (2), Charadriidae (2), Diomedidae (2), Formicariidae (2), Furnariidae (2), Momotidae (2), Nyctibiidae (2), Palaeognathae (2), Quercymegapodiidae (2), Ramphastidae (2), Threskiornithidae (2), Troglodytidae (2), Trogonidae (2), Turdidae (2), Vireonidae (2), Alcenidae (1), Anhimidae (1), Apodidae (1), Cardinalidae (1), Cariamidae (1), Corvidae (1), Fregatidae (1), Gracilitarsidae (1), Jacanidae (1), Mimidae (1), Neognathae (1), Odontophoridae (1), Opisthocomidae (1), Ornithuromorpha (1), Palaelodidae (1), Passerellidae (1), Pelagornithidae (1), Phoenicopteridae (1), Spheniscidae (1), Strigiformes (1), Teratornithidae (1), and Tytonidae (1). Among these, 16 extinct genera and 21 extinct species were described. Most of the material was found in limestone caves of quaternary age and represents almost exclusively neospecies. In general, a large quantity of material awaits deeper analyses, including elements that are non-diagnostic, non-accessible or that may represent neospecies in the case of more recent material.

**Keywords:** Ornithology. Paleontology. Archeology. History of science. South America.

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## 1. INTRODUCTION

Brazil currently has 1,971 recognized bird species (Pacheco *et al.* 2021), being the country with the most expressive diversity in the world. This diversity corresponds to the geological moment between the Holocene and the Anthropocene and represents a very small fraction of the time of existence of birds. In a country of continental dimensions such as Brazil, it is reasonable to assume that the number of species that existed overtime in its territory is equally significant, comprising an enormous diversity of shapes, sizes, colors, and habits that, even in a fortunate situation, will have only a relatively small portion known from the fossil record.

While the living species in Brazil are particularly well studied (Sick 1997), knowledge on their prehistoric representatives has been progressing slowly, especially when compared to countries like Germany, China, the United States, and Argentina, the last of which holds the most complete and diverse record in South America. The fossil record of birds is notably biased, especially when compared to mammals, due to the fragile nature of their bones (Agnolin 2016b). In addition, the small number of specialized researchers working in the field and the lack of osteological collections hinder, among other factors, the development of both paleornithology and systematics in Brazil (Alvarenga 1992). Despite this, in the last decades, we witnessed 21 extinct species being formally described from paleontological sites across the country, with the oldest records dating back to the early Cretaceous (Winge 1887; Ameghino 1891; Alvarenga 1982; 1983; 1985a; 1985b; 1988; 1990; 1995; 1999; Baird & Vickers-Rich 1997; Olson & Alvarenga 2002; Alvarenga & Guilherme 2003; Alvarenga & Olson 2004; Alvarenga *et al.* 2008; Faure *et al.* 2010; Mayr *et al.* 2011a; Mayr *et al.* 2011b; Carvalho *et al.* 2015; 2021). Material of Quaternary age was found in considerable number, such as the records from Bahia (e.g., Penido *et al.* 2012), Piauí (e.g., Guérin *et al.* 1996), and Minas Gerais (e.g., Souza Cunha & Guimarães 1978), but relatively little has been published on it.

The avian remains found in the country are represented by bones, feathers, mummified specimens, eggs, coprolites, pellets, and alleged tracks (e.g., Castro *et al.* 1988; Alvarenga 1997; Figuti 2005; Lopes *et al.* 2011; Marsola *et al.* 2014) and are housed in museums or private collections in Brazil, Denmark, the United States,

England, France, Germany, and Japan (e.g., Reinhardt 1881; Winge 1887; Ameghino 1891; Olson 1981; Alvarenga 1982; Naish *et al.* 2007). In addition, rock paintings made by the ancient human inhabitants of the territory also testify to their presence (Sick 1997).

Published studies are focused almost entirely on taxonomy (Taranto 2012: 24). Most of the Brazilian material determined so far belongs to extant species, and yet its attribution to specific taxa cannot be accepted without a doubt (Olson 1985). Rarely have older studies been considered in more recent ones, and several mentions are limited to lists of taxa without specifying the state and nature of the material. Some studies are even overlooked due to being published in volumes focused on other areas of prehistory's knowledge.

The lack of comparative material is a significant hindrance to the determination of the fossils, becoming even more critical when treating materials from older geological periods. Referring to younger material from caves, Sales (2003: 212) noted that, besides the rare preservation of bird remains in these environments, which disappear before the calcification process, this material's location is also compromised by the lack of knowledge and records of Brazilian caves, added to the scarcity of biologists and speleologists working in this line of research. In Brazil, there is virtually no specialist dedicated exclusively to the study of fossil birds, a scenario prompted by several factors that include nationally generalized poor valorization of science to possibly the idea that birds do not fossilize well and, therefore, there are no materials of this group to be studied intending a full-time dedication. There are several mentions of bird material, generally regarded as indeterminate or referred to as neospecies, in conference abstracts by undergraduate students, and, in rare exceptions, this line of research is carried on in their careers. Most of the recent bird material described in full articles is done by researchers who also cover other groups (generally vertebrates) in their publications.

Therefore, it is necessary to organize this fragmented information on Brazilian paleornithology and start new studies to expand its components. Besides broadening the understanding of the taxonomic diversity and the evolution of birds, such knowledge is an essential source of paleobiogeographic and paleoenvironmental information

(Alvarenga & Höfling 2000: 590). Furthermore, it may assist in future strategies for managing living species (Dietl & Flessa 2011).

## **2. OBJECTIVES**

Based on the above, this study aims to:

1) Conduct a critical review of the history of paleornithological studies in Brazil, from the first mentions available in the literature to the most recent activities. The events will be contextualized within the history of science and the country, introducing the geological settings of the most important fossiliferous sites with maps. Highlights will be given to individuals with more significant contributions, with illustrations and historical photographs. The structuring of the historical review will follow a chronological model of phases established in this study, divided, at first, in the periods of the region of Lagoa Santa (c. 1835–1881), the Tremembé Formation (c. 1915–2011), the São José de Itaboraí Basin (c. 1948–2011), the Solimões Formation (c. 1989–2003), the Crato Formation (c. 1988–2021), and the Bauru Group (c. 2005–2021). Further noteworthy sites will also be briefly discussed.

2) Catalog the fossil and subfossil records of Brazilian birds present in the literature. The records in this catalog will be organized by taxonomy (orders and families following the classification adopted by Pacheco *et al.* [2021]). Their disposition of records within these categories will follow the date of their publication, to maintain the historical context. Each record will have information about its synonymy, discovery process (e.g., locality, age, discoverer, descriptor), material content (e.g., known elements, holotypes and paratypes, state of preservation, housing institution, institutional identification), implications for diversity, ecology, evolution, classification, temporal and spatial distribution, photographs of the material when available, and type locality and etymology for newly named paleospecies.

3) Update the nomenclature given to the fossil materials, according to the literature. Materials of very dubious attribution in the literature will have their generic or specific attribution revoked, given the impossibility of examination in hand.



4) Include unpublished material present in collections of Brazilian institutions, with their information on provenance, historical context, and institutional and taxonomic identification, when available.

5) The availability of information originally published in Danish (such as the studies of Peter Wilhelm Lund, Oluf Winge, and Johannes Reinhardt, pioneers in paleornithology in Brazil) also aims to solve a historical problem already mentioned by the Danish zoologist Theodor Mortensen (1925: 517) when he commented on Herluf Winge's work: the lack of recognition and reach of ideas when not published in a universal language that, when they finally reach researchers from other parts of the world, are often either ignored or misinterpreted because of this language barrier, causing significant damage to science and also to the author's recognition.

### **3. JUSTIFICATION**

Reviewing and cataloging works is essential given the dispersion of knowledge about Brazilian paleornithology, where a picture of its history and the diversity of known taxa are absent, and of South America's in general, of which the bird fossil record is notably biased (Agnolin 2016b). The published historical approaches are, as already mentioned, incomplete. The absence of a panorama of this diversity impacts the studies at the national and global levels, mainly concerning biogeographic and evolutionary issues (e.g., the relationship between the avifaunas of the early Paleogene of South America and Europe [Mourer-Chauviré 1999]).

The inexistence of an updated and comprehensive catalog of records and species known from fossil and subfossil material is a significant impediment to this area's progress in the country, the knowledge of these bird's taxonomic and distributive diversity over time, the type of material preserved, their paleoecology, and to the state of knowledge of the national paleontological heritage in general. This also affects the understanding of the fossil history of birds for South America in general, on which there is little that is informative in its fragmentary information (Agnolin 2016b).

The published Brazilian material was mentioned, never in its entirety, in the lists of Lambrecht (1933), Brodkorb (1963; 1964; 1967; 1971; 1978), Mones (1986), and Cuello (1988). The absence of an updated listing of these records is in line with the

global paleornithological scenario, with the final part of Brodkorb's work being the last global listing to be published so far. The lists of Mones (1986) and Cuello (1988), the most recent, are in short reproductions of secondary mentions. It is coupled with the fact that much of the published data is obscure, and its citation indirectly increases the possibility of disseminating misinformation.

The gathering of data and the inclusion of unpublished information will serve as a basis for further studies and in-depth reviews of the material already published, offering new perspectives on the knowledge of these birds and the environments with which they are associated.

#### **4. MATERIALS AND METHODS**

This study consists of a review of bibliographic and documentary material and the inclusion of some unpublished information on fossil material.

During the bibliographic review, both specialized technical publications and popular texts were consulted, the latter mainly to obtain historical material from any date, as long as they offer reliable and relevant information. In addition, previously unpublished documentary material will also be consulted. Finally, figures of fossils of historical significance that were only mentioned in the literature or figured through images without good resolution were included. Undergraduate theses are not included in this review.

Great efforts were made to cover as much as possible of the literature regarding the fossil and subfossil remains of birds discovered in Brazilian territory. However, since subfossils are more obscurely mentioned in the literature, there is a greater chance that some records are not included here.

In-depth information about taphonomic processes regarding the treated localities should be consulted in the cited bibliography and references therein. Site names follow the original publications, with updated Portuguese spelling when necessary.

Additionally, there is an unaccounted amount of unpublished remains waiting to be studied in several Brazilian museums (and even outside the country), and these, naturally, are not included in this study.

All direct quotations are translated into English.

A basic avian skeletal scheme is presented in Fig. 1.

The BP abbreviation stands for “before present”.

Tables and figures are in the end of this document.

#### **4. 1. Institutional abbreviations**

The institutional abbreviations present in this study are summarized in Table 1, including historical denominations. Non-recurrent abbreviations are explained in their respective texts.

### **5. HISTORY**

The history of bird fossil research in Brazil was never explored in detail, being partially summarized by a few authors over time. We can divide the work done in this line into two main parts, conducted by Danish and Brazilian researchers, respectively, though its timeline is not continuous, as, for example, the first half of the twentieth century saw just a handful of studies published. In some scenarios (i.e., in Lagoa Santa and Taubaté and Bauru Basins), the paleornithological finds are associated mostly with the action of individuals, while others were the result of decentralized combined efforts. The most important events are summarized in Table 2.

In Denmark, Reinhardt (1881) commented on the fossil bird material gathered in the Lagoa Santa region by his fellow countryman, the naturalist Peter Wilhelm Lund, and on other authors’ related publications. While describing the collection gathered by Lund, Winge (1887) included a summary of what was published on the subject until then.

In Brazil, an extract of Winge’s study was published and commented in Portuguese by Padberg Drenkpol (1931), dealing with the paleontology of parrots. The compilation of Lund’s translated theses by Paula Couto (1950) included mentions of the bird material with comments. Valle & Carnevalli (1973) mentioned Lund’s research on fossil birds and his study on the relationship of barn owls with the formation of small

bone heaps in caves. Ruschi (1979) also summarized the finds, including mentions of zooarcheological material. Sick (1984a: 64, 65) briefly cited the Paleogene finds from Rio de Janeiro and São Paulo, and Lund's and Winge's research (Sick 1984a: 111; 1993: 34; 1997: 53), as well as subfossils and rock paintings depicting birds, mentioning the occurrence of some fossil representatives in the texts in which he addressed the families. He further noted that Pierce Brodkorb provided most paleontological data, and, perhaps because of this, his coverage of Winge's work is sparse, although he mentioned having a translated version of it. Alvarenga (1993; 1997) briefly mentioned the earliest finds, focusing on the material found in the country's Southeast Region, on which he was working. Alvarenga & Höfling (2001; 2004; 2011) highlighted most of the extinct taxa in their reviews of avian paleontology. Taranto *et al.* (2009) and Taranto (2012) briefly mentioned the extinct species, and Stefano *et al.* (2012) commented on the bird collections gathered by Lund, both living and fossil, although somewhat inconsistently, at times not specifying the nature of the mentioned material. Finally, the author of the present work has contributed with a thorough review of the history of the fossil material found by Lund and other researchers in the Lagoa Santa region (Nascimento & Silveira 2020) and an abstract of the present study (Nascimento & Silveira 2021).

The country's record of extinct fossil species was further mentioned, in various degrees, in general reviews of South American fossil birds such as Tambussi & Noriega (1996), Mayr (2009; 2016), Tambussi & Degrange (2013), and Agnolin (2016b).

As chronologically as possible, the following sections explore the history of the most important fossil-bearing areas with bird remains in Brazil. Information was gathered concerning the sites' geological aspects and their exploration's history, emphasizing the discovery of bird material, paleoenvironmental aspects and associated fossil taxa.

## **5. 1. Lagoa Santa Karst (MG)**

### **5. 1. 1. General information**

Being an object of study since the early nineteenth century, the Lagoa Santa region (Fig. 2.9), in the state of Minas Gerais, is the best-known and most researched karstic

landscape in Brazil, having been one of the first places to be the object of systematic paleontological and archeological research in the country. It is about 30 km north of Belo Horizonte and encompasses nine municipalities, in total or part, in the São Francisco sedimentary basin, where the rocks of the Bambuí Group are deposited. It bears the highest density of caves in Brazil, with nearly 1,400 known, many of which provided a wealth of paleontological and archeological material. The fossils findings, with age ranging from the middle Pleistocene to the early Holocene (360,000–9,100 years BP), along with the archeological material, sparked a wide range of interdisciplinary scientific studies, from physical to biological and socio-cultural fields, being especially important to the question regarding the antiquity of human occupation in the Americas. Albeit being unique in some respects, this karst shares similarities with other sites in limestone areas throughout the states of Minas Gerais, Bahia, and Goiás (Auler 2020a; Auler 2020b; Galvão & Peñaranda 2020).

Although the proximity to Belo Horizonte (the new state capital established in 1897) made it easily accessible to generations of researchers, it also brought a wide array of threats to the karst's integrity, some already present since colonial times. The marked increase of human occupation in the last several decades, along with mining and industrial processing, results in degradation through landform and cave destruction, impoverished ecology, air, soil and water pollution, and damage to paleontological and archeological sites. Since 1980, several protected areas of varying usage categories were implemented in the karst territory, from federal, state, and municipal initiatives, such as the Lagoa Santa Karst Environmental Protection Area (established in 1990), but they are still incomplete and fragile and face several challenges regarding the application of their concepts and assumptions (Alt & Moura 2020).

The karst is intensely researched to this day, and much of the early international attention it received was due to the Danish naturalist Peter Wilhelm Lund (1801–1880) (Fig. 3.A). Although not all caves visited by Lund in the early years of his research were part of what today is referred to as Lagoa Santa Karst (e.g., Gruta de Maquiné), these reports are a necessary inclusion in any study regarding him or the Lagoa Santa region due to their essential contribution to Lund's initial trajectory (Auler & Piló 2016), and, therefore, a requisite to the history of Brazilian paleornithology.

## 5. 1. 2. Lund on fossil birds

Paleontological studies began in Brazil with natural history expeditions carried out during the 19th century by foreign researchers, with fossils being discovered in caves in Minas Gerais as early as 1809 (Cartelle 2012). In this context, during his second and permanent visit to Brazil, Lund established himself in the town of Lagoa Santa, after a fortuitous encounter with his fellow countryman Peter Claussen (1807?–1860?<sup>1</sup>) in the town of Curvelo. Claussen showed Lund several of the saltpeter-bearing caves in the region, which he commercially exploited and sold the fossils he found to European museums<sup>2</sup>. This shifted Lund's focus from general botany and zoology to paleontology, immediately putting him in a path of notable specialization that distinguished him from various other naturalists that explored Brazil during that century (Paula Couto 1950; Cartelle 1994; Auler & Piló 2016).

Between 1835 and 1844 (Padberg Drenkpol 1927), Lund inspected over 800 caves in the region (Lund 1845–1849), although only a small number of them contained fossils. He published, besides paleontology, essential contributions on archeology, karst geomorphology, and speleology (Auler 2020a).

Although Lund focused on studying fossil mammals, he was responsible for the first published records of bird fossils in the country. In his first thesis about his research in the region, written in 1836 and published the next year, in which he described the cave Lapa Nova de Maquiné (now Gruta de Maquiné, located in the current municipality of Cordisburgo), Lund (1837) mentioned bones of various animals, including birds, in the stalagmite crust that lines the floor of one of its chambers. In the same study, when discussing the remains found in that cave, he mentioned bones of a pigeon-sized bird found next to the remains of a giant sloth, located underneath the stalagmite crust.

Bird remains were reported several times in his publications (Lund 1839; 1840; 1841a; 1841c; 1842b; 1842c; 1845–1849), but never in-depth. He planned work on the

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<sup>1</sup> Following Holten & Sterll (2011).

<sup>2</sup> Claussen published mentions of bird finds in 1841 (but read on), in the same work where he comments that it was from the knowledge of William Buckland's work in 1831 that he came up with the idea of looking for fossils in the Brazilian caves, finding mammalian remains the following year. Among the bird fossils that he collected, we can highlight the material that served as a type for the description of *Ciconia lydekkeri* (Ameghino). However, by the date of his publication, it is not possible to determine the exact year in which such fossils were found, and Lund's accounts are then the first documents on the ancient remains of birds in Brazilian territory.



numerous unexamined remains but occupied himself with the already-ongoing work on the mammal remains more than once. However, he sent to publication in 1841 a small treatise on what he found at the time, which, because of his own will (Winge 1887), was never published. What was published was only a small extract (Lund 1841d; Lund 1842a) where he reported his provisional results with 34 species belonging to 26 genera: one bird of prey, eighteen songbirds, six climbers, four gallinaceous birds, and five waders, almost all of genera still living in the region, except for a rhea-sized *Alectorides* he believed was extinct. He concluded that the most important result of this research is the continuity of the rules (e.g., the concept that extinct fauna presented greater diversity and larger forms) established from the comparative study between living and extinct mammals, which were also applicable to the birds. It agrees with Lund's support to Cuvier's theory of catastrophism (Cartelle 1994).

Lund (1846) reported the finds of Lapa da Escrivânia V (Winge 1887; Paula Couto 1950), of the Escrivânia complex, in the current municipality of Prudente de Morais. The excavation took place in 1844 and was the site with the most important bird material that he found, with many individuals with an estimated total of 7,569,650 (the vast majority being small mammals), of which about 350,000 were birds. The remains of birds in this cave were far more numerous than any other and increased his collection numbers for this group tenfold. Lapa da Escrivânia XI also provided material in considerable numbers. This large number of small bones in a single site was associated with predation by owls, with the larger bones coming from animals that fell into the caves. Lund estimated as 5,000 years the smallest time interval for the accumulation of these smaller bones, assuming that a couple of owls brought daily, under an optimistic perspective, four prey items, and also considering the time between the change of cave occupants. It constitutes one of the first qualified attempts to estimate the age of paleontological material with accuracy through empirical observations. The work in the Escrivânia complex was Lund's last cave study, who thought to have depleted the region's fossil novelties (Holten & Sterll 2011).

The components of Lund's collection, with some exceptions, were sent to Copenhagen between 1845 and 1849 (Fig. 3.D) (Padberg Drenkpol 1927; Cartelle 1994). They were donated to King Christian VIII and Denmark, and the reimbursement of Lund's expenses was used in the collection's benefit, such as the payment of a

curator, for which position Lund indicated Johannes Theodor Reinhardt (1816–1882) (Fig. 3.B), his professor’s son. Reinhardt joined the Galathea expedition that left Copenhagen in June 1845 for Lagoa Santa. However, political changes in Denmark prompted a significant delay in the collection’s proper exhibition and study (Fig. 3.E) (Holten & Sterll 2011).

### **5. 1. 3. Other contemporary studies**

Other authors contemporary to Lund published about fossil birds from the Lagoa Santa region, but most were simply mentions or reproductions of his studies. Claussen (1841) published data that were almost exact copies of Lund’s observations and this threat to Lund’s reputation, of which Clausen did not retract, worsened their relationship, which was tense most of the time, driving Lund to publish a rectification (Lund 1843) (Holten & Sterll 2011). Gervais (1844a; 1844b) referenced Lund’s data and reported material purportedly found by Claussen, who had recently returned to Europe. According to Reinhardt (1881), this material was sold to the Muséum d’Histoire Naturelle in Paris. Lund received several researchers in his home, such as Helmreichen (1846), who reproduced information on his bird material numbers, and Liais (1872), who found a sternum of a hummingbird in a cave in the region and attributed the alleged finds of Claussen to Lund. Wallace (1876), besides from reproducing data that Lund published, also cited “a new species of the very isolated South American genus *Opisthocomus*” (Wallace 1876: 164), indeed a mistake, as pointed out by Newton (1881) and Reinhardt (1881), but which was eventually kept in Lambrecht (1933).

Further studies on the bird remains discovered by Lund would be published only after his death. Reinhardt (1881; 1882) carefully re-analyzed the purported giant Alectorides of which Lund believed to have found the remains, including possibly associated fragments and illustrations of lost material, and concluded that they belonged to the living *Rhea americana*. This led him to propose that there are no indications that the region’s ancient bird fauna had large extinct representatives, thus eliminating the integral parity between this group and the mammals as to the rules employed by Lund. Truly giant extinct birds would only be discovered in South America in the late 1880s (Buffetaut 2013).

#### 5. 1. 4. Winge on fossil birds

A thorough examination of the mammalian (including human) and bird remains of Lund's collection was published under the collective title "*E Museo Lundii*" between 1887<sup>3</sup> and 1915. His fellow countryman Herluf Winge (1857–1923), a specialist in mammals, wrote most of the monographs that comprise this work, based on the fossil material and Lund's scientific documents, published or not (Paula Couto 1950). The ornithologist Oluf Winge (1855–1889) (Fig. 3.C), his brother, wrote the monograph dedicated to the bird remains, published in 1887.

By invitation of Reinhardt, Winge began studying the bird remains in the boreal summer of 1881. Reinhardt died the following year, and Winge's studies continued under the auspices of Professor Christian Frederik Lütken. Winge determined 126 taxa from the material, several probably including more than one species. Most of them represented extant taxa that still can be found in the Lagoa Santa region.

Winge described a single new extinct species from numerous remains of three sites, the anatid *Chenalopex pugil* (now *Neochen pugil*). It was larger than its purported closest living relative, the Orinoco goose *Neochen jubata* (Spix). It was the first species of fossil bird (and of dinosaur) to be named for Brazil.

Lund's bird fossil collection was never thoroughly reviewed. Olson (1985a) noted that, due to a probably limited comparative material, even some of the most positive determinations in Winge's work could not be accepted without contestation: 58 taxa, almost half of the total, show some degree of uncertainty regarding their determination. Winge himself did not exclude the possibility that some of the determined fragments could represent related species of territories elsewhere or even extinct forms. However, he noted that, given the general similarity between the fossil and the living avifauna, this probably would not essentially affect his results. Nevertheless, these factors do not take away the merit of Winge's work, who had perceived certain traits that would result in the description of a new genus and species, over a century later (see below).

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<sup>3</sup> On the publication date of the first parts of "*E Museo Lundii*", see Nascimento & Silveira (2020).

### **5. 1. 5. Further work on bird remains**

The next known new species from the region, the ciconiid *Ciconia lydekkeri* (Ameghino), was described in a convolute nomenclatural act (see below) by Lydekker (1891) and Ameghino (1891), from remains that Claussen sold to the British Museum (Natural History).

Alvarenga (1998; 2007) associated material excavated by the French-Brazilian Archeological Mission (1971–1976) in Lapa Vermelha IV (municipality of Confins) with the living species *Vultur gryphus* and *Anodorhynchus glaucus* or *Anodorhynchus leari*.

Besides the two taxa described in the nineteenth century, only in the 2000s new species would be published from the region, both being condors of opposite sides of a line regarding body size: the small *Wingegyps cartellei*, described by Alvarenga & Olson (2004) from material collected by Lund along with material from Gruta dos Brejões, Bahia, and the large *Pleistovultur nevesi*, described by Alvarenga *et al.* (2011) from Gruta Cuvieri, in the municipality of Matozinhos.

From the literature, Nascimento & Silveira (2020) attributed 161 records from pleistocenic to early holocenic age that were determined to a taxonomic level below Aves to the region. Additionally, many undescribed materials await study (e.g., Souza Cunha & Guimarães 1978). As they purportedly belong to living species, some records were mentioned simply as “birds” in the literature, and their younger age and poor conservation support this reduced interest (e.g., Paula Couto 1958). This is particularly true for the remains excavated in archeological sites (of which Walter [1958] noted that they are quite common in camp refuse), which were reported in the literature on several occasions (e.g., Veloso 1983; Veloso & Resende 1992; Cartelle *et al.* 1998; Hubbe 2008; Perez 2009; Kipnis *et al.* 2010a; 2010b; Hubbe *et al.* 2011; Mayer 2011; Mingatos 2017; Chim 2018).

### **5. 1. 6. Concluding remarks**

Establishing a chronology for the avifauna described by Winge is difficult. Cenizo *et al.* (2015) followed available data (Dias 2004; Bueno *et al.* 2013) that estimate ages between 12.000 and 8.000 years BP, and suggested it may correspond to the stadial

event of Younger Dryas in the post-Late Glacial Maximum. Some remains are of a more recent age (Reinhardt 1881; Winge 1887). Winge (1887) assumed that bodies of water and forest extension could have been more abundant in the region in the past because of the diversity of anatids (at least six taxa versus the four living in the area now) and the presence of large psittacids and the genera *Crax* and *Xiphocolaptes*, respectively, among the material collected by Lund. Nevertheless, he noted that drastic changes in the landscape do not seem to have happened according to the general picture of the bird remains found. Cartelle (2020) used this interpretation of more significant forest extension inferred from the bird remains to support the occurrence of different mammalian megafauna taxa in the region compared to other pleistocenic intertropical sets in Brazil, which included larger giant sloth and proboscidean species. Pollen assemblages recovered in the region indicate a wetter and cooler climate than nowadays, with a mixture of typical cold-climate elements co-occurring with cerrado and tropical forest taxa during the Pleistocene–Holocene transition (Raczka *et al.* 2013; Raczka *et al.* 2018).

These avian remains are particularly important due to their taxonomic diversity and historical significance, especially due to the ancient avifauna of Brazil being very poorly known, as is South America's in general (Olson 1985a; Alvarenga 1997; Tambussi & Degrange 2013). They also allow us to faithfully picture the bird community of the Pleistocene–Holocene transition in the region, enabling us not only to understand the composition of ancient biotas but also to understand the changes in the environments and their faunas over time. Besides birds, remains of invertebrates, fishes, amphibians, reptiles, and mammals (including humans) were also found in the region (e.g., Lund 1837; Paula Couto 1950; Hansen 2012). The mammalian megafauna stands out by being numerous and diverse, including proboscideans, giant sloths, glyptodonts, camelids, equids, litopterns, short-faced bears, and saber-toothed cats (Cartelle 2016).

## **5. 2. Tremembé Formation (SP)**

### **5. 2. 1. General information**

Discovered in the nineteenth century, the Taubaté Basin is a valley approximately 150 km long (northeast-southwest) and width ranging between 10 and 25 km, surrounded by

the Serra do Mar and Serra da Mantiqueira mountain ranges, between the municipalities of Cachoeira Paulista and Jacareí in the east of the State of São Paulo (Melo *et al.* 2007: 78; Kellner & Campos 1999: 246; Couto-Ribeiro 2010: 1). It is divided into three stratigraphic units, the Resende, Tremembé, and Pindamonhangaba Formations (Couto-Ribeiro 2010: 3).

The Tremembé Formation (Fig. 2.7) is of lacustrine origin, with an alternating sequence of pyrobituminous shales and bentonite clay attributed to the late Oligocene or the early Miocene (late Deseadan SALMA, 24–22 million years BP; Mayr *et al.* 2011: 962). The fossil birds of the formation, comparable with European finds of a well-defined age, support this hypothesis (Alvarenga *et al.* 2007: 4R). The locality provided vital contributions to Brazilian paleontology, whether in paleobotany or in paleozoology of invertebrates and vertebrates (Alvarenga 1988: 321). Particularly crucial for paleornithology, this is the locality with the most paleospecies described in Brazil.

Its main outcrops are in Taubaté, Tremembé, and Pindamonhangaba, where they are commercially exploited for montmorillonite clay (Couto-Ribeiro 2010: 5). Most fossils come from Fazenda Santa Fé, belonging to the Sociedade Extrativa Santa Fé, which corresponds to a smectitic clay exploration quarry, located in the Padre Eterno neighborhood, near the right bank of the Paraíba do Sul River, in Tremembé. Its fine sediments preserve, under different fossilization processes, a wide variety of taxa, from microfossils, ichnofossils, and remains of invertebrates, vertebrates, and plants, making it the most important geological and paleontological site of the Brazilian Lower Tertiary. Despite its importance, much of its information is being lost with the progressive exploration of the quarry (Bernardes-de-Oliveira *et al.* 2002: 63, 64), although, paradoxically, without this process, the systematic paleontological exploration in this site would be practically unfeasible (Couto-Ribeiro 2010: 30).

Fossils from the formation were described as early as 1898 in a study dealing with fish remains (Paula Couto 1958: 1). The first mention of a bird remain was published in 1916. In the previous year, the German-Brazilian zoologist Hermann von Ihering (1850–1930), then director of the Museu Paulista, sent a fossil feather preserved as a carbonized trace (Davis & Briggs 1995: 784) from the Taubaté Basin to be examined by Robert Wilson Shufeldt (1850–1934), an American specialized in



osteology and paleontology of birds. Shufeldt (1916) published the description of the specimen, associating it with a large species, noting that it was of particular interest as it furnished evidence that “highly developed birds” existed in that formation.

The second bird record was another feather from the shale levels, and it was described by paleoichthyologist Rubens da Silva Santos (1918–1996) in 1950 as belonging to a passeriform. Gilberto H. William found the fossil in July 1948, while collecting along with Silva Santos and Alberto Lopa in Nossa Senhora da Guia Mine during a paleontological survey carried out by the Divisão de Geologia e Mineralogia do Departamento Nacional de Produção Mineral (DNPM). This mine is currently deactivated (Alvarenga 1988: 321).

Additional feather specimens from the gray shales of Fazenda Santa Fé were firstly published by Prado & Anelli (2015) and Prado et al. (2016b). Prado & Anelli reported a contour feather (GP/2E-8125) they performed Scanning Electron Microscopy (SEM) analysis finding microbodies interpreted as eumelanosomes, which in turn suggested that the feather was dark colored. Prado *et al.* also reported a second specimen, describing them as preserved carbonized traces (although they show different degrees of preservation due to taphonomic processes) and tentatively attributing them to aquatic taxa.

### **5. 2. 2. Alvarenga on fossil birds**

The next big step, which would effectively be a new beginning in the study of fossil birds in the country, would come with the work of Herculano Alvarenga on the fossils of Taubaté Basin and the early Eocene of the São José de Itaboraí Basin, in Rio de Janeiro (see below) (Alvarenga 1992: 254). His body of work and his influence on the subject essentially founded the age of modern studies of this nature in the country, which could easily give him the title of father of Brazilian paleornithology.

Herculano Marcos Ferraz de Alvarenga (Fig. 4.B) was born in Taubaté in 1947 and, from an early age, showed an avid interest in birds, gathering a collection of skins that he prepared himself. He graduated from the Faculdade de Medicina de Taubaté in 1973, specializing in orthopedics. Two years later, he joined the institution as a professor and, in 1977, due to a long college strike, he toured the Taubaté Basin in

search of fossils, where he came across the remains of a huge bird in the clay mine in the Padre Eterno neighborhood. After analyzing these remains at his home for a while, he sought out the geologist Diógenes de Almeida Campos, from the DNPM in Rio de Janeiro, searching for help with the fossils' description. The two exchanged correspondences about the material, and Campos encouraged Alvarenga to continue his studies and publish a scientific article on the bird, an action that would start his paleontological career (Pivetta 2003: 55; Moon 2012: 73; Andrade 2017: 98). Financial support from the National Geographic Society was received for fieldwork carried out in the Tremembé Formation (Alvarenga 1995: 33).

The well-preserved fragments of this bird's skeleton were collected during several months between 1977 and 1978, with the help of local workers (Alvarenga 2008) and were found in the bentonite clay some 2 or 3 meters below the pyrobituminous shales, scattered in an area of approximately 100 m<sup>2</sup> (Alvarenga 1982: 697; 2003: 15). After restoration, the material provided the incomplete skeleton of a large bird (Fig. 4.A), described as the new phorusrhacid species *Physornis brasiliensis* in 1982, initially classified in the genus originally described for Argentinean material (Alvarenga 1982: 697).

In January 1978, at the same locality and level as the phorusrhacid fossils, new fragments were collected, this time of a cathartid. Alvarenga analyzed this material at the Natural History Museum of Los Angeles County, and this study resulted in the 1985 description of the new genus and species *Brasilogyys faustoi*, the oldest representative of the family in South America, of a somewhat larger size than the living *Coragyps atratus* (Bechstein) (Alvarenga 1985b; 1997: 123).

In 1988, from material sent by Silva Santos, Alvarenga described the genus and species *Taubacrex granivora* from an incomplete skeleton preserved in a shale fragment that had been found about 6 m deep in 1950 by the Petrobrás engineer Mustafá Hanzagic in Nossa Senhora da Guia Mine, former Petrobrás property in Tremembé (Couto-Ribeiro 2010: 5). Part of the fossil was lost, probably during collection, but the piece has remains of ossified tendons, imprints of feathers, and gizzards containing gastroliths. In the same work, Alvarenga (1988: 321) already pointed out other

fragments of bird bones not yet studied from the same source (as in Olson & Alvarenga 2002: 701).

In the same year, Castro *et al.* (1988a; 1988b) reported coprolitic nodules associated with birds from Fazenda Santa Fé. From their analysis, it was possible to infer data on the ecology of these animals, demonstrating that they had varied eating habits, in addition to information on the evolution of the Tremembé Formation's sedimentation paleoenvironments.

Between 1984 and 1989, fossils determined as phoenicopteriforms, among others, were collected in Fazenda Santa Fé. They had their formal description published in 1990, with the new species *Agnopterus sicki* (honoring the ornithologist Helmut Sick) and material showing great affinity with the European species *Palaelodus ambiguus* (Alvarenga 1990). The study of this material also contributed to the knowledge of the paleoenvironment and the site's geological age.

After comparing the fossils of *Physornis brasiliensis* with museum specimens in Argentina, the United States, and Europe and finding significant differences, Alvarenga published in 1993 a new genus for the bird, *Paraphysornis*. This fossil's importance in the paleornithology development in the country is indisputable, and its solid and curious figure would make it a kind of symbol of the Brazilian paleoavifauna.

Alvarenga, Silva Santos, and other professors at the Universidade Estadual do Rio de Janeiro found, in July 1989, in the pyrobituminous shales of Fazenda Santa Fé, the impression of part of the incomplete skeleton of a small galliform, soon mentioned and figured by Alvarenga (1993b: 24, 25). It was the basis for the description, in 1995, of the new genus and species *Ameripodius silvasantosi* (Alvarenga 1995b). The bird was included in the family Quercymegapodiidae, initially described for the European Paleogene, showing to be of particular paleobiogeographic interest, especially in the observed similarities between the paleoavifaunas of South America and Europe (Mourer-Chauviré 1999). Eventually, *Taubacrex granivora*, initially associated with the Rallidae, was transferred to the Quercymegapodiidae by Mourer-Chauviré (2000: 486, 488). These two are the oldest known galliform records for South America (Agnolin 2016b: 160).

In 1995, Alvarenga joined the doctoral program in zoology at the Instituto de Biociências da Universidade de São Paulo (IB/USP), while still teaching and attending in his orthopedics office (Andrade 2017: 98). His work (“Revisão sistemática das aves Phorusrhacidae”; Borges 2008: 85), conceived as early as 1988 (Alvarenga in Mourer-Chauviré 1990: 1) and completed in 1999, resulted in the publication in 2003 of the revision of the family Phorusrhacidae, along with his supervisor Elizabeth Höfling (Alvarenga & Höfling 2003).

Azevedo & Carvalho (1998) reported small and thin eggshell fragments from the upper level (dark shales) that showed structural arrangement strongly reminiscent of the ratite pattern. This occurrence was the first (and only, so far) record of eggshells for this unit and the first for fossil avian eggs for the country.

Alvarenga published the description of the new genus and species *Chaunoides antiquus* in 1999, from several fragments of the montmorillonite clays of Fazenda Santa Fé that he collected between 1978 and 1993. He had already mentioned the existence of remains attributed to the family on an earlier occasion (Alvarenga 1993b: 24). It was the first anhimid fossil species to be recognized, representing a slightly smaller and slender bird than the smallest living species, *Chauna chavaria* (Linnaeus) (Alvarenga 1999: 223, 229).

The renowned American paleornithologist Storrs Lovejoy Olson (1944–2021) (Smithsonian Institution, the United States) came to Brazil (on one of at least three occasions; Pivetta 2003: 55) and worked with Alvarenga on the study of bone fragments from the montmorillonite clays of Fazenda Santa Fé. This study (Olson & Alvarenga 2002) described the new genus and species *Taubatornis campbelli*, the smallest (although comparable in size to *Pelecanus thagus* Molina) and the oldest known teratornithid. The bird was found syntopic with the cathartid *Brasilogyps faustoi*, and the Tremembé Formation conforms to the almost invariable association pattern of the two families when teratornithids are found. This discovery supports the hypothesis of the family’s origin in South America.

In 2011, Alvarenga, Gerald Mayr (Forschungsinstitut Senckenberg, Germany) and Cécile Mourer-Chauviré (Université Lyon 1, France) described the genus and species *Hoazinavis lacustris*, the oldest known opisthocomiform, from fossils found in

2008. Additionally, they revised and reclassified the fossils of the species *Namibiavis senutae* (early Miocene of Namibia) also as an opisthocomiform, leading to the hypothesis of the dispersion of the group's representatives from Africa to South America through a transatlantic route in a vegetation raft, being the first known example for birds (Mayr *et al.* 2011b).

Furthermore, Alvarenga (in Castro *et al.* 1988b: 2360; Alvarenga 1993b: 24; 1997: 123) mentioned undescribed fossils from the Anatidae, Podicipedidae, and Phalacrocoracidae families, among others. This material's state of conservation prevents a more detailed analysis, but in any case, they are added to this deposit's rich fossiliferous bird record. Castro *et al.* (1988b: 2362) also mentioned the occurrence of the Ardeidae family in the formation, and Garcia (1993: 329) mentioned feather impressions. There are also three specimens of fossil feathers in the collection of the Instituto de Geociências da Universidade de São Paulo, collected in 2006 in Fazenda Santa Fé.

### **5. 2. 3. Taubaté's Natural History Museum**

Over the years, Alvarenga gathered a large collection in his home, exchanging copies of skeletons with Brazilian and foreign researchers and institutions. Argentinean technicians Pablo Puerta and Raul Vacca were in Taubaté for two months in 1988 to assist Alvarenga in the restoration of the *Paraphysornis brasiliensis* skeleton, with two resin copies being ready for exchange in 1990. A total of 12 were produced, exchanged with institutions from Brazil, Argentina, Japan, the United States, and several European countries. This practice was ended in 2005 due to customs bureaucracies (Alvarenga in Mourer-Chauviré 1988: 4; Alvarenga in Mourer-Chauviré 1990: 1; Tuffani 2002; Alvarenga 2007a; Moon 2012: 74; Venceslau 2014: 6).

The prestige of his scientific career led the Taubaté City Hall to initiate, in 1995, the first talks about creating a natural history museum. In 1998, the City Hall set aside land for erecting a building, which it would also finance, and it was completed in late 2000. The Museu de História Natural de Taubaté (MHNT) (Fig. 4.C) would be inaugurated in 2004, with Alvarenga as its director, being maintained by the Fundação de Apoio à Ciência e Natureza (FUNAT), which was created for this purpose (Tuffani

2002; Venceslau 2014: 6, 7; Andrade 2017: 98). Its collection currently has about 14 thousand pieces from all geological periods (Andrade 2017: 98)—including extinct bird fossils from other countries (e.g., Alvarenga 1990: 338; Alvarenga & Höfling 2003: 58). Its importance for paleornithology is highlighted, with the richest skeleton collection of modern birds in Latin America (MHNT undated B). Alvarenga also published several articles on living birds (e.g., Alvarenga *et al.* 2002; Antunes *et al.* 2007) and fossils from other vertebrate groups (e.g., Soria & Alvarenga 1989; Vucetich *et al.* 1993).

The species *Paraphysornis brasiliensis* is the symbol of the MHNT (Alvarenga 2007a), being crucial for its creation (Alvarenga 2008; Moon 2012: 73). Its original bones were shown to the public for the first time during the 2009 “Museum Week” (Alvarenga 2009: 38). The MHNT also has as its mascot an animated version of the bird, “Fisó”, created by the artist Marcos Sachs (MHNT undated A). Academic projects were carried out based on the Museum’s collection or copies of its materials, such as the use of *P. brasiliensis* as the basis for an animatronic robot (Almeida *et al.* 2005) and its reconstruction and digitalization with the use of three-dimensional virtual modeling (Lima *et al.* 2008).

## **5. 2. 4. Concluding remarks**

The Tremembé Formation is interpreted as an ancient shallow and alkaline lake (Alvarenga 1999: 223)—it would receive water from tributary rivers and, without connection to the ocean, would reach high salt concentrations, allowing ostracods and decapods to reach large numbers, serving as a base for feeding fossil flamingos (Alvarenga 1990: 342). The paleoclimate was probably subtropical or tropical in the valley’s interior where the lake was located and colder in the higher areas around it (Melo *et al.* 2007: 78). The shales suggest an alternation between wet and dry seasons, with the fossils indicating periodic mortality of many small fishes; this probably attracted predators and scavengers such as the cathartiforms *Brasilogyps faustoi* and *Taubatornis campbelli* (Olson & Alvarenga 2002: 704). The fauna associated with the formation includes notoungulates, astrapotheres, pyrotheres, litopterns, cingulates, sparassodonts, caviomorph rodents, bats, chelonians, crocodilians, snakes, anurans, caecilians, bone fishes, insects, arachnids, crustaceans, and mollusks. Fossils of plants, palynomorphs, and other microfossils, such as ostracods, sponge spicules, and

scolecodonts, were also found (Bernardes-de-Oliveira 2002: 64; Couto-Ribeiro 2010: 6, 12; Melo & Bergqvist 2010: 94).

### **5. 3. São José de Itaboraí Basin (RJ)**

#### **5. 3. 1. General information**

The São José de Itaboraí Basin (Fig. 2.3), discovered in 1928 by engineer Carlos Euler, is located in the São José neighborhood, in the district of Cabuçu, municipality of Itaboraí, State of Rio de Janeiro, about 60 km from the capital. It is one of the smallest Brazilian sedimentary basins, with an approximate length of 1.4 km (northeast-southwest) and a minor axis width of approximately 0.5 km (northwest-southeast), with an area of approximately 1 km<sup>2</sup>. It is, however, richly fossiliferous, being filled by a sequence of clastic and chemical (travertine) limestones that are cut vertically by dissolution channels filled with marl, in which most of the fossils were found. The basin's limestone was exploited between 1933 and 1984 for the manufacture of cement used in constructions such as the Maracanã Stadium and the Rio-Niterói Bridge, and this exploitation was responsible for the discovery of a large number of fossils. The area, originally owned by the Companhia Nacional de Cimento Portland Mauá, was expropriated in 1990 by the Municipality of Itaboraí, which created in 1995 the “Parque Paleontológico de São José de Itaboraí”, aiming at its preservation and the dissemination of its geo-paleontological importance (Bergqvist *et al.* 2006: 13, 14, 15, 16; Bergqvist *et al.* 2009: 413, 414, 418, 428). The age attributed to the basin is the early Eocene (Itaboraian SALMA, 53–50 million years BP; Woodburne *et al.* 2014a: 39; Woodburne *et al.* 2014b: 109, 116). In addition, fossils of pleistocenic age and archeological materials have been found in the basin's vicinity (Bergqvist *et al.* 2006: 34, 35; Bergqvist *et al.* 2009: 421, 423)

#### **5. 3. 2. Avian remains**

The first publication on the basin's fossils appeared as early as 1929, dealing with incomplete internal molds of gastropods (Bergqvist *et al.* 2006: 33). In 1948, the naturalist Ney Vidal, from the former Geology Division of MN, collected some fragments of bird bones there. Later, in 1949, Júlio de Carvalho collected in the same

place most of the components of a small collection of sparse and fragmented bird bones, which were included in the vertebrate collection assembled by the DNPM Paleontology Section (Alvarenga 1983: 1). These fossils were briefly mentioned by Paula Couto (1953; 1958: 11; 1970: 909), who cited several unidentified birds, Palma (1973: 40) and Palma & Brito (1974: 400), who cited long bone fragments, Price (*in lit.* 1977 in Sick 1984a: 65), who mentioned the remains of several birds (“metatarsals, vertebrae, premaxillae, etc.”), Francisco & Cunha (1978: 390, 402, 408), who also mentioned long bones, and Rich (1979: 323, 324), who mentioned small birds. However, no detailed description would be published until Déa Regina Bouret Campos, then responsible for the DNPM paleontological collection, and Fausto Luiz de Souza Cunha, paleontologist at MN, sent the material collected by Carvalho and Vidal, respectively, for Herculano Alvarenga to study, as Cunha was aware of Alvarenga’s interest in paleornithology (Alvarenga 1983: 1).

Alvarenga prepared and restored these fossils, concluding that most of them belong to a single bird species, which he described in 1983 as the new genus and species of small opisthodactylid *Diogenornis fragilis*, honoring Diógenes de Almeida Campos for his support. The species was considered a possible ancestor of the living rheas and one of the oldest known ratites (Alvarenga 1983: 1, 2).

The fragments collected by Vidal and Carvalho contained yet another species, which Alvarenga described in 1985 as the new psilopterid genus and species *Paleopsilopterus itaboraiensis* (Alvarenga 1985a). The bird was considered the oldest known representative of the phorusrhacoids (Alvarenga 1985a: 20).

In 1997, paleontologists Robert F. Baird (Melbourne University, Australia) and Patricia Vickers-Rich (Monash University, Australia) described the genus and species *Eutreptodactylus itaboraiensis*, from an incomplete tarsometatarsus collected by Ney Vidal in 1950 and deposited at MN, of which the study was allowed by Fausto Luiz de Souza Cunha. The taxon was considered the oldest known cuculid, probably from a new subfamily, and one of the oldest records for an extant family (Baird & Vickers-Rich 1997). Unfortunately, after being studied, the fossil was lost, leaving only casts and illustrations in collections.



Mourer-Chauviré (1999) pointed out the similarities between the fossil avifaunas of the early Tertiary in Europe and South America (including the records from Itaboraí and Taubaté), in addition to recent discoveries that indicated that a similar fossil avifauna was also present in North America. Thus, it was possible to define an association of terrestrial or non-marine aquatic taxa that constitute a continental basal avifauna common to Europe, North America, and South America, of which some elements survived only in the latter. In the face of the inability or low flight ability of some of these components, Mourer-Chauviré proposed that these taxa underwent diversification during the Late Cretaceous or the Paleocene, and dispersed through land routes that existed then, from South America to North America and then Europe, or the other way around.

Alvarenga, Gerald Mayr, and Julia A. Clarke (University of Texas, the United States) described in 2011 several avian remains present in the collection of MN, composed of indeterminate fossils (including material perhaps belonging to *Eutreptodactylus itaboraiensis*) and the new genus and species *Itaboravis elaphrocnemoides* (Mayr *et al.* 2011a), similar in size to *Crypturellus tataupa*. The associated elements of this newly described taxon, briefly mentioned by Mourer-Chauviré (1999: 87), show characters akin to those of the European Paleogene genus *Elaphrocnemus*, associated with the Cariamiformes.

Furthermore, phalanges referable to *Diogenornis fragilis* and *Paleopsilopterus itaboraiensis* were reported by subsequent authors (Taranto & Bergqvist 2009: 51R; Taranto *et al.* 2009a: 287; Taranto & Bergqvist 2010: 118; Alvarenga *et al.* 2011: 191, 192; Metello *et al.* 2012a: 525; Metello *et al.* 2012b: 140; Metello 2013: 176; Metello *et al.* 2014: 84; Metello & Bergqvist 2014: 151).

### **5. 3. 3. Concluding remarks**

As observed in the Paleocene of Europe, the Itaboraí paleoavifauna seems to include a significant number of representatives with little or no flight capacity. Whether this indicates particular characteristics of early Cenozoic ecosystems, such as the absence of large predatory mammals, remains to be addressed in future studies (Mayr *et al.* 2011a: 684). There is, however, a record of large terrestrial predatory crocodylians for the basin

(Pinheiro *et al.* 2018: 88). The associated paleofauna includes marsupials, litopterns, notoungulates, astrapotheres, xenungulates and cingulates (the site is regarded as the “cradle of mammals” in Brazil), chelonians, lizards, snakes, crocodylians, anurans, caecilians, and gastropods. Fish or any benthic animals were not found, possibly because the lake that filled the original tectonic depression was formed by scalding thermal waters and/or due to the high concentration of calcium carbonate dissolved in its waters (Bergqvist *et al.* 2006: 13, 33, 34; Bergqvist *et al.* 2009: 421, 423). Fossil plants and microfossils of ostracods and palynomorphs have also been found (Bergqvist *et al.* 2009: 421). Moderately dense woodlands or forests existed in and around the basin area, in a hot and humid tropical environment (Paula Couto 1970: 913; Alves 2012a: 63; Woodburne *et al.* 2014a: 40, 51).

With the cessation of extractive activities on the site in 1984, water drainage was also interrupted, which started to accumulate in the depression of approximately 70 m left by the excavations, forming a lake currently used for the water supply of the community in the São José neighborhood. This prevents new geological studies and collection activities (Bergqvist *et al.* 2006: 13; Bergqvist *et al.* 2009: 414, 416; Kellner & Campos 1999: 246).

## **5. 4. Solimões Formation (AC, AM)**

### **5. 4. 1. General information**

Sediments from the late Cenozoic are present in several localities in the Western Amazon (west of Manaus), and their deposits originated in a fluvial-tidal wetland system that existed before the final establishment of the Amazon River system (Negri *et al.* 2010: 245). They contain a wide variety of aquatic and terrestrial fossil vertebrates, and the most diverse faunas are found in the upper Solimões Formation of Solimões Basin in the State of Acre, of late Miocene age (Huayquerian SALMA; Cozzuol 2006: 198; Latrubesse *et al.* 2007: 78; Latrubesse *et al.* 2010: 106; Negri *et al.* 2010: 245, 246; Guilherme *et al.* 2020).

The Solimões Formation (Fig. 2.8) is a succession of claystones and lignites with sandstone beds, and its upper part, as observed in the state of Acre, is dominated by sandstones and contains few clay intervals. Samples of its vertebrate fauna were

collected at dozens of sites found along the banks of rivers and on roads (Negri *et al.* 2010: 246, 247). Between 1989 and 1998, the team at the Laboratório de Pesquisas Paleontológicas (LPP) at the Universidade Federal do Acre collected several bird fossils at two of these sites: Cachoeira do Bandeira (between Brasiléia and Assis Brasil) and Niterói (in Seringal Niterói, Senador Guimard), on the banks of the Acre River, among more than 5,000 pieces of vertebrates recovered and identified in the region. Cachoeira do Bandeira was discovered by the RadamBrasil staff in 1976, while Niterói was discovered in 1987 in a conjoined expedition by the Laboratório de Pesquisas Paleontológicas (LPP) of UFAC and MPEG (Souza-Filho & Guilherme 2015).

#### 5. 4. 2. Avian remains

Brazilian fossil birds in the region have been mentioned in the literature since then, but always in very brief and sometimes confusing notes. Campbell (in Mourer-Chauviré 1987: 7) mentioned a giant undescribed anhinga. Wall *et al.* (1991: 397) mentioned fossil material from this group. Alvarenga (1992: 254), through communication with Campbell, mentioned fossils of an extinct anhingid and a giant phorusrhacid, collected by the team of the Natural History Museum of Los Angeles County. Noriega (1992: 218) mentioned a very large anhingid, through communication with Campbell. Alvarenga (1993b: 21) mentioned the genus *Macranhinga* as known from the bordering region between Acre (Brazil) and Bolivia (probably Sítio Cachoeira do Bandeira), from material collected by the Universidade [Federal] do Acre. Latrubesse *et al.* (1997: 112) and Bocquentin & Silva (1998: 154) listed the genus *Anhinga* and an indeterminate phorusrhacid. Bocquentin & Janoo (1997: 111) reported a new species of *Anhinga* (but without describing the new taxon). Finally, Negri & Ferigolo (1999: 18) listed an indeterminate phorusrhacid.

Campbell, responsible for the first mentions of Brazilian fossil anhingid remains, described in 1996 the species *Anhinga fraileyi*, from late Miocene Peruvian material from the Patos (LACM 4611; Negri *et al.* 2010: 258) and Cachoeira do Bandeira (LACM 5158; Negri *et al.* 2010: 257) sites<sup>4</sup>. The Patos site was discovered in the 1970s

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<sup>4</sup> Campbell (1992: 20A) mentioned fossils of a giant *Anhinga* from the Amazon, without specifying the location; even though he also mentioned fossils from Brazil (in Alvarenga 1992: 254), they may be the *Anhinga fraileyi* material he described in 1996. Campbell (1996: 2, 3) referred all the material described as *A. fraileyi* to Peru, with the holotype and referred material from the LACM 4611 locality, and the proximal end with the axis of a left humerus

and explored in 1985 in a conjoined expedition by the LPP of UFAC and the Los Angeles County Museum (Souza-Filho & Guilherme 2015).

Brazilian anhingid material would only be formally described in 2003. The ornithologist Edson Guilherme, who started a collection of living bird skeletons in the LPP, located and reidentified the fossils of birds that were “lost” within the lab’s paleovertebrate collection. Because of the significant morphological similarity, some fossils were identified as reptiles and stored on the shelves next to hundreds of fragments, mostly crocodylians. After reviewing the entire collection, Guilherme contacted Herculano Alvarenga to study the material jointly (Guilherme 2016: 46). This partnership resulted in the description of two new species: *Anhinga minuta* and *Macranhinga ranzii*, respectively the smallest and the (then) largest known anhingas, in addition to material determined as *Anhinga* cf. *grandis* and *Anhinga* cf. *fraileyi*, taxa originally described from the United States and Peru, respectively (Alvarenga & Guilherme 2003).

Bandeira *et al.* (2015) briefly reported on two specimens from Cachoeira do Bandeira locality that were collected during the RadamBrasil project. A humerus was associated with *Anhinga* cf. *A. minuta* and a tarsometatarsus with *Anhinga* indet.

Guilherme *et al.* (2020) published on new specimens tentatively attributed to *Macranhinga ranzii* representing new skeletal elements from a new locality named Cajueiro at the left margin of the Purus River, municipality of Boca do Acre, Amazonas (Loboda *et al.* 2019). Morphological and myological data enabled them to recognize the

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(LACM 135362) and the axis of a right humerus (LACM 135363) from the LACM 5158 locality. Diederle (2015: 132; 2017: 342) associated these two humeri fragments to the Brazilian territory, based on Negri *et al.* (2010: 258), who listed LACM 5158 as “Bandeira – Acre River (Brazil)”. Souza-Filho & Guilherme (2015) lists the Acre 6 locality as the same of LACM 4611 of Frailey (1986) as a site bordering Peru (providing the Peruvian coordinates 10°56’15”S and 69°55’41”W), which may be the source for these disagreements. Campbell (1996: 8) also mentioned that “a similar but less diverse paleofauna is known from Cachuela Bandeira, Bolivia, the second locality (LACM 5158) bringing bones of *Anhinga fraileyi*”. There is also the possibility that the mentions of Campbell (in Mourer-Chauviré 1989: 7), Wall *et al.* (1991: 397), Alvarenga (1992: 254), Noriega (1992: 218), and Latrubesse *et al.* (1997: 112; they include Niterói and Patos as sources for the provided faunal list, without further details) refer to the *A. fraileyi* material described from Peru. Alvarenga & Höfling (2000: 589) mentioned *Anhinga frailegyi* [*sic*] as coming from the State of Acre, citing Campbell (1996) as a source. In that study’s second edition (Alvarenga & Höfling 2004: 827), they said the same for *A. fraileyi*. In the third edition (Alvarenga & Höfling 2011: 127), they mentioned *A. fraileyi* in Acre, citing both Campbell (1996) and Alvarenga & Guilherme (2003). Additionally, Bocquentin & Melo (2006: 188), when listing the fauna recovered from Patos and Cavalcante localities (the State of Acre, according to the map in fig. 1, pp. 188; LACM 4611 and LACM 4418 localities, respectively), among others that provided fossils used in the description of the giant turtle *Stupendemys souzai*, included *A. fraileyi*. This mention needs to be revised since it is unclear whether it refers to the Peruvian material used in the original description by Campbell (LACM 4611=Patos, Acre River, Peru, according to Negri *et al.* 2010: 258).

taxon as a powerful swimmer and diver, being able to proficiently hunt fishes in deep waters (such as the frequently recovered *Paleohoplias assisbrasilensis* and *Hoplosternum* sp.), and to provide new phylogenetic hypotheses and improvements in the diagnosis of anhingid taxa.

Furthermore, Souza-Filho & Guilherme (2015) mentioned Anhingidae material from the Talismã site in the right bank of Purus River, Amazonas, and avian material from the Morro do Careca site, in the BR-364 highway, between the municipalities of Feijó and Tarauacá, Acre. Diederle (2015; 2017) revised the anhingid fossil species from South America, treating as *Macranhinga* sp. the specimens that Alvarenga & Guilherme (2003) determined as *Anhinga* cf. *grandis* and *Anhinga* cf. *fraileyi*, and published (Diederle 2016) a contribution on the body mass and means of locomotion of *Anhinga minuta*. The phorusrhacid remains still await a formal description and were briefly summarized by Agnolin (2009b: 56).

### **5. 4. 3. Concluding remarks**

The associated fauna of the South-Western Amazon region, one of the last before the Great American Biotic Interchange, encompasses a great diversity of crocodylians and chelonians, as well as lizards, snakes, marsupials, caviomorph rodents, ground sloths, cingulates, litopterns, notoungulates, astrapotheres, sirenians, cetaceans, bats, primates, bony and cartilaginous fishes, crustaceans, and mollusks (Latrubesse *et al.* 1997: 111, 112, 113, 114; Bocquentin & Silva 1998: 154, 155; Alvarenga & Guilherme 2003: 620; Cozzuol 2006: 198, 199; Bocquentin & Melo 2006: 187, 188; Latrubesse *et al.* 2010: 107, 108, 111, 113; Negri *et al.* 2010: 245, 248). The anhingids are good indicators of what the environment was like in the region, being attributed to marginal forests of clear lakes and slow-flowing rivers, and along with the associated fauna and flora, indicate an area with large water bodies surrounded by open vegetation mixed with gallery forests that are subject to water fluctuation levels in a tropical seasonal to tropical wet-dry climate (Alvarenga & Guilherme 2003: 620; Latrubesse *et al.* 2007: 75; Negri *et al.* 2010: 253).

The extreme deep diving capacity presented by this group was probably one of the factors that drove its evolutionary history and its extinction (Diederle & Agnolin

2017: 1062). The radiation of these large anhingids in South America appeared during the Miocene, in tropical and subtropical climates, and disappeared at the beginning of the Pliocene (the Pliocene/Pleistocene age attributed to *G. kiyuensis* is disputed), probably due to the combination of deteriorating climatic conditions, the regression of the epicontinental seas and the subsequent disappearance of several freshwater environments, the arrival of carnivorous placental mammals from North America, and the probable competition with the phalacrocoracids, better adapted to survive in more severe climatic conditions (Cenizo & Agnolin 2010: 507, 508, 509).

## **5. 5. Crato Formation (CE)**

### **5. 5. 1. General information**

The Crato Formation (Fig. 2.1) (*sensu* Martill *et al.* 2007; Crato Member of the Santana Formation in some studies) outcrops around the northern, eastern, and southern-eastern flanks of the Chapada do Araripe plateau, at the boundaries of southern Ceará, western Pernambuco, and south-eastern Piauí. It comprises a heterolithic sequence of clastic and carbonate strata currently restricted within the Araripe Basin and some smaller, interconnected basins (Martill 2007: 8). Martill & Heimhofer (2007: 33, 39) recognized four members in the formation, beginning from the most basal: Nova Olinda, Caldas, Jamaru, and Casa de Pedra. Only in the Nova Olinda Member, a series of laminated limestones up to 14 m thick, fossils occur in an astoundingly large number, often preserving exceptional details. The lowest part of the sequence of the Crato Formation, which includes the Nova Olinda Member, is presumably of late Aptian age in the Early Cretaceous (119–113 million years BP; Martill & Heimhofer 2007; Carvalho *et al.* 2015b).

The sediments of the Crato Formation were deposited in an equatorial mid-continental setting, with a hot and arid climate, in a lacustrine environment with a suggested minimum extent of about 18,000 km<sup>2</sup> (Martill 2007: 16; Carvalho *et al.* 2015b). The water body was inferred to have considerably deep waters, with hypersaline events and anoxia in the bottom waters that assisted to some degree the exquisite preservation of the fossils, inhibiting efficient decomposition and disarticulation (Heimhofer & Martill 2007). However, it is noteworthy that these and

other aspects remain debatable, and different approaches exist in the literature (see Martill & Bechly 2007).

Information on strata included in the Crato Formation was first published in 1846, but only by the 1940s and 1950s fossils began to be noted in the literature. It was not until the 1980s that serious paleontological research commenced, with a considerable number of fossils being found due to the significant increase in the extraction of limestones for commercial purposes (Martill & Heimhofer 2007: 27, 28).

Commercial mining for cement manufacture and limestones used as building stones, tabletops, and paving slabs occurs in the Nova Olinda Member and some of the overlying argillaceous strata, making it of considerable economic importance to the region (Andrade 2007; Martill & Bechly 2007: 3). Most of the fossils existing in scientific collections result from these commercial activities, including the subsequent illegal fossil trade. Quarry workers find the fossils while manually extracting the limestones, selling them at meager prices to “middle-men” based in Santana do Cariri and Nova Olinda, in most of the cases, which in turn sell them to dealers based in São Paulo and abroad (Martill & Bechly 2007: 5).

The Nova Olinda Member is an essential lagerstätte due to the diverse and abundant fauna and flora—with the most diverse non-marine fossil assemblage of Gondwana (Martill *et al.* 2007: xii)—and for the exceptional quality of preservation, with a high level of anatomic fidelity, mostly in three dimensions, and many unweathered specimens retaining color patterns (Martill & Frey 1995: 126). The fossil assemblage is dominated by arthropods, with insects being the most abundant group in both number and taxonomic diversity, but also represented by chilopods, arachnids, and crustaceans. The vertebrates include fishes, with the gonorynchiform *Dastilbe crandalli* Jordan being the most abundant, anurans, turtles, lizards, crocodylians, and pterosaurs (Martill *et al.* 2007). Besides birds and indeterminate feathers, the only other known dinosaur record is the compsognathid *Ubirajara jubatus* Smyth *et al.* (2020), which preserved filamentous integumentary structures. The small, volant birds known from the locality may have been responsible for predation marks observed in some fossil insects (Naish *et al.* 2007: 530). The fossil flora is diverse, dominated by gymnosperms (such

as conifers, cycadophytes and gnetophytes) and angiosperms, but also includes several spore-bearing plants (Mohr *et al.* 2007).

### **5. 5. 2. Feathers**

In the Crato Formation, remains of possible birds are extremely rare, being so far reported only from the Nova Olinda Member (Naish *et al.* 2007). Small, isolated feathers were likely blown into the Crato lagoon, where they sunk and were rapidly buried in the anoxic bottom (Martill & Davis 2001) and occur predominantly as carbonized traces, though melanosome and possibly iron oxide preservation are also present (Prado *et al.* 2016a). Apart from being categorized by comparison with modern feather morphotypes, these specimens could not be assigned to any particular taxon. They possibly represent several different and disparate taxa, and not even their origin from birds can be secured since some non-avian theropod groups also possessed true feathers (Naish *et al.* 2007). However, after their association in one case with avian skeletal remains (Carvalho *et al.* 2015a; 2015b), Smyth *et al.* (2020) postulated that most are likely from enantiornithiform ornithothoraceans rather than from non-avian dinosaurs. The deposit represents the only case of fossil feathers associated with skeletal remains where feathers occur frequently in South America. It is also one of the few localities that bear Mesozoic bird remains in Gondwana. Apart from the Yixian Formation in China, where complete avian fossils associated with feathers are common, it is one of the richest Mesozoic feather localities (Naish *et al.* 2007: 529, 530), constituting the only known record of feathers of this age from Brazil (Metello 2017).

The first-ever fossil described as Mesozoic avian remains from Brazil was one of these isolated feathers, a probable remex associated with a well-flighted bird by Martins-Neto & Kellner (1988). This record was also the first description of a fossil feather for South America as a whole. Its exact place of origin is not known but probably was collected around the municipality of Santana do Cariri, Ceará. It is preserved as a limonitic by-product of a weathered pyritic permineralization (Martill & Filgueira 1994: 483). This feather's discovery in a site that provided small, well-preserved vertebrate fossils (e.g., fishes and anurans) along with other fossils (such as insects and seeds) indicating abundant and varied food sources offered prospects for future discoveries of more complete bird fossils (Kellner *et al.* 1991: 376).



The second feather, this time a semiplume, was reported by Martill & Filgueira (1994), being overall the third reported occurrence of Mesozoic avian remain from Brazil. The fossil comes from the then recently discovered locality of Mina de Antone Phillipe, near the Tatajuba Reservoir and about 10 km west of Nova Olinda, Ceará, Crato Formation's main commercial exploitation area. One of the quarry workers collected it and passed it down to Sr. Antone Phillipe, the quarry owner, as a fortunate event despite being in a site outside the main commercial collecting area, where most of the fossils were ignored. The fossil appears to have been preserved organically, although no tests were conducted in fear of damaging it further. The Crato Formation at this locality was probably deposited close to the ancient shoreline of the Crato lagoon.

Kellner *et al.* (1994) described a fossil down feather without attributing it to a specific locality. Nevertheless, the record was considered empirical evidence that the early Cretaceous birds had already developed an effective thermoregulatory insulation cover and increased the expectation of finding skeletal remains of birds in the same deposit.

Martill (1994: 115) pointed out fake fossil feathers among the fabrications done by local quarry workers intended to supply the illegal fossil trade. Modern feathers were glued to limestone slabs, with some fakes being challenging to detect. He purchased two specimens (figure 8 in the article) that could not be determined as fabrications in the field without a good microscope. Their slight elevation on the bedding plane and the fact that one slab had two feathers in suspiciously similar orientations were clues to their possible fake identity.

Martill & Frey (1995) reported feathers from exposures of unweathered, gray-colored laminites at the Mina de Antone Phillipe. One of them, an incomplete contour feather with alternating dark and light bands, was regarded as perhaps the earliest recorded occurrence of color patterning in birds. The authors deposited part and counterpart of the specimen in different institutions aiming for a wider availability for examination. In the same field trip in which this banded feather was obtained, several other non-flight feathers were collected. These feathers are preserved as organic material of black appearance. Martill & Frey did not risk examining the feather's color pattern (as in insect specimens with the same kind of preservation) by electron

microscopy as the pattern preservation could be masked by gold or carbon coating. Instead, they choose to analyze another feather from the same locality which had a similar style of preservation despite lacking color patterning. At high magnifications, it showed that the feather's organic material is composed of elongated and roughly aligned rod-shaped bodies that the authors considered to be autolithified bacteria similar to material described from the Eocene oil shales of Messel, Germany.

An almost symmetrical feather with possible ectoparasite eggs was described by Martill & Davis (1998; 2001). The specimen was obtained in June 1996 from a commercial fossil dealer by the National Science Museum of Japan, and, although the locality was given only as Crato Formation, its matrix is well comparable with that of weathered, laminated limestones of the Nova Olinda Member, probably being collected in one of the small quarries operated between Nova Olinda and Santana do Cariri. It is too weathered for its original preservation mode to be satisfactorily established. The numerous spherical, hollow structures of about 75  $\mu\text{m}$  in diameter were interpreted as probably feather mites and regarded as possibly the oldest occurrence of ectoparasitism on feathered maniraptorans. It is the longest feather known from the Crato Formation and a little larger than all Cretaceous feathers reported until then, with a length of 85 mm.

Kellner & Campos (2000) noted that several morphotypes of feathers had been unearthed in the formation, with most being undescribed. They mentioned about two dozen, noting that their exact site of provenance was unknown. Although they suspected that all published specimens might have come from outcrops around Nova Olinda (as several specimens were, in any case) since in the past all the mining sites in the formation were in that area, the expansion of the quarrying activities in the region led to the opening of several new mining pits around Santana do Cariri and along the Nova Olinda–Santana do Cariri road. Thus, some of the newer specimens possibly came from them. Regarding their identity as avian or non-avian dinosaurs, they considered that down and flight feathers likely belong to birds, as “true downs” were not known in non-avian dinosaurs, and a strongly asymmetrical remex was more consistent with a well-flighted animal—though Bittencourt & Langer (2011: 28) noted that the occurrence of asymmetrical feathers in non-avian eumaniraptorans challenges this attribution. The nature of the other morphotypes remained inconclusive, but they also noted that they

did not know about semiplumes occurring in non-avian forms. The development of distinct coloration patterns known on some contour feather specimens was also highlighted, showing that artifices observed in modern species (such as behavioral and communicational) were likely present or had similar variants in this stage of dinosaur evolutionary history.

Kellner (2002) described a complete contour feather preserving banded color pattern, previously figured by Kellner & Campos. Additionally, he mentioned that several very small feathers (less than 20 mm), either down feathers or semiplumes, are housed in the American Museum of Natural History, New York, and MN.

Semiplumes frequently occur in the Crato Formation, with Naish *et al.* (2007) reported having examined some 20 or more, compared to only one possible remex and two or three symmetrical rectrices. These feathers are mostly small, being 10–20 mm long, but some larger ones are also present, with one reaching 22 mm.

Vinther *et al.* (2008) analyzed the part specimen of the banded feather originally described by Martill & Frey (1995) in a study about the color of fossil feathers, along with Eocene material from the Fur Formation of Denmark. By comparing the structure of black feathers of a living icterid, they interpreted the elongate, oblate carbonaceous bodies making up the dark bands of the Crato feather as eumelanin-containing melanosomes. Their observations indicated that structures present on fossil feathers previously reported as bacteria (as the second feather mentioned by Martill & Frey) are melanosomes, of which the distribution can preserve the color pattern of the original feather in the fossil. Thus, this study proposed that exceptionally preserved melanosomes were a more plausible scenario as the chief explanation for integumentary preservation in vertebrate fossils rather than lithified bacteria (Smithwick & Vinther 2020).

A down feather and a semiplume collected at Mina do Demar, on the road connecting Nova Olinda and Santana do Cariri, during the field season of 2009 by biology student Laiz Karla of CAV were briefly described by Sayão & Uejima (2009; 2010) and later figured by Sayão *et al.* (2011). Additionally, from the same locality, Sayão *et al.* (op. cit.) described a third feather with a morphotype similar to that of down or ornamental feathers. They also speculated on the nature of the covert feathers

in the deposit, relating their number, besides taphonomic aspects, to molting processes, and framed the described morphotypes to the developmental stages II (the third feather from Mina do Demar), III (semiplumes and down feathers) and possibly V (primary remex) defined by Prum (1999), still not confirming the presence of Aves in the deposit.

Eight seemingly contour feathers, an isolated specimen, and a set of seven feathers in the same block from Mina do Triunfo, in Nova Olinda, were reported by Leite & Hessel (2011). The set is unique as the only published example of this kind of conservation without associated osteological remains. Based on similarities with fossil feathers from the Early Cretaceous of Liaoning, China described by Zhang *et al.* (2006), the authors tentatively attributed the specimens to small non-avian dinosaurs, being possible contour feathers from the upper part of the hindlimbs. The set of seven feathers was analyzed by Campos *et al.* (2019) through combined microscopy and spectroscopy techniques, aiming minimal damage to the specimen, and their result confirmed the feather identity of the fossil, plus revealing eumelanosomes in its composition that indicate the feathers originally were dark-colored.

Prado & Anelli (2013) briefly described a semiplume and a down feather which were apprehended by the Brazilian Federal Police and the IPHAN and then deposited in the collection of the Laboratório de Paleontologia Sistemática of IGc/USP. They noted that the different feather morphotypes could represent ontogenetic stages or be interpreted as signs of intraspecific and behavioral relationships, such as the presence of neonates or parental care. Later, Prado *et al.* (2016a) described further these specimens, classifying both as down feathers and assigned them to Coelurosauria and presented an additional semiplume with the same origin as apprehension, which they referred to as Maniraptoriformes. They also developed on questions regarding taphonomy and paleoecology of the animals that provided the fossil feathers, speculating that the specimens initially described by Prado & Anelli were possible auricular feathers of a chicken-sized animal, while the third feather had both protective and thermoregulatory roles. Also, even though the evidence is lacking, possible roles in camouflage, communication, and sexual selection were suggested. They also speculated that birds might have lived by the shoreline of the Crato lagoon, which enhanced the probability of preservation of their remains. Finally, they developed on the absence of feathered

dinosaurian remains in the Romualdo Formation<sup>5</sup> (the second, younger lagerstätte in the Araripe Basin known for preserving soft tissues such as muscle fibers and blood vessels), which was possibly related to different taphonomic conditions. Overall, the IGc collection has 82 Crato feathers with origin as apprehensions (Prado, personal communication).

Additionally, Prado & Anelli (2015) performed SEM analysis in two feathers, one from the Crato Formation (GP/2E-8771) and other from the Tremembé Formation (GP/2E-8125) and found oblate microbodies in both fossils (not occurring in the matrix), which were interpreted as fossilized eumelanosomes. Most of them are “broken”, but indicate a high density and organization, varying in size from 500 to 1800 nm, morphologically suggesting an association with iridescent pattern. In accordance with the known environmental settings from both sites, dry and arid for the Crato and hot and humid for the Tremembé Formation, they suggested that dinosaurs from both units had dark or iridescent feathers, being well adapted to the ecological niches they occupied.

In his master dissertation, Metello (2017) analyzed the plumage of *Cratoavis cearensis* (see below) and described all the 45 isolated fossil feathers in the collection of UFRJ (though he figured only six), constituting 28 contour feathers, 8 plumes, and 9 semiplumes<sup>6</sup>, preserved as carbonized traces in all cases except for one preserved as an impression with a faded carbon contour. These specimens were collected between 2000 and 2016 in Mina Pedra Branca, in Nova Olinda, Ceará.

Fourteen fossil feathers were mentioned by Nascimento & Oliveira (2018), consisting of two from the collection of UFRPE, five from Museu de Paleontologia Plácido Cidade Nuvens of URCA in Santana do Cariri and seven from the Laboratório de Paleontologia of URCA in Crato. They were determined as five plumes, three semiplumes, and six contour feathers, all showing good preservation with identifiable rachises, barbs, and barbules, with two of them showing alternating color patterns.

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<sup>5</sup> Vidal & Campos (2008) mentioned birds among the material from the Romualdo Formation, possibly in error.

<sup>6</sup> Following the study's Table 1. There is some conflicting information regarding the feather's classification in the study, with two semiplumes being also regarded as contour feathers in some sections.

Other isolated reports of fossil feathers include that of Teixeira & Saraiva (2010). Several other unpublished examples are held in national and international collections, public or private. In addition, specimens taken illegally from Brazil can often be seen available for sale on foreign sites, such as a down feather costing \$1,100.00 in an American online shop.

### **5. 5. 3. Skeletal remains**

Skeletal remains were first mentioned and figured in literature by Naish *et al.* (2007), although these authors stated that this kind of fossil was already known from anecdotal accounts and personal observations. Two specimens were preliminary described, the first consisting of feathers associated with presumed carpal bones and deposited in the Senckenberg Museum in Frankfurt. The second consists of a poorly preserved partial skeleton with associated feathers, held in the private collection Masayuki Murata (MURJ) in Kyoto. By 2006, Martill and four other researchers were disputing the private museum's permission to describe the fossil, which was considered the oldest Gondwanan avian fossil known from skeletal remains (if indeed representing a basal bird), but only photographs became available. It reportedly reached Japan through Germany, being sold for US\$ 100.000 (Amorim 2006).

Herzog *et al.* (2008) reported rumors of a nearly complete and excellently well-preserved avian skeleton sold and smuggled out of the country, with no information about its destination. It is unclear whether this refers to the MURJ specimen (as they do not cite Naish *et al.*) or another trafficked specimen. The first seems more likely.

A fully articulated skeleton associated with feathers of a very small euenantiornithean bird was firstly described by Carvalho *et al.* (2015a) and further by Carvalho *et al.* (2015b), who classified it as the new genus and species *Cratoavis cearensis*. It is the first Mesozoic bird named from Brazil and the Early Cretaceous of South America and the most complete avian specimen of this age known from Gondwana. The fossil was found in Mina Pedra Branca by Cleudson Dias, Devânio Ferreira Lima, and Antonio Josieudo Pereira Lima, who provided it to the authors to be studied. The specimen preserved long, rachis-dominated rectrices in relief, shedding light on the anatomical structure and probable function of this feather

morphotype, previously known only from two-dimensional slabs and unknown among living birds, assisting, for example, in the determination of fossil material with complicated history as a true feather of this kind (Agnolin *et al.* 2017b). Possibly, some color patterning was also preserved in the form of a row of lunar transversal bands in the tail feathers that, despite the specimen's possible juvenile nature, resemble the feathering of modern adult birds. A South American record of this type of tail feathering also broadened this morphotype's paleobiogeographic distribution, which was only reported until then from China.

In 2020, it was reported that researchers at the LACEV (Laboratorio de Anatomía Comparada y Evolución de los Vertebrados) of MACN were working on new contributions on the Early Cretaceous birds from Brazil (SAPE 2020). In the next year, Carvalho *et al.* (2021) described as an ornithuromorph the new genus and species *Kaririavis mater* from an isolated foot found in Mina Pedra Branca, adding to the otherwise enantiornithean-restricted avifauna of the Crato Formation. This small bird possibly belongs to an unknown clade with some cursory similarities to extant flightless ratites and represents the oldest known ornithuromorph for Gondwana. This record in South America demonstrates that basal ornithuromorphs were present and probably diversified in the southern hemisphere by the Aptian.

## **5. 6. Bauru Group (SE Brazil)**

### **5. 6. 1. General information**

The Bauru Group (*sensu* Soares *et al.* 1980) is the most widespread continental rock unit with vertebrate remains of Cretaceous age in South America, being exposed over an area of 240,000 km<sup>2</sup> in western São Paulo, western Minas Gerais, northwestern Paraná, east Mato Grosso do Sul, and south Goiás (Bertini *et al.* 1993; Candeiro 2005; Bittencourt & Langer 2011).

Four formations proposed by Soares *et al.* (1980) are traditionally recognized constituting the Bauru Group as part of the Paraná Basin (in ascending order): Caiuá, Santo Anastácio, Adamantina and Marília, with the last two being richly fossiliferous (Bertini *et al.* 1993). The view of these deposits as an individualized Bauru Basin was proposed by Fernandes & Coimbra (1996), who erected the Caiuá Group, divided into

Santo Anastácio, Rio Paraná and Goio Erê Formations, and the Bauru Group, divided into Adamantina, Uberaba and Marília Formations. A new review by Fernandes & Coimbra (2000) and Fernandes (2004) divided the Bauru Group into the Uberaba, Marília, Vale do Rio do Peixe, Araçatuba, São José do Rio Preto and Presidente Prudente Formations (the last four once making up the former Adamantina Formation). These different views regarding its tectonic context and stratigraphic units pose problems while referring to earlier fossil findings into these new units of more elaborated stratigraphic frameworks, resulting in most paleontological works still relying on the traditional nomenclature (Bittencourt & Langer 2011). Avian material has been associated in the literature to the Adamantina (and its dismembered formations) and Marília Formations of São Paulo and Minas Gerais.

The Adamantina Formation is generally regarded as Campanian–Maastrichtian in age, but an older Turonian–Santonian age was also suggested, based on its vertebrate fossil remains (Dias-Brito *et al.* 2001; Bittencourt & Langer 2011; Candeiro *et al.* 2013); nevertheless, its origin in different depositional cycles and some faunal elements suggest it congregates rocks of significantly different ages with still poorly sampled individual biotas (Bittencourt & Langer 2011). The unit encompasses aeolian, lacustrine and fluvial deposits formed under a warm, seasonal and arid to semi-arid climate intercalated with more humid intervals (Bittencourt & Langer 2011). It is exposed in the States of Goiás, São Paulo and in the Triângulo Mineiro region of Minas Gerais, and, based on its vertebrate remains, it was deposited during the Turonian–Santonian (Dias-Brito *et al.* 2001; Candeiro *et al.* 2013). Although occurring over a large geographic area, both the Adamantina and Marília Formations present very few natural exposures, with fossil localities being site-specific and restricted. Most fossils have been collected during the construction of roads and railways and excavations of buildings and wells (Bertini *et al.* 1993). The Adamantina Formation is predominantly composed of reddish clays and sands of fluvial-lacustrine origin (Bertini *et al.* 1993; Candeiro *et al.* 2013). The Adamantina Formation is about 190 m thick (Bertini *et al.* 1993); maximum nearly 200 m (Candeiro *et al.* 2013). Studies in sedimentology suggest that the Adamantina Formation was deposited in a warm, humid climate (Bertini *et al.* 1993).

The Marília Formation is generally attributed to the Maastrichtian (Dias-Brito *et al.* 2001), being exposed in Goiás, São Paulo and the Triângulo Mineiro region of



Minas Gerais (Candeiro *et al.* 2013). It is divided into three members: the Serra da Galga and Ponte Alta, both restricted to the Triângulo Mineiro region, and Echaporã, exposed in Goiás and São Paulo (Candeiro *et al.* 2013). The unit is composed of alluvial fans associated with braided canals and subordinated levels of aeolian sediments and calcrete (Bittencourt & Langer 2011). The Marília Formation is dominated by whitish calcareous conglomeratic sandstones of fluvial origin (Bertini *et al.* 1993). The Marília Formation is about 160 m thick (Bertini *et al.* 1993), 180 m in Minas Gerais (Fernandes & Coimbra 1996). Studies in sedimentology suggest that the Marília Formation was deposited in relatively drier conditions (Bertini *et al.* 1993). It consists of fine to medium sandstones intercalated by conglomerate levels (Candeiro *et al.* 2013). The Marília Formation consists of a sequence of coarse to conglomeratic sandstones, mudstones and carbonate layers (Martinelli & Teixeira 2015).

Vertebrate fossils from the Bauru Group were firstly reported in 1911, with only large terrestrial vertebrates being extensively discovered until the end of the 1980s (Bertini *et al.* 1993). It contains one of the richest Late Cretaceous vertebrate assemblages of Brazil and it includes theropod and sauropod dinosaurs, crocodylians, turtles, and fishes, with relatively rarer occurrences of anurans, squamates, and mammals (Candeiro 2005). Invertebrate remains include bivalves, crustaceans, worm burrows and tubes, and the fossil flora includes charophytes, spores, gymnosperms and angiosperms (Bertini *et al.* 1993).

Bird remains are uncommon in the Bauru Group (Azevedo *et al.* 2007). Chiappe (1991) mentioned an unpublished fragmentary proximal end of an avian carpometacarpus from the Bauru Formation through communication with Alvarenga in 1988. Later (Chiappe 1996), he was informed by Alvarenga that the Cretaceous material was contaminated, and the bone belonged to the extant *Coccyzus americanus* (Linnaeus). True fossil avian material was only discovered beginning the next decade in localities in São Paulo and Minas Gerais.

### **5. 6. 2. São Paulo**

The first true Mesozoic bird osteological remains from Brazil were revealed to the public on 10 August 2005 during the II Congresso Latino-Americano de Paleontologia

de Vertebrados in Rio de Janeiro. They were found just two months before in a site of 2 x 1 m and 50 cm deep discovered in September 2004 by paleontologist William Roberto Nava (MPM), who studied them along with Herculano Alvarenga (MHNT) (Castilhos 2005; Thomé 2005; Chiappe *et al.* 2018a). Alvarenga & Nava (2005) reported the occurrence of three to four different sparrow-sized enantiornithean taxa from the Adamantina Formation of Presidente Prudente (Fig. 2.2), based on dozens of well-preserved, isolated, and partially articulated bones showing no evidence of reworking. The material is very similar to *Enantiornis leali* Walker from the Late Cretaceous of El Brete, Argentina, but no new taxa were named due to difficulties in associating the bones.

More material was discovered in hundreds of excavation trips—about 2,000 bones of dozens or even hundreds of individuals of small to medium-sized taxa (Chiappe *et al.* 2018a; 2018b; 2019; Fonseca 2019a), and in 2015, during a paleontological event in Uruguay, Nava and paleontologist Luis M. Chiappe (Natural History Museum of Los Angeles County) formed a partnership to study the material, with Alvarenga and paleontologist Agustín G. Martinelli (MACN) also contributing. Chiappe visited the region two times in 2017 and a third time in 2018 along with fossil preparator Maureen Walsh and illustrator and photographer Stephanie Abramowicz (Prefeitura de Marília 2018). He returned in 2019 when more material was found in the fourth excavation phase (the second along with American and Argentinean researchers), which also integrated technician Guillermo Aguirrezabala and doctorate student Sebastián Rozadilla (MACN), as well as technician Jonatan Kaluza (Fundación Félix de Azara) from Argentina (Fonseca 2019a; Tomazela 2019).

The site, located in an urban public plot in the district of Parque dos Girassóis, was firstly dubbed “Enantiornithes outcrop” (Nava 2013; 2015) and later “William’s Quarry” (Chiappe *et al.* 2018a; 2018b; 2019), with the fossils being concentrated in a very small area of about 6 m<sup>2</sup> of red-pink fluvial sandstones and claystones, possibly as the result of a catastrophic event (Nava *in* Lopes 2020). It also provided, in smaller numbers, remains of other small vertebrates such as fishes, anurans, chelonians, squamates (including the new lizard *Brasiliguana prudentis* Nava & Martinelli), and teeth of mesoeucrocodylians and theropod and sauropod dinosaurs, besides gastropods and coprolites (Nava 2013; 2015; Nava *et al.* 2015; Fonseca 2019a). The site constitutes

the most abundant Mesozoic avian locality in the Americas and the richest of the Late Cretaceous age globally. It provides critical information for contrasting hypothesis of avian diversification during the Cretaceous–Paleogene transition and the earliest divergences of modern birds, indicating, along with other contemporary Gondwanan localities, a notable abundance of enantiornitheans during the interval of 80–70 million years BP, which is difficult to reconcile with the hypotheses of a southern hemisphere origin for neornitheans during this time (Chiappe *et al.* 2018a; 2018b; 2019).

The site also provided the first confirmed examples of toothed birds from the Late Cretaceous of South America, adding important information to its otherwise meager cranial anatomy knowledge (Nava *et al.* 2015). Wu *et al.* (2019; 2021) performed micro-computer tomography ( $\mu$ CT) imaging on a premaxilla and a partial dentary to understand the occurrence of polyphyodonty in Mesozoic birds better, with the results indicating a conserved pattern in archosaurs as the alternating tooth replacement pattern of toothed birds is shared with that of crocodylians. They also developed a new morphologic framework for organizing tooth diversity in enantiornitheans that can be applied to other toothed avian clades to understand dental evolution in stem birds better.

Due to its importance, Nava and the associated researchers first requested the Presidente Prudente city managers to protect the site during the first phase of group excavations in May 2017 (Fonseca 2019a; 2019b). The protection was granted in a municipal decree on 14 February 2020 and the site area was fenced on 28 July 2020, with the city intending to transform it into a paleontological park (Prefeitura de Presidente Prudente 2020).

Azevedo *et al.* (2007) reported a phalanx fragment of a possible bird among microvertebrate material collected through screenwashing technique at the Jales locality in Furnas Farm of Adamantina [Vale do Rio do Peixe] Formation in Alfredo Marcondes, western São Paulo state (Candeiro 2015; Alves *et al.* 2016), which shows sandstone sediments that are reddish, sometimes conglomeratic, and cemented by calcium carbonate. The fossil was collected in 2001 during an expedition led by paleontologist Lílian Paglarelli Bergqvist (UFRJ).

Marsola *et al.* (2012) reported the first Mesozoic avian egg from Brazil, found in July 2011 in a well-defined intraformational conglomerate level exposed within white-reddish sandstones attributed to the Vale do Rio do Peixe Formation along road SP-270, near the municipality of Álvares Machado. The nearly complete specimen was attributed to a basal Ornithothoraces and is one of the smallest known Mesozoic bird eggs (Marsola *et al.* 2012; Marsola 2013; Marsola *et al.* 2014).

Other studies include Cardia (2019), which featured bird remains in the Bauru Group vertebrate material analyzed for mercury concentrations aiming at trophic chain reconstructions. Taranto *et al.* (2010) mentioned bird remains among the material collected starting in 2002 in Presidente Prudente Formation in the municipalities of Flórida Paulista and Alfredo Marcondes. Pinheiro *et al.* (2019) mentioned bird material among fossils collected in Presidente Prudente Formation (likely in William's Quarry) during field work organized by Faculdade de Formação de Professores of UERJ in 2019.

### **5. 6. 3. Minas Gerais**

The first record of Cretaceous bird material from Minas Gerais was that of Candeiro *et al.* (2010), who reported an isolated pedal phalanx of an indeterminate Aves of Late Maastrichtian age from the Serra da Galga Member of the Marília Formation in the municipality of Uberaba in the Triângulo Mineiro region, which contains one of the richest Late Cretaceous continental biotas in Brazil (Candeiro *et al.* 2013). Candeiro *et al.* (2012) added an ungual phalanx of indeterminate Aves and a metatarsal of a possible Enantiornithes. The specimens were found during screen washing performed by the CPPLIP from 2009 in “Ponto 1 do Price” site of Peirópolis locality. The material is similar in degree of incompleteness to the material from the Adamantina Formation of Jales locality in São Paulo. The Peirópolis area provided a diverse Late Cretaceous fauna, including bivalves, ostracods, fishes, turtles, lizards, mesoeucrocodylians and theropod and sauropod dinosaurs. Rédua *et al.* (2016) hypothesized that these birds possibly fed on small freshwater or terrestrial invertebrates.

On the lack of avian records from the Adamantina Formation in the Triângulo Mineiro region, Candeiro (2015) pointed that this is probably associated with the lack of more intensive prospecting in that unit.

## 5. 7. Further records

Besides these sites, several others in the country harbor fossil and subfossil material of birds. The most notable ones with the material described to the family level will be cited in the following subsections, with further details available in the records accounts. Indeterminate fragments of varying temporal and spatial distribution were reported in the literature, and as many examples as possible will be cited in the following paragraphs. This is not an exhaustive survey of every mention of bird material, which permeates the literature, especially the archeological, in a vast and decentralized manner.

- **Acre:** Late Miocene of Morro do Careca site, BR-364 (Souza-Filho & Guilherme 2015).
- **Alagoas:** Pleistocene of Picos II site (Oliveira *et al.* 2013; Silva *et al.* 2013).
- **Bahia:** Pleistocene of Gruta Ioiô (Langer *et al.* 2013); Quaternary of Gruta dos Ossos (Oliveira *et al.* 2016).
- **Goiás:** Archeofaunal remains from the early Holocene of GO-JA-01 site, Serranópolis (Schmitz 1990; Dias 2004).
- **Minas Gerais:** Quaternary of Lagoa Santa region (Winge 1887); Holocene of Lapa do Marciano, Pedro Leopoldo (Walter 1958); Quaternary of Lapa Vermelha (Souza Cunha & Guimarães 1978); Quaternary of Lapa do Carroção, Pedro Leopoldo (Veloso 1983; Veloso & Resende 1992); Quaternary of Gruta do Pomar, Matozinhos (Cartelle *et al.* 1998); Quaternary of Gruta Cuvieri, Matozinhos (Hubbe 2008; Perez 2009; Hubbe *et al.* 2011; Mayer 2011); Gruta do Janelão (Ferreira *et al.* 2005); Lapa do Carlúcio (Oliveira 2008); Holocene of Lapa do Santo, Matozinhos (Perez 2009; Mingatos 2017); Holocene of Lapa das Boleiras, Matozinhos (Kipnis *et al.* 2010a; 2010b); Holocene of Lapa Grande do Taquaruçu, Jaboticatubas (Chim 2018).

- **Mato Grosso:** Holocene of Santa Elina rock shelter (Figuti 2005; Vialou 2005).
- **Pará:** Archeofaunal remains from the early Holocene of Caverna da Pedra Pintada, Monte Alegre (Roosevelt *et al.* 1996; Dias 2004).
- **Pernambuco:** Late Pleistocene tanks of Lagoa da Pedra, Conceição das Crioulas, Salgueiro (Guérin 1993).
- **Piauí:** Quaternary of Toca da Janela da Barra do Antonião, Coronel José Dias (Guérin *et al.* 1993a; 1993b; 1996; Moraes 2014); Toca da Baixa das Cabaceiras, Parque Nacional Serra da Capivara (Guidon *et al.* 2009a).
- **Rio de Janeiro:** Holocene of Sambaqui do Forte, Cabo Frio (Kneip *et al.* 1975); Holocene of Sambaqui do Zé Espinho (Vogel 1987); Holocene of Saco and Madressilva sambaquis (Kneip *et al.* 1997); Holocene of Beirada, Moa, and Pontinha sambaquis (Kneip *et al.* 1994; 1995; 1997; Kneip 2001; Magalhães *et al.* 2001); Holocene of Sambaqui de Sernambetiba (Rodrigues *et al.* 2013).
- **Rio Grande do Norte:** Various taxa from the Pleistocene of Olho d'água da Escada, Mossoró (Souza Cunha 1962; 1966; 1978); Holocene of Pedra do Alexandre site (Silva 2014).
- **Rio Grande do Sul:** Late Pleistocene of Sanga da Cruz (Oliveira 1999; Kerber & Oliveira 2008b); Holocene of Vale do Rio dos Sinos (Dias 2004).
- **São Paulo:** Quaternary of Abismo Ponta de Flecha, Iporanga (Chahud 2001).

### **5.7.1. Natural tanks in Itapipoca (CE)**

Natural tanks with associated fossiliferous deposits are found throughout Northeast Brazil and primarily preserve late Pleistocene megafauna remains (Ximenes 2009). Bird remains are rare in these sites, with just a handful of records in the literature.

During January and February 1961, an MN expedition led by paleontologist Carlos de Paula Couto with the collaboration of geologist Fausto Luiz de Souza Cunha took place in the João Cativo paleontological site in Itapipoca, Ceará. They recovered bird material in a tank deposit (tank “2”) and roughly reported it as indeterminate

neognath orders and genera in their expedition reports, being the first records of bird fossils for the Northeast region of the country (Souza Cunha 1961; Paula Couto 1961). Later, part of this material was associated with the genus *Rhea* (Paula Couto 1962; 1980) and a hawk (Metello & Araújo Júnior 2013). However, as other materials deposited in MN, their current status is not known.

Also, in Itapipoca, another tank deposit in the Jirau paleontological site (tank “1”) provided indeterminate bird material during work done between 2003 and 2008 by Celso Lira Ximenes and Antônio Sílvio Teixeira dos Santos (Araújo Júnior 2012; Araújo Júnior *et al.* 2013).

### **5.7.2. Gruta dos Brejões and Toca da Boa Vista (BA)**

The paleontologist Castor Cartelle (PUC Minas, then UCMG) and his team collected numerous quaternary bird bones associated with mammalian fauna from caves in middle east Brazil in the 1980s (Mourer-Chauviré 1988: 4). In 1980 and 1984, 2,000 bird bones (Cartelle & Santos 1985; 1,800 according to Penido *et al.* 2012) were collected in Gruta dos Brejões (Fig. 2.10), in the municipality of Morro do Chapéu, Bahia. The roof collapse in three points along the eleven kilometers of the cave created openings that facilitated the access to birds, especially in the area dubbed “Salão das Aves”, where most of the material, belonging to non-cave dwelling families, was found. In addition, many small bones interpreted as disaggregated from owl pellets by water infiltration were also found in the same area. By 1983 this material already numbered more than 900 pieces and was being studied by the ornithology team of UFMG-UCMG (Cartelle 1983). Cartelle & Santos (1985) reported a complete ciconiid skeleton and 33 skulls belonging to nine families. By 1988 this material was taken to Taubaté by Cartelle’s student José Enemir dos Santos to be analyzed in collaboration with Herculano Alvarenga (Mourer-Chauviré 1988: 4). By 2012 it was still being revised, and three taxa were determined to the species level, including the extinct condor *Wingegyps cartellei* (Alvarenga & Olson 2004; Silva *et al.* 2012b; Penido *et al.* 2012).

Unregistered and unidentified quaternary bird fossils are included in the paleontology collection of the MHNJB/UFMG (Greco & Cozzuol 2012). From Toca da Boa Vista in Campo Formoso, Bahia, some advance was made regarding the cataloging

and determination of material collected in the 1980s by Cartelle and his team (Silva 2010, not consulted by us; Cozzuol, personal communication). Silva & Cozzuol (2010) reported seven taxa associated with dry savannas, of which the preservation status suggested an age between the late Pleistocene and Holocene. Unfortunately, the MHNJB suffered a fire on 15 June 2020, but the paleontological collection was not affected (Cozzuol, personal communication).

### **5.7.3. São Raimundo Nonato region (PI)**

Guérin *et al.* (1993a; 1993b) briefly reported avian remains of quaternary age from the rock shelter Toca da Janela da Barra do Antonião, in the municipality of Coronel José Dias, São Raimundo Nonato archeological area (Fig. 2.11), southeastern Piauí. It is the most important one of the hundred cavities situated in a reduced karstic area in the southeastern vicinity of the Parque Nacional Serra da Capivara, which provided a wealth of archaeological and paleontological remains and paleoclimatic indicators. Discovered in 1986, this large rock shelter was excavated up to 1990 by archeologist Niède Guidon. It further provided a rich pleistocenic fauna, human burial, rock paintings and lithic tools associated with megafaunal remains (Guérin *et al.* 2002). Cenizo *et al.* (2015) followed an age of  $9670 \pm 140$  years BP to this avian assemblage based on data by Martin (1996).

The avian remains come mainly from the superficial levels of sector C (0.05–0.50 m deep) and from the surrounds of a human skeleton with age estimated at about 9.700 years old (0.55 m deep), as well as from slightly deeper levels of sectors A and B (0.74–1.37 m deep). No significant differences were observed between the composition of these two parts of the deposit other than that the superficial levels of sector C are richer and more diversified.

Due to the lack of comparative material for the living South American avifauna in European osteological collections, it was not possible for them at that moment to determine the material in the generic and specific levels. Later, with the aid of American collections, Guérin *et al.* (1996) preliminarily reported, besides indeterminate Passeriformes, 32 taxa (Simões [2001] later reported the total number to be 42). Though minimum numbers of individuals, both adult and young, were provided for most taxa,



no skeletal elements and their conservation status were specified, nor where the material was deposited. Guérin *et al.* (1993a) included, in the preliminary report, the occurrence of Phasianidae among the material, a record which was not present in their other publication of the same year nor in the one of 1996.

Most of the recorded taxa can still be found living in the Parque Nacional Serra da Capivara and adjacent areas, with the absence of some taxa today possibly indicating environmental changes that caused some reduction of forested areas. There is also a notable scarcity of aquatic forms among the rock shelter material when compared to the living avifauna (two versus 12 families, respectively), possibly due to alimentary preferences of the ancient human inhabitants or the raptorial birds responsible for the accumulation of the material, as aquatic and semiaquatic mammals and large amphibians are well represented.

More avian materials from levels 1 and 3 of sector A of Toca da Janela da Barra do Antonião were later reported by Moraes (2014), including apparently burned indeterminate material. She also attributed to owls' the pellets of small rodent bones found in the same site.

The surprising absence of *Rhea* among the remains of Toca da Janela do Antonião was noted by Guérin *et al.* (1993b; 1996), which is well represented in the Nordeste Tradition rock paintings dated between 12.000 and 6.000 years, although it no longer occurs in the region today. From Toca do Serrote das Moendas, a new site also in the vicinity of Parque Nacional Serra da Capivara that began to be excavated in 2006 under the direction of Elaine Ignacio, Guidon *et al.* (2009b) firstly mentioned the finding of *Rhea*<sup>7</sup> as part of a rich late Pleistocene fauna associated with human remains and lithic tools. Later, Faure *et al.* (2010) associated the fossil with *Rhea fossilis*, a species first described from Argentina. Remains of *Blastocerus* and *Hydrochoerus* were also firstly unambiguously reported from these deposits. The nature of this publication, in a volume specialized in rock art, prompted this record to be largely ignored in publications concerning the bird fossil diversity in Brazil.

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<sup>7</sup> Faure *et al.* (2010) stated that this is the first record of the genus for the Brazilian Northeast but seems to have overlooked Paula Couto (1980).

#### **5.7.4. Entre-Córregos Formation (MG)**

The Aiuruoca Basin, located between the northern border of Serra da Mantiqueira and southern border of Serra de Minduri, in Planalto do Alto Rio Grande, southern Minas Gerais is composed of the Entre-Córregos and Pinheirinho Formations, and was firstly described by Santos (1999). Its sedimentary packing suggests it was deposited on a terminal lacustrine system (Bedani & Haddad 2002).

The Entre-Córregos Formation (Fig. 2.5) is fossiliferous and is composed of pelite, in the form of shales with argillite intercalations. Its remains are characterized by plant megafossils, insects, fishes, anurans, coprolites, and palynomorphs (Bedani & Haddad 2002; Franco-Delgado & Bernardes-de-Oliveira 2004). These palynomorphs indicate an Eocene–Oligocene age for the outcropping section of the Formation (Garcia *et al.* 2000), and the leaf architecture of the plant fossils indicate the region had high temperatures and wet weather (Castro-Fernandes *et al.* 2013).

Among these remains there is also the presence of some fossil feathers. They occur in the medium-gray argillaceous, papyraceous shales in the 1.42 m thick basal layer of the Formation, along with rare plant material, fishes, and insects, and abundant pipid anurans. They have been collected in the area of the left margin of the Entre-Córregos creek near the road that connects the municipalities of Minduri, Cruzília, Andrelândia, São Vicente de Minas, and Aiuruoca (Bedani & Haddad 2002; Franco-Delgado & Bernardes-de-Oliveira 2004). Brief mentions exist in the literature (Bedani & Haddad 2002; Franco-Delgado & Bernardes-de-Oliveira 2004; Castro-Fernandes *et al.* 2013), but unfortunately, these specimens do not seem to have been described in detail nor figured anywhere. Nevertheless, they attest to the presence of birds in these deposits and give hopes of future finds of osteological material.

#### **5.8. Brazilian contribution to international research**

Brazilian researchers also contributed to international research on fossil birds. Alvarenga published on a flightless bird from the Cretaceous of Argentina (Alvarenga & Bonaparte 1992), on an anhingid from the Miocene of Chile (Wall *et al.* 1991; Alvarenga 1995a), and a phorusrhacid from the Pleistocene of Uruguay (Alvarenga *et al.* 2010). Paleontologists Douglas Riff and Alexander Kellner published on an avian

vertebra from the Cretaceous of Morocco (Riff *et al.* 2004). Ornithologist Luís Fábio Silveira published on an aquatic twig-nest with phoenicopteriform eggs from the Miocene of Spain (Grellet-Tinner *et al.* 2012). Paleontologist Ismar de Souza Carvalho published on a fossil feather from the Jurassic of Kazakhstan (Agnolin *et al.* 2017b).

## 5.9. Other studies on prehistoric avifauna

Inferences about the prehistory of the avifauna in the country were also made from other sources than physical remains. Yamashita (1997) hypothesized that *Anodorhynchus* macaws were followers of giant herbivorous mammals during the Pleistocene—dubbed as anachronistic survivors by Agnolin (2016b), consuming the palm nuts stripped off the pulp by them and that this conservative and primitive behavior is now present again in their association with the domestic cattle introduced in their native range, which similarly affects the landscape. Among other factors, the *Anodorhynchus* material from the Lagoa Santa region, with its well-documented extinct mammalian megafauna, was cited to support the hypothesis.

The presence of prehistoric rock paintings made by the ancient human inhabitants of the territory now corresponding to Brazil also testify to the presence of these animals, together with biological remains. Naturally, most identifications are tentative, but in sites where multidisciplinary studies have been taken place some paintings could be assigned to family or genus level. Rhea-like figures are abundant in Northeast rock shelters, such as those from the São Raimundo Nonato region (e.g., Guidon 1991; Pessis 2003; Faure *et al.* 2010), a flamingo-like figure was found in São Rafael, Rio Grande do Norte (Souza & Medeiros 1982), and a macaw-like figure was found in Serranópolis, Goiás (Dias 2004), among others, often generic-like representations throughout the country (e.g. Silva *et al.* 2007). Besides rock paintings, other artistic manifestations also testify to the presence of birds, such as the zoomorphic figures found in sambaquis (1997). A thorough, multidisciplinary review of these records will certainly contribute to the understanding of the biology, biogeography, and relationship with humans of late Pleistocene-early Holocene avifaunas of Brazil.

## 5.10. Osteological studies

Osteological studies are fundamental sources of information for avian comparative anatomy, systematics, phylogeny, paleontology, archeology, biomechanics, and functional anatomy (Sick 1997: 86; Olson 2003; Höfling 2004). Unfortunately, the field is still developing at a slow pace in Brazil, despite showing indications of growth since the beginning of the 2000s (SAPE 2002). The lack of comparative collections is a determining factor (Alvarenga 1992), as are the few avian anatomists, who work mainly with living taxa (Höfling 2004). Today, the country's five largest bird skeleton collections are held, beginning from the largest, in MHNT, PUC-MG, MZUSP, MNRJ, and MPEG. A significant part of the work developed in this field results of undergraduate and graduate programs (Borges 2008; Mallet-Rodrigues 2016), especially at Universidade de São Paulo (in São Paulo) and Universidade Estadual Paulista (in Botucatu).

The following groups are included among articles and theses (those of which were not published as articles) dealing with non-paleontological and non-veterinary osteology (not including conference abstracts), with examples of studies: Tinamiformes (Silveira & Höfling 2007), Anseriformes (Previatto 2012), Galliformes (Silveira 2003; Marceliano *et al.* 2007c), Columbiformes (Andrela & Donatelli 1995; Marceliano *et al.* 2007b), Cuculiformes (Posso & Donatelli 2001; Posso & Donatelli 2005; Posso & Donatelli 2006; Posso & Donatelli 2007; Posso & Donatelli 2010), Nyctibiiformes (Mahecha & Oliveira 1998; Höfling & Alvarenga 2001; Costa & Donatelli 2009; Costa 2014; Costa *et al.* 2017; Costa *et al.* 2021), Caprimulgiformes (Höfling & Alvarenga 2001; Costa 2014), Apodiformes (Höfling & Alvarenga 2001), Opisthocomiformes (Marceliano 1996), Gruiformes (Marceliano *et al.* 1997; Alves 2012b), Eurypygiiformes (Marceliano *et al.* 2007a), Procellariiformes (Dénes & Silveira 2007), Ciconiiformes (Guzzi 2007; Guzzi *et al.* 2014a; Santos *et al.* 2018; Oliveira *et al.* 2019), Pelecaniformes (Ferreira & Donatelli 2005; Ferreira 2007; Silva 2011), Cathartiformes (Brito 2008), Accipitriformes (Migotto 2008; Migotto 2013), Strigiformes (Mahecha & Oliveira 1998; Höfling & Alvarenga 2001; Salomão 2015), Coliiformes (Höfling & Alvarenga 2001), Trogoniformes (Höfling & Alvarenga 2001), Coraciiformes (Calonge-Méndez 1998; Flausino *et al.* 1999; Höfling & Alvarenga 2001; Pascotto & Donatelli 2003; Pascotto *et al.* 2006a; Pascotto *et al.* 2006b; Calonge-Méndez &

Höfling 2007), Galbuliformes (Donatelli 1992; Alvarenga *et al.* 2002; Ladeira & Höfling 2007; Posso *et al.* 2020), Piciformes (Höfling & Gasc 1984a; Höfling & Gasc 1984b; Höfling 1991; Höfling 1995; Donatelli 1996; Höfling & Alvarenga 2001; Donatelli 2012a; Donatelli 2012b; Novaes 2013; Araújo 2014; Caldas *et al.* 2019), Falconiformes (Silva *et al.* 2012a; Guzzi *et al.* 2014b; Guzzi *et al.* 2015a; Guzzi *et al.* 2015b), Psittaciformes (Porto 2004; Gaban-Lima 2007; Ferraroni 2015), and Passeriformes (Donatelli 1997; Höfling & Alvarenga 2001; Almeida 2003; Calonge-Méndez 2004; Donatelli & Marceliano 2007; Cid 2011; Araújo 2012; Previatto & Posso 2015; Guzzi *et al.* 2016). Additionally, Aires (2019) and Aires *et al.* (2021) worked with the osteology of both fossil and living birds.

## **6. CATALOG OF RECORDS**

In this section, the records of fossil and recent material attributed to birds (and those of dubious attribution) in the literature obtained from our survey are listed, in addition to some unpublished material present in collections.

### **6.1. Composition**

The records are grouped herein according to the political geographical unit established as the Brazilian territory, thus being an artificial composition. Chronologically, they range from the emergence of the Aves clade (although its definition is problematic [Mayr 2016]) to recent (archeological) material (Table 3), including bone remains, feather impressions, eggs, coprolites, traces, and mummifications, found in cave, tank, lake, fluvial and coastal deposits. Fossil feathers of uncertain determination, which may represent non-avian dinosaurs, were also included and flagged as such.

There is an unaccounted quantity of remains awaiting study in several Brazilian institutions (and even outside the country), and these, naturally, are not included in this study when not mentioned in the literature. Furthermore, this study does not intend to be a complete catalog of all material unearthed in Brazil since this is not a possible task but rather the closest approximation as possible to this objective.

Great efforts were made to cover as much as possible of the literature regarding the remains of birds, fossil and recent, discovered in Brazilian territory. However, since

the recent (archeological) material is more obscurely mentioned in the literature, it is more likely that some records have not been included here as a result. Taxa determined in the species level are most likely to be included, and, therefore, the coverage of this type of occurrence is biased, in addition to the biases that already exist regarding this kind of material inside archeological methods.

Considering the occurrence of certain groups in North America and southern South America, such as the Presbyornithidae (Mourer-Chauviré 1999; Agnolin 2016b), it is very likely that they also occurred in Brazil, although fossils were not found so far. Alvarenga (1993b: 21), emphasizing the enormous wingspan (about 6 m) of *Argentavis magnificens* Campbell & Tonni (Miocene of Argentina), commented that “it is reasonable to accept that this giant also flew over Brazilian territory”. Odontopterygiform birds, besides a dubious record (see below), likewise inhabited the territory, considering they were recorded throughout the globe, with South American records in Chile, Peru and Venezuela (e.g., Chávez *et al.* 2007; Mayr & Rubilar-Rogers 2010; Solórzano & Rincón 2015).

Despite some material attributed to indeterminate birds, historical and noteworthy records will be discussed in proper accounts (e.g., indeterminate material from Itaboraí Basin).

## 6.2. Notes on descriptions

Each record account is structured as follows: the general number in this study, the designation used in this study, the temporal (geological period) and spatial (Brazilian State) source, the type locality and etymology for extinct described taxa, a chronological synonym list, and the descriptive text.

A “†” preceding a determination indicates the taxon is confirmedly extinct. It is not adopted when the material is not determined with security. A “?” after the determination of a taxon indicates the attribution of such a name is uncertain. A “cf.” before a genus or species indicates the material is comparable, but not securely determined, to such taxon. A “(spp.)” following a determination indicates that multiple indeterminate species-level taxa are included in that record. Different indeterminate

records with the same designation (e.g., “Passeriformes indet.”) are numbered and ordered first geochronologically and then by their first mention in the literature.

The items in the synonym lists include the name the record was referred to (generally the most exclusive term in the publication; vague terms such as “bones” or “feathers” are avoided when known to refer to several specimens previously mentioned with most exclusive names) and the author, year and page (that describes the material or name it) of the publication (including theses and conference abstracts), besides figures (abbreviated as “fig.” or “figs.”) and plates (abbreviated as “pl.” or “pls.”) when available. Tables are not included. The criteria for inclusion of names in the synonym lists are based on the most important publications within ornithology and paleontology, on publications of historical importance, and/or on publications that differ from the current dominant designation for such material. The valid taxonomic binominal name originally used to describe the taxon stands out in bold. A name followed by “[in part]” indicates that such designation refers to only a part of the total material included in that record. A name followed by “[?]” indicates that such designation is tentatively attributed to that record.

As the bird fossil record in Brazil and its history are fluid, we refrained from following a rigid scheme of standardization in the descriptive texts, as would be sectioning them into topics. Instead, the descriptive text of the extinct taxa follows the basic script for presenting data on the fossil material’s discovery, its known elements and collection in which it was deposited (generally only once for numerous collections such as Lund’s), and, finally, data related to its classification, related species, biology, and other observations. Regarding the extant taxa present in the fossil record or cases of information scarcity (as in indeterminate remains), generally, only one paragraph is adopted summarizing the available data. The original references should be consulted regarding technical descriptions, material measurements, and taphonomic details.

### **6.3. Notes on nomenclature and taxonomy**

The records are ordered primarily following classification, followed by the date of the first mention in the literature. The taxonomic nomenclature and systematic order adopted here follows Pacheco *et al.* (2021) for the Brazilian taxa and [Cornell Birds of

the World] for taxa from elsewhere. Extinct taxa nomenclature follows specific authors, as can be seen in their respective texts. Extinct taxa are included chronologically in the end of living taxa systematic order. Authorship is provided for specific names only.

The revised name attributions to the fossil materials follow largely on the lists of Lambrecht (1933), Brodkorb (1963; 1964; 1967; 1971; 1978), Mones (1986), and Cuello (1988), in addition to this study's observations. However, these authors simplify most determinations given with uncertainties, such as those by Winge (1887), and some indeterminate material is not mentioned at all. In some cases, even records attributed to specific names (as some materials described by Winge) are lacking in Mones. These approaches are not adopted here.

#### **6.4. Notes on terms**

The osteological terminology adopted here follows Baumel & Witmer (1993), with terms adapted to English. Feather terminology follows the original descriptions.

Site names follow the original publications, with updated Portuguese spelling.

#### **6.5. Records**

The records here are divided into four groups regarding the nature of their preservation: feathers, eggs, ichnofossil, and skeletal remains (including mummifications, which are less common).

In addition to these, there are records in the literature that have been initially associated with birds, but further examination proved them to belong elsewhere. Klein & Ferreira (1979: 530) mentioned bird remains, although with some uncertainty, from the Itapecuru Formation (Early Cretaceous) of Maranhão. Through verbal communication with Diógenes de Almeida Campos, Martins-Neto & Kellner (1988: 64) stated these small-sized remains were being studied at the time and did not belong to birds.



## 6.5.1. Feathers

Fossil feathers are usually of little taxonomic importance but serve to demonstrate the presence of birds in certain deposits (Martill & Filgueira 1994: 483), even though, regarding Mesozoic sediments, they could belong to other feathered dinosaur clades. Due to their fragility and requirement of special conditions that allow their fossilization (Kellner *et al.* 1994: 491), the rarity of such structures in the fossil record makes it worthwhile to comment on these records here. Specimens preserving coloration patterns and possible remains of parasites are of particular importance.

### 6.5.1.1. Mesozoic feathers

#### 1. †Fossil feather 1 (GP/2T-136)

Early Cretaceous - Ceará

- “Pena” - Martins-Neto & Kellner 1988: 61–68, figs. 1A, 1B, 2E.
- “isolated feather” - Chiappe 1991: 61.
- “Undetermined feather” - Kellner *et al.* 1991: 376, fig. in pp. 377.
- “feather, family *incertae sedis*” - Martill 1993: 150.
- “small flight feather” - Martill & Frey 1995: 121.
- “flight feather” - Chiappe 1996: 535, 538–539, fig. 3A.
- “penas de diferentes formas e tamanho” [in part] - Kellner 1998: 657.
- “Flight feather” - Kellner & Campos 2000: 523, 527, fig. 19.
- “markedly asymmetrical wing contour feather” - Martill & Davis 2001: 252.
- “flight feather” - Kellner 2002: 396, fig. 16.9.
- “flight feathers” [*sic*] - Machado & Kellner 2007: 300.
- “Asymmetrical remex” - Naish *et al.* 2007: 526, fig. 18.1A.
- cf. Aves [in part] - Bittencourt & Langer 2011: 28, 38.
- “Penas isoladas - de contorno, das asas, da cauda e semi-plumas” [in part] - Campos 2011: 90.
- “small flight feather” - Sayão *et al.* 2011: 198, 203.
- “provável pena remex” - Leite & Hessel 2011: 2.
- “One primary remex” - Prado *et al.* 2016a: 4.

Martins-Neto & Kellner (1988) reported a fossil feather (GP/2T-136) from the Crato Formation, being the first record of this kind for the Mesozoic of South America and the first record of Mesozoic bird remain from Brazil. The relatively well-preserved fossil was provided to one of the authors by Pedro Luiz Novaes Ferreira, from São Paulo, and,

although its exact provenance is unknown, it was likely collected around the municipality of Santana do Cariri, Ceará, from an indeterminate area around Nova Olinda according to Chiappe (1996) through communication with Kellner. It shows a limonitic/imprint preservation (Prado *et al.* 2016a: 4). Unfortunately, the slab was fractured into some pieces, with one of the fractures dividing the fossil into two parts. The material reached the authors already glued, and, due to its fragility, it could not undergo further preparation. It is an asymmetric feather with identifiable calamus (of about 5 mm long), rachis and barb impressions (about 19 barbs per centimeter of rachis), with a total length of about 64 mm, and maximum width of about 8 mm. No barbule impressions are preserved, but due to the disposition of the barbs, the authors concluded they existed and were not preserved. The fossil was attributed to a bird that was possibly well-adapted to flight due to the rachis curvature and vane asymmetry, probably a primary remex of a neornithea or an enantiornithea. Chiappe (1991: 61) suggested that it could belong to an enantiornithea, although there is no direct supporting evidence. Later, Barrowclough (in Kellner *et al.* 1991: 376) suggested it may represent either one of the trailing primaries or a secondary remex, and if it was indeed capable of flight, the bird had approximately the size of a brush-finch, perhaps weighing between 35 and 40 g. A horizontally inverted color picture of the specimen was included in the same publication. Sayão *et al.* (2011) commented that the feather could have belonged to a flightless form due to its similarity with that of flightless birds, as in the absence of barbules, although, as noted by Martins-Neto & Kellner, this could be a preservation artifact.

## 2. †Fossil feather 2 (LEIUG 114369)

Early Cretaceous - Ceará

- “Feather” - Martill & Figueira 1994: 483–487, fig. 2.
- “demiplume” [*sic*] - Martill & Frey 1995: 121.
- “semiplume” - Chiappe 1996: 539.
- “Semiplume” - Kellner & Campos 2000: 523, 528.
- “small semiplume” - Kellner 2002: 396–397.
- “semiplume” - Machado & Kellner 2007: 300.
- “semiplume” - Naish *et al.* 2007: 525.
- “Several types of feathers” [in part] - Bittencourt & Langer 2011: 28.
- “Penas isoladas – de contorno, das asas, da cauda e semi-plumas” [in part] - Campos 2011: 90.

- “two small semiplumes” [in part] - Sayão *et al.* 2011: 198, 202.
- “semipluma” - Leite & Hessel 2011: 2.
- “Semiplume” - Prado *et al.* 2016a: 4.

Martill & Filgueira (1994) reported a fossil feather (LEIUG 114369) from the Mina de Antone Phillipe locality near the Tatajuba Reservoir, in the Nova Olinda Member of Crato Formation, collected by one of the quarry workers. The fossil is preserved as a carbonized trace (Prado *et al.* 2016a) and suffered damage somewhat since or during the collection. It is a semiplume associated with a bird, lacking the proximal part of the calamus. The preserved impression is 21 mm long along the slightly curved rachis and has a maximum width of 18 mm, partly due to the spreading of the loose and plumaceous barbs. The longest barbs range from 8 to 10 mm in length. Some of them are separated from adjacent barbs, with some being folded back toward the proximal end of the rachis. Barbules, both proximal and distal, are identifiable in some barbs, being up to 0.04 mm long with up to sixteen barbules per millimeter in the parts of the barbs where counting them is easy. The feather is overall dark gray distally to light gray proximally. It is similar to the feathers found in the posterior part of the body of modern passeriforms<sup>8</sup> and has a size comparable to those of birds between 150 and 300 mm long. The authors noted a remarkable similarity in size, morphology, and preservation with a fossil feather figured by Talent *et al.* (1966) from the Early Cretaceous of Koonwarra, Victoria, Australia.

### 3. †Fossil feather 3 (MCT 1493-R)

Early Cretaceous - Ceará

- “Fossil down feather” - Kellner *et al.* 1994: 489–492, fig. 2.
- “down feather” - Chiappe 1996: 538–539.
- “penas de diferentes formas e tamanho” [in part] - Kellner 1998: 657.
- “Down feather” - Kellner & Campos 2000: 523, 528, fig. 17.
- “very small and fluffy down feather” - Kellner 2002: 397, fig. 16.10.
- “Pena fóssil” - Kellner 2006: 84, fig. 46.
- “down feather” - Machado & Kellner 2007: 300.
- “isolated down feather” - Naish *et al.* 2007: 525.
- “Several types of feathers” [in part] - Bittencourt & Langer 2011: 28.
- “Penas isoladas – de contorno, das asas, da cauda e semi-plumas” [?; in part] - Campos 2011: 90.

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<sup>8</sup> Prado *et al.* (2016b) mistakenly mentioned it being assigned to passerine birds in Martill & Filgueira’s work.

- “down feather” - Sayão *et al.* 2011: 198.
- “pluma” - Leite & Hessel 2011: 2.
- “Down feather” - Prado *et al.* 2016a: 4.

A fossil down feather (MCT 1493-R)<sup>9</sup> associated with a bird was described by Kellner *et al.* (1994) from the Crato Formation in the Araripe Basin, without attributing it to a specific locality. According to Chiappe (1996), through communication with Kellner, it is from an indeterminate area around Nova Olinda. It is a comparatively small feather, preserved as a carbonized trace (Prado *et al.* 2016a), with a length of about 7.5 mm from the weakly visible calamus to the largest barb and is of a dark-brown color in a grayish slab. The very slender rachis is about 3.4 mm long. Some barbs are almost as thick as the rachis. They show individual sizes that decrease towards the shaft’s distal end, with the last and smallest barb on the shaft’s terminal portion about 2.9 mm long, while the largest barb near the shaft’s base is about 5.3 mm long. There are about three to four barbs per millimeter of the rachis. Barbules are longer on the barbs’ proximal parts, increasing the down density of the feather towards the rachis. On the left upper portion of the matrix above the feather there is a long barb-like structure, at least 25 mm in length, straight distally and curved proximally. It was possibly originally connected to the largest basal barb or not part of the feather at all, as no barbules were observed in the structure.

#### 4. †Fossil feather 4 (LEIUG 115562/SMNK 1247 PAL)

Early Cretaceous - Ceará

- “small ?breast feather” - Martill & Frey 1995: 120–121, fig. 1.
- “contour, body feather” - Chiappe 1996: 539.
- “Contour feathers” [in part] - Kellner & Campos 2000: 523, 528.
- “incomplete contour feather” - Kellner 2002: 397.
- “contour feathers showing part of the color pattern” [in part] - Machado & Kellner 2007: 300.
- “colour-banded feather” [in part] - Vinther *et al.* 2008: 522–525, fig. 1A–C.
- cf. Aves [in part] - Bittencourt & Langer 2011: 28, 38.
- “Penas isoladas - de contorno, das asas, da cauda e semi-plumas” [?; in part] - Campos 2011: 90.
- “contour feathers” [in part] - Sayão *et al.* 2011: 198, 202.
- “pena de contorno” - Leite & Hessel 2011: 2.
- “Contour feather” - Prado *et al.* 2016a: 4.

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<sup>9</sup> Deposited in the collection of MN according to Kellner (2006).

- “striped fossil feather” [in part] - Smithwick & Vinther 2020: 190–191, fig. 11.5.
- “feather” [in part] - Roy *et al.* 2020: 254.

Martill & Frey (1995) reported a fossil feather with a preserved color pattern from the Nova Olinda Member locality of Mina de Antone Phillipe near Tatajuba reservoir, Ceará. The part (LEIUG 115562) and the counterpart (SMNK 1247 PAL) were collected and deposited in different institutions. It is a small body feather, possibly from the breast, 7 mm long with a maximum width of 4 mm, from a bird probably slightly larger than a living fringillid. The specimen was split through the middle, with the color pattern being preserved on both part and counterpart. It comprises a series of transverse bands of alternating dark and light appearance with relatively sharp limits between the colored bands. Three dark bands exist perpendicularly to the rachis, the most proximal one beginning at the quill’s distal portion. The proximal portion of the feather is partly concealed by matrix, preventing knowing the quill’s entire length in LEIUG 115562, which also has overall darker-appearing bands. A small distal extension of color exists along the rachis, but it does not reach the succeeding dark color band. A dark band includes the feather’s tip, where there is also a proximal extension of the band along the rachis that almost unites with the distal extension of the central dark band. The authors commented that this barred feather pattern probably gave the bird a speckled appearance, such as seen in the breast of some turdids and fringillids. According to Kellner (2002: 397), it most likely represents only the apex of the pennaceous portion of a body feather.

A study conducted by Vinther *et al.* (2008) showed that the dark bands of LEIUG 115562 are preserved as elongate, oblate carbonaceous bodies 1–2  $\mu\text{m}$  long, aligned along with the barbs and barbules, whereas the light bands retained only relief traces in the matrix. These oblate bodies were interpreted as eumelanosomes, as seen in the structure of black feathers in the living icterid *Agelaius phoeniceus* (Linnaeus). Their observations indicated that the specimen was originally banded with a black and white eumelanin pattern.

## **5. †Fossil feather 5 (LEIUG 115563/SMNK 1251 PAL)**

Early Cretaceous - Ceará

- “feather” - Martill & Frey 1995: 125–126, fig. 4.
- “Contour feathers” [in part] - Kellner & Campos 2000: 523.
- cf. Aves [in part] - Bittencourt & Langer 2011: 28, 38.
- “Penas isoladas - de contorno, das asas, da cauda e semi-plumas” [?; in part] - Campos 2011: 90.

Martill & Frey (1995) reported a second feather from the same locality as the specimen above. It is about 15 mm long and 1.5 to 2.0 mm wide, as all of the barbs are pressed together. To avoid risking color-patterned specimens (including insects) by examining them through electron microscopy, as coating with gold or carbon would mask the pattern preservation, the authors selected this second feather for this purpose. It is preserved in a visibly similar way to the color-patterned feather, although it lacks such pattern, possibly as it was of an original uniform color. The specimen was split in the middle, with half of the feather remaining on each counterpart slab. One half remained preserved (SMNK 1251 PAL) while the other (LEIUG 115563) was trimmed with a diamond saw so it could be mounted on a flat-topped aluminum stub and later sputter coated with gold and examined in a scanning electron microscope. At high magnifications, it showed that the feather’s organic material is composed of roughly aligned elongate, rod-shaped bodies 0.5–2.2  $\mu\text{m}$  long with a diameter of 0.3–0.5  $\mu\text{m}$  that the authors considered to be autolithified bacteria, resembling that from the Eocene oil shales of Messel, Germany. The feather per se was not figured, but bacteria’s micrographs were included in the study. However, as noted above, Vinther *et al.* (2008) interpreted similar structures in the banded feather described from the same locality as melanosomes.

## 6. †Fossil feather 6 (NSM PV 20059)

Early Cretaceous - Ceará

- “fossil feather” - Martill & Davis 1998: 528–529, fig. 1.
- “feather” - Martill & Davis 2001: 241–259, figs. 1–5.
- “isolated feather with a symmetrical vane” - Naish *et al.* 2007: 526, 528, figs. 18.1B–F.
- “Penas isoladas – de contorno, das asas, da cauda e semi-plumas” [in part] - Campos 2011: 90.
- “possible rectrices” [in part] - Sayão *et al.* 2011: 202.
- “pena de contorno” - Leite & Hessel 2011: 2.
- “One symmetrical feather” - Prado *et al.* 2016a: 4.

Martill & Davis (1998) described a fossil feather with possible ectoparasite eggs (NSM PV 20059) from the Crato Formation, describing it further later (Martill & Davis 2001). The specimen was purchased from a commercial fossil dealer by the National Science Museum of Japan in June 1996. Although the locality was given only as Crato Formation, the authors confirmed that the specimen matrix is similar to that of weathered, laminated limestones of the Nova Olinda Member, highly likely from one of the small quarries between Nova Olinda and Santana do Cariri in southern Ceará. Martill & Davis noted that, although seemingly preserved as a carbonized trace, the fossil is too weathered to satisfactorily establish its original preservation mode, but was regarded so by Prado *et al.* (2016a).

The fossil comprises both part and counterpart (this one less preserved), orange/brown in coloration on a buff-colored slab. The feather is 85 mm long and has a maximum width of 11 mm, while the calamus is 19 mm long and 1.5 mm at its widest part. The umbilical sulcus is possibly represented by a 33 mm long dark-colored band lying centrally within the scapus. The rachis (which the authors consider to be the part of the scapus bordered by the barbs) is 66 mm long and slightly curved. In the apex, possibly two or three millimeters are missing. The rachis' margins seem to diverge proximally at about 48 mm from the distal apex, possibly being the termination of the rachis part occupied by medullary tissue combined with the taphonomic artifact of the rachis collapse along the umbilical sulcus from a three-dimensional state to the fossil's almost two-dimensional state. Although there is a real slight asymmetry, the main slab specimen shows a visually apparent asymmetry due to the barbs being damaged distally on the right vane's margin. The maximum length of the barbs is 17 mm at a point about 35 mm from the proximal umbilicus at the proximal tip of the calamus. Although not well-preserved, the barbules are visible on many of the barbs. They are single, fine distolateral projections, about 25 mm long, in the barbs' proximal and distal margins, where they appear to be densely distributed. A narrow space running between the barbs results from the apparent lack of interaction between barbules of adjacent barbs in most regions of the vane. The feather is almost complete, seeming to lack only very small portions of the distal tips of the most distal few barbs and showing some damage distally in some of the more proximal barbs.

Adhered to the barbs, barbules, and calamus are numerous, spherical to sub-spherical egg-like structures, of which the authors ruled out as artifacts of preservation or a pollen affinity in favor of an identity as true eggs. They are reddish-brown and slightly shiny, present over most of the feather's surface, with a minimum number of 242 units being counted on the most well-preserved slab. They have a diameter of 68–75  $\mu\text{m}$  and a wall 5–7  $\mu\text{m}$  thick in split units that allow measurement, mainly occurring in insolation, although few irregular clusters of between 5 and 15 units are also present. The structures are hollow (now filled with calcite), and some of them display a circular aperture on the surface facing away from the feather, perhaps indicating that they had hatched (Naish *et al.* 2007: 528). The association between the feather and eggs are not unequivocal, and possibly they were from a microscavenger rather than a parasite. However, their number and close resemblance to the eggs of modern bird mites suggest they are at least eggs of mites (Acari), if not parasitic mites. Proctor (2003) suggested that if these structures are indeed eggs, they may be from ostracods, arguing that modern feather mite eggs are larger (150–400  $\mu\text{m}$  long), sausage-shaped, and have longitudinal seams rather than circular apertures and that ostracods readily deposit their small, round eggs on submerged detritus. While there are no records of ostracods in the Nova Olinda Member, they occur in abundance in the strata immediately beneath (Naish *et al.* 2007: 528).

The feather is possibly precluded from being a flight feather due to its near symmetry, being similar in this aspect to the rectrices of *Archaeopteryx lithographica* Meyer. If a primary wing feather, it would be similar in asymmetry range to recent flightless birds. The barbs are straight for most of their length, but hooked barbules are absent, resembling those in the elongated body feathers of large ratites such as *Rhea*. The authors suggested that the specimen may have belonged to an animal with similar ecology, a ground-dwelling avian or feathered non-avian dinosaur, but did not assign it to any group.

The feather's isolated nature suggests it was possibly molted, being slightly damaged due to abrasion sustained during life (as in preening) or natural wear. The authors suggested the feather was self-plucked due to severe infestation based on many of the supposed eggs on its surface being unhatched and on many of the same deposit fossils appearing to have been blown into the Crato lagoon.



## 7. †Fossil feather 7 (MCT 1509-R)

Early Cretaceous - Ceará

- “Pena fóssil” - Kellner *et al.* 1999: 53, fig. 41.
- “Contour feather” - Kellner & Campos 2000: 523, 528, fig. 18.
- “complete contour feather” - Kellner 2002: 397, fig. 16.11.
- “contour feathers showing part of the color pattern” [in part] - Machado & Kellner 2007: 300.
- cf. Aves [in part] - Bittencourt & Langer 2011: 28, 38.
- “Penas isoladas – de contorno, das asas, da cauda e semi-plumas” [?; in part] - Campos 2011: 90.
- “contour feathers” [in part] - Sayão *et al.* 2011: 198, 202.

Kellner (2002) described a complete fossil contour feather (MCT 1509-R), previously figured by Kellner *et al.* (1999) and Kellner & Campos (2000), from a quarry of the Crato Formation near Nova Olinda, Ceará. It is possibly a feather from the body and has a length of almost 22 mm. The rachis is curved, the vanes are symmetrical, and the proximal portion of the calamus was not preserved. Five pairs of alternating dark and light bands, essentially perpendicular to the rachis, compose the feather’s color pattern, being more visible toward the apex of the pennaceous part and fading towards the basal portion, which lacks any banding.

## 8. †Fossil feather 8 (Chiappe 2007)

Early Cretaceous - Ceará

- “Some fossil feathers” [in part] - Chiappe 2007: 78, fig. in pp. 78.

Chiappe (2007) figured a 5-cm-long fossil feather with a preserved banded color pattern, only stating that it comes from the Early Cretaceous of Brazil. The feather is similar to specimens by Kellner (2002, fig. 16.11) and Naish *et al.* (2007, pl. 25E).

## 9. †Fossil feather 9 (Naish *et al.* 2007 1)

Early Cretaceous - Ceará

- “isolated down feathers” [in part] - Naish *et al.* 2007: 528, pl. 25A.

Naish *et al.* (2007) figured an isolated down feather about 18 mm long from the Crato Formation. It is of dark color, and its distal half barbs are preserved clumped together.

## **10. †Fossil feather 10 (Naish *et al.* 2007 2)**

Early Cretaceous - Ceará

- “isolated down feathers” [in part] - Naish *et al.* 2007: 528, pl. 25B.

Naish *et al.* (2007) figured an isolated down feather about 18 mm long and 14 mm wide (due to the spreading of the barbs) from the Crato Formation. A darker tone is present in the distal barbs and the middle barbs’ distal parts.

## **11. †Fossil feather 11 (Naish *et al.* 2007 3)**

Early Cretaceous - Ceará

- “isolated down feathers” [in part] - Naish *et al.* 2007: 528, pl. 25C.

Naish *et al.* (2007) figured an isolated down feather about 17 mm long and 12 mm wide (due to the spreading of the barbs) from the Crato Formation. It has an overall dark coloration.

## **12. †Fossil feather 12 (Naish *et al.* 2007 4)**

Early Cretaceous - Ceará

- “small down feather with pattern of transverse bands” - Naish *et al.* 2007: 528, pl. 25E.

Naish *et al.* (2007) figured a small down feather about 18 mm long from the Crato Formation. It preserves a pattern of transverse bands, similar to specimens figured by Kellner (2002, fig. 16.11) and Chiappe (2007, fig. in pp. 78).

## **13. †Fossil feather 13 (Naish *et al.* 2007 5)**

Early Cretaceous - Ceará

- “single elongate down feather” - Naish *et al.* 2007: 528, pl. 25F.

Naish *et al.* (2007) figured a single elongate down feather about 19 mm long from the Crato Formation.

## **14. †Fossil feather 14 (Naish *et al.* 2007 6)**

Early Cretaceous - Ceará

- “feather with pattern of fine, diagonally arranged banding” - Naish *et al.* 2007: 528, pl. 25G.

Naish *et al.* (2007) figured a feather preserving a fine, diagonally arranged banding pattern, with a length of about 18 mm.

## **15. †Fossil feather 15 (Naish *et al.* 2007 7)**

Early Cretaceous - Ceará

- “elongate symmetrical feather with pattern of offset bands” - Naish *et al.* 2007: 528, pl. 25H.
- “One of the rare and excellently preserved feathers of a bird with preserved color patterns” - Herzog *et al.* 2008: 38, fig. 31.

Naish *et al.* (2007) figured a well-preserved elongate, symmetrical feather with a pattern of offset bands (about 10 dark bands are visible in the right vane, fading towards the calamus), with a length of about 18 mm. The specimen was later figured by Herzog *et al.* (2008), who commented that no information was available on the collection where the fossil is deposited (probably Europe).

## **16. †Fossil feather 16 (CAV 0001-V)**

Early Cretaceous - Ceará

- “plúmula” - Sayão & Uejima 2009: 22.
- “plúmula” - Sayão & Uejima 2010: 54.
- “penas plumáceas” [in part] - Freitas *et al.* 2010: 32.
- “down feather” - Sayão *et al.* 2011: 199, fig. 2.
- “plumas” [in part] - Leite & Hessel 2011: 2.
- “One plume” - Prado *et al.* 2016a: 4.

Two fossil feathers collected during the field season of 2009 by biology student Laiz Karla of CAV at Mina do Demar, on the road connecting Nova Olinda and Santana do Cariri were briefly described by Sayão & Uejima (2009; 2010) and then figured by Sayão *et al.* (2011). They are presumably preserved as carbonized traces (Prado *et al.* 2016a). The first is a down feather (CAV 0001-V), which has a total length of 18.81 mm (excluding the calamus, which was not preserved) and maximum width of 13.66 mm. The rachis is 5.07 mm long and is shorter than the barbs. The largest barb is 11.85 mm long, while the smallest is 5.4 mm long. The barbules are more abundant in the base of the barb and decrease in number and size distally.

## 17. †Fossil feather 17 (CAV 0002-V)

Early Cretaceous - Ceará

- “semi-plúmula” - Sayão & Uejima 2009: 22.
- “semi-plúmula” - Sayão & Uejima 2010: 54.
- “penas plumáceas” [in part] - Freitas *et al.* 2010: 32.
- “semiplume” - Sayão *et al.* 2011: 199, 201, fig. 3.
- “plumas” [in part] - Leite & Hessel 2011: 2.
- “One semiplume” - Prado *et al.* 2016a: 4.

The second feather from Mina do Demar described by Sayão & Uejima (2009; 2010), and later figured by Sayão *et al.* (2011), is a semiplume (CAV 0002-V). The feather is preserved in a dark brown color contrasting with the light-yellow matrix. A variation in the staining tone is present, darker in the calamus base of the calamus and lighter closer to the rachis. A very light band pattern can be observed distally in the barbs, interposed between light and dark shades. The feather has a total preserved length of 8.55 mm. The calamus is 0.47 mm long and has been displaced from its original position, likely during fossilization. The very slender rachis is 4.76 mm long and is longer than the barbs. The barbs decrease in size toward the shaft’s distal part. The largest barb is 4.71 mm long, while the smallest is 3.34 mm long. Both proximal and distal barbules are identifiable in some barbs. It was reported as the smallest semiplume described from the formation.

## 18. †Fossil feather 18 (Teixeira & Saraiva 2010)

Early Cretaceous - Ceará

- “pluma isolada proveniente de Theropoda ou aves” - Teixeira & Saraiva 2010: 46.

Teixeira & Saraiva (2010), two researchers associated with the URCA, reported finding an isolated feather, of a bird or a non-avian theropod, during systematic collecting in quarries of Nova Olinda.

## 19. †Fossil feather 19 (MPSC-PN 2221)

Early Cretaceous - Ceará

- “Fossil feather” - Sayão *et al.* 2011: 201–202, 204, fig. 5.
- “plumas” [in part] - Leite & Hessel 2011: 2.
- “Down feather” [?] - Prado *et al.* 2016a: 4.

A third fossil feather (MPSC-PN 2221) from Mina do Demar was described by Sayão *et al.* (2011). The feather has a long calamus and a rachis (which is also somewhat flattened) with a total length of about 75 mm. The loose barbs are long and filamentous and lack barbules. It is overall similar to down or ornamental feathers but differs from them in the rachis morphology. The authors also noted the similarity with a fossil feather preserved in amber from the Early Cretaceous of France described by Perrichot *et al.* (2008) and suggest a non-avian origin based on comparison with the developmental stages defined by Prum (1999). Conversely, Prado *et al.* (2016a) mentioned it under “feathers assigned to a bird” preserved as carbonized traces in their Table 1, separately mentioning the two other specimens firstly reported by Sayão & Uejima (2009).

## **20. †Fossil feather 20 (UFC.0022V)**

Early Cretaceous - Ceará

- “pena isolada” - Leite & Hessel 2011: 1–5, fig. 1A.
- “Eight contour feathers” [in part] - Prado *et al.* 2016a: 4.

Leite & Hessel (2011) reported a total of eight dark-colored feathers from Mina do Triunfo in Nova Olinda, which they tentatively attributed to contour feathers from the upper part of the hindlimbs of non-avian dinosaurs, noting similarities with the feathers from the Early Cretaceous of Liaoning, China described by Zhang *et al.* (2006). The slender rachis has almost the same width as the barbs, attached to the rachis at about 15°. The barbules are attached with a small angle and almost coalesce with the barbs forming a kind of sheath, especially in the distal barbs. One of these specimens is an isolated, apparently symmetrical feather (UFC.0022V) 22 mm long.

## **21. †Fossil feathers 21 (UFC.0023Va/UFC.0023Vb [MN 7754-V])**

Early Cretaceous - Ceará

- “conjunto de sete penas” - Leite & Hessel 2011: 1–5, fig. 1B.
- “Eight contour feathers” [in part] - Prado *et al.* 2016a: 4.
- “several feather-like structures” [in part] - Campos *et al.* 2019: 17–24, figs. 1–2, 4–5, 7.

The other feathers reported by Leite & Hessel (2011) from Mina do Triunfo are a set of seven feathers in the same matrix block, preserved in part and counterpart

(UFC.0023Va/UFC.0023Vb). They are almost symmetrical and range from 15 to 25 mm long. The feathers are united by their basal region and no traces of calami could be observed, but this area preserved a finely punctate epidermis impression of about 2 mm<sup>2</sup>.

Campos *et al.* (2019) analyzed the specimen through combined microscopy and spectroscopy techniques (they were aiming at minimal damage, only 1 mm<sup>3</sup> was scrapped from the surface) and confirmed the fossils' feather identity, distinguishing six (not seven) plumulaceous down feathers. The analysis also revealed preserved eumelanosomes with a mean length of  $1.293 \pm 0.317 \mu\text{m}$  and a mean width of  $0.298 \pm 0.032 \mu\text{m}$  in its composition that indicate the feathers were originally dark-colored. Barbules similar to that of extant plumulaceous feathers and long prong barbicels were also distinguishable. These conclusions should also be valid to specimen UFC.0022V, as it is of the same aspect. Oddly, however, the set of feathers is referred to as MN 7754-V, and no further information was provided, nor Leite & Hessel were cited. It was also not specified if it was the part or counterpart (as such feature is not mentioned), though the pictured unit from both studies matches well.

## 22. †Fossil feather 22 (GP/2E-7853)

Early Cretaceous - Ceará

- “semiplúma” - Prado & Anelli 2013: 266.
- “downy feather” - Prado *et al.* 2016a: 6–8, fig. 2C, H.

Prado & Anelli (2013) briefly described two fossil feathers from the Crato Formation, apprehended by the Brazilian Federal Police, which were further described and referred to Coelurosauria by Prado *et al.* (2016a). The first is a down feather (GP/2E-7853) of orange coloration in a weathered beige slab, possibly being preserved as limonite. A nearly complete *Dastilbe* sp. is present in the same matrix block. The feather has a width of 12.36 mm and a length (excluding the calamus) of 16.14 mm. The calamus was not preserved and was supposedly very thin. The rachis is 0.49 mm wide and 9.43 mm long, and has barbs of varying size, ranging from 4.85 mm to 8.65 mm. Barbules have been only subtly preserved in some regions of the barbs. Prado *et al.* tentatively assigned both this and GP/2E-7854 specimens to stage IIIb of Prum & Brush's (2002) evolutionary model and to morphotype 4 of Xu & Guo (2009) and noted the possibility

of them being auricular feathers of an animal of a maximum size similar to that of a chicken.

### **23. †Fossil feather 23 (GP/2E-7854)**

Early Cretaceous - Ceará

- “plúmula” - Prado & Anelli 2013: 266.
- “Downy feathers” [in part] - Prado *et al.* 2016a: 8–9, fig. 2B, E–G.

The second feather described by Prado & Anelli (2013) and Prado *et al.* (2016a) is a down feather (GP/2E-7854) of varying brownish tones, due to different preservation in carbonaceous traces, in a weathered beige slab. It has a width of 12.76 mm and a length of 19 mm. The thin calamus, inferred from a slight-line structure consisted of an external molt, is 0.24 mm long. The rachis is 0.49 mm wide and 12.03 mm long, and the barbs range from 4.3 mm to 17.83 mm. The barbules are present as vestigial traces.

### **24. †Fossil feather 24 (GP/2E-8771)**

Early Cretaceous - Ceará

- “countour feathers” [in part] - Prado & Anelli 2015: 148.
- “Semiplume” - Prado *et al.* 2016a: 9–10, fig. 2A, D.

In addition to the previous two apprehended specimens, Prado *et al.* (2016a) described a semiplume (GP/2E-8771) of blackish color, possibly preserved as a carbonized trace in a grayish (likely unweathered) slab. It has a width of 15.63 mm and a length of 33.50 mm. The rachis is 0.03 mm wide and 29.35 mm long, and the barbs range from 4.12 mm to 16.45 mm. The barbules are clearly visible and vary in size, suggesting some degree of cohesion between the barbs, though no barbicels can be observed. A V-shaped structure reminiscent of afterfeather, larger than the vanes, is attached to the basal part, though it does not show afterfeather diagnostic features. Markings done with a scraper tool, especially in the region where the calamus was supposed to be found, were made by the illegal dealers to make it more commercially attractive. The authors referred the specimen to Maniraptoriformes and assigned it to stage IIIa+b of Prum & Brush's (2002) evolutionary model and morphotype 6 of Xu & Guo (2009). They also suggested that it might have had protective and thermoregulatory functions while also speculating on camouflage, communication, and sexual roles.

Previously, Prado & Anelli (2015) performed SEM analysis in the specimen and the observed microbodies were interpreted as eumelanosomes, suggesting it had an iridescent pattern demonstrating that the dinosaur fauna of that unit was well adapted to its ecological niche.

## **25. †Fossil feather 25 (UFRJ-DG 05 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 05 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum width of 2.9 mm. As for general, the contour feathers described by him have pennaceous vanes, formed by parallel barbs with intertwined barbules. The calami are short and thin, difficult to distinguish in the matrix, and the rachises are preserved as a thin dark line between the vanes. The size of the plumulaceous areas varies.

## **26. †Fossil feather 26 (UFRJ-DG 08 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 08 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 20.9 mm, a maximum width of 14.9 mm, a rachis 14.76 mm long, and the longest barb 15.1 mm long.

## **27. †Fossil feather 27 (UFRJ-DG 09 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 09 Av” - Metello 2017: 19–20.

A fossil contour feather described by Metello (2017). It has a maximum length of 16.7 mm, a maximum width of 10.9 mm, the rachis is 11.3 mm long, and the longest barb is 11.4 mm long. It is curved, with the barbs being loose in the feather edge, similar to wing coverts of modern birds.

## **28. †Fossil feather 28 (UFRJ-DG 10 Av)**

Early Cretaceous - Ceará



- “UFRJ-DG 10 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 10.8 mm, a maximum width of 11.9 mm, the rachis is 3.2 mm long, and the longest barb is 7.9 mm long. As for general, the plumes described by him have a slender rachis (not always easily recognizable), poorly preserved calami, and vanes formed by long and slender disarranged barbs with non-intertwined barbules that show a fuzzy texture. The longest barbs are longer than their respective rachises.

### **29. †Fossil feather 29 (UFRJ-DG 11 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 11 Av” - Metello 2017: 19–20, fig. 10.

A fossil contour feather described by Metello (2017). It has a maximum length of 14.4 mm, a maximum width of 8.6 mm, the rachis is 12.1 mm long, and the longest barb is 6.1 mm long. It lacks a plumulaceous portion. The barbs are equally spaced in a single plan, indicating pennaceous vanes with intertwined barbules.

### **30. †Fossil feather 30 (UFRJ-DG 12 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 12 Av” - Metello 2017: 20, 24, fig. 13.

A fossil semiplume (but also classified as a contour feather in the same study) described by Metello (2017). It has a maximum length of 17.5 mm, a maximum width of 5.8 mm, the rachis is 13 mm long, and the longest barb is 11.6 mm long. The barbs are collapsed with the rachis. As for general, the semiplumes described by him have rachis present as a thin dark line, poorly preserved as the calami. The vanes have long and slender disarranged barbs, with non-intertwined barbules that show a fuzzy texture. The longest barbs are shorter than their respective rachises.

### **31. †Fossil feather 31 (UFRJ-DG 13 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 13 Av” - Metello 2017: 24.

A fossil semiplume described by Metello (2017). It has a maximum length of 23 mm, a maximum width of 16 mm, the rachis is 19.7 mm long, and the longest barb is 13.8 mm long.

### **32. †Fossil feather 32 (UFRJ-DG 14 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 14 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 19.2 mm, a maximum width of 4.9 mm, the rachis is 16 mm long, and the longest barb is 10.2 mm long.

### **33. †Fossil feather 33 (UFRJ-DG 15 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 15 Av” - Metello 2017: 24.

A fossil semiplume described by Metello (2017). It has a maximum length of 20.7 mm, a maximum width of 10.6 mm, the rachis is 14.9 mm long, and the longest barb is 10.4 mm long.

### **34. †Fossil feather 34 (UFRJ-DG 16 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 16 Av” - Metello 2017: 24, fig. 14.

A fossil semiplume described by Metello (2017). It has a maximum length of 18.9 mm, a maximum width of 13.2 mm, the rachis is 10.9 mm long, and the longest barb is 10.3 mm long.

### **35. †Fossil feather 35 (UFRJ-DG 17 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 17 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 10.6 mm, a maximum width of 7.6 mm, the rachis is 3.7 mm long, and the longest barb is 5.6 mm long.

### **36. †Fossil feather 36 (UFRJ-DG 18 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 18 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 17.3 mm, a maximum width of 4.8 mm, the rachis is 10.4 mm long, and the longest barb is 11.4 mm long.

### **37. †Fossil feather 37 (UFRJ-DG 19 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 19 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 16.5 mm, a maximum width of 14.6 mm, the rachis is 11.1 mm long, and the longest barb is 10.8 mm long.

### **38. †Fossil feather 38 (UFRJ-DG 20 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 20 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 14.15 mm, a maximum width of 8.7 mm, the rachis is 9.2 mm long, and the longest barb is 9.4 mm long.

### **39. †Fossil feather 39 (UFRJ-DG 21 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 21 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 17.2 mm, a maximum width of 10.2 mm, the rachis is 11.8 mm long, and the longest barb is 11.5 mm long.

#### **40. †Fossil feather 40 (UFRJ-DG 22 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 22 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 13.5 mm, a maximum width of 4.7 mm, the rachis is 5.7 mm long, and the longest barb is 9.3 mm long.

#### **41. †Fossil feather 41 (UFRJ-DG 23 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 23 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 20.8 mm, a maximum width of 10.1 mm, the rachis is 15.3 mm long, and the longest barb is 10.5 mm long.

#### **42. †Fossil feather 42 (UFRJ-DG 24 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 24 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 16.2 mm, a maximum width of 8.1 mm, the rachis is 8.4 mm long, and the longest barb is 12.4 mm long.

#### **43. †Fossil feather 43 (UFRJ-DG 25 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 25 Av” - Metello 2017: 24.

A fossil semiplume described by Metello (2017). It has a maximum length of 15.8 mm, a maximum width of 7.4 mm, the rachis is 10.2 mm long, and the longest barb is 9.8 mm long.

#### **44. †Fossil feather 44 (UFRJ-DG 26 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 26 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 10.7 mm, a maximum width of 6.6 mm, the rachis is 5 mm long, and the longest barb is 7.2 mm long.

#### **45. †Fossil feather 45 (UFRJ-DG 27 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 27 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 15.8 mm, a maximum width of 10.9 mm, the rachis is 9.7 mm long, and the longest barb is 10.9 mm long.

#### **46. †Fossil feather 46 (UFRJ-DG 28 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 28 Av” - Metello 2017: 24.

A fossil semiplume described by Metello (2017). It has a maximum length of 15.9 mm, a maximum width of 9 mm, the rachis is 10.8 mm long, and the longest barb is 9.1 mm long.

#### **47. †Fossil feather 47 (UFRJ-DG 29 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 29 Av” - Metello 2017: 24.

A fossil semiplume described by Metello (2017). It has a maximum length of 20 mm, a maximum width of 17.5 mm, the rachis is 15.1 mm long, and the longest barb is 10.7 mm long.

#### **48. †Fossil feather 48 (UFRJ-DG 32 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 32 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 20.2 mm, a maximum width of 9.8 mm, the rachis is 8.5 mm long, and the longest barb is 14.6 mm long.

#### **49. †Fossil feather 49 (UFRJ-DG 33 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 33 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 31.7 mm, a maximum width of 4.5 mm, the rachis is about 16.9 mm long, and the longest barb is 9.12 mm long.

#### **50. †Fossil feather 50 (UFRJ-DG 35 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 35 Av” - Metello 2017: 19–20, 31, fig. 12.

A fossil contour feather described by Metello (2017). It has a maximum length of 19.4 mm, a maximum width of 14.2 mm, the rachis is 12.9 mm long, and the longest barb is 12 mm long. It shows open and loose vane edges, perhaps a feather that was used in sexual display.

#### **51. †Fossil feather 51 (UFRJ-DG 36 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 36 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 18.1 mm, a maximum width of 7.6 mm, the rachis is 10.2 mm long, and the longest barb is 10.8 mm long.

### **52. †Fossil feather 52 (UFRJ-DG 37 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 37 Av” - Metello 2017: 19–20.

A fossil contour feather described by Metello (2017). It has a maximum length of 15.5 mm, a maximum width of 7.5 mm, the rachis is 9.1 mm long, and the longest barb is 8.9 mm long. It is curved, with the barbs being loose in the feather edge, similar to wing coverts of modern birds.

### **53. †Fossil feather 53 (UFRJ-DG 38 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 38 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 21.3 mm, a maximum width of 18.2 mm, the rachis is 13.4 mm long, and the longest barb is 14.3 mm long.

### **54. †Fossil feather 54 (UFRJ-DG 39 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 39 Av” - Metello 2017: 19–20, fig. 11.

A fossil contour feather described by Metello (2017). It has a maximum length of 21.6 mm, a maximum width of 15.3 mm, the rachis is 15.9 mm long, and the longest barb is 11.6 mm long. The barbs are collapsed with the rachis. The plumulaceous area of the feather accounts for about half of the total length of the vanes.

### **55. †Fossil feather 55 (UFRJ-DG 40 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 40 Av” - Metello 2017: 19–20.

A fossil contour feather described by Metello (2017). It has a maximum length of 25.9 mm, a maximum width of 6.8 mm, the rachis is 18.2 mm long, and the longest barb is 12 mm long. The barbs are collapsed with the rachis.

### **56. †Fossil feather 56 (UFRJ-DG 41 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 41 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 15.8 mm, a maximum width of 6.5 mm, the rachis is 8.9 mm long, and the longest barb is 6.3 mm long.

### **57. †Fossil feather 57 (UFRJ-DG 42 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 42 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 15.5 mm, a maximum width of 15.2 mm, the rachis is 11.2 mm long, and the longest barb is 11.3 mm long.

### **58. †Fossil feather 58 (UFRJ-DG 43 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 43 Av” - Metello 2017: 20, 24.

A fossil semiplume (but also hinted as a contour feather in the same study) described by Metello (2017). It has a maximum length of 14.1 mm, a maximum width of 4.85 mm, the rachis is 8.9 mm long, and the longest barb is 6.7 mm long. The barbs are collapsed with the rachis.

### **59. †Fossil feather 59 (UFRJ-DG 44 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 44 Av” - Metello 2017: 19–20.



A fossil contour feather described by Metello (2017). The barbs are equally spaced in a single plan, indicating pennaceous vanes with intertwined barbules. The longest barb is 6.9 mm long.

### **60. †Fossil feather 60 (UFRJ-DG 45 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 45 Av” - Metello 2017: 24.

A fossil plume described by Metello (2017). It has a maximum length of 9.1 mm, a maximum width of 6.9 mm, the rachis is 4.8 mm long, and the longest barb is 6.6 mm long.

### **61. †Fossil feather 61 (UFRJ-DG 46 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 46 Av” - Metello 2017: 19–20.

A fossil contour feather described by Metello (2017). It has a maximum length of 16.7 mm, a maximum width of 7.9 mm, the rachis is 11.9 mm long, and the longest barb is 9.3 mm long. The barbs are equally spaced in a single plan, indicating pennaceous vanes with intertwined barbules.

### **62. †Fossil feather 62 (UFRJ-DG 47 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 47 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 23.5 mm, a maximum width of 17.5 mm, the rachis is 15.8 mm long, and the longest barb is 7.5 mm long.

### **63. †Fossil feather 63 (UFRJ-DG 48 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 48 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 19.3 mm, a maximum width of 6.8 mm, the rachis is 14.9 mm long, and the longest barb is 10.3 mm long.

#### **64. †Fossil feather 64 (UFRJ-DG 49 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 49 Av” - Metello 2017: 19–20.

A fossil contour feather described by Metello (2017). It has a maximum length of 19.9 mm, a maximum width of 5.7 mm, the rachis is 13.4 mm long, and the longest barb is 11.9 mm long. The barbs are collapsed with the rachis.

#### **65. †Fossil feather 65 (UFRJ-DG 50 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 50 Av” - Metello 2017: 19–20.

A fossil contour feather described by Metello (2017). It has a maximum length of 19.1 mm, a maximum width of 4.5 mm, the rachis is 10.3 mm long, and the longest barb is 14.4 mm long. It is curved, with the barbs being loose in the feather edge, similar to wing coverts of modern birds.

#### **66. †Fossil feather 66 (UFRJ-DG 51 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 51 Av” - Metello 2017: 24.

A fossil semiplume described by Metello (2017). It has a maximum length of 21.5 mm, a maximum width of 8.5 mm, the rachis is 18 mm long, and the longest barb is 13.1 mm long.

#### **67. †Fossil feather 67 (UFRJ-DG 52 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 52 Av” - Metello 2017: 24, fig. 15.

A fossil plume described by Metello (2017). It has a maximum length of 14.7 mm, a maximum width of 11.9 mm, the rachis is 7.4 mm long, and the longest barb is 8.7 mm long.

### **68. †Fossil feather 68 (UFRJ-DG 53 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 53 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 17.1 mm, a maximum width of 4.8 mm, the rachis is 10.3 mm long, and the longest barb is 10.1 mm long.

### **69. †Fossil feather 69 (UFRJ-DG 54 Av)**

Early Cretaceous - Ceará

- “UFRJ-DG 54 Av” - Metello 2017: 19.

A fossil contour feather described by Metello (2017). It has a maximum length of 13.7 mm, a maximum width of 6.4 mm, the rachis is 8.7 mm long, and the longest barb is 8.2 mm long.

### **70. †Fossil feather 70 (MPSC-PN 2383)**

Early Cretaceous - Ceará

A small fossil down feather (MPSC-PN 2383) in the collection of MPSC.

## **6.5.1.2. Cenozoic feathers**

### **71. †Fossil feather 71 (Museu Paulista 111)**

Late Oligocene/Early Miocene - São Paulo

- “Fossil feather” - Shufeldt 1916: 206–207.
- Aves [“Indeterminadas”; in part] - Paula Couto 1958: 2, 5.
- Aves [“Indeterminadas”; in part] - Paula Couto 1970: 922.
- “penas fósseis” [in part] - Sick 1984a: 65.
- “penas fósseis na bacia de Taubaté” [in part] - Alvarenga 1997: 123.
- “penas isoladas” [in part] - Kellner 1998: 659.

- “primary feather of a large bird” - Sayão *et al.* 2011: 198.
- “One primary remex” - Prado *et al.* 2016a: 4.

Shufeldt (1916) reported a fossil feather from the shales of the Taubaté Basin. The specimen, No. 111 at the Museu Paulista, was sent to him by the director of the institution Dr. von Ihering in a letter of transmission dated 8 January 1915.

The fossil matrix has a dark chocolate-brown color, with roughness similar to leather on the face on which the feather is found, while the posterior face is lighter in color, with evidence of horizontal cleavage. The plate is 14 x 7.5 cm and has an average thickness of 3 mm, with markings that indicate it was collected with some sharp instrument, such as a knife. When the plate is wet, the feather, which is quite faint, becomes more evident (Shufeldt 1916: 206, 207). The feather was preserved as a carbonized trace (Prado *et al.* 2016a).

The feather has a total length of 11.3 cm, where the calamus has 4 cm and the vane 7.3 cm. Despite its plumular appearance, Shufeldt (1916: 207) believed it to be a primary feather of a sizable bird.

Shufeldt took a life-size photograph of the specimen for archiving with similar ones in his collection (but this has not been published); he further noted that it is impossible to perceive the feather impressions smallest structures, even with a powerful lens. Although Silva Santos (1950: 446) reiterated that the specimen was at the time at the Museu Paulista (probably only reproducing what Shufeldt published), when, and if, the fossil was returned is unknown. The zoological and paleontological collections of the Museu Paulista were eventually transferred to MZUSP. The fossil feather, however, could not be located.

## **72. †Fossil feather 72 (DGM 1-A)**

Late Oligocene/Early Miocene - São Paulo

- “uma das penas de cobertura do corpo-pluma de um passeriforme” - Silva Santos 1950: 445–446, fig. in pp. 445.
- Aves [“Indeterminadas”; in part] - Paula Couto 1958: 2, 5.
- Aves [“Indeterminadas”; in part] - Paula Couto 1970: 922.
- “penas fósseis” [in part] - Sick 1984a: 65.

- “Pena de ave não identificada” - Lima 1989: 76, fig. in pp. 76.
- “penas fósseis na bacia de Taubaté” [in part] - Alvarenga 1997: 123.
- “penas isoladas” [in part] - Kellner 1998: 659.
- “isolated feathers imprints” [*sic*] - Sayão *et al.* 2011: 198.
- “One contour feather” - Prado *et al.* 2016a: 4.

A second fossil feather from the Tremembé Formation was described by Silva Santos (1950: 445, 446). Gilberto H. William collected the material (DGM 1-A) in July 1948 in Nossa Senhora da Guia Mine, Tremembé, in a layer of dark green shales approximately 12.5 m deep, during the paleontological research carried out by the Divisão de Geologia e Mineralogia of DNPM and is deposited in their collection (Lima 1989: 76).

Silva Santos described it as a contour feather of a passeriform, of size close to a turdid<sup>10</sup>. The preserved carbonized impression is 27 mm long (Lima 1989: 76; Prado *et al.* 2016a: 4). The calamus is absent, but if we consider the average length for such structure, the complete feather should have around 30 mm. Silva Santos also noted that, although the specimen appears very well preserved to the naked eye, no study under a microscope could be done on its minute structure, preventing an attempt at classification.

### 73. †Fossil feather 73 (Pirabas Formation)

Early Miocene - Pará

- “Pena de Ave fossilizada” - Ackermann 1964: 61–62, figs. 20–21.
- “pena fóssil” - Alvarenga 1997: 123.
- “Two pennaceous feathers” - Prado *et al.* 2016a: 4.

Ackermann (1964) reported a fossil feather preserved as a carbonized trace in limestone from the Caieira fossiliferous site (Olaria), Pirabas Formation (Fig. 2.6), early Miocene, near Capanema, Pará (Távora *et al.* 2010: 208, 211; Prado *et al.* 2016a). He noted that the fossil “still retains the beautiful dark gray color as the living black heron has”. Alexander Wetmore (in Ackermann 1964: 62), when asked about the possible identity of the feathers in communication by letter, could only indicate that, due to the wide and loose barbs, it could be tail coverts. He also suggested that Ackermann should include mention of the feathers in a publication about his finds due to its scientific interest, on

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<sup>10</sup> Prado *et al.* (2016) mistakenly mentioned it being assigned to *Turdus rufiventris* Vieillot in Silva Santos’ study.

which Ackermann commented “although the species of the bird to which it belonged cannot be determined, it deserves to be highlighted due to its rarity and preservation”.

Although Ackermann mentioned a single feather in the text, two photographs (1964: 61) in black and white and with scale were included, which clearly show two distinct specimens, and an excerpt from Wetmore’s letter also mentions them in the plural. The specimens measure approximately 6 cm and 7 cm. Prado *et al.* (2016a) considered them to be possible semiplumes or contour feathers.

In the same locality, fossils of cnidarians, bivalves, gastropods, cartilaginous fishes, and several plant species were found, indicating an estuarine environment (Távora *et al.* 2010: 211; Góes *et al.* 1990: 9).

#### **74. †Fossil feather 74 (Tremembé Formation)**

Late Oligocene/Early Miocene - São Paulo

- “impressões de penas” - Garcia 1993: 329.

Garcia (1993: 329) mentioned feather prints while briefly reporting the fossils of the Taubaté Basin from the collection of the Universidade de Guarulhos (Garcia & Saad 1996: 36), from the deposits of Fazenda Santa Fé, Mineração Aligra S/A, and Nossa Senhora da Guia, in Tremembé and Taubaté. Additionally, she reported fragments of eggshells, but without attributing them to any specific group of vertebrates.

#### **75. † Fossil feathers 75 (Entre-Córregos Formation)**

Eocene/Oligocene - Minas Gerais

- “penas” - Bedani & Haddad 2002: 37.
- “penas de aves” - Franco-Delgado & Bernardes-de-Oliveira 2004: 118.
- “avian feathers” - Martins Neto & Pesenti 2006.
- “algumas penas de aves” - Castro-Fernandes *et al.* 2013: 36.

The occurrence of avian fossil feathers in the Entre-Córregos Formation of the Aiuruoca Basin, Minas Gerais, was firstly reported by Bedani & Haddad (2002). Subsequent authors (e.g., Franco-Delgado & Bernardes-de-Oliveira 2004; Martins Neto & Pesenti 2006; Castro-Fernandes *et al.* 2013) also mentioned them, but without a proper description or figures.

## **76. †Fossil feather 76 (GP/2E-8125)**

Late Oligocene/Early Miocene - São Paulo

- “countour feathers” [in part] - Prado & Anelli 2015: 148.
- Neognathae - Prado *et al.* 2016b: 170–171, fig. 2A, D.

Prado & Anelli (2015) reported a contour feather (GP/2E-8125) from the Tremembé Formation. They performed SEM analysis in the specimen and the observed microbodies were interpreted as eumelanosomes, suggesting it had a dark pattern demonstrating that the dinosaur fauna of that unit was well adapted to its ecological niche. Prado *et al.* (2016b) described it as an incomplete contour feather composed only by the mid portion, presenting a black hue, with preserved barbs and barbules. It is 17.17 mm wide and 26.42 mm long. The largest barb is 19.62 mm, and the smallest is 1.88 mm long. Ostracod shells were preserved in the matrix.

## **77. †Fossil feather 77 (GP/2E-8126/GP/2E-8127)**

Late Oligocene/Early Miocene - São Paulo

- Neognathae - Prado *et al.* 2016b: 171, fig. 2B-C, E-F.

Prado *et al.* (2016b) reported an incomplete rectrix preserved in part and counterpart (GP/2E-8126/GP/2E-8127) with identifiable barbs and thick rachis. The specimen GP/2E-8126 is 23.65 mm wide and 67.90 mm long, its largest barb is 19.47 mm and the smallest is 4.21 mm long, and its rachis is 64.74 mm long and 1.36 mm thick. The specimen GP/2E-8127 is 32.33 mm wide and 52.33 mm long, its largest barb is 26.67 mm and the smallest is 3.33 mm long, and its rachis is 52.33 mm long and 3.67 mm thick. Apparently, the rachis and the vanes were severely crushed and chemically altered. A small fish vertebra is present in the surrounding matrix. The authors suggested that it possibly belonged to aquatic taxa considering its taphonomic history, with its size indicating a medium-sized bird not more than 80–90 cm long.

### **6. 5. 2. Eggs**

The paleological record of birds in Brazil include just two reports, representing both Mesozoic and Cenozoic sediments. No ootaxa were erected.

## 78. †Ornithothoraces indet. (LPRP-USP 0359)

Late Cretaceous - São Paulo

- “ovo fossilizado afim a Aves” - Marsola *et al.* 2012: 49.
- “ovo de aves Enantiornithes” - Marsola 2013: 25, 49–55, figs. 10, 23–27.
- Ornithothoraces - Marsola *et al.* 2014: 563–566, fig. 2.
- “ave” - Reis *et al.* 2014: 184.
- Ornithothoraces - Martinelli & Teixeira 2015: 147, 149.

Marsola *et al.* (2014) reported a fossil egg which they attributed to the Ornithothoraces, from the Late Cretaceous of Vale do Rio do Peixe Formation in the Bauru Group of São Paulo, being the first recorded occurrence of a Mesozoic fossil egg for Brazil. The fossil was previously provisionally described by Marsola *et al.* (2012) and Marsola (2013). It was found during July 2011 in a site along road SP-270, near the municipality of Álvares Machado.

A combination of Scanning Electron Microscopy, Wave Dispersion Energy analyses and Computed Tomography was used to determine the taxonomic identity and structural features of the biomineralized tissues of the fossil egg. The specimen (LPRP-USP 0359) is a nearly complete, slightly compressed egg, with its main axes measuring 31.4 mm x 19.5 mm. It is one of the smallest known Mesozoic bird eggs. The deformation was probably caused by lithostatic compression during sedimentation. There is a small polar portion damaged, possibly by erosion during exposure in the outcrop. The 125.5- $\mu$ m-thick shell is externally smooth with rounded pore openings and incorporates three structural layers of similar thickness with both prismatic and aprismatic boundaries. It is somewhat fragile compared with the eggs of modern neognaths and paleognaths and represents one of the thinnest shelled Mesozoic avian eggs known. There are no signs of predation, hatching or trampling, nor embryonic remains (Marsola 2013).

The fossil egg shows a close similarity with those of enantiornitheans from the Late Cretaceous of Bajo de la Carpa Formation (Río Colorado Subgroup) of Argentina. Marsola *et al.* (2012) and Marsola (2013) initially attributed it to Enantiornithes, while Marsola *et al.* (2014) preferred an affinity with basal Ornithothoraces. Furthermore, the coherency of their depositional contexts suggests a compatible preference for breeding



and nesting environments, with that of the Vale do Rio do Peixe Formation being closely comparable with the semi-arid landscape with eolian dunes interspersed with wide, shallow, and slightly anastomosing river systems that were ephemeral and subject to seasonal fluctuation of the Bajo de la Carpa Formation.

### **79. †Aves indet. (MN 4705-V)**

Late Oligocene/Early Miocene - São Paulo

- “cascas de ovos fósseis isoladas” - Carvalho (in Kellner 1998): 659.
- “Avian eggshells” - Azevedo & Carvalho 1998: 25A.
- “cascas de ovos fossilizadas de aves” - Souto 2017: 39.

Azevedo & Carvalho (1998) reported several small and thin eggshell fragments (MN 4705-V) from the upper level of the Tremembé Formation. Analysis through Scanning Electron Microscopy and microscopes of the fractured and polished surfaces of mainly radial sections showed a structural arrangement strongly resembling the typical ratite pattern. Four layers could be differentiated, an innermost zone of radial calcite plates (~0.03 mm), a basal tabular crystallite aggregates layer (~0.14 mm), a spongy layer (~0.19 mm) and a thin external zone (~0.02 mm), with pores distributed randomly between the shell units.

## **6. 5. 3. Ichnofossils**

### **80. †Coprolites**

Late Oligocene/Early Miocene - São Paulo

- “Os nódulos coprolíticos teriam sido, pelo resultado descrito, produzidos por uma ave de porte médio de hábito alimentar múltiplo” - Castro *et al.* 1988a: 109.
- “Coprólitos de aves” - Castro *et al.* 1988b: 2358–2370, figs. 3–6.

Castro *et al.* (1988a; 1988b) reported coprolites associated with birds coming from the shales (predominantly) and clays of Fazenda Santa Fé (Castro *et al.*, 1988b: 2360). These records provide information about the ecology of these animals and the evolution of the sedimentary paleoenvironments of the Tremembé Formation (Castro *et al.* 1988b: 2358).

The coprolitic nodules are beige, allowing a good distinction from the matrix, with ellipsoidal (more frequent), circular, semicircular, or reniform shapes and dimensions ranging from 6 to 50 mm along the major axis and commonly 5 to 20 mm along the minor axis (Castro *et al.* 1988a: 109; 1988b: 2360). The material is deposited in the collection of fossil invertebrates of the Departamento de Geologia e Paleontologia of MN under numbers 5.619-I (samples C-1 to C-6) and 5.620-I (illustrated in figures 2-6 of Castro *et al.* 1988b).

By analyzing its content and the chemical elements that make up the coprolitic nodules, it was possible to infer the feeding eating habits and the conditions in which its generators lived (Castro *et al.* 1988b: 2362). Some of the nodules contain undigested ossicles and fish scales (Castro *et al.* 1988a: 109; 1988b: 2361), and elements that form a set of micronutrients essential to the development of plants were found, corroborating the variation in these birds' feeding habits (Castro *et al.* 1988a: 109; 1988b: 2362). The indication that these birds were not exclusive fish consumers agrees with the unfavorable environmental conditions to this type of diet, where periodic fish deaths were caused by the lake bottom's anoxic characteristics, which limited their availability (Castro *et al.* 1988b: 2361). The different diets of fossil birds known from the Tremembé Formation (from generalists to exclusive fish and carrion feeders) demonstrate the relationship between the chemical composition of the coprolites and the habits of the organisms that generated them (Castro *et al.* 1988b: 2362).

The type of deposition of the coprolites suggests that they were projected vertically in shallow water (Castro *et al.* 1988b: 2361). Its occurrence corroborates the tendency of the drying up of the Tremembé paleolake, also evidenced by the accumulation of fish, traces of invertebrates, and vegetation in the swampy environment, until its complete drying (Castro *et al.* 1988b: 2362).

## **81. †Footprints**

Late Cretaceous - Roraima

- “Icnofóssil de pegadas de aves” - Lopes *et al.* 2011: 1–4, fig. 2.

Lopes *et al.* (2011) reported ichnofossils of bird tracks from the Late Cretaceous of Serra do Tucano Formation in the Tacutu Basin. In the same formation, ichnofossils

from arthropods and other invertebrates were also found, possible footprints of small non-avian dinosaurs, imprints of plants and coprolites, in addition to material not yet determined. As for the occurrence of footprints of small non-avian dinosaurs along with footprints of birds, Lopes *et al.* noted that the environment could have been a feeding or passage site. However, as pointed by Gustavo Prado (personal communication), this record needs to be revised since it could have a non-vertebrate origin.

#### **6. 5. 4. Osteological material and mummifications**

Osteological remains make up the bulk of the known fossil bird material for Brazil. Most of the extinct taxa were described from truly fossilized remains, but many subfossil materials are also known, especially from archeological sites. The literature concerning these remains is sparse and usually does not go beyond family level taxonomical determinations. Mummified remains associated with these sub-recent materials are rarer, being mentioned in the literature on a handful of occasions.

### **Aves**

#### **82. †Aves indet. (SMF)**

Early Cretaceous - Ceará

- “partial “wing”” - Naish *et al.* 2007: 528, pl. 25D.
- cf. Aves [in part] - Bittencourt & Langer 2011: 28–29, 38.
- “Three other asymmetrical feathers found in association with bone fragments” - Sayão *et al.* 2011: 198.
- “possíveis aves” [in part] - Leite & Hessel 2011: 2.
- “materiais osteológicos de aves” [in part] - Pinheiro & Fernandes-Ferreira 2014: 125.
- “avian skeletons associated with poorly preserved feathers” [in part] - Carvalho *et al.* 2015a: 2.
- “presumed carpal bones associated with three asymmetrical feathers” - Carvalho *et al.* 2015b: 162.
- “materiais isolados de aves” [in part] - Metello 2017: 6.
- “enantiornithines” [?; in part] - Pittman *et al.* 2020: 61.

Naish *et al.* (2007) briefly described and figured an unaccessioned specimen from the Crato Formation in the SMF collection. It comprises a single large asymmetric “primary” flight feather similar to that described by Martins-Neto & Kellner (1988),

five smaller asymmetric feathers, and two unidentifiable, presumed carpal bones<sup>11</sup>. The longest and smallest feathers are, respectively, 81 mm and 14 mm long.

### **83. †Aves indet. (UFRJ-DG 06-Av)**

Late Cretaceous - São Paulo

- Aves indet. - Azevedo *et al.* 2007: 546, fig. 2R–S.
- cf. Aves - Bittencourt & Langer 2011: 38.
- Aves indet. - Candeiro *et al.* 2012: 618.
- Aves cf [?; in part?] - Brum & Simbras 2015: 119.
- Aves indet. - Martinelli & Teixeira 2015: 147.
- Aves indet. - Alves *et al.* 2016: 87–88, fig. 4I–J.

From the Jales locality of Adamantina [Vale do Rio do Peixe] Formation in western São Paulo state, Azevedo *et al.* (2007) reported a bone fragment (UFRJ-DG 06-Av) about 1 mm long that they tentatively attributed to the distal end of a phalanx of an indeterminate bird. The fossil was also described and figured by Alves *et al.* (2016).

### **84. †Aves indet. (CPPLIP 470)**

Late Cretaceous - Minas Gerais

- Neornithes indet. - Candeiro *et al.* 2010: 33.
- Aves gen. et sp. indet. [in part] - Candeiro *et al.* 2012: 619–620, fig. 1B.
- Aves indet. - Candeiro 2015: 165, fig. 36H–I.
- Avialae indet. - Martinelli & Teixeira 2015: 147, fig. 10B.
- Theropoda indet. [?; in part] - Pereira *et al.* 2015: 175.

From the “Ponto 1 do Price” site of Peirópolis locality of Marília Formation in Uberaba, Minas Gerais, Candeiro *et al.* (2012) assigned to an indeterminate Aves a complete, robust isolated pedal phalanx 1 of left digit II<sup>12</sup> (CPPLIP 470), discovered in 2009 and previously briefly mentioned by Candeiro *et al.* (2010). The authors noted similarities with the larger specimen MACN PV RN 1107 described by Agnolin & Martinelli (2009) from the Late Cretaceous Los Alamitos Formation of Río Negro Province, Argentina, including features reminiscent of derived neornithine predatorial birds (such

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<sup>11</sup> Adapted from the plate’s caption. In the text, Naish *et al.* (2007: 526, 528) mention it as a “feather, associated with two or three smaller feathers and with some indeterminate bones” or “three asymmetrical feathers are preserved in association with several presumed carpal bones”.

<sup>12</sup> Candeiro (2015: 165) mistakenly described it as front limb phalanx.

as Falconiformes), but with Candeiro *et al.* (2010) tentatively assigning it to Neornithes indet. and Candeiro *et al.* (2021) only to Aves indet.

## 85. †Aves indet. (CPPLIP 481)

Late Cretaceous - Minas Gerais

- Aves gen. et sp. indet. [in part] - Candeiro *et al.* 2012: 619, fig. 1A.
- Avialae indet. - Martinelli & Teixeira 2015: 147, fig. 10A.
- Theropoda indet. [?; in part] - Pereira *et al.* 2015: 175.

From the “Ponto 1 do Price”, Candeiro *et al.* (2012) assigned to an indeterminate Aves a small, isolated bone identified as a possible pedal ungual phalanx lacking its proximal end (CPPLIP 481). Its position on the pes could not be determined due to its incomplete nature.

## †Enantiornithes

### 86. †?Enantiornithes indet. (MURJ)

Early Cretaceous - Ceará

- “probable enantiornithine bird” - Naish *et al.* 2007: 528–529, pl. 26.
- “a nearly complete and excellently well preserved skeleton of a bird” [?] - Herzog *et al.* 2008: 38.
- “bird, possibly enantiornithine” - Close *et al.* 2009: 617.
- “enantiornithine bird” - O'Connor & Dyke 2010: 19.
- Enantiornithes indet. [in part] - Bittencourt & Langer 2011: 28–29, 38.
- “ave enantiornitínea” - Campos 2011: 90.
- “supposed presence of an enantiornithine bird” - Sayão *et al.* 2011: 203.
- “possivelmente aves euenantiornitiformes” - Leite & Hessel 2011: 2.
- Enantiornithes indet. - Bittencourt & Langer 2012: 305–306.
- “possível enantiornitíneo” - Pinheiro & Fernandes-Ferreira 2014: 125.
- “avian skeletons associated with poorly preserved feathers” [in part] - Carvalho *et al.* 2015a: 2.
- “poorly preserved articulated specimen” - Carvalho *et al.* 2015b: 162.
- “materiais isolados de aves” [in part] - Metello 2017: 6, fig. 5.
- “enantiornithines” [in part?] - Pittman *et al.* 2020: 61.

Naish *et al.* (2007) preliminary described a partial skeleton associated with feathers of a probable enantiornithean from the Crato Formation held in the MURJ private collection, in Japan. The poorly preserved fossil is somewhat crushed and partially articulated,

preserved in part and counterpart. Many of the bones are represented only by external molds. The skull is preserved in palatal view and is incomplete, with a braincase, mid-line palatal elements, and possible rod-like jugal bar being discernible in the photographs that were available to the authors. About 25 vertebrae are preserved, including cervical (several are preserved in ventral view), dorsal and caudal. The dorsal vertebrae show features comparable to that of euenantiornitheans. At least three caudal vertebrae are preserved, two of which are articulated. Fragments of other caudal vertebrae are also present. A presumably present pygostyle was not preserved. Part of the ilium and a possible ischium have been tentatively identified. A hindlimb, possibly the left one, is the best-preserved part of the specimen, comprising the femur, tibiotarsus, tarsometatarsus, and hallux. The latter appears proportionally large, fully reversed, and retaining its unguis claw sheath. Feather impressions are present alongside the tarsometatarsus and adjacent to the femur. The specimen is 156 mm long from the rostral-most preserved tip of the skull to the last preserved caudal vertebrae, being about the same size as the fringillid *Fringilla coelebs* Linnaeus.

A nearly complete and excellently well-preserved skeleton was mentioned by Herzog *et al.* (2008) to be rumored sold and smuggled out of Brazil, with unknown whereabouts. It is not clear if this refers to the MURJ specimen, though this seems likely.

### **87. †cf. *Enantiornithes* indet. (CPPLIP 482)**

Late Cretaceous - Minas Gerais

- cf. *Enantiornithes* gen. et sp. indet. - Candeirol *et al.* 2012: 620, fig. 1C.
- *Enantiornithes* indet. - Candeirol *et al.* 2013: 17, 18, 19.
- *Enantiornithes* - Candeirol 2015: 165, fig. 36J.
- cf. *Enantiornithes* gen. et sp. indet. - Martinelli & Teixeira 2015: 147, fig. 10C.
- Theropoda indet. [?; in part] - Pereira *et al.* 2015: 175.

From the “Ponto 1 do Price” site, Candeirol *et al.* (2012) assigned an incomplete left metatarsal III lacking its proximal portion (CPPLIP 482) to a possible enantiornithean.

### **88. †*Enantiornithes* indet. (spp.) (William’s Quarry)**

Late Cretaceous - São Paulo

- Enantiornithes - Alvarenga & Nava 2005: 20.
- “at least three indetermined different Enantiornithes” - Agnolin & Martinelli 2009: 42.
- Enantiornithes - Alvarenga & Höfling 2011: 119.
- Enantiornithes indet. - Bittencourt & Langer 2011: 33, 38.
- Enantiornithes indet. - Bittencourt & Langer 2012: 310–311.
- Enantiornithes indet. - Candeiro *et al.* 2012: 618.
- Enantiornithes - Marsola *et al.* 2012: 49.
- “pequenas aves relacionadas aos Enantiornithes” [in part?] - Nava 2013: 253.
- Aves cf [in part?] - Brum & Simbras 2015: 119.
- “pequenas aves relacionadas aos Enantiornithes” [in part?] - Nava 2015: 138.
- “indeterminate enantiornithine birds” - Carvalho *et al.* 2015b: 161.
- Enantiornithes indet. - Martinelli & Teixeira 2015: 147.
- “enantiornithine birds” [in part] - Nava *et al.* 2015: 73.
- Enantiornithes [in part] - Alves *et al.* 2016: 87–88.
- “enantiornithine birds” [in part] - Chiappe *et al.* 2018a: 170.
- “enantiornithine birds” [in part] - Chiappe *et al.* 2018b: 105.
- “enantiornithine birds” [in part] - Chiappe *et al.* 2019: 232–233.
- “enantiornithines” [in part] - Pittman *et al.* 2020: 61.

Alvarenga & Nava (2005) reported enantiornithean remains from William’s Quarry site (Chiappe *et al.* 2018a) of Adamantina Formation around Presidente Prudente, São Paulo, being the first avian osteological material of Mesozoic age to be reported to the country. The first material was collected two months before their public announcement on 10 August 2005. It is represented by several dozens of three dimensionally preserved and delicate bones, isolated and partially articulated, of about three or four different birds morphologically very close to *Enantiornis leali* Walker<sup>13</sup> from the Late Cretaceous of El Brete, Argentina, but much smaller, of size comparable to small living passeriforms. Differences in phalanx thickness indicated that disparate taxa are represented (Alvarenga in Castilhos 2005), as well one form having four while the other has three fingers (Lopes 2005). Despite their great diagnostic value, the bones were difficult to associate, which prevented the description of new taxa.

Alvarenga & Höfling (2011) described the still-under study material as including several bones, many associated in incomplete skeletons, representing at least four

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<sup>13</sup> Alves *et al.* (2016) mistakenly reported that Alvarenga & Nava (2005) compared the specimens to *Neuquenornis volans* Chiappe & Calvo from the Late Cretaceous of Río Colorado Formation of Argentina.

genera and species that did not seem to have teeth and were hummingbird or sparrow-sized.

The material still awaits formal description, but several bones were figured in contemporaneous news media (e.g., Castilhos 2005; Lopes 2005), including a humerus with associated radius and ulna and other fragments (MHNT-VT-5240), a complete left coracoid (MHNT-VT-5241), and an incomplete tarsometatarsus (MHNT-VT-5242). In addition, toothless skulls, vertebrae, hindlimb elements, and other fragments were also mentioned by Lopes (2005).

- “pequenas aves relacionadas aos Enantiornithes” [in part?] - Nava 2013: 253.
- Aves cf [in part?] - Brum & Simbras 2015: 119.
- “pequenas aves relacionadas aos Enantiornithes” [in part?] - Nava 2015: 138.
- “enantiornithine birds” [in part] - Nava *et al.* 2015: 73.
- Enantiornithes [in part] - Alves *et al.* 2016: 87–88.
- “enantiornithine birds” [in part] - Chiappe *et al.* 2018a: 170.
- “enantiornithine birds” [in part] - Chiappe *et al.* 2018b: 105.
- “enantiornithine birds” [in part] - Chiappe *et al.* 2019: 232–233.
- “enantiornithine birds” [in part] - Wu *et al.* 2019: 221.
- “enantiornithines” [in part] - Pittman *et al.* 2020: 61.
- “enantiornithines” [in part] - Wu *et al.* 2021: 1–12, figs. 1–4.

More material from William’s Quarry was excavated in the subsequent years after the publication of Alvarenga & Nava (2005) but mentions in the literature do not provide specifications about which elements they are referring to. This material is deposited in MPM and under preparation at that institution and the Natural History Museum of Los Angeles County (Fonseca 2019b; SAPE 2020). Nava (2013; 2015) mentioned cranial and post cranial materials, including associated sacral and lumbar vertebrae forming a synsacrum, furcula, and partially fused carpometacarpus and tarsometatarsus.

Nava *et al.* (2015) briefly described two three-dimensionally preserved, dorsally V-shaped toothed premaxillae, which were found associated with postcranial elements of unquestionably enantiornithean identity.

Chiappe *et al.* (2018a; 2018b; 2019) reported the material of at least three small to medium-sized taxa in the hundreds, including numerous postcranial elements and many skull portions, such as isolated rostra, mandibles, and crania.



To understand better the occurrence of polyphyodonty in Mesozoic birds, Wu *et al.* (2019; 2021) performed a  $\mu$ CT scan at 3  $\mu$ m resolution in a premaxilla (MPM 90) and a partial dentary (MPM 351). The results showed preservation of replacement teeth and their tooth families, and a 3D reconstruction of the replacement tooth rows showed a conserved alternating pattern, as observed in other archosaurs.

## †Euenantiornithes

### 89. †*Cratoavis cearensis* Carvalho, Novas, Agnolin, Isasi, Freitas & Andrade

Early Cretaceous - Ceará

Fig. 16.A

*Type locality:* Mina Pedra Branca, municipality of Nova Olinda, state of Ceará, Brazil (7° 6'51.9'' S and 39° 41'46.9'' W).

*Etymology:* *Cratoavis*, “Crato bird”, and *cearensis* referring to the state of Ceará.

- Indeterminate genus and species - Carvalho *et al.* 2015a: 1–5, suppl. 1–19, figs. 1–2, suppl. figs. 1–7.
- *Cratoavis cearensis* **nov. gen. et sp.** - Carvalho *et al.* 2015b: 161–171, figs. 3–4.
- *Cratoavis cearensis* - Metello 2017: 7–8, 28, 30, figs. 1, 16.
- *Cratoavis cearensis* - Agnolin *et al.* 2017b: 2, fig. 1A.
- “UFRJ-DG 031Av” - Knoll *et al.* 2018: 6–7.
- “*Cratoavis*” - O'Connor 2020: 157.
- *Cratoavis cearensis* - Foth 2020: 176–177.
- “UFRJ-DG 031Av” - O'Connor *et al.* 2020: 37, 39, 40.
- “*Cratoavis* (valid?)” - Pittman *et al.* 2020: 61.

Carvalho *et al.* (2015a) described an articulated skeleton associated with feathers of a minute euenantiornithean from Mina Pedra Branca, Nova Olinda, found by Cleuduardo Laurentino Dias, Devânio Ferreira Lima, and Antonio Josieudo Pereira Lima. Later in the same year, they described it further and erected the new genus and species *Cratoavis cearensis* for the material (Carvalho *et al.* 2015b).

The specimen (UFRJ-DG 031 Av, holotype) is a nearly complete skeleton preserved in part and counterpart, about 6 cm long from the snout to the tip of the pygostyle. The skeleton is exposed in lateral view, except for the proximal caudal vertebrae and pygostyle (including the rectrices), which are exposed in dorsal view. The

skull and neck are exposed on the left side, being rotated ventrally regarding the rest of the body, whereas most of the remaining skeleton elements are exposed on the right side. The bones have a dark-brown coloration and are preserved in three dimensions, but as common in fossils preserved in part and counterpart, several elements are cracked, with crushing and displacement occurring in some of them (e.g., in the skull and jaw). The smaller counterpart shows better preservation but contains only imprints of the skull, forelimbs, and pectoral girdle fragments.

The identified elements, both as bones or impressions of varying degrees of preservation, include parts of the poorly-preserved skull (parietal, frontal, nasal, and lacrimal bones), sclerotic ring, maxilla with minute alveoli (indicating it was toothed), vertebrae (five cervical preserved in articulation, six dorsal and eight free caudal, as well as sacral), pygostyle (composed of eight fused vertebrae), most right dorsal ribs and the distal end of some left ones, sternal ribs, both ilea, pubes, both coracoids, left scapula, both humeri, both radii, both ulnae, both carpometacarpi, left-wing phalanges (represented by digits I and II, including unguals, and only the base of the first phalanx of digit III), both femora, both tibiotarsi, both metatarsals (best represented by right I, II, III and IV ones), and pedal phalanges of both feet (represented by digits I, II, III and IV, including unguals). In addition, long, thin bones in the abdominal region are probably part of a gastrarium. The ischia and the sternum were not preserved; Knoll *et al.* (2018) noted that the latter was presumably completely cartilaginous.

Different elements of the plumage have been preserved, most as impressions (Metello 2017). The most remarkable are the paired dorsoventrally depressed, rachis-dominated symmetrical rectrices 79.9 mm long, roughly 30% longer than the length of the skeleton, similar to that observed among other enantiornitheans and confuciusornithiforms. The feather's proximal portion was interpreted as the calamus, which is inserted on the third proximal pygostyle vertebra. Its preservation in relief helped recognize key characters in this feather morphotype: a narrow groove extends from the base to the distal tip; the robust scapus is nearly flat at the calamus, becoming slightly convex in the rachis at mid-length (with its reconstruction indicating it was nearly 8-shaped in cross section), flattening again distally where it became vaned; the first recognizable barbs of the pennaceous vanes appear at nearly mid-length of the scapus, increasing in size distally; no signs of interlocking barbules are visible.

According to O'Connor (2020), the three-dimensional specimens preserved Cretaceous Burmese amber, showing that the wide rachis observed in compression fossils was originally C-shaped with a thickness of 3-10  $\mu\text{m}$ , indicate that rectrices of *C. cearensis* are dorsally exposed and flattened. However, Foth (2020) noted that this particular morphology could be the result of miniaturization and that Carvalho *et al.* provided no compelling evidence that the rectrices were de facto preserved in dorsal view (other than the caudal vertebrae and pygostyle being preserved in the same view), with the longitudinal groove most likely representing the ventral furrow of the rachis and not a dorsal groove, in analogy to modern pennaceous feathers. The third proximal part of the rachis bears a row of five lunar dark granulate transversal bands, interpreted as remnants of an ornamental color pattern, preserved as carbonized traces (Metello 2017). The presence of this kind of pattern reinforces the interpretation that such elongated rectrices could have been sexually dimorphic and associated with sexual display, specific recognition, or visual communication among early birds. Small brownish contour feathers with pennaceous and plumulaceous vanes cover the wings and body, including a crown at the top of the head. Ten asymmetrical secondary remiges have been incompletely preserved (longest right one 10.3 mm, longest left one 8.6 mm), and asymmetrical alular feathers are also observable, with at least three of them preserved on the left hand. Feathers on the hind limbs were not observed. Around the skull, there are probable preserved soft tissues, in some cases appearing like a dotted surface similar to fragments of skin, and small plumes appearing like a brownish tinge. Elongate, yellowish-white muscle fibers are preserved bordering the femur.

The ontogenetic state of the specimen is uncertain. Carvalho *et al.* (2015b) pointed out the very small body size and unfused tarsometatarsus, tibiotarsus, and carpometacarpus in favor of being a young individual. Fused vertebral centra, well-defined epiphyses of long bones, extensive pubic apron, and the absence of surface pitting indicate that it was probably an adult individual, though. A well-developed plumage is also contrasting, especially the long rectrices, similar to the observed in adult individuals of modern birds. The early ontogenetic emergence of these tail feathers is also indicated by the presence of well-developed plumage, especially the ornamental rectrices, in young enantiornitheans from the Jehol Group (Early Cretaceous of northeast China). If correct, this could indicate that significant differences in plumage

development probably existed between enantiornitheans and modern birds. It was referred to as an immature specimen by Knoll *et al.* (2018), O'Connor (2020), and O'Connor *et al.* (2020).

Carvalho *et al.* (2015a; 2015b) classified it as a euenantiornithean of unresolved phylogenetic position, highlighting similarities with the genera *Pengornis* and *Eoenantiornis*. Agnolin *et al.* (2017b) referred to it as a basal enantiornithean. O'Connor (2020) referred to the taxon as “*Cratoavis*” and Pittman *et al.* (2020) as “*Cratoavis* (valid?)”, with neither of them developing it further.

## Ornithuromorpha

### 90. †*Kaririavis mater* Carvalho, Agnolin, Rozadilla, Novas, Ferreira Gomes Andrade & Xavier-Neto

Early Cretaceous - Ceará

Fig. 16.B

*Type locality:* Pedra Branca Mine, Nova Olinda County, Ceará State Brazil (7°7'25"S, 39°42'7"W).

*Etymology:* *Kaririavis*, “Kariri bird”, referencing the Karirí people of northeastern Brazil combined with the Latin *avis*, and *mater*, Latin for “mother”, as it is the oldest ornithuromorph known for South America.

- “early Cretaceous birds from Brazil” - SAPE 2020: 3.
- *Kaririavis mater* gen. et sp. nov. - Carvalho *et al.* 2021: 1–12, figs. 2–4, 6.

Carvalho *et al.* (2021) described a small, partial isolated foot from the Crato Formation of Mina Pedra Branca, Nova Olinda, Ceará as the new genus and species *Kaririavis mater*. Work being done on the fossil was reported already in the previous year (SAPE 2020), but with no more details than its age and country of origin.

The fossil (UFRJ-DG 116 Av) is preserved as part and counterpart and includes partial right pes, a nearly complete tarsometatarsus (exposed in plantar view) and several apparently unconnected pedal phalanges, tentatively identified as digit II phalanges 1 and 2, digit III phalanges 1 to 3, two indeterminate phalanges of digit IV, and ungual phalanx of digit II covered with a keratinous sheet, along with at least 10

poorly-preserved dark-brownish contour feathers preserved in close association, which the authors believed they probably belong to this individual.

The sparrow-sized bird was referred to Ornithuromorpha. Its unique foot morphology precludes a clear knowledge of its habits and the paleoecological niche that it occupied, but the morphology of its tarsometatarsus strongly suggests it may belong to an unknown ornithuromorph clade with terrestrial habits, in contrast with most Early Cretaceous ornithuromorphs, which are interpreted as semiaquatic.

Up to its description, the knowledge of Early Cretaceous ornithuromorphs was almost restricted to Asia and absent from Gondwanan landmasses. The discovery of *K. mater* considerably expands the paleobiogeographic distribution of Ornithuromorpha, being one of the oldest worldwide occurrences, as well as the first from Gondwana, with similar age to species from China. The record reinforces the idea that the diverse early Aptian basal ornithuromorphs known as “Jehol Birds” were probably not unique to eastern Asia but represent an example of biota from multiple lagerstätte sites serendipitously firstly found in that continent. Despite Early Cretaceous birds being still insufficiently known, *K. mater* exhibits a very different morphology when compared with contemporary Asian avifaunas, possibly being a result of biogeographic differences and indicating that the phylogenetic diversity of Mesozoic avifaunas of Gondwana is likely far greater than what has been discovered so far.

## Neornithes

### 91. †Aves indet. 1

Early Eocene - Rio de Janeiro

- Aves indet. A - Mayr *et al.* 2011a: 680–682, fig. 1.
- “Indetermined birds” [in part] - Tambussi & Degrange 2013: 32.

Mayr *et al.* (2011a: 680, 681, 682, 683) reported an indeterminate right carpometacarpus (MN 4115-V) from the early Eocene of the São José de Itaboraí Basin.

Due to the assignment of two humeri and a coracoid to *Itaboravis elaphrocnemoides* (see Cariamiformes), Mayr *et al.* (2011a: 683) pointed out that that seems to be among the most abundant small birds in Itaboraí, a fact that could support

the attribution of this carpometacarpus of comparable size to that species. However, the Itaboraí material also includes tibiotarsi of four small to medium size forms (see below), demonstrating a considerable diversity, and, unlike one of the humeri and the coracoid, which were found in the same matrix block, there is no evidence beyond the size to support this attribution with *I. elaphrocnemoides*.

The carpometacarpus morphology does not correspond to any known avian taxon, seemingly closer to the tinamids (but differing from them in different characters) and clearly different from the European Paleogene genus *Elaphrocnemus*.

## 92. †Aves indet. 2

Early Eocene - Rio de Janeiro

- Aves indet. B (“cf. *Eutreptodactylus itaboraiensis* gen. et sp. nov.”) - Mayr *et al.* 2011a: 682, fig. 2.
- “Indetermined birds” [in part] - Tambussi & Degrange 2013: 32.

Mayr *et al.* (2011a: 682) reported the distal end of an indeterminate left tibiotarsus (MN 4119-V) from the early Eocene of the São José de Itaboraí Basin. This bone belonged to a small bird, much smaller than *Itaboravis elaphrocnemoides*, perhaps belonging to *Eutreptodactylus itaboraiensis*, the only bird of comparable size known from the same locality, from which the holotype came from the same set of bones. However, because the holotype of *E. itaboraiensis* is a tarsometatarsus and has been lost, further comparisons are not possible for a reliable attribution of MN 4119-V.

## 93. †Aves indet. 3

Early Eocene - Rio de Janeiro

- Aves indet. C - Mayr *et al.* 2011a: 682–683, fig. 2.
- “Indetermined birds” [in part] - Tambussi & Degrange 2013: 32.

Mayr *et al.* (2011a: 682, 683) reported the indeterminate distal end of a right tibiotarsus (MN 4116-V) from the early Eocene of the São José de Itaboraí Basin. The specimen belonged to a bird the size of *Itaboravis elaphrocnemoides* and has a distinct morphology, which does not correspond to any living taxon.

Tambussi & Degrange (2013: 31) mentioned a tibiotarsus possibly belonging to *Itaboravis*, probably referring to this specimen, although Mayr *et al.* (2011a: 682) only referred to similar dimensions.

#### **94. †Aves indet. 4**

Early Eocene - Rio de Janeiro

- Aves indet. D - Mayr *et al.* 2011a: 683, fig. 2.
- “Indetermined birds” [in part] - Tambussi & Degrange 2013: 32.

Mayr *et al.* (2011a: 683) reported the distal end of an indeterminate left tibiotarsus (MN 4117-V) from the early Eocene of the São José de Itaboraí Basin. the bone is similar to the tinamids in one of its characters, but its fragmentary state does not allow a reliable determination.

#### **95. †Aves indet. 5**

Early Eocene - Rio de Janeiro

- Aves indet. E - Mayr *et al.* 2011a: 683, fig. 2.
- “Indetermined birds” [in part] - Tambussi & Degrange 2013: 32.

Mayr *et al.* (2011a: 683) reported the distal end of an indeterminate left tibiotarsus (MN 4118-V) from the early Eocene of the São José de Itaboraí Basin. Its state of preservation is precarious and has no distinctive characters.

#### **96. †Aves indet. 6**

Early Eocene - Rio de Janeiro

- Aves indet. (?D or E) - Mayr *et al.* 2011a: 683, fig. 2.

Mayr *et al.* (2011a: 683) reported the fragmented distal end of an indeterminate left tarsometatarsus (MN 4120-V) from the early Eocene of the São José de Itaboraí Basin. This fragment consists only of the metatarsal III trochlea, with a size that corresponds approximately to that of the two tarsometatarsals mentioned above (Aves indet. 4 and 5).

## 97. Aves indet. 7

Late Pleistocene - Rio Grande do Sul

- Aves indet. - Hsiou 2009a: 146.

In addition to the part of a tarsometatarsus attributed to *Mycteria cf. americana*, Hsiou (2009a: 146) also noted that another single fragment, this time of a tibiotarsus (MCN-PV 8806), was found in the Touro Passo Formation, but due to its high degree of fragmentation and fragility, attribution to the family level was not possible.

## 98. Aves indet. 8 (spp.?)

Pleistocene - Alagoas

- “ossos de ave” - Oliveira *et al.* 2013: 259.
- “osso de ave” [in part] - Silva *et al.* 2013: 281.

From Picos II, a lagoon deposit at Fazenda Picos in the municipality of Piranhas, Alagoas, Oliveira *et al.* (2013) reported fragments of pleistocenic-age avian bones associated with megafaunal remains. They figure among material collected in January 2011 and January 2012, though Silva *et al.* (2013) mentioned a bird bone from the site collected in 2010. Nevertheless, this is the first record of bird bones for this kind of deposit in Alagoas. The fragments are small and could not be determined at a more specific level. The largest fragment (SGP-MHN-UFAL 0931-V) is part of a diaphysis of a long bone 70 mm long with a diameter of 10 mm showing preserved trabeculae, being similar to a femur, a tibiotarsus, or a tarsometatarsus of an aquatic bird or a bird of prey.

## Palaeognathae

### 99. Palaeognathae indet.

Quaternary - Ceará

- Aves *incertae sedis* - Araújo Júnior 2012: 70.
- Struthioniformes - Metello & Araújo Júnior 2013: 70.
- Aves *incertae sedis* - Araújo Júnior *et al.* 2013: 57.
- Aves *incertae sedis* - Araújo Júnior 2015: 191.
- *Rhea?* [?; in part?] - Araújo Júnior 2016: 150.



- *Rhea?* [?; in part?] - Waldherr *et al.* 2017: 471.
- *Rhea?* [?; in part?] - Waldherr *et al.* 2019: 115.

Araújo Júnior (2012: 70, 110) and Araújo Júnior *et al.* (2013: 57) reported a fragment of a long bone of a large indeterminate adult bird from the Jirau site in Itapipoca, Ceará, noting that only *Rhea* was recorded in natural tanks, but the status of the material precluded a more detailed description and therefore it was determined only as *Aves incertae sedis*. The fossil is deposited in the collection of MUPHI.

## Ratitae

### 100. †*Diogenornis fragilis* Alvarenga

Early Eocene - Rio de Janeiro

Fig. 12.A

*Type locality:* Limestone Itaboraí Basin, about 700 m east of the village of São José, district of Cabuçu, municipality of Itaboraí, state of Rio de Janeiro, Brazil.

*Etymology:* *Diogenornis*, with Greek *ornis*, “bird of Diógenes”, honoring Brazilian paleontologist Diógenes de Almeida Campos, then in the Departamento Nacional de Produção Mineral, for the support given to Alvarenga, and *fragilis* portraying the idea that the bird was vulnerable to predators because of its terrestrial habit.

- Aves [“Ainda por determinar”; in part?] - Paula Couto 1958: 11.
- Aves [“Diversas, não identificadas”; in part?] - Paula Couto 1970: 909.
- Aves [“fragmentos de ossos longos”; in part?] - Palma 1973: 40.
- Aves [“fragmentos de ossos longos”; in part?] - Palma & Brito 1974: 400.
- “restos de diversas aves, metatarsais, vértebras, pré-maxilas, etc.” [in part?] - Price (*in lit.* 1977 in Sick 1984a): 65.
- Aves [“representadas por ossos longos”; in part?] - Francisco & Cunha 1978: 390, 402, 408.
- *Diogenornis fragilis*, **sp. n.** - Alvarenga 1983: 1–8, figs. 1–17.
- *Diogenornis fragilis* - Mones 1986: 75.
- *Diogenornis fragilis* - Cuello 1988: 4.
- *Diagenornis* [*lapsus*] - Peters 1988: 226.
- “fragmentos de ossos longos de aves” [in part?] - Brito 1989: 60.
- *Diogenornis fragilis* - Alvarenga 1993a: 62, fig. 33.
- *Diogenornis fragilis* - Alvarenga 1993b: 22, fig. 14.
- *Diogenornis fragilis* - Alvarenga 1997: 123, fig. 33.
- *Diogenornis fragilis* - Kellner 1998: 654, 658–659.
- *Diogenornis* - Kellner & Campos 1999: 247, fig. 9.

- *Diogenornis fragilis* - Alvarenga & Höfling 2000: 587.
- *Diogenornis fragilis* - Alvarenga & Höfling 2004: 825.
- *Diogenornis fragilis* - Bergqvist *et al.* 2006: 55, fig. 62.
- *Diogenornis fragilis* - Bergqvist *et al.* 2009: 422, fig. 9G.
- *Diogenornis fragilis* - Mayr 2009: 32, fig. 5.2.
- *Diogenornis fragilis* - Alvarenga & Höfling 2011: 123.

Alvarenga described the genus and species in 1983 from sparse and fragmented bones from the Departamento Nacional de Produção Mineral (DNPM) collection, most of which were collected in 1949 by Júlio Carvalho. The material was not examined in detail until the then responsible for the DNPM paleontological collection, Déa Regina Bouret Campos, aware of Alvarenga's interest in fossil birds, invited him to study the material. Subsequently, paleontologist Fausto Luiz de Souza Cunha from MN sent to Alvarenga fragments of bird bones of the same origin collected in 1948 by naturalist Ney Vidal, from the former Divisão de Geologia of MN. After preparing and restoring several pieces, Alvarenga concluded that most of the material belonged to a single species, representing 4 or 5 individuals (Alvarenga 1983: 1).

The bones are deposited in the collection of the Seção de Paleontologia of the DNPM (Museu de Ciências da Terra - DNPM/RJ; under the acronym DGM) and in the collection of MN. The holotype comprises the complete left and right tibiotarsi and a right tarsometatarsus lacking the distal end of a young specimen (DGM 1421-R). The paratypes consist of a right tarsometatarsus of an adult individual, lacking the diaphysis' distal half, but retaining the distal extremity (DGM 1422-R); a left tarsometatarsus of a young adult lacking the diaphysis' distal shaft, also preserving the distal extremity (DGM 1423-R); the proximal end of a right tarsometatarsus (MN 4033-V); the middle segment of the diaphysis of a right tarsometatarsus (MN 4034-V); a segment corresponding to the distal metaphysis of a left tarsometatarsus, lacking the lateral part (MN 4035-V); the middle trochlea of a left tarsometatarsus (MN 4036-V); the proximal end of a left humerus (DGM 1424-R), which appears to be larger than that of *Rhea*, although *Diogenornis* is overall much smaller; the proximal phalanx of the second digit of the left wing (DGM 1430-R), narrower and longer than in *Rhea*; anterior part of the premaxilla (DGM 1428-R), showing a robust beak, higher than wide, very different from that of the living rheas, resembling that of a chicken, or even a cassowary, as noted by Olson (1985b: 106); posterior part of the vertebral bodies of five cervical vertebrae

(DGM 1425-R), probably C-5 to C-9; nine cervical vertebrae, probably associated, including atlas, axis, and others identified as C-3, C-4, C-5, C-7, C-9, C-10, and C-11 (DGM 1426-R); six thoracic vertebrae (DGM 1427-R), probably the last pre-sacral; axis (DGM 1429-R); thoracic vertebra (MN 4037-V), probably the first or second, and another thoracic vertebra (MN 4038-V), probably the pre-sacral penultimate or antepenultimate (Alvarenga, 1983: 2, 3, 4).

The bird, with dimensions estimated between 80 and 90 cm in height and weight of 4.138 kg, was probably flightless, but its wings were proportionally much more developed than those of *Rhea*, raising the possibility that its close ancestors were flighted (Alvarenga 1983: 5, 6; Taranto & Bergqvist 2010: 118). Furthermore, Taranto *et al.* (2011: R58, R59), while studying the bird's hind limbs, estimated the length of the absent femur and concluded that the legs' morphology is comparable to that of *Rhea americana*, but with the dimensions of a young specimen, suggesting possible congruence in the biomechanical locomotion between the genera. This topic was addressed in greater detail by Taranto (2012: e.g., 24, 32, 33, 35, 37), who pointed out that *Diogenornis*, being a cursorial bird, digitigrade, and with three large and robust fingers, would be well adapted to running, being able to achieve speed close to the 50 km/h that *Rhea* is capable of<sup>14</sup>.

The discovery of several individuals together, of different sizes and ages, may indicate the presence of sexual dimorphism and gregarious habits (Alvarenga 1983: 6).

Alvarenga (1983: 1, 4) initially classified the species within the Opisthodontidae as a probable representative of the ancestors of living rheas and highlighted the beak's shape as an essential differentiating character between this family and Rheidae. Peters (1998) and Peters & Storch (1993) noted similarities with the European ratite genus *Palaelotis*. Tambussi (1995: 122, 123, 127) associated it with the Rheiformes, considering the species, along with proximal phalanges from Las Flores (Grupo Río Chico in Chubut, Argentina; early Eocene [Woodburne *et al.* 2014b: 109]) associated with Rheidae<sup>15</sup>, as the oldest records for the order. She also concluded that

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<sup>14</sup> This study includes an annex of the final manuscript of this analysis, authored by Taranto, Bergqvist, Loguercio & Rocha-Barbosa, in the form submitted to the journal *Acta Paleontologica Polonica*. However, apparently it was not published.

<sup>15</sup> Bourdon *et al.* (2009: 653) erroneously attribute this record to *Diogenornis fragilis*.

the Rheidae family would have been represented since the time of its earliest records by two morphotypes, one including the slender forms of the Eocene of Brazil and the other with a structural pattern present in living species, such as the bird of Las Flores. On its classification as an opisthodactylid, Mayr (2009: 32) noted that the similarities between these ancient forms are probably plesiomorphic and preferred to treat them as stem rheids. He also pointed out the osteological similarities between the Itaboraí species and the birds of the Palaeotididae and Remiornithidae families. Later, Mayr (2016: 100) added that there is no solid basis for an affinity between *Diogenornis* and the Rheiformes, but this is very likely for biogeographic reasons and the general similarity to the living rheas, as also pointed out by Agnolin (2016b).

After re-studying the material, comparing it with all ratite families, Alvarenga (2010: 143) considered the species much closer to the Australian casuariids than to the South American rheids, reinforcing the theory of a Gondwanan origin for these birds, the close relatedness between rheids and casuariids (including Dromaiidae) and the importance of the transantarctic biotic exchange between South America and Australia in the early Cenozoic. This possible relation was briefly mentioned earlier by Alvarenga & Höfling (2000: 587; 2004: 825).

Agnolin & Cenizo (2014: 3) tentatively maintained the classification as a casuariid and referred to the genus *Diogenornis* the distal end of a tibiotarsus from the locality Río Chico (middle Paleocene) in Chubut, Argentina. They also mentioned the distal end of another tibiotarsus from the Bryn Gwyn locality (Oligocene) in Chubut, which is similar to *Diogenornis* and the casuariids. Later, Agnolin (2016a: 2, 3) referred to the Río Chicos tibiotarsus as cf. *Diogenornis* within the Ratitae, pointing out similarities with the casuariids, and the tibiotarsus from Bryn Gwyn, due to its fragmentary nature, was left as indeterminate Aves after a detailed review (Agnolin, personal communication). In the face of the new hypothesis of a relationship between the oldest South American ratites with the casuariids, Agnolin (2016a: 2, 7, 8) began to review unpublished specimens deposited in several Argentinean institutions and to reevaluate published specimens from different sites in the country due to the new anatomical information available, with his results suggesting that during the Paleogene and the beginning of the Neogene, South American ratites were quite diverse, encompassing not only rheids but also several taxa of uncertain affinity that were

possibly extinct with the change of their warm forested habitats for arid areas at the end of the Miocene. This unexpected ratite diversity in South America and the equivalent scenario in Europe and Africa fossil finds, along with recent molecular analyses, made him question the model of the modern ratites' origin as exclusive products of the breakup of Gondwana.

- *Diogenornis fragilis* - Metello *et al.* 2012a: 525.
- *Diogenornis fragilis* [in part] - Metello 2013: 176.
- *Diogenornis fragilis* [in part?] - Metello *et al.* 2014: 84.
- *Diogenornis fragilis* [in part] - Metello & Bergqvist 2014: 151.

Metello *et al.* (2012a: 525) associated with this species an ungual phalanx (UFRJ DG 305-M), of the same origin as the other known elements, erroneously deposited in the Mammal Collection of the Geology Department of UFRJ<sup>16</sup>.

- *Diogenornis fragilis* [in part] - Metello 2013: 176.
- *Diogenornis fragilis* [in part?] - Metello *et al.* 2014: 84.
- *Diogenornis fragilis* [in part] - Metello & Bergqvist 2014: 151.

Metello (2013: 176) mentioned two ungual phalanges attributed to this species (including the record mentioned above), noting that they are digits III and IV, probably of the left foot. This other material is identified in the collection as MCT 1839-R (Metello & Bergqvist 2014: 151). The phalanges to that of *Struthio*, probably due to the basal position of *Diogenornis*, and its description reinforce the cursorial habit attributed to the taxon (Metello *et al.* 2012a: 525; Metello 2013: 176). Metello & Bergqvist (2014: 151), while evaluating the curvature of the phalanges, agreed on the terrestrial habits, interpreting it as a well-established terrestrial bird, even though it still retained some reduced flight capacity, and that it possibly behaved like a tinamid, feeding and raising their offspring on the ground and flying short distances to escape predators.

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<sup>16</sup> Metello *et al.* (2014: 84) mentioned the ungual phalanges referable to *Diogenornis fragilis* and *Paleopsilopterus itaboraiensis* (see Cariamiformes) present in the DNPM fossil mammal collection, without specifying which or how many were the specimens, referring to them only as distinct morphotypes.

## Rheiformes

### Rheidae

#### 101. *Rhea* sp.

Quaternary - Ceará

- “Neornithes: indeterminadas” [in part] - Souza Cunha 1961: 5.
- “Neornithes, Ordens e gêneros indeterminados” [in part] - Paula Couto 1961: 8.
- “aves (indeterminadas)” [in part] - Paula Couto 1962: XIX.
- *Rhea* - Paula Couto 1980: 145.
- *Rhea* - Ximenes 2009: 472.
- *Rhea* - Souto & Carvalho 2010: 116.
- *Rhea* sp. - Araújo Júnior 2012: 70.
- *Rhea* sp. - Araújo Júnior *et al.* 2013: 59.
- *Rhea?* [?; in part?] - Araújo Júnior 2016: 150.
- *Rhea?* [?; in part?] - Waldherr *et al.* 2017: 471.
- *Rhea?* [?; in part?] - Waldherr *et al.* 2019: 115.

Paula Couto (1980: 145) reported the genus *Rhea* among the quaternary fauna recovered from a tank (tank “2”) in the João Cativo locality in Itapipoca, Ceará. In the face of material from Piauí being assigned to *Rhea fossilis* (Faure *et al.* 2010), this record needs a reevaluation.

#### 102. *Rhea americana* (Linnaeus)

Quaternary - Goiás, Minas Gerais

- “deux espèces d’Autruches (*Rhea*) dont l’une bien plus grande que l’espèce actuelle” [in part] - Lund 1840: 319.
- “uddöd Art af Familien Alectorides Ill. af Störrelse som den amerikanske Struds” [in part?] - Lund 1841d: 18.
- “deux espèces d’autruche, dont l’une bien plus grande que l’espèce actuelle” [in part] - Claussen 1841: 20.
- “to Arter Struds, hvoraf den ene betydelig større end den her nulevende Art” [in part] - Lund 1842b: 130.
- “un genre voisin des *Dicholophus* ou *Cariamias*” [?] - Gervais 1844a: 294.
- “Autruche du genre *Rhea*, plus grande que les deux espèces actuelles” - Gervais 1844b: 33.
- “l’une des plus remarquables par sa grande taille est de la famille des Alectoridés ou Hocos” -

Gervais 1844b: 34.

- "une espèce plus grande que les espèces vivantes. Mais celle-ci n'appartient pas à un nouveau genre. Elle était du type du Nandou, ou autruche du Brésil, et appartenait comme elle au genre *Rhea*" - Liais 1872: 302.
- "le genre *Cariama* (*Dicholophus* d'Illiger, *Microdactylus* de Geoffroy, *Seriema* du Brésil)" [?] - Liais 1872: 303.
- "two species of American ostrich (*Rhea*), one larger than either of the living species" [in part] - Wallace 1876: 164.
- "gigantisk Styltegænger" - Lund (in Reinhardt 1881): 147.
- *Rhea americana* [in part] - Reinhardt 1881: 141-153, figs. 1-3.
- *Rhea americana* (et aff.) [in part] - Winge 1887: 18.
- *Rhea americana* [in part] - Lambrecht 1933: 729.
- *Rhea americana* [in part] - Brodkorb 1963: 201.
- *Rhea americana* [in part] - Mones 1986: 75.
- *Rhea americana* [in part] - Cuello 1988: 26.
- *Rhea americana* [in part] - Nascimento & Silveira 2020: 489.

Lund (1840: 319; 1842b: 130) identified remains of *Rhea americana* among his finds of the Lagoa Santa region, interpreting them as two species, one larger than the living one. Later (Lund 1841d: 18), in the summary of his unpublished treatise, he mentioned only one species for the genus, and one form that he believed to be an extinct *Alectorides*, but with the dimensions of a *Rhea*. Reinhardt (1881: 142, 143; 1882: 323) noted that Lund, in his unpublished treatise, apparently did not believe he had the remains of more than one species of *Rhea*, and from that, it can be concluded, although not explained, that the *Alectorides* is the same bird as one of these species of *rhea*.

Several subsequent authors repeated this treatment as two species of rheas represented in the material (e.g., Claussen 1841: 20; Wallace 1876: 164). Gervais (1844b: 33, 34) mentioned the two rhea species and the large *Alectorides*. Liais (1872: 302) mentioned the two rhea species and "le genre *Cariama* (*Dicholophus* d'Illiger, *Microdactylus* de Geoffroy, *Seriema* du Brésil)", noting that it provided a species in quaternary times, probably referring to Gervais' account of "un genre voisin des *Dicholophus* ou *Cariamias*" supposedly found by Claussen, whose alleged finds Liais attributed to Lund. Winge (1887) stated that he does not know what this designation referred to.

The bones initially determined as the Alectorides are the proximal end of a right tarsometatarsus and a pedal phalanx lacking the proximal joint surface, both impregnated with incrustations (Reinhardt 1881: 146; 1882: 326). Reinhardt (1881: 146; 1882: 326, 327) reported that, according to Lund's own words in his unpublished treatise, both fragments were found in the same place in the same cave, Lapa da Anna Felicia (Winge 1887: 18), and had all the markings that indicated they belonged to the same individual. Colored illustrations of both (done by Peter Andreas Brandt) were included in this treatise (with monochrome versions reproduced in Reinhardt 1881: 150; 1882: 330).

The Alectorides was erected based on these two fragments. However, after sending his treatise to Denmark, Lund must have realized that he had a third bone of that bird: the middle part of a right tibiotarsus covered in incrustations, which was marked in his catalog (erroneously as a femur) as No. 8 and coming from the same cave as the other two fragments, under the name of "gigantisk Styltegænger" ("giant wader"), the same under which the tarsometatarsus, of No. 9, was cataloged (Reinhardt 1881: 146, 147, 151; 1882: 327, 331). Reinhardt noted that both correspond in form, appearance, and condition, and it can be concluded that they are the remains of the same individual, and that Lund does not appear to have found more than these three fragments of this bird since such name does not appear again in his catalog, nor any mention of Alectorides.

According to Reinhardt (1881: 148, 149; 1882: 328, 329), Lund's opinion that the giant Alectorides was generically different from *Cariama*—the only component of this unnatural group of which Lund was more familiar and could compare bones—and that it was the missing link between this and *Palamedea* was based not only on the differences observed between the tarsometatarsi<sup>17</sup> but also, and perhaps mainly, on the pedal phalanx, which would indicate longer fingers than those of the seriemas. However, unfortunately, this bone seems to have been lost or destroyed, still in Brazil, since there is no mention of it in Lund's catalog and neither Reinhardt (1881: 147, 148; 1882: 327, 328) was able to locate it in the collection.

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<sup>17</sup> Erroneously translated from "Løb" ("tarsometatarsus") in Reinhardt (1881: 149) to "tibia" ("tibiotarsus") in Reinhardt (1882: 329).



The thorough examination of the fragments and the illustration of the pedal phalanx led Reinhardt (1881: 149, 150, 151, 152; 1882: 329, 330, 331) to conclude that these bones belong to an adult specimen of *Rhea americana*. The tarsometatarsus, when compared to a fresh, grown but young specimen, presents specific differences. On the possibility of dealing with another species of the genus, he noted (Reinhardt 1881: 152/1882: 332) that, although he has not recognized anything that goes against his conclusion, the discovery of new bones can bring out differences that could not be inferred in such limited material.

While agreeing with Reinhardt's conclusion about the identity of the tibiotarsus and tarsometatarsus fragments, Winge (1887: 18) considered that the pedal phalanx is most likely the first phalanx of a llama, and the lack of its proximal part contributed to the confusion. He also noted that Lund might have realized this, and perhaps it is the reason for the absence of this piece's mention in his catalog.

- “deux espèces d’Atruches (*Rhea*) dont l’une bien plus grande que l’espèce actuelle” [in part] - Lund 1840: 319.
- “*Rhea*” - Lund 1841d: 18.
- “deux espèces d’autruche, dont l’une bien plus grande que l’espèce actuelle” [in part] - Claussen 1841: 20.
- “to Arter Struds, hvoraf den ene betydelig større end den her nulevende Art” [in part] - Lund 1842b: 130.
- *Rhea* - Gervais 1844b: 34.
- “Outre cette grande espèce, le D<sup>r</sup> Lund en a encore trouvé une seconde du même genre, plus voisine de l’espèce actuelle par sa taille” - Liais 1872: 302.
- “two species of American ostrich (*Rhea*), one larger than either of the living species” [in part] - Wallace 1876: 164.
- *Rhea* - Reinhardt 1881: 142.
- *Rhea* [in part] - Lund (in Winge 1887): 18.
- *Rhea* aff. *americanæ* [in part] - Lund (in Winge 1887): 18.
- *Rhea americana* (et aff.) [in part] - Winge 1887: 18–19.
- *Rhea americana* [in part] - Lambrecht 1933: 729.
- *Rhea americana* [in part] - Brodkorb 1963: 201.
- *Rhea americana* [in part] - Mones 1986: 75.
- *Rhea americana* [in part] - Cuello 1988: 26.
- *Rhea americana* [in part] - Nascimento & Silveira 2020: 489.

From the material of *Rhea americana* that was not primarily determined as the Alectorides, Winge (1887: 18, 19) reported from Lapa da Anta I a second phalanx of the third digit (“*Rhea*” in the Lund’s catalog), slightly smaller than in *R. americana*. From Lapa da Escrivânia I several bones; a sixth cervical vertebra, lacking the anterior part, the distal end of a tibiotarsus (“*Rhea aff. americanae*” in Lund’s catalog), with slight variation in morphology, the fragment of a distal end of a tarsometatarsus (“*Rhea aff. americanae*” in Lund’s catalog), and a first phalanx of the second digit, smaller than in *R. americana*. Regarding the possibility that these smaller bones from Lapa da Anta and Lapa da Escrivânia I were from a different species, Winge noted that it is very uncertain, with no reason to think about any other species besides the living one.

- *Rhea americana* - Dias 2004: 255.
- *Rhea americana* - Paulo 2009: 141.

Dias (2004) mentioned the species among archeofaunal remains from the GO-JA-01 shelter of Serranópolis, Goiás, dating from the early Holocene. Paulo (2009: 141) reported these remains to be represented by the maxilla, mandible, axis, vertebra, sternum, coracoid, humerus, radius, ulna, carpometacarpus, sacrum, femur, and tarsometatarsus, besides eggshells. They were collected by IGPA in partnership with Unisinos, which carried out surveys within the scope of the Projeto Paranaíba in the Programa Arqueológico de Goiás, and are deposited at the Museu da Unisinos (Paulo, 2009: 17, 38, 128).

On the occurrence of *Rhea americana* remains in archeological sites in South America, Tambussi & Noriega (1996) commented that it was a probably human food resource in Argentina, Uruguay and Brazil.

### **103. †*Rhea fossilis* Moreno & Mercerat**

Quaternary - Piauí

- *Rhea* - Guidon *et al.* 2009b: 80.
- *Rhea fossilis* - Faure *et al.* 2010: 5–7, fig. 8.

Rock paintings of the Nordeste Tradition interpreted as rheas exist in rock shelters of the Parque Nacional Serra da Capivara, such as those pictured grouped in a row from Toca do Boqueirão da Pedra Furada, Toca da Pinga do Boi, Baixão do Perna I, Toca do

Boqueirão do Puxa and Toca do Vento (Guidon 1991; Pessis 2003; Faure *et al.* 2010). However, despite a rich vertebrate fauna being excavated in the region since the 1980s, surprisingly no remains of these birds were found (Guérin *et al.* 1993a; 1993b; 1996). This changed when Guidon *et al.* (2009b) firstly reported the genus *Rhea* from Toca do Serrote das Moendas, a rock shelter that began being excavated in 2006.

Faure *et al.* (2010) attributed the material, the distal end of a left tarsometatarsus (labelled as 113–145606) from sector 1, layer 15 of that site to *Rhea fossilis*, a taxon originally described from the Argentinean late Pleistocene that was similar but slenderer than *Rhea americana*. The bone is incompletely preserved and bears some rodent teeth markings. Remains of pampatheriines, dasypodids, glyptodontids, scelidotheriines, macraucheniids, equids, cervids, tayassuids, camelids, canids, felids, small rodents, various reptiles, and amphibians were also found in the same layer.

The name *Rhea fossilis* had a convolute nomenclatural history. Ameghino (1882) firstly used the name for material from the deposits of Olivera and Arrecifes, province of Buenos Aires but without description or figures. Moreno & Mercerat (1891) attributed the name *Rhea pampeana* to that material, which they described and figured, and assigned *Rhea fossilis* to material from Mar del Plata instead. Later, Ameghino (1891) rebutted, synonymizing *Rhea pampeana* with *Rhea fossilis* Ameghino and *Rhea fossilis* Moreno & Mercerat with *Rhea americana*. Faure *et al.* (2010), following Tonni & Laza (1980), Cuello (1988) and Mones (1986), treats *Rhea fossilis* Moreno & Mercerat as the valid designation, in opposition to Tambussi (1995).

## **Tinamiformes**

### **Tinamidae**

#### **104. Tinamidae indet.**

Quaternary - Goiás

- Tinamidae indet - Paulo 2009: 141.

Paulo (2009: 141) reported an indeterminate record of the family to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

## 105. *Tinamus solitarius* (Vieillot)

Quaternary - Minas Gerais

- *Tinamus major* - Winge 1887: 16.
- *Tinamus major* - Lambrecht 1933: 730.
- *Tinamus major* - Brodkorb 1963: 194.
- *Tinamus major* - Mones 1986: 75.
- *Tinamus major* - Cuello 1988: 27.
- *Tinamus solitarius* - Nascimento & Silveira 2020: 489.

Winge (1887: 16) reported from Lapa da Escrivânia V the proximal and distal ends of a tibiotarsus, and from "various caves"<sup>18</sup> a coracoid, an ulna, and the distal end of a tibiotarsus. He noted little difference between this material and a fresh skeleton, not enough to belong to another species. The distal end of the tibiotarsus is somewhat different from that observed in *Crypturellus*, *Nothura*, and *Rhynchotus*, and the other fragments were determined mainly by their size.

Winge followed Reinhardt's survey of the avifauna from the "Brazilian campos" (1870: 50), which reported *Tinamus major* in the Lagoa Santa region. This record was synonymized with *Tinamus solitarius* by Hellmayr & Conover (1942: 10) and Rodrigues (2008: 150), which is supported by the geographic distribution of these species: *T. major* occurs mainly in the North and part of the Midwest Brazil (Sick 1997: 162; Cabot *et al.* 2017a), and *T. solitarius* occurs in the Southeast (Sick 1997: 162; Cabot *et al.* 2017b), although it is now extinct in the Lagoa Santa region (Rodrigues 2008: 150). *T. solitarius* has also been considered conspecific with *T. major* (Hellmayr & Conover 1942: 10; Cabot *et al.* 2017b). This record, which needs to be revised as Lund's material as a whole, is then better provisionally referred to as *Tinamus solitarius*.

## 106. *Crypturellus* sp. 1

Quaternary - Goiás

- *Crypturellus* indet - Paulo 2009: 141.

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<sup>18</sup> Winge (1887: 11) used the term "Forskjellige Huler" ("various caves") for what Lund seemed to refer to the Lapas da Anna Felicia, dos Coxos, dos Ossinhos, and da Serra das Abelhas. The bones' surface and fracture are similar to that observed in the material of Lapa do Capão Seco.

Paulo (2009: 141) reported the genus to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

### **107. *Crypturellus* sp. 2**

Quaternary - Bahia

- *Crypturellus* sp. - Silva & Cozzuol 2010: 111.

An incomplete tarsometatarsus lacking the proximal epiphysis was associated with the genus by Silva & Cozzuol (2010: 111), being one of the two tinamids reported from material found in the 1980s at Toca da Boa Vista, in Campo Formoso, Bahia. The fossil is deposited in the collection of the MHNJB/UFMG.

### **108. *Crypturellus obsoletus* (Temminck)**

Quaternary - Minas Gerais

- *Crypturus obsoletus* - Winge 1887: 16.
- *Crypturus obsoletus* - Lambrecht 1933: 730.
- *Crypturellus obsoletus* - Brodkorb 1963: 194.
- *Crypturellus obsoletus* (“*Crypturus obsoletus*”) - Mones 1986: 74.
- *Crypturellus obsoletus* - Cuello 1988: 27.
- *Crypturellus obsoletus* - Nascimento & Silveira 2020: 489.

Winge (1887: 16) reported from Lapa do Baú a femur fragment; from Lapa do Capão Seco a coracoid and a carpometacarpus, of at least two individuals; from Lapa da Escrivânia V several individuals, represented by the sternum, coracoid, humerus, and tibiotarsus; from Lapa do Marinho II several bones, which he considered to belong to a single individual, represented by the coracoid, humerus, femur, and tarsometatarsus; from Lapa do Taquaral III a humerus (No. 12209 in the Lund's catalog about this cave), and a sternum, an ulna, a femur, and a tibiotarsus without recorded origin, but very similar in appearance with the humerus. Winge noted that the humerus' proximal end is firmly encrusted in the carpometacarpus' upper part (both on the left side), with the carpal<sup>19</sup> and the first phalanx of the alular digit in their place. There are also several bones from “various caves”<sup>18</sup> and of unknown origin.

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<sup>19</sup> “bageste Haandrodsben” (“posterior carpal”) in the original.

## **109. *Crypturellus noctivagus* (Wied)**

Quaternary - Minas Gerais, Piauí

- *Crypturus noctivagus* - Winge 1887: 16.
- *Crypturus noctivagus* - Lambrecht 1933: 730.
- *Crypturellus noctivagus* - Brodkorb 1963: 194.
- *Crypturellus noctivagus* (“*Crypturus noctivagus*”) - Mones 1986: 74.
- *Crypturellus noctivagus* - Cuello 1988: 27.
- *Crypturellus noctivagus* - Nascimento & Silveira 2020: 490.

Parts of at least two individuals, coming from “various caves”<sup>18</sup> were reported by Winge (1887: 16): coracoid, humerus, ulna, carpometacarpus, and femur, of which he noted that only the humerus and the femur were compared to fresh bones, the other parts probably belonging to the same set of bones. There are also two humeri of unknown origin. Brodkorb (1963: 194) wrongly listed it as coming from Lapa da Escrivânia, an error repeated by Cuello (1988: 27).

- Tinamidae [in part] - Guérin *et al.* 1993a: 198.
- Tinamidae [in part] - Guérin *et al.* 1993b: 328.
- *Crypturellus noctivagus* - Guérin *et al.* 1996: 84.
- *Crypturellus noctivagus* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

## **110. *Crypturellus parvirostris* (Wagler)**

Quaternary - Minas Gerais, Piauí

- *Crypturus parvirostris* - Winge 1887: 17.
- *Crypturus parvirostris* - Lambrecht 1933: 730.
- *Crypturellus parvirostris* - Brodkorb 1963: 194.
- *Crypturellus parvirostris* (“*Crypturus parvirostris*”) - Mones 1986: 74.
- *Crypturellus parvirostris* - Cuello 1988: 27.
- *Crypturellus parvirostris* - Nascimento & Silveira 2020: 490.

Winge (1887: 17) reported a good number of bones from Lapa da Escrivânia V and several individuals of recent age<sup>20</sup>, which included skulls. He noted that although the bones of this species as a whole are supposedly quite distinct from those of *Crypturellus tataupa*, this is often questionable.

- Tinamidae [in part] - Guérin *et al.* 1993a: 198.
- Tinamidae [in part] - Guérin *et al.* 1993b: 328.
- *Crypturellus parvirostris*- Guérin *et al.* 1996: 84.
- *C. parvirostris* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least two adults and one young individual are present in the material.

### **111. *Crypturellus tataupa* (Temminck)**

Quaternary - Minas Gerais

- *Crypturus* [?; in part] - Lund 1841d: 18.
- “le genre Tinamou (*Tinamus* de Lath., *Crypturus* d’Illig., le Nhambú du Brésil)” [?] - Liais 1872: 303.
- *Crypturus* [in part] - Lund (in Winge 1887): 16.
- *Crypturus inter obsoletum et tataupam* [in part] - Lund (in Winge 1887): 17.
- *Crypturus tataupa* - Winge 1887: 16-17.
- *Crypturus tataupa* - Lambrecht 1933: 730.
- *Crypturellus tataupa* - Brodkorb 1963: 194.
- *Crypturellus tataupa* (“*Crypturus tataupa*”) - Mones 1986: 74.
- *Crypturellus tataupa* - Cuello 1988: 27.
- *Crypturellus tataupa* - Nascimento & Silveira 2020: 490.

Winge (1887: 16, 17) reported several bones from Lapa da Escrivânia V, more bones from Lapa do Marinho II, two left carpometacarpus fragments from Lapa do Capão Seco, which may be *Crypturellus parvirostris*, and a "dissolved" skeleton of recent age<sup>20</sup> found in a cave and determined by Lund. There is a humerus from Lapa do Baú (“1138 *Crypturus*” in Lund’s catalog) of a form with an intermediate size between *C.*

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<sup>20</sup> Winge (1887: 12) uses the term "Fra nyeste Tid" ("of recent time") associated with younger bones, often with dry tendons, found in the floor of the caves. Owls have mostly brought them, but they can also have belonged to individuals who took shelter or were lost in these places. Skulls and other fragile parts are generally well preserved. Winge noted that the species represented in the collection only by these more recent bones were not included in his general list. Lambrecht's "prähistorisch" (1933).

*obsoletus* and *C. tataupa*, but closer to the latter (of which it can be a very large individual). There is also a skeleton of recent age<sup>20</sup> determined by Lund as “*Crypturus inter obsoletum et tataupam*”, about which Winge commented that if it is not this species, there is no corresponding contemporary form in the region. As this tinamid record received a designation in Lund’s catalog, it possibly maybe what he referred to as belonging to the genus *Crypturus* (Lund 1841d), and what Liais (1872: 303) called “le genre Tinamou (*Tinamus* de Lath., *Crypturus* d’Illig., le Nhambú du Brésil)”, noting that it provided a species in quaternary times.

### **112. *Rhynchotus rufescens* (Temminck)**

Quaternary - Minas Gerais

- *Rhynchotus rufescens* - Winge 1887: 18.
- *Rhynchotus rufescens* - Lambrecht 1933: 730.
- *Rhynchotus rufescens* - Brodkorb 1963: 195.
- *Rhynchotus rufescens* - Mones 1986: 75.
- *Rhynchotus rufescens* - Cuello 1988: 27.
- *Rhynchotus rufescens* - Nascimento & Silveira 2020: 490.

Winge (1887: 18) reported from Lapa da Escrivânia V bones of several individuals; from Lapa da Escrivânia IX a humerus; from Lapa da Escrivânia XI two bones; and from Lapa da Lagoa do Sumidouro more bones. The material is represented by the coracoid, scapula, humerus, ulna, radius, carpometacarpus, first phalanx of the second digit of the wing, femur, tibiotarsus, and tarsometatarsus.

### **113. *Nothura minor* (Spix)**

Quaternary - Minas Gerais

- *Nothura minor* - Winge 1887: 17.
- *Nothura minor* - Lambrecht 1933: 730.
- *Nothura minor* - Brodkorb 1963: 195.
- *Nothura minor* - Mones 1986: 74.
- *Nothura minor* - Cuello 1988: 27.
- *Nothura minor* - Nascimento & Silveira 2020: 490.

Several bones from Lapa da Escrivânia V, some of unknown origin (two of them probably from Lapa da Lagoa do Sumidouro) and a scapula of recent age<sup>20</sup> were



reported by Winge (1887: 17). He noted that of all the medium-sized species of *Nothura* and *Crypturellus* included in his study, there are mostly bones of the shoulder girdle and forelimbs. As for a large number of hindlimb bones, he decided to leave them indeterminate, given the substantial similarity between the genera.

#### **114. *Nothura maculosa* (Temminck)**

Quaternary - Bahia, Minas Gerais

- *Nothura maculosa* - Winge 1887: 17.
- *Nothura maculosa* - Lambrecht 1933: 730.
- *Nothura maculosa* - Brodkorb 1963: 195.
- *Nothura maculosa* - Cuello 1988: 28.
- *Nothura maculosa* - Nascimento & Silveira 2020: 490.

Winge (1887: 17) reported a considerable number of bones from Lapa da Escrivânia V, an ulna from Lapa da Escrivânia XI, a humerus from Lapa da Lagoa do Sumidouro, and a coracoid of recent age<sup>20</sup>.

- *Nothura maculosa* Silva & Cozzuol 2010: 111.

Silva & Cozzuol (2010: 111) associated an incomplete tarsometatarsus lacking the proximal epiphysis with the species, one of the two tinamids reported from material found in the 1980s at Toca da Boa Vista, in Campo Formoso, Bahia. The fossil is deposited in the collection of the MHNJB/UFGM.

#### **115. *Taoniscus cf. nanus* (Temminck)**

Quaternary - Minas Gerais

- *Tinamus* sp. [in part] - Lund (in Winge 1887): 17.
- *Nothura (Taoniscus) nana* (fere certe) - Winge 1887: 17–18.
- *Nothura (Taeniscus) nana* [sic] - Lambrecht 1933: 730.
- *Taoniscus nanus* - Brodkorb 1963: 195.
- *Taoniscus nanus* (“*Nothura (Taoniscus) nana?*”) - Mones 1986: 74–75.
- *Taoniscus nanus* - Cuello 1988: 28.
- *Taoniscus cf. nanus* - Nascimento & Silveira 2020: 490.

Winge (1887: 17, 18) reported several bones from Lapa da Escrivânia V, two bones from Lapa da Escrivânia XI, some isolated parts of unknown origin, and bones of

several individuals of recent age<sup>20</sup>, of which a humerus was determined as “*Tinamus* sp.” by Lund. The material is represented by the notary, coracoid, sternum, humerus, ulna, radius, carpometacarpus, synsacrum, femur, tibiotarsus, and tarsometatarsus. Although he had no fresh bones for comparison and the species was not recorded alive in the Lagoa Santa region by Lund or Reinhardt, Winge (1887: 9, 17, 18) determined the material with almost certainty. He commented that, given the finds of recent remains, it is unlikely that the species would not occur commonly in the region, since the birds that exist in its geographic range generally coincide with those existing in the Lagoa Santa region, and it may not have been found due to its reclusive habits or by sheer coincidence.

## Neognathae

### 116. Neognathae indet.

Early Eocene - Rio de Janeiro

- “muito similar ao *Paleopsilopterus [sic] itaboraiensis*” - Taranto & Bergqvist 2009: 51R.
- “nova forma de Phorusrhacidae” - Taranto *et al.* 2009a: 287.
- “tamanho e características muito próximas a tauracos (Musophagiformes) e urias (Charadriiformes), mas não foi associado a estes grupos pela ausência da porção proximal, onde está a maior parte das sinapomorfias” - Taranto & Bergqvist 2010: 118.

Taranto & Bergqvist (2009: 51R) and Taranto *et al.* (2009a: 287) reported the distal end of a right tibiotarsus (UFRJ 02-AV) from the early Eocene of São José de Itaboraí, present among material long stored in the collection of the Departamento de Geologia at UFRJ. They noted the bone is similar to that of *Paleopsilopterus itaboraiensis*, but better preserved and of a size close to that of a pigeon, and belonged to an adult individual, suggesting another form of the family in the São José de Itaboraí Basin. Taranto & Bergqvist (2010), however, when mentioning the materials, associated the “size of a pigeon” with a femur (UFRJ 01-AV) and described the tibiotarsus as similar in size and characteristics to the Musophagiformes and Charadriiformes, but not associating it to none of these groups due to the lack of the bone’s proximal end, where most synapomorphies are concentrated.

## Anseriformes

### Anhimidae

#### 117. †*Chaunoides antiquus* Alvarenga

Late Oligocene/Early Miocene - São Paulo

Fig. 14.A

*Type locality:* Fazenda Santa Fé, 2 km north of Tremembé, state of São Paulo, Brazil (22°30'S, 45°32'W).  
Montmorillonite clay, about 4 m below the level of the shallowest shales.

*Etymology:* *Chaunoides*, with the Latinized suffix *oideus*, “similar to *Chauna*”, and *antiquus*, Latin for “ancient”.

- Anhimidae - Alvarenga 1993b: 24.
- Anhimidae - Alvarenga 1997: 123.
- Anhimidae - Mourer-Chauviré 1999: 87.
- *Chaunoides antiquus* - Alvarenga 1999: 223–230, figs. 3–4, 6–10.
- *Chaunoides antiquus* - Alvarenga & Höfling 2000: 589.
- *Chaunoides antiquus* - Alvarenga & Höfling 2004: 827.
- *Chaunoides antiquus* - Alvarenga & Höfling 2011: 127.

From fossils collected on different occasions between 1978 and 1993 in the montmorillonite clays of the Tremembé Formation at Fazenda Santa Fé, about 4 m below the shallowest shales, Alvarenga (1999) named *Chaunoides antiquus*, the first fossil genus and species of anhimid. It was smaller and more gracile than the smallest living species in the family, *Chauna chavaria*, with slender leg bones and less pneumatized skeleton than the living anhimids (Alvarenga 1999: 229).

Remains of at least three individuals are known, making it the best represented (or most abundant) bird in the Tremembé Formation (Alvarenga & Höfling 2011: 127). The material consists of an almost complete left coracoid (MNRJ-4619-V, holotype), another incomplete left coracoid (MNRJ-4620-V) associated with an almost complete left femur (MNRJ-4621-V), the distal end of a left ulna (MNRJ-4622-V), the distal end of a right radius (MNRJ-4623-V), a left radius lacking the proximal end (MNRJ-4624-V), a left ulna lacking the proximal end (MNRJ-4632-V) associated with a segment of the distal axis of a left tibiotarsus (MNRJ-4631-V), two segments of the distal end of left tibiotarsi (MNRJ-4625-V and MNRJ-4629-V), the latter associated with the

proximal end of a left tarsometatarsus (MNRJ-4630-V), and three unassociated segments of distal axes of right tibiotarsi (MNRJ-4626-V, MNRJ-4627-V and MNRJ-4628-V).

Although *Chaunoides antiquus* is the only described fossil species that is safely associated with the Anhimidae family, remains that possibly belong to the group were reported from the early Eocene of North America and Europe, and poorly preserved material from Australia (Mayr 2016: 113). In addition, the genus *Paranyroca*, from the Miocene of South Dakota, is possibly related to the family (Mayr 2016: 113).

## **Anatidae**

### **118. ?Anatidae indet.**

Late Oligocene/Early Miocene - São Paulo

- Anatidae - Alvarenga (in Castro *et al.* 1988b): 2360, 2362.
- “fósseis ainda não descritos de Anatidae” - Alvarenga & Höfling 2000: 589.
- “fósseis ainda não descritos de Anatidae” - Alvarenga & Höfling 2004: 827.
- “fósseis ainda não descritos de Anatidae” - Alvarenga & Höfling 2011: 127.

Alvarenga (in Castro *et al.* 1988: 2360) and Alvarenga & Höfling (2000: 589; 2004: 827; 2011: 127) mentioned undescribed anatid remains among fossil material from the Taubaté Basin. These mentions seem to be exchanged for Podicipedidae in further studies (Alvarenga 1993b: 24; 1997: 123).

### **119. *Dendrocygna* sp.**

Quaternary - Minas Gerais

- *Dendrocygna* sp. 1 v. 2 (vel *D. viduata* et sp. alia; vel sp. una, non *D. viduata*) - Winge 1887: 19.
- *Dendrocygna* sp. (“cfr. *viduata* und andere Arten”) - Lambrecht 1933: 740.
- *Dendrocygna viduata* - Brodkorb, 1964: 237.
- *Dendrocygna viduata* - Cuello 1988: 34.
- *Dendrocygna* sp. - Nascimento & Silveira 2020: 490.

Winge (1887: 19) reported from Lapa da Escrivânia XI the distal end of a tibiotarsus and a tarsometatarsus, the latter slightly thinner than in *Dendrocygna viduata*, and a humerus and a carpometacarpus from Lapa da Lagoa do Sumidouro, which correspond

pretty well to *D. viduata*, in addition to a femur that possibly fits here, but there were only bones of a mounted specimen for comparison, lacking the femora. Winge noted that it is possible to consider that the bones from Lapa da Lagoa do Sumidouro are of *D. viduata*, and those from Lapa da Escrivânia XI are of a related species, or both materials belong to this related species.

## 120. †*Neochen pugil* (Winge)

Quaternary - Minas Gerais

Figs. 5–7, 8.A–F, 15.A

*Type locality*: Figured material from Lapa da Escrivânia V (Hansen 2012: 98, 99).

*Etymology*: *pugil*, Latin for “boxer” (Lambrecht 1933: 377).

- “*Chauna* eller *Palamedea*” [in part] - Reinhardt 1881: 145.
- *Chenalopex pugil* n. sp., affinis *jubatae* (Spix) sed multo major - Winge 1887: 19–22, figs. 1–6.
- *Chenalopex pugil* [in part] - Lambrecht 1933: 376, 377, 390, 741, 880, fig. 194A.
- *Alopochen pugil* - Rothschild 1907: ix.
- *Neochen pugil* - Howard 1964: 281–282, pl. VI: C, D [May 1964].
- *Neochen pugil* - Brodkorb 1964: 216 [26 June 1964].
- “Fighting shelduck, *Neochen pugil*” - HRH The Prince Philip, Duke of Edinburgh & J. Fisher 1970: 193.
- *Neochen pugil* (“*Chenalopex pugil*”) - Mones 1986: 81–82.
- *Neochen pugil* - Cuello 1988: 10.
- *Neochen pugil* - Alvarenga 1993a: 62.
- *Neochen pugil* - Alvarenga 1997: 123.
- “*Neochen pugil* (Winge, 1887).-Greater Orinoco Sheldgoose” - Livezey 1997: 475.
- *Neochen pugil* - Alvarenga 1998: 60.
- *Chenalopex pugil* [original name] - Hansen 2012: 98–99, figs. 41A, 41B.
- *Neochen pugil* [in part] - Nascimento & Silveira 2020: 490, fig. 3.

Based on several bones from three localities, Winge (1887: 19, 20, 21, 22) described *Chenalopex pugil*, the first species of fossil bird (and dinosaur) named for Brazil. This large-sized anatid, larger than its putative closest living relative, the Orinoco goose *Neochen jubata* (Spix), had its remains found in three localities: several bones from Lapa da Escrivânia V, belonging to at least three males, more bones from Lapa da Escrivânia XI, mainly from a female, and some fragments associated with a male, coming from Lapa do Tatu.

The material is represented by the cervical vertebrae, coracoid (not listed by Winge, but figured and mentioned in the description), a rib, a fragment of the anterior part of the sternum, part of the synsacrum and pelvis, proximal and distal ends of the humerus, proximal end of the ulna, proximal and distal ends of the radius, carpometacarpus, first phalanx of the second digit of the wing, femur, distal end of the tibiotarsus, tarsometatarsus, and first phalanx of the second digit and first phalanx of the third digit of the foot. No elements were designed as a type (Howard 1964). However, a right coracoid (ZMUC 12115), the proximal end of a left humerus (ZMUC 12017), a right carpometacarpus (ZMUC 12044), a left tibiotarsus lacking the proximal end (ZMUC 12122), and a left tarsometatarsus (ZMUC 12084) associated with the male sex, from Lapa da Escrivânia V, were figured. This material was listed as type by Brodkorb (1964) and Hansen (2012).

The species is quite similar to *Neochen jubata* but larger and different in certain aspects (e.g., in the cervical vertebrae, coracoid, sternum, humerus, and radius). It is well-differentiated from *Alopochen aegyptiaca*, *Plectropterus gambensis*, *Chloephaga melanoptera*, and *Chloephaga picta*. There are two sets of bones, one of larger size and one smaller, which Winge believed belong to males and females, respectively, and correspond almost precisely to the difference observed between two specimens of *N. jubata* that were available for comparison—a taxidermied specimen with no defined sex, but probably a male, and a disarticulated skeleton of a young female. The carpometacarpus and tarsometatarsus are proportionally longer, and the femur, pedal phalanges, and coracoid are proportionally slightly shorter than in *N. jubata*. Winge noted that, if both sexes of the two species could be appropriately compared, the differences observed in the radius and cervical vertebrae, and perhaps even in the sternum, could disappear. As in *N. jubata*, there is a well-developed spur in the alular metacarpal, probably used for fighting. Unregistered fragments in Lund's collection belonging to this species were attributed to *Chauna* or *Anhima* by Reinhardt (1881: 145), but there is no known trace of anhinmids among the material from the caves.

Winge proposed that this species might still be found alive in remote areas in the inner regions of Brazil, near the southern tributaries of the Amazon River. Nevertheless, so far, there has been no record of its existence in historical times. Lambrecht (1933:

377), probably by confusion, commented, “Reinhardt collected the same from the Brazilian Campos”.

The first mentions for the combination *Neochen pugil* are Howard (May 1964<sup>21</sup>) and Brodkorb (26 June 1964). Howard noted that the species of “*Chenalopex*” are then recognized as *Neochen* in South America and *Alopochen* in Africa. Winge himself found the placement of *Chenalopex jubata* and *C. pugil* in the same genus as *C. aegyptiaca* (Linnaeus) something to be debated. Due to the differences in size and structure, Andrews (1897) suggested classifying *C. pugil* in a new genus apart from *C. jubata*. Rothschild (1907) listed it under *Alopochen*, possibly following the classification of *Chenalopex jubata* and *C. aegyptiaca* in this new genus by Stejneger (1885). The name *Neochen* was only proposed for the then *Alopochen jubata* by Oberholser in 1918, without a diagnosis for the described fossil species of South America, *Chenalopex pugil* and the Argentinean *C. debilis* Ameghino (now *Neochen debilis*), of middle pleistocenic age (Agnolin 2006a). A third fossil species associated with the genus, *Neochen barbadiana* Brodkorb, was described in 1965 from fossils of the late Pleistocene of Barbados (Brodkorb 1965).

Andrews (1897: 350) made a parallel between the two living species of “*Chenalopex*”, *C. aegyptiaca* and *C. jubata*, where both are represented in their respective range by a much larger pleistocenic form, *Centronis majori* and *Chenalopex pugil*, respectively. He noted that they differ in the shape of the legs but have an almost identical wing structure, where the similarities between the carpometacarpi are a “remarkable example of parallel modification”, but not in a way that suggests a generic relationship between the two fossil taxa (Howard 1964: 282, 283, 284).

- *Chenalopex pugil* - Lydekker 1891: 98–99.
- *Chenalopex pugil* [in part] - Lambrecht 1933: 377.
- *Neochen pugil* [in part] - Nascimento & Silveira 2020: 490.

Lydekker (1891: 98, 99), while cataloging the fossil birds in the British Museum (Natural History) collection, associated a right carpometacarpus (NHMUK PV OR 18906), described as “imperfect”, with the bird named by Winge. The institution acquired this bone in 1848 as part of the Claussen Collection, and it comes from a cave

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<sup>21</sup> According to a review by J.J. (in McEvey 1968).

in the same region as Lund's finds. Lambrecht (1933: 377) erroneously listed a tarsometatarsus present in the collection of the British Museum.

## 121. *Cairina moschata* (Linnaeus)

Quaternary - Minas Gerais, Piauí, Rio de Janeiro

- *Anas* [in part] - Lund (in Winge 1887): 22.
- Anatid. sp., s. under *Cairina moschata* [in part] - Winge 1887: 13.
- *Cairina moschata* [in part] - Winge 1887: 14.
- *Cairina moschata* (et forte sp. alia) - Winge 1887: 22.
- *Cairina moschata* - Lambrecht 1933: 743.
- *Cairina moschata* - Brodkorb 1964: 238.
- *Cairina moschata* - Cuello 1988: 35.
- *Cairina moschata* - Nascimento & Silveira 2020: 490.

Winge (1887: 22) reported a humerus (“*Anas*” in Lund’s catalog) from Lapa da Pedra dos Índios, and an ulna and a tibiotarsus from Lapa da Lagoa do Sumidouro, besides the first part of a third foot digit that possibly belongs to this species. The distal end of a tibiotarsus and the proximal end of a carpometacarpus that possibly belong to a female were also found in the latter locality. Several bones were found in Lapa da Escrivânia XI, including a humerus that Winge considered with much uncertainty that it might belong to a small female.

- Anseriformes? [in part] - Guérin *et al.* 1993a: 198.
- Anseriformes? [in part] - Guérin *et al.* 1993b: 328.
- *Cairina moschata* - Guérin *et al.* 1996: 84.
- *Cairina moschata* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

- *Cairina moschata* - Kneip *et al.* 1994: 50.
- Anatidae (“marreca, pato-do-mato”) [in part] - Kneip *et al.* 1995: 7.
- Anatidae (“marreca, pato-do-mato”) [in part] - Kneip *et al.* 1997: 19, 37.
- Anatidae (“marreca, pato-do-mato”) [in part] - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Pontina I (1 piece) and Pontinha III (1 piece), in Saquarema, Rio de Janeiro.



## 122. *Amazonetta brasiliensis* (Gmelin)

Quaternary - Minas Gerais, Piauí, Rio de Janeiro

- *Anas* sp., s. Anm. under 14. *Anas brasiliensis* [in part] - Winge 1887: 15.
- *Anas brasiliensis* (et aff.) - Winge 1887: 22.
- *Anas brasiliensis* - Lambrecht 1933: 740.
- *Nettion brasiliense* - Brodkorb 1964: 243.
- *Nettion brasiliense* (“*Anas brasiliensis*”) - Mones 1986: 81–82.
- *Amazonetta brasiliensis* - Cuello 1988: 35.
- *Amazonetta brasiliensis* - Nascimento & Silveira 2020: 490.

Winge (1887: 22) reported several bones from Lapa da Escrivânia V, including an uncertain femur, several bones from Lapa da Escrivânia XI, probably from a single individual, and more bones from Lapa da Lagoa do Sumidouro. The material is represented by the coracoid, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. Additionally, he reported from Lapa da Escrivânia V the distal end of a humerus that is quite similar to that of *Amazonetta brasiliensis* but larger, besides a coracoid and a carpometacarpus, and from “various caves”<sup>18</sup> two coracoids, slightly larger than in *A. brasiliensis* and different from it and each other, noting that even the genus assignment is uncertain, in addition to a cervical vertebra of a considerably large anatid.

- Anseriformes? [in part] - Guérin *et al.* 1993a: 198.
- Anseriformes? [in part] - Guérin *et al.* 1993b: 328.
- *Amazonetta brasiliensis*- Guérin *et al.* 1996: 84.
- *Amazonetta brasiliensis* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

- *Amazonetta brasiliensis* - Kneip *et al.* 1994: 50.
- Anatidae (“marreca, pato-do-mato”) [in part] - Kneip *et al.* 1995: 7.
- Anatidae (“marreca, pato-do-mato”) [in part] - Kneip *et al.* 1997: 19, 37.
- Anatidae (“marreca, pato-do-mato”) [in part] - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Moa I (1 piece), Pontinha I (2 pieces of at least one individual), and Pontinha III (2 pieces of at least one individual), in Saquarema, Rio de Janeiro.

### 123. *Mergus cf. octosetaceus* Vieillot

Quaternary - Minas Gerais

- *Mergus* sp., verisimillime *M. octosetaceus* Vieill. (*brasilianus* Vieill. postea) - Winge 1887: 23.
- *Mergus* sp. (“cfr. *M. octosetaceus*”) - Lambrecht 1933: 736.
- *Mergus octosetaceus* - Brodkorb 1964: 249.
- *Mergus octosetaceus* - Mones 1986: 82.
- *Mergus octosetaceus* - Cuello 1988: 36.
- *Mergus cf. octosetaceus* - Nascimento & Silveira 2020: 490.

Winge (1887: 23) reported two humeri and two tarsometatarsi from Lapa da Escrivânia V, besides the distal end of a tibiotarsus that probably belongs to the same species, possibly *Mergus octosetaceus*, of which there were no records in Minas Gerais. He noted that the tarsometatarsus is quite similar to that of *Mergus merganser*, *Mergus serrator*, and *Mergellus albellus*, and it is shorter and stouter than in *Merganetta armata* and longer than in *Lophodytes cucullatus*. The humerus has almost the same size as in *Mergellus albellus* (but the tarsometatarsus is larger) and is slightly larger than in *Oxyura leucocephala* (of which the humerus used in comparison lacked the proximal end).

### 124. *Nomonyx dominicus* (Linnaeus)

Quaternary - Minas Gerais

- *Erismatura dominica* - Winge 1887: 22.
- *Erismatura dominica* - Lambrecht 1933: 736.
- *Nomonyx dominicus* - Brodkorb 1964: 248.
- *Nomonyx dominicus* (“*Erismatura dominica*”) - Mones 1986: 81–82.
- *Oxyura dominica* - Cuello 1988: 36.
- *Nomonyx dominicus* - Nascimento & Silveira 2020: 490.

Winge (1887: 22) reported a tarsometatarsus from Lapa da Escrivânia V that is very similar to the one of a fresh specimen, and a femur of a small merganser from Lapa da Lagoa do Sumidouro, which possibly belongs to this species.

## Galliformes

### Cracidae

#### 125. *Penelope* sp. 1

Quaternary - Minas Gerais

- *Penelope* sp. (fere certe sp. 2, vel 3) [in part] - Winge 1887: 23–24.
- *Penelope* sp. (“cfr. *supercilius* Ill. oder *vetula*”) [in part] - Lambrecht 1933: 752.
- *Penelope obscura* - Brodkorb 1964: 306.
- *Penelope obscura* - Mones 1986: 85.
- *Penelope obscura* - Cuello 1988: 40.
- *Penelope* sp. 1 - Nascimento & Silveira 2020: 490.

Winge (1887: 23-24) divided the material referable to the genus *Penelope* into three sets, based on the size of the bones, which can represent up to three species in total. He had available for comparison *Penelope superciliaris* and a larger species, “*Penelope cristata?*”, which he believes to be well determined. The first and larger set is composed of two right femora, much larger than in *P. superciliaris* and similar to “*P. cristata?*”, coming from “various caves”<sup>18</sup>, and the lower end of a coracoid, of equivalent size to the femora, coming from “a saltpeter cave near Escrivânia”—erroneously listed as “Lapa da Escrivânia” by Brodkorb (1964: 306) and Cuello (1988: 40).

#### 126. *Penelope* sp. 2

Quaternary - Minas Gerais

- *Penelope* [in part] - Lund (in Winge 1887): 23.
- *Penelope* sp. (fere certe sp. 2, vel 3) [in part] - Winge 1887: 23–24.
- *Penelope* sp. (“cfr. *supercilius* Ill. oder *vetula*”) [in part] - Lambrecht 1933: 752.
- *Penelope superciliaris* - Brodkorb 1964: 306.
- *Penelope superciliaris* - Mones 1986: 85.
- *Penelope superciliaris* - Cuello 1988: 40.
- *Penelope* sp. 2 - Nascimento & Silveira 2020: 490.

The set of medium-sized bones attributed to *Penelope* by Winge (1887: 23-24) consists of two left humeri (“*Penelope?*” in Lund's catalog) coming from Lapa do Baú—one without recorded origin, but with a very similar aspect to the other, both larger than in

*Penelope superciliaris* and slightly smaller than in “*Penelope cristata*”, differing slightly from both, and parts of the same individual—mandible, a cervical vertebra, humerus, ulna, first phalanx of the second digit of the wing, femur, tibiotarsus, tarsometatarsus, and some pedal phalanges, coming from Lapa da Escrivânia III. The total size is slightly larger than *P. superciliaris* and slightly smaller than “*P. cristata*”. The humerus is very similar to that of Lapa do Baú. The tibiotarsus is slightly thinner and somewhat shorter than in “*P. cristata*”, and the first phalanx of the second digit of the wing and the pedal phalanges are as large as on it.

### **127. *Penelope* sp. 3**

Quaternary - Minas Gerais

- *Falco* [in part] - Lund (in Winge 1887): 24.
- *Penelope* sp. (fere certe sp. 2, vel 3) [in part] - Winge 1887: 23–24.
- *Penelope* sp. (“cfr. *superciliosus* Ill. oder *vetula*”) [in part] - Lambrecht 1933: 752.
- *Ortalis guttata* - Brodkorb 1964: 306.
- *Ortalis guttata* - Mones 1986: 85.
- *Ortalis guttata* - Cuello 1988: 40.
- *Penelope* sp. 3 - Nascimento & Silveira 2020: 490.

The third set of bones attributed to *Penelope* by Winge (1887: 23, 24), of smaller size, consists of the distal end of a humerus from Lapa da Escrivânia V, slightly smaller than in *Penelope superciliaris*, but probably of this species, two coracoids of young individuals from “various caves”<sup>18</sup>, of which one is very similar to *P. superciliaris*, although somewhat larger, and the other is shorter and slightly different, and a humerus lacking the proximal end (“*Falco*” in Lund’s catalog), coming from a “cave near Mocambo”, slightly larger and slightly divergent when compared to *P. superciliaris*.

Brodkorb (1964: 306), probably based on the sizes, associated the three sets, from the largest to the smallest respectively, to *Penelope obscura*, *P. superciliaris*, and *Ortalis guttata*.

### **128. *Penelope* sp. 4**

Quaternary - Piauí

- Cracidae - Guérin *et al.* 1993a: 198.
- Phasianidae [?] - Guérin *et al.* 1993a: 198.
- Cracidae - Guérin *et al.* 1993b: 328.
- *Penelope superciliaris* ou *jacucaca* - Guérin *et al.* 1996: 84.
- *Penelope superciliaris* ou *P. jacucaca* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material associable with *Penelope superciliaris* or *P. jacucaca* from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

## **129. *Penelope* spp. 5**

Pleistocene - Bahia, Minas Gerais

- “Espécies ainda não descritas do gênero *Penelope*” - Alvarenga & Silveira (in Silveira *et al.* 2008): 20.
- “Undescribed *Penelope* species” - Nascimento & Silveira 2020: 504.
- *Penelope* spp. 4 - Nascimento & Silveira 2020: 490.

Alvarenga & Silveira (in Silveira *et al.* 2008: 20) reported the occurrence of undescribed species of *Penelope* among the approximately 20,000 years old fossils found in caves of Minas Gerais and Bahia.

## **130. *Penelope superciliaris* Temminck**

Quaternary - Minas Gerais

- *Penelope superciliaris* sp. - Sales 2003: 214.

Sales (2003: 214) reported two specimens among the bones and carcasses in an advanced state of natural mummification found between 2001 and 2002 in the Zona II of Lapa do Rezar<sup>22</sup>, in the Parque Nacional do Peruáçu, Minas Gerais.

## **131. *Crax* sp.**

Quaternary - Minas Gerais

- *Crax?* [in part] - Lund (in Winge 1887): 24.
- *Crax* sp. 1 vel 2 - Winge 1887: 24.

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<sup>22</sup> Regarding the total material, Sales (2003: 213) specified that 18 bone sets and five mummified carcasses were found but did not attribute the material's nature to each species or age.

- *Crax* sp. - Lambrecht 1933: 752.
- *Crax fasciolata* - Brodkorb 1964: 306.
- *Crax fasciolata* - Mones 1986: 85.
- *Crax fasciolata* - Cuello 1988: 40–41.
- *Crax* sp. - Nascimento & Silveira 2020: 490.

Winge (1887: 24) described material that he considers to be one or two *Crax* species: a coracoid, the proximal and distal ends of a tibiotarsus, and part of a tarsometatarsus from Lapa da Escrivânia V, all larger than in a fresh skeleton; part of the proximal end of a humerus and a tibiotarsus (approximately the same size as the one from Lapa da Escrivânia V) from Lapa da Escrivânia N° XI; a humerus (“*Crax?*” in Lund’s catalog) and a tibiotarsus from Lapa do Capão Seco, of sizes close to that observed in fresh skeletons (although the humerus is more robust), but considerably smaller than the material of the other caves; and the distal end of an ulna from “various caves”<sup>18</sup>, slightly larger than in fresh skeletons. Only two fresh skeletons of similar sizes were available for comparison but with no precise species definition.

## Odontophoridae

### 132. *Odontophorus capueira* (Spix)

Quaternary - Minas Gerais

- *Perdix dentata* [in part] - Lund 1841d: 18.
- “les Perdix” [in part] - Liais 1872: 303.
- *Perdix* aff. *dentata* [in part] - Lund (in Winge 1887): 24.
- *Odontophorus dentatus* - Winge 1887: 24–25.
- *Odontophorus dentatus* - Lambrecht 1933: 752.
- *Odontophorus gujanensis* - Brodkorb 1964: 327.
- *Odontophorus gujanensis* (“*Odontophorus dentatus*”) - Mones 1986: 85–86.
- *Odontophorus gujanensis* - Cuello 1988: 41.
- *Odontophorus gujanensis* (= *O. dentatus*) - Tambussi & Noriega 1996: 251.
- *Odontophorus capueira* - Nascimento & Silveira 2020: 490.

Winge (1887: 24, 25) reported a tarsometatarsus from Lapa da Escrivânia V, two paired humeri and two tibiotarsi from Lapa do Marinho II, a coracoid and an ulna from Lapa do Periperi I, a humerus (“*Perdix* aff. *dentata*” in Lund’s catalog) from Lapa Vermelha (Lagoa Santa), a tibiotarsus and a tarsometatarsus from “various caves”<sup>18</sup>, and several

humeri (two of them determined as “*Perdix aff. dentatae*” from “caves in Mocambo” in the Lund’s catalog), a coracoid, and a tarsometatarsus of unknown origin. Winge further noted that some of these humeri are probably from Lapa da Escrivânia V.

This material was listed as *Odontophorus gujanensis* by Brodkorb (1964: 327), which was followed by Mones (1986) and Cuello (1988: 41), but this species is not found, at least nowadays, in Minas Gerais. Winge (1887: 4) probably based the name *Odontophorus dentatus* (Temm.) on Reinhardt's (1870: 52, 53) *Odontophorus dentatus* (Licht.). Krabbe (2007: 336), during a revision of the skins collected by Lund and Reinhardt, associated the name *Odontophorus dentatus* given by Reinhardt with *Odontophorus capueira capueira*.

## †Quercymegapodiidae

### 133. †*Taubacrex granivora* Alvarenga

Late Oligocene/Early Miocene - São Paulo

Fig. 14.C

*Type locality:* Tremembé Formation, Taubaté Basin, municipality of Tremembé, state of São Paulo, Brazil.

*Etymology:* *Taubacrex*, portmanteau of Taubaté and the Greek *krex*, a rallid, and *granivora*, “grain eater”.

- *Taubacrex granivora* - Alvarenga 1988: 321–328, figs. 1–3, 6.
- *Taubacrex granivora* - Alvarenga 1993a: 63.
- *Taubacrex granivora* - Alvarenga 1997: 123.
- *Taubacrex granivora* - Kellner 1998: 654, 659.
- *Taubacrex granivora* - Alvarenga & Höfling 2000: 589.
- *Taubacrex granivora* - Alvarenga & Höfling 2004: 827.
- *Ameripodius granivora* - Mourer-Chauviré *et al.* 2011: 620.
- *Taubacrex granivora* - Alvarenga & Höfling 2011: 128.

The fossil remains, preserved in a pyrobituminous shale fragment, were collected approximately six meters deep at the Mina Nossa Senhora da Guia (now deactivated), near the Tremembé center, by Petrobrás engineer Mustafá Hanzagic in 1950, and described by Alvarenga in 1988 as the new genus and species *Taubacrex granivora*. The specimen’s appearance indicates that the remains were preserved completely, but, probably during their collection, parts of the skeleton were lost (Alvarenga 1988: 321).

The specimen consists of an incomplete and fragmented post-cranial skeleton (IG-208-V, holotype), with bone remains and impressions, including the right coracoid, a humerus, the left radius, the left pelvis, the femora, the tibiotarsi, and the left tarsometatarsus, in addition to ossified tendons in the tibiotarsus and tarsometatarsus (Alvarenga 1988: 321, 322, 323). The preservation of the gizzard with nine spheroidal gastroliths and seed impressions indicates its eating habits (Alvarenga 1988: 325, 326) and consists of the oldest record of this nature for the Galliformes (Mayr 2009: 42). There are also feather impressions showing a carbonized/imprint preservation (Prado *et al.* 2016a), without relief, which are apparently small tectrices and upper wing coverts, and some larger ones may be secondary remiges. Primary remiges or larger rectrices are absent (Alvarenga 1988: 327). A preserved ungual phalanx and the impression of another with relatively short and slightly curved claws suggest, along with other features of the skeleton, that it was cursorial, although capable of flying (Alvarenga 1988: 326, 327). Its dimensions were close to those of *Gallinula chloropus* (= *G. galeata*; Alvarenga 1988: 327). The fragment of the shale containing the fossil has a triangular shape and measures about 22 x 20 cm and is deposited in the collection of the Seção de Paleontologia e Estratigrafia of the Instituto Geológico de São Paulo (Alvarenga 1988: 321, 324).

Alvarenga (1988: 323, 324, 327) provisionally placed the taxon within the Rallidae (Gruiformes) in its description, pointing out that similarities to the Galliformes were observed but always secondarily to the previous group. Through reanalysis of the material, also comparing it with the *Ameripodius* fossils found in France, Mourer-Chauviré (2000: 486, 488) attributed it to the Quercymegapodiidae. Contemporarily, Alvarenga & Höfling (2000: 589, 590) also suggested a classification as a galliform close to megapodiids. The bird was mentioned as *Ameripodius granivora* by Mourer-Chauviré *et al.* (2011: 620), which was followed by Tambussi & Degrange (2013: 43, 44). This combination's usage, however, was possibly a mistake (Mourer-Chauviré, personal communication). Mayr (2009: 42) noted that even though *T. granivora* and *Ameripodius silvasantosi* differ in the shape of the coracoid (according to Mourer-Chauviré 2000: 489), such bone is slightly crushed in the holotype of the first, requiring a direct comparison between the two specimens so that the possibility that they belong to the same genus is ruled out.



### 134. †*Ameripodius silvasantosi* Alvarenga

Late Oligocene/Early Miocene - São Paulo

Fig. 14.B

*Type locality:* State of São Paulo, municipality of Tremembé, Fazenda Santa Fé; Taubaté Basin, Tremembé Formation, most superficial layer of pyrobituminous shales at indeterminate level.

*Etymology:* *Ameripodius*, a portmanteau of America and the Greek *podius* (foot), in reference to the similarity with the Megapodiidae, and *silvasantosi* honoring the Brazilian paleoichthyologist Rubens da Silva Santos (1918–1996).

- Galliformes - Alvarenga (in Mourer-Chauviré 1992b): 7, 8.
- Galliformes - Alvarenga 1993b: 24, fig. 18.
- *Ameripodius silvasantosi* - Alvarenga 1995b: 33–44, figs. 2–8.
- *Ameripodius silvasantosi* - Alvarenga 1997: 123.
- *Ameripodius silvasantosi* - Kellner 1998: 654, 659.
- *Ameripodius silvasantosi* - Alvarenga & Höfling 2000: 589.
- *Ameripodius silvasantosi* - Alvarenga & Höfling 2004: 827.
- *Ameripodius silvasantosi* - Alvarenga & Höfling 2011: 128.

In July 1989, at Fazenda Santa Fé, in Tremembé, the partial impression of the skeleton of this *Odontophorus*-sized bird was found through the cooperative work of Herculano Alvarenga along with Rubens da Silva Santos, and other professors from the Universidade Estadual do Rio de Janeiro. Alvarenga described the new genus and species *Ameripodius silvasantosi* in 1995, being then considered the first record of a galliform for the Tertiary of South American (Alvarenga 1993b: 24; 1995b: 33, 34, 43; see *Taubacrex*).

The material (MNRJ-4488-V, holotype) is a part of the shoulder girdle and wings, preserved in a pyrobituminous shale plate divided into part and counterpart. The cranial half of the right coracoid, the left coracoid, and the left carpometacarpus were almost completely removed from the shale. The humeri were removed in fragments, leaving an impression cast. Partial impressions of the right radius, ulna, and carpometacarpus were also obtained. The anterior margin of the sternal keel, the left clavicle, including the symphysis region, the fragmented and incomplete right scapula, the almost complete left radius, and the first and second phalanges of the second digit of the left wing were embedded in the matrix. The relatively robust and slightly arched ulna suggests that its wings were relatively short and strong.

Alvarenga attributed it to the Quercymegapodiidae, which at the time included only *Quercymegapodius depereti* from the late Eocene and *Quercymegapodius brodkorbi* from the middle and late Eocene, both from Phosphorites du Quercy, France (Mourer-Chauviré 1992a: 77; Mourer-Chauviré 77a; 2006: 137). A second, larger species of the Brazilian genus was described by Mourer-Chauviré in 2000 as *Ameripodius alexis*, from the early Miocene of Saint-Gérard-le-Puy, France (Mourer-Chauviré 2000: 482, 489). The presence of the genus on both continents emphasizes the similarity between the South American and European avifaunas during the beginning of the Paleogene (Mourer-Chauviré 2000: 481). Mourer-Chauviré (1999: 88; 2000: 489, 491) hypothesized that, as with the Megapodiidae, capable of crossing large extensions of water and colonizing islands, possibly there was a direct dispersion across the ocean between Europe and South America, or vice versa, when the Atlantic was considerably narrower than it is today. According to Mayr (2016: 110), the very narrow carpometacarpus of the quercymegapodiids indicates that they differed from the living Galliformes in their flight capacity, which is in agreement with the fact that they are the only stem group of Galliformes known to have reached the geographically isolated South American continent.

## †Odontopterygiformes

### †Pelagornithidae

#### 135. †*Pelagornis longirostris* (Spulski)

Neogene? - Brazil?

*Type locality*: None attributed.

*Etymology*: *Pelagornis* “sea bird” e *longirostris* “long face”.

- *Odontopteryx longirostris* - Spulski 1910: 507–521, figs. 1–7.
- *Pseudodontornis longirostris* - Lambrecht 1930: 1–17, figs. 3, 6, pls. 1–2.
- *Pseudodontornis longirostris* - Brodkorb 1963: 263.
- *Pseudodontornis longirostris* - Harrison & Walker 1976: 15–17, figs. 15C, 17D, 21A, 24, 25B, 25D, 26B, 30B.
- *Pseudodontornis longirostris* (“*Odontopteryx*” *longirostris*) - Mones 1986: 79.
- *Pelagornis longirostris* - Mayr & Rubilar-Rogers 2010: 1327.
- *Pelagornis (Pseudodontornis) longirostris* - Ksepka 2014: 10624.

Spulski erected the species *Odontopteryx longirostris* in 1910 for an incomplete skull and jaw of unknown age and origin, characterized by pseudo teeth. The skull also had conserved the right eye's sclerotic ring, which was lost in an accident before the analysis. The specimen was supposedly brought from Brazil to Germany by a sailor five years earlier, who sold it to the rarities dealer J. Schulze in Königsberg, and was then acquired in 1905 by Prof. Braun for the Zoologische Institut (Spulski 1910: 508).

Spulski compared it to *Odontopteryx toliapica* from the lower Eocene, described by Richard Owen in 1873. Lambrecht (1930: 1, 10), however, after further preparation and study of the specimen, in addition to also examining Owen's fossil, found it distinct enough, based on the pseudo teeth and other characters, to be classified into the new genus *Pseudodontornis*.

Spulski (1910: 508) noted that the orbits were filled with pure and granular limestone and speculated that the fossil could date from the Eocene, based on the significant similarity he found with the *Odontopteryx toliapica* skull, as well as its "primitive characters". Lambrecht (1930: 2) disagreed with these arguments, citing that the mere presence of pseudo teeth (which differ it from Owen's fossil) does not work as a comparison and that the *Pseudodontornis longirostris* skull is quite specialized, and these two isolated points cannot serve as a basis for age determination.

During the fossil reanalysis, Lambrecht (1930: 3) presented a portion of the matrix to Prof. Friedrich von Huene, who had returned from South America, to give his opinion on its origin. He was, however, unaware of any similar rock. Lambrecht achieved the same result by showing Prof. von Fryberg, who had been to Brazil three times. Due to the "impression of being surprisingly new" and the highly crystalline character of the rock, Lambrecht (1930: 3) discarded an origin associated with freshwater. The presence of traces of brachiopods reinforced the association with a marine coastal environment. Regarding the possible age of the fossil, he also observed there is a negative impression of a bivalve shell, "close to *Cardium (Laevicardium) cingulatum*", from the late Oligocene of Europe ("but that also occurred in the Pliocene") but noting that it may be a secondary deposition in the matrix.

Lambrecht (1930: 11; 1933: 306, 307) did not exclude the possibility that the fossil was found in Germany and was attributed to Brazil so that it could be sold at a

higher price. However, the pelagornithids had a worldwide distribution from the late Paleocene to the late Pliocene (Mayr 2016: 121), including records from four Neogene formations in South America—in Chile, Peru, and Venezuela (Solórzano & Rincón 2015: 1, 6)—and it would not be unlikely that representatives of the group had inhabited Brazil, especially given its extensive coastline. Mayr & Rubilar-Rogers (2010: 1313) speculated that the species probably lived during the Neogene. Brodkorb (1963: 263) raised the possibility of Miocene age and German origin. Mones (1986: 79) associated it, with doubt, with the Eocene. Mlíkovský (2002: 82), in contrast to Brodkorb's assumption, argued there are no suitable locations of Miocene age in that part of Europe, and that if the fossil came from the continent, it would have come from Eocene marine deposits in the North Sea Basin, which are well represented in northern Germany, Denmark, and England.

The specimen was deposited in the collection of the Geological-Paleontological Museum of the Institutes der Albertus-Universität Königsberg, then in Prussia. Königsberg was heavily bombed by the Allies during World War II and by the end of the war was annexed to the Soviet Union and renamed Kaliningrad. The fossil appears to have been destroyed during these events (Mayr & Rubilar-Rogers 2010: 1313; Ksepka & Habib 2016: 67). Harrison & Walker (1976: 4, 15, 61), during the revision of the Odontopterygiformes, tried to locate the specimen with the help of Dr. E.N. Kurotchkin (Paleontological Museum of the Moscow Academy of Sciences) but had no success.

Remains of pelagornithids were reported from South Carolina, in the United States, by Hopson (1964), including a fragment of the mandible which he associated with *Pseudodontornis longirostris*, initially attributed to the early Miocene, but probably coming from the late Oligocene, according to Olson (1985b: 196, 197). Hopson (1964: 7) commented that the discovery of this material strengthens the assumption that the type specimen came from the Western Hemisphere, but not necessarily from North America, arguing that an oceanic bird of this size probably had a wide distribution. In addition, the distal portion of a tarsometatarsus that he attributed almost certainly to *Palaeochenoides mioceanus* (1964: 8)—a species initially described from an incomplete femur from the same deposit by Shufeldt in 1916—was later

considered to belong to *P. longirostris* by Howard & Warter (1969: 354) and Harrison & Walker (1976: 15, 17).

Gamble (1985; *apud* Harrison 1985: 23) associated a jaw fragment from the Oldhaven formation in Shelford Sandpit, England (Paleocene) with *Pseudodontornis longirostris*. The specimen, as well as another indeterminate jaw fragment associated with the Odontopterygiformes, does not appear to be of a bird, possibly being fish remains, according to Harrison (1985: 23).

Chávez & Stucchi (2002: 26) associated with *Pseudodontornis* cf. *longirostris* cranial remains from the Bahía Inglesa Formation, northern Chile. However, the same fossils, dating from the middle Miocene, have been reassigned to Pelagornithidae indet. cf. *Pelagornis* by Chávez *et al.* (2007: 183, 186), adopting more conservative criteria while waiting for new materials.

Other forms were associated with the genus erected by Lambrecht, but due to the general poor preservation state of this group's fossils, their classification is uncertain (Mayr & Rubilar-Rogers 2010: 1313). In New Zealand, remains found in South Island were originally described as *Pseudodontornis stirtoni* by Howard & Warter (1969), of Miocene or Pliocene age (Howard & Warter 1969: 345, 346; McKee 1985: 181). From North Island, McKee (1985: 181, 183) reported unidentified pelagornithid remains from the middle Pliocene, which he thought might belong to *Pseudodontornis*, as it was the only genus described for the country. In England, *Pseudodontornis tenuirostris* was described from the late Paleocene by Harrison (1985). From Kazakhstan, of the same age, *Pseudodontornis tshulensis* was described by Averianov *et al.* (1991), both forms with questionable validity due to little knowledge about the intraspecific variability of pseudo teeth in pelagornithids (Mayr 2009: 56). From the early Eocene of England, there is also *Pseudodontornis longidendata*, described by Harrison & Walker (1976), which is possibly synonymous with *Dasornis emuinus* (Bowerbank 1854) according to Mayr (2008: 1114; 2009: 56). The genus was also mistakenly listed (in place of "pseudodontornithids") by Becker (1987 *apud* Goedert 1989; Goedert 1989: 939, 940) for the Miocene of Astoria Formation, central coast of Oregon, United States.

Olson (1985b: 198) noted the possibility that *Pseudodontornis* is synonymous with *Pelagornis*, a genus originally proposed by Lartet in 1857 to *P. miocaenus*, from

the Miocene of France. Mayr & Rubilar-Rogers (2010: 1327), reviewing the taxonomy of the Neogene pelagornithids, considering the present knowledge and aiming at the clarity in the study of the materials, proposed that all its components be classified under *Pelagornis*, which would include, in addition to *P. miocaenus*, the following species then recognized as valid: *P. longirostris*, *P. stirtoni*, *P. orri* (Howard) from the Miocene of California, *P. mauretanicus* Mourer-Chauviré & Geraads from the Pliocene of Africa, and *P. chilensis* Mayr & Rubilar-Rogers from the Miocene of Chile (see also Mayr *et al.* 2013). *Pelagornis sandersi* Ksepka, notable for its enormous wingspan (Ksepka 2014: 1), was later described from material from the Oligocene of South Carolina.

## Phoenicopteriformes

### Phoenicopteridae

#### 136. †*Agnopterus sicki* Alvarenga

Late Oligocene/Early Miocene - São Paulo

Fig. 14.E

*Type locality*: Brazil, state of São Paulo, municipality of Tremembé, Fazenda Santa Fé, Taubaté Basin, Tremembé Formation; layer of montmorillonite clay below the most superficial strata of pyrobituminous shales.

*Etymology*: *Agnopterus*, Greek for “unknown wing” (Milne-Edwards 1869–1871: 84), and *sicki* honoring German-Brazilian ornithologist Helmut Sick (1910-1991).

- *Agnopterus sicki* - Alvarenga, 1990: 335–345, figs. 1–2.
- *Agnopterus sicki* Alvarenga 1990 - Alvarenga, 1997: 123.
- *Agnopterus sicki* - Kellner 1998: 654, 659.
- *Agnopterus* - Alvarenga & Höfling 2000: 591.
- *Agnopterus* - Alvarenga & Höfling 2004: 829.
- *Agnopterus sicki* - Alvarenga & Höfling 2011: 127.

Alvarenga (1990) described flamingo remains among material collected between 1984 and 1989 at Fazenda Santa Fé, from montmorillonite clay below the most superficial pyrobituminous shales of the Tremembé Formation, Taubaté Basin, São Paulo, of which a new species of phoenicopterid was named *Agnopterus sicki*.

The material consists of a well-preserved distal fragment of the right tibiotarsus (holotype, MNRJ-4257-V), possibly from an individual that has not reached adulthood, and a diaphysis fragment (MNRJ-4258-V), which perhaps belongs to the same bone.

The genus *Agnopterus* was erected by Milne-Edwards (1869–1871: 83, 84) for *A. laurillardi*, from material of the late Eocene of France. In 1940, Tugarinov described a second species, *Agnopterus turgaiensis*, from material of the late Oligocene of Kazakhstan (Mayr 2009: 107; Zelenkov 2013: 1323). The Brazilian species is similar to the latter, both in morphology and in measures and proportions (Alvarenga 1990: 339). Alvarenga (1990: 340) noted that genus must be revised. The inclusion of *A. turgaiensis* was questioned by Olson & Feduccia (1980: 44) due to the significant age difference from the material described by Milne-Edwards. Mayr (2009: 108) also commented that both *Agnopterus sicki* and *A. turgaiensis* are based on very fragmented material for a safe placement within the Phoenicopteriformes. Another species, *Agnopterus hantoniensis*, was associated with the genus by Lydekker (1891: 95, 96, 97) from material of the late Eocene of England, but its status is uncertain (Mayr 2009: 106; Zelenkov 2013: 1326). Mayr (2009: 106) considered it a stem member of the Phoenicopteriformes.

## †Palaelodidae

### 137. †*Palaelodus* cf. *ambiguus* Milne-Edwards

Late Oligocene/Early Miocene - São Paulo

Fig. 14.D

- *Palaelodus* cf. *ambiguus* - Alvarenga 1990: 335-345, figs. 3–9.
- *Palaelodus* - Alvarenga 1993a: 63.
- *Palaelodus* sp. - Alvarenga 1993b: 24.
- *Palaelodus* - Alvarenga (in Sick 1993): 152.
- *Palaelodus* sp. - Alvarenga 1997: 123.
- *Palaelodus* - Alvarenga (in Sick 1997): 226.
- *Palaelodus* aff. *ambiguus* - Kellner 1998: 654, 659.
- *Palaelodus* - Alvarenga & Höfling 2000: 591.
- *Palaelodus* - Alvarenga & Höfling 2004: 829.
- *Palaelodus* - Alvarenga & Höfling 2011: 129.
- *Palaelodus* aff. *ambiguus* [*lapsus*] - Tambussi & Degrange 2013: 44.

In addition to the fragments described as *Agnopterus sicki*, Alvarenga (1990) also associated five other dissociated fragments to the genus *Palaelodus*.

The material consists of the distal end of a left tibiotarsus (MNRJ-4259-V), the distal end of a right tarsometatarsus lacking the lateral trochlea (MNRJ-4261-V), a right coracoid lacking the upper end and the lateral half of the sternum joint (MNRJ-4262-V), the proximal end of a left tibiotarsus (MNRJ-4260-V), and the proximal half of a left first wing phalanx (MNRJ-4263-V).

The genus *Palaelodus* is represented by *P. ambiguus*, *P. crassipes*, and *P. gracilipes* in Europe, described initially from the early Miocene of France, with the validity of the last two questioned (Worthy *et al.* 2010: 77, 84); *P. aotearoa* of the early Miocene of New Zealand (Worthy *et al.* 2010); *P. kurochkini* from the middle Miocene of Mongolia (Zelenkov 2013); and *P. pledgei* and *P. wilsoni* from the late Oligocene to the middle Miocene of Australia, where a specimen from the middle Pleistocene was also associated with *P. wilsoni*, but its specific status is still uncertain (Baird & Vickers-Rich 1998; Worthy *et al.* 2010: 78). Alvarenga (1990: 341; 1997: 123) noted that the remains found in the Tremembé Formation may represent a new species, but, due to the state of the material, it is not possible to establish a specific diagnosis. However, there is a great affinity in size and form with *Palaelodus ambiguus* - at the end of the Oligocene or beginning of the Miocene the family Palaelodidae had already reached an almost global distribution (Mayr 2016: 132).

Noriega & Agnolin (2008: 278) reported the distal end of a right tarsometatarsus (MACN PV 12756) from the “Mesopotamiense”, Ituzangó Formation (late Miocene), Entre Ríos Province, Argentina referred to as *Palaelodus cf. ambiguus* and on which its measurements and morphology coincide with the Brazilian material.

## **Podicipediformes**

### **Podicipedidae**

#### **138. Podicipedidae indet.**

Late Oligocene/Early Miocene - São Paulo



- Podicipedidae - Alvarenga 1993b: 24.
- Podicipedidae - Alvarenga 1997: 123.

Podicipedid remains are among the poorly preserved birds from the Taubaté Basin that await the discovery of new specimens for further study (Alvarenga 1993b: 24; 1997: 123). Alvarenga (in Castro *et al.* 1988b: 2360) mentioned indeterminate remains of anatids that appear to be reassigned to podicipedids in subsequent mentions (Alvarenga 1993b: 24; 1997: 123).

### **139. *Tachybaptus dominicus* (Linnaeus)**

Quaternary - Minas Gerais

- *Tachybaptus dominicus* - Winge 1887: 25.
- *Tachybaptus (Podicipes) dominicus* - Lambrecht 1933: 731.
- *Podiceps dominicus* - Brodkorb 1963: 228.
- *Podicipes dominicus* (“*Tachybaptus dominicus*”) - Mones 1986: 76.
- *Tachybaptus dominicus* - Cuello 1988: 28.
- *Tachybaptus dominicus* - Nascimento & Silveira 2020: 490.

A femur, a tibiotarsus, and a coracoid from Lapa da Escrivânia V, a rather large tarsometatarsus from Lapa da Escrivânia IX, a rather large femur from Lapa da Escrivânia XI, and a humerus from an uncertain location were listed by Winge (1887: 25). He noted that some may show only small differences from fresh bones, probably individual variations, and that two fresh skeletons are also not very different.

### **140. *Podilymbus podiceps* (Linnaeus)**

Quaternary - Minas Gerais

- *Podilymbus (antarcticus vel podiceps, si sp. dist.)* - Winge 1887: 25.
- *Podilymbus antarcticus* oder *podiceps* - Lambrecht 1933: 732.
- *Podilymbus podiceps* - Brodkorb 1963: 230.
- *Podilymbus podicipes* - Mones 1986: 76.
- *Podilymbus podiceps* - Cuello 1988: 28.
- *Podilymbus podiceps* - Nascimento & Silveira 2020: 490.

From Lapa da Escrivânia V, Winge reported the remains of at least three individuals, represented by the posterior part of a mandibular branch, scapula, coracoid, humerus, synsacrum, femur, and tarsometatarsus. Winge described the remains belonging to

*Podilymbus antarcticus* (Lesson) (= *Podilymbus podiceps antarcticus*) or *P. podiceps*, if they were de facto different taxa (treated as different subspecies by Pacheco *et al.* 2021). Only the tarsometatarsus was determined by comparison, being available only bones from the skin of a male from the first, to which the tarsometatarsus is very similar, only slightly smaller, and differs from that of a *P. podiceps* in being slightly larger and narrower in the proximal end. The other bones correspond well to the tarsometatarsus if compared to the equivalents in *Podiceps* and *Tachybaptus*.

### **141. *Podilymbus podiceps antarcticus* (Lesson)**

Holocene - Rio de Janeiro

- *Podilymbus podiceps antarcticus* - Kneip *et al.* 1994: 48.
- Podicipedidae (“mergulhão”) - Kneip *et al.* 1995: 7.
- Podicipedidae (“mergulhão”) - Kneip *et al.* 1997: 19, 37.
- Podicipedidae (“mergulhão”) - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the subspecies from the sambaquis of Beirada I (3 pieces of at least one individual), Beirada II (4 pieces of at least one individual), and Pontinha III (6 pieces of at least two individuals), in Saquarema, Rio de Janeiro.

## **Columbiformes**

### **Columbidae**

#### **142. Columbidae indet. 1**

Quaternary - Minas Gerais

- “en mindre Due (muligvis en af de ellers opførte Arter)” - Winge 1887: 11.
- “d’un petit pigeon (peut-être une des espèces déjà citées)” - Winge 1887: 3 [French abstract].
- Columbidae indet. 1 - Nascimento & Silveira 2020: 492.

From Lapa do Capão Seco, among the many fragile, hard-to-determine bones, Winge (1887: 11) mentioned a small-sized columbid, without specifying the skeletal elements found, and he thinks it can represent some of the species already mentioned in his study.

## 143. Columbidae indet. 2

Quaternary - Minas Gerais

- *Chamaepelia* (et g. aff.) sp. 3 (fere certe): ut videtur: *Ch. griseola* vel *Ch. (Columbula) campestris*; *Ch. talpacoti*; *Ch. (Scardafella) squamosa* [in part] - Winge 1887: 39.
- *Chamoepelia* sp. (“cfr. *griseola*, *campestris*, *talpacoti* und *Scardafella squamosa*”) [in part] - Lambrecht 1933: 769.
- *Uropelia campestris* (?) - Brodkorb 1971: 198.
- *Columbigallina passerina* (?) - Brodkorb 1971: 198.
- *Uropelia campestris* (?) - Brodkorb 1971: 198.
- *Columbigallina passerina* (“*Chamaepelia* sp.” [in part]) - Mones 1986: 93.
- *Uropelia campestris* (“*Chamaepelia* sp.” [in part]) - Mones 1986: 93–94.
- *Columbina passerina* - Cuello 1988: 51.
- *Uropelia campestris* - Cuello 1988: 52.
- Columbidae indet. 2 - Nascimento & Silveira 2020: 492.

Remains representing at least two species, probably three or even four, were reported by Winge (1887: 39) from Lapa da Escrivânia V, except a tibiotarsus from Lapa da Escrivânia XI associated with *Columbina talpacoti*. Winge divided them into four sets, noting that two *Columbina talpacoti* and two *Columbina squammata* skeletons were available for comparison. The first set is composed of two small humeri, shorter and thinner than those of the other sets, which may represent *Columbina passerina* (*griseola*) or *Uropelia campestris*.

## 144. Columbidae indet. 3

Quaternary - Minas Gerais

- *Chamaepelia* (et g. aff.) sp. 3 (fere certe): ut videtur: *Ch. griseola* vel *Ch. (Columbula) campestris*; *Ch. talpacoti*; *Ch. (Scardafella) squamosa* [in part] - Winge 1887: 39.
- *Chamoepelia* sp. (“cfr. *griseola*, *campestris*, *talpacoti* und *Scardafella squamosa*”) [in part] - Lambrecht 1933: 769.
- *Chamaepelia* sp. [in part] - Mones 1986: 93.
- Columbidae indet. 3 - Nascimento & Silveira 2020: 492.

The second set of small columbid bones from Lapa da Escrivânia V defined by Winge (1887: 39) is composed of elements that are larger than the first set, but still smaller than in *Columbina talpacoti*, represented by the humerus, ulna, radius, and tarsometatarsus (of which some may belong to the first set).

#### **145. Columbidae indet. 4**

Quaternary - Goiás

- Columbidae indet - Paulo 2009: 142.

Paulo (2009: 142) reported an indeterminate record of the family to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

#### **146. *Patagioenas picazuro* (Temminck)**

Quaternary - Piauí

- Columbidae [in part] - Guérin *et al.* 1993a: 198.
- Columbidae [in part] - Guérin *et al.* 1993b: 328.
- *Columba picazuro* - Guérin *et al.* 1996: 84.
- *Columba picazuro* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

#### **147. *Patagioenas cayennensis* (Bonnaterre)**

Quaternary - Minas Gerais

- *Columba rufina* - Winge 1887: 38.
- *Columba rufina* - Lambrecht 1933: 768.
- *Columba cayennensis* - Brodkorb 1971: 197.
- *Columba cayennensis* (“*Columba rufina*”) - Mones 1986: 93.
- *Columba cayennensis* - Cuello 1988: 49.
- *Patagioenas cayennensis* - Nascimento & Silveira 2020: 493.

Winge (1887: 38) reported several bones from Lapa da Escrivânia V, somewhat larger than in a recent skeleton, represented by the scapula, coracoid, humerus, ulna, carpometacarpus, and femur; from Lapa da Escrivânia XI, the front part of a sternum, larger and slightly different, but still considered belonging to this species; and, of recent age<sup>20</sup>, an ulna.

#### **148. *Patagioenas plumbea* (Vieillot)**

Quaternary - Minas Gerais

- *Columba plumbea* - Winge 1887: 38.
- *Columba plumbea* - Lambrecht 1933: 768.
- *Columba plumbea* - Brodkorb 1971: 197.
- *Columba plumbea* - Mones 1986: 93.
- *Columba plumbea* - Cuello 1988: 50.
- *Patagioenas plumbea* - Nascimento & Silveira 2020: 493.

Winge (1887: 38) reported bones of several individuals from Lapa da Escrivânia V, represented by the coracoid, humerus, ulna, femur, tibiotarsus, and tarsometatarsus. In addition, there is a carpometacarpus and part of a skull from an unknown location.

### **149. *Geotrygon montana* (Linnaeus)**

Quaternary - Minas Gerais

- *Geotrygon montana* - Winge 1887: 40.
- *Geotrygon montana* - Lambrecht 1933: 769.
- *Geotrygon montana* - Brodkorb 1971: 199.
- *Geotrygon montana* - Mones 1986: 93.
- *Geotrygon montana* - Cuello 1988: 52.
- *Geotrygon montana* - Nascimento & Silveira 2020: 493.

Winge (1887: 40) reported from Lapa da Escrivânia V a tibiotarsus, of which he noted that it corresponds very closely to this species, showing only individual variation, and is quite distinct from *Leptotila verreauxi*, and a coracoid and a femur of recent age<sup>20</sup>, which when compared to a recent skeleton are, respectively, somewhat longer and slightly shorter.

### **150. *Leptotila spp.***

Quaternary - Minas Gerais

- *Leptotila spp.* - Sales 2003: 214.

Sales (2003: 214) attributed to the genus four specimens that appear among bones and mummified carcasses found in Zona II of Lapa do Rezar, Minas Gerais.

### **151. *Leptotila verreauxi* Bonaparte**

Quaternary - Minas Gerais, Piauí

- *Engyptila ochroptera* - Winge 1887: 39–40.
- *Engyptila ochroptera* - Lambrecht 1933: 769.
- *Leptotila verreauxi* - Brodkorb 1971: 199.
- *Leptotila verreauxi* (“*Engyptila ochroptera*”) - Mones 1986: 93–94.
- *Leptotila verreauxi* - Cuello 1988: 52.
- *Leptotila verreauxi* - Nascimento & Silveira 2020: 493.

Winge (1887: 39, 40) reported many bones from Lapa da Escrivânia V, notably humeri, which present a high degree of individual variation, particularly some tarsometatarsi, noting that this variation is also observed in three fresh skeletons, a humerus from Lapa da Escrivânia XI, some bones from “various caves”<sup>18</sup>, and two bones of recent age<sup>20</sup>. The total material is represented by the scapula, coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus.

- *Leptotila verreauxi* - Moraes 2014: 46, 60, fig. 25.

Moraes (2014) reported the species among archeofaunal remains from the most superficial layers in sector A of Toca da Janela da Barra do Antonião. The remains figure among material collected between 1988 and 1990 and are deposited in the Laboratório de Vestígios Orgânicos of FUMDHAM.

Only post-cranial remains were reported. About 90% of the analyzed humeri presented a dark coloration, possibly indicating they were burned. Some superficial fractures were also observed. A left humerus was figured (labelled as 8257-7). A single ulna was analyzed, also showing a dark coloration.

## **152. *Zenaida auriculata* (Des Murs)?**

Quaternary - Minas Gerais

- Columbidae indet. (s. under *Zenaida maculata*) [in part] - Winge 1887: 13.
- *Zenaida maculata* (?) - Winge 1887: 39.
- *Zenaida maculata* (?) (“kann auch *Chamoepelia* – *Scardafella* – *squamosa* sein”) - Lambrecht 1933: 769.
- *Zenaidura auriculata* (?) - Brodkorb 1971: 198.
- *Zenaidura auriculata* (“*Zenaida maculata*?”) - Mones 1986: 94.
- *Zenaida auriculata* - Cuello 1988: 50.
- *Zenaida auriculata*? - Nascimento & Silveira 2020: 493.

Winge (1887) reported four humeri From Lapa da Escrivânia V, which vary in size but are smaller than in *Zenaida auriculata*. However, the similarity with the species is very high, being well-differentiated from *Paraclaravis geoffroyi* and *Geotrygon montana*. Additionally, from Lapa da Escrivânia XI there is a similar humerus, but even smaller, closer in size to that of *Columbina squammata* than *Z. auriculata*.

### **153. *Zenaida auriculata* (Des Murs)**

Quaternary - Piauí

- Columbidae [in part] - Guérin *et al.* 1993a: 198.
- Columbidae [in part] - Guérin *et al.* 1993b: 328.
- *Zenaida auriculata* - Guérin *et al.* 1996: 84.
- *Zenaida auriculata* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least eight adult and one young individuals are present in the material.

### **154. *Zenaida auriculata noronha* Sharpe**

Holocene - Pernambuco

- *Zenaida auriculata noronha* - Olson 1981: 484.

In 1973, Olson, on his expedition to the archipelago of Fernando de Noronha, found fossilized remains of this eared dove subspecies, indicating that its occurrence on the islands is not new. This insular taxon is the same as that found in parts of Northeast Brazil, probably due to the frequent inflows of individuals from the continent (Olson 1981: 484).

### **155. *Columbina minuta* (Linnaeus)**

Quaternary - Piauí

- Columbidae [in part] - Guérin *et al.* 1993a: 198.
- Columbidae [in part] - Guérin *et al.* 1993b: 328.
- *Columbina minuta* - Guérin *et al.* 1996: 84.
- *Columbina minuta* [sic] - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least five adult and one young individuals are present in the material.

### **156. *Columbina cf. talpacoti* (Temminck)**

Quaternary - Piauí

- Columbidae [in part] - Guérin *et al.* 1993a: 198.
- Columbidae [in part] - Guérin *et al.* 1993b: 328.
- cf. *Columbina talpacoti* - Guérin *et al.* 1996: 84.
- cf. *C. talpacoti* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material comparable with the species from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **157. *Columbina talpacoti* (Temminck)**

Quaternary - Minas Gerais

- *Chamaepelia talpacoti* [in part] - Winge 1887: 13.
- *Chamaepelia* (et g. aff.) sp. 3 (fere certe): ut videtur: *Ch. griseola* vel *Ch. (Columbula) campestris*; *Ch. talpacoti*; *Ch. (Scardafella) squamosa* [in part] - Winge 1887: 39.
- *Chamaepelia* sp. (“cfr. *griseola*, *campestris*, *talpacoti* und *Scardafella squamosa*”) [in part] - Lambrecht 1933: 769.
- *Columbigallina talpacoti* - Brodkorb 1971: 198.
- *Columbigallina talpacoti* (“*Chamaepelia* sp.” [in part]) - Mones 1986: 93.
- *Columbina talpacoti* - Cuello 1988: 51.
- *Columbina talpacoti* - Nascimento & Silveira 2020: 493.

The third set of small columbid bones established by Winge (1887: 39) corresponds to *Columbina talpacoti* and is represented by two humeri and three ulnae from Lapa da Escrivânia V and a tibiotarsus from Lapa da Escrivânia XI.

### **158. *Columbina squammata* (Lesson)**

Quaternary - Minas Gerais

- *Chamaepelia* (et g. aff.) sp. 3 (fere certe): ut videtur: *Ch. griseola* vel *Ch. (Columbula) campestris*; *Ch. talpacoti*; *Ch. (Scardafella) squamosa* [in part] - Winge 1887: 39.



- *Chamoepelia* sp. (“cfr. *griseola*, *campestris*, *talpacoti* und *Scardafella squamosa*”) [in part] - Lambrecht 1933: 769.
- *Scardafella squammata* - Brodkorb 1971: 198.
- *Scardafella squammata* (“*Chamaepelia* sp.” [in part]) - Mones 1986: 93–94.
- *Scardafella squammata* - Cuello 1988: 52.
- *Columbina squammata* - Nascimento & Silveira 2020: 493.

The fourth set of small columbid bones established by Winge (1887: 39) from remains from Lapa da Escrivânia V is composed of four humeri, a carpometacarpus, and a tibiotarsus, and corresponds to *Columbina squammata*, being only slightly smaller than in it, but somewhat larger than in *Columbina talpacoti*.

### **159. *Columbina picui* (Temminck)**

Quaternary - Piauí

- Columbidae [in part] - Guérin *et al.* 1993a: 198.
- Columbidae [in part] - Guérin *et al.* 1993b: 328.
- *Columbina picui* - Guérin *et al.* 1996: 84.
- *C. picui* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **160. *Claravis pretiosa* (Ferrari-Pérez)?**

Quaternary - Minas Gerais

- *Peristera cinerea*? - Winge 1887: 39.
- *Peristera cinerea* (?) - Lambrecht 1933: 769.
- *Claravis pretiosa* - Brodkorb 1971: 198.
- *Claravis pretiosa* (“*Peristera cinerea*?”) - Mones 1986: 93–94.
- *Claravis pretiosa* - Cuello 1988: 51.
- *Claravis pretiosa*? - Nascimento & Silveira 2020: 493.

Winge (1887: 39) reported some humeri from Lapa da Escrivânia V, considerably smaller than in *Paraclaravis geoffroyi* but equivalent in form, of which he noted they almost certainly belong to *Claravis pretiosa*.

## **161. *Paraclaravis geoffroyi* (Temminck)**

Quaternary - Minas Gerais

- “un Perroquet (*Psittacus*)” [?; in part] - Gervais 1844a: 294.
- *Psittacus* [in part] - Lund (in Winge 1887): 39.
- *Peristera geoffroyi* - Winge 1887: 39.
- *Peristera Geoffroyi* - Lambrecht 1933: 769.
- *Psittacus* sp. [?; in part] - Lambrecht 1933: 770.
- *Claravis godefrida* - Brodkorb 1971: 199.
- *Claravis godefrida* (“*Peristera geoffroyi*”) - Mones 1986: 93–94.
- *Claravis godefrida* - Cuello 1988: 51.
- *Paraclaravis geoffroyi* - Nascimento & Silveira 2020: 493.

Winge (1887: 39) reported some humeri from Lapa da Escrivânia V, of which he noted that they are easily distinguishable from other genera, and a humerus from a “cave near Sumidouro”, other than Lapa da Lagoa do Sumidouro, determined as “*Psittacus*” in Lund’s catalog.

## **Cuculiformes**

### **Cuculidae**

## **162. Cuculidae indet.**

Quaternary - Goiás

- Cuculidae indet - Paulo 2009: 141.

Paulo (2009: 141) reported an indeterminate record of the family to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

## **163. *Crotophaga ani* Linnaeus**

Quaternary - Minas Gerais

- *Crotophaga ani* - Winge 1887: 45.
- *Crotophaga ani* - Lambrecht 1933: 769.
- *Crotophaga ani* - Brodkorb 1971: 206.
- *Crotophaga ani* - Mones 1986: 94.

- *Crotophaga ani* - Cuello 1988: 54.
- *Crotophaga ani* - Nascimento & Silveira 2020: 493.

Winge (1887: 45) reported four humeri and a mandibular branch from Lapa da Escrivânia V.

#### **164. *Tapera naevia* (Linnaeus)**

Quaternary - Minas Gerais

- *Diplopterus naevius* - Winge 1887: 45.
- *Diplopterus naevius* - Lambrecht 1933: 769.
- *Tapera naevia* - Brodkorb 1971: 206.
- *Tapera naevia* (“*Diplopterus naevius*”) - Mones 1986: 94.
- *Tapera naevia* - Cuello 1988: 55.
- *Tapera naevia* - Nascimento & Silveira 2020: 493.

Winge (1887: 45) reported bones of several individuals from Lapa da Escrivânia V, represented by the coracoid, humerus, ulna, carpometacarpus, fêmur, and tarsometatarsus. Winge had only available bones from taxidermized specimens for comparison. He noted that the coracoid and femur were not determined by this process and are quite distinct from the same bones as the other living cuculids found in the region.

#### **165. *Piaya cayana* (Linnaeus)**

Quaternary - Minas Gerais

- *Coccyzus cajanus* [in part] - Lund 1841d: 18.
- “un Coua (*Coccyzus* de Vieillot)” [in part] - Liais 1872: 303.
- *Coccyzus* aff. *cayano* [in part] - Lund (in Winge 1887): 45.
- *Pyrrhococcyx cayanus* - Winge 1887: 45.
- *Coccyzus* sp. (“angeblich aus den Knochenhöhlen Brasiliens”) [in part] - Lambrecht 1933: 769.
- *Pyrrhococcyx cayanus* - Lambrecht 1933: 769.
- *Piaya cayana* - Brodkorb 1971: 206.
- *Piaya cayana* (“*Pyrrhococcyx cayanus*”) - Mones 1986: 94.
- *Piaya cayana* - Cuello 1988: 54.
- *Piaya cayana* - Nascimento & Silveira 2020: 493.

Winge (1887: 45) reported six humeri and a fragment of carpometacarpus from Lapa da Escrivânia V, and an incomplete humerus (“*Coccyzus* aff. *cayano*” in Lund’s catalog) from “a cave in Mocambo”.

- *Piaya cayana* sp. Sales 2003: 214.

Sales (2003: 214) reported a specimen among the bones and mummified carcasses found in Zona II of Lapa do Rezar, in Minas Gerais.

## Nyctibiiformes

### Nyctibiidae

#### 166. *Nyctibius* sp.

Quaternary - Minas Gerais

- *Nyctibius* sp. e mediis, fere certe *N. jamaicensis* - Winge 1887: 43–44.
- *Nyctibius* sp. - Lambrecht 1933: 774.
- *Nyctibius griseus* - Brodkorb 1971: 236.
- *Nyctibius griseus* - Mones 1986: 96.
- *Nyctibius griseus* - Cuello 1988: 57.
- *Nyctibius griseus* - Sick 1984a: 334.
- *Nyctibius griseus* - Sick 1993: 300.
- *Nyctibius griseus* - Sick 1997: 408.
- *Nyctibius* sp. - Nascimento & Silveira 2020: 493.

Winge (1887: 43, 44) reported the proximal end of a left carpometacarpus from Lapa da Escrivânia V, and a right carpometacarpus of recent age<sup>20</sup>, lacking the upper part. He noted that both fragments appear to belong to the same species, being much smaller and somewhat different from *Nyctibius aethereus*, and postulated that they might belong, due to their measurements, to *Nyctibius jamaicensis*, since the other smaller species are too small. However, this species does not occur in Brazil, which is almost certainly why Brodkorb (1971: 236) listed the material as *Nyctibius griseus*.

#### 167. *Nyctibius griseus* (Gmelin)

Pleistocene - Bahia

- *Nyctibius griseus* - Silva *et al.* 2012b: 368.

Silva *et al.* (2012b: 368) reported remains that Herculano Alvarenga associated with the species among the material collected in 1980 and 1984 by the team of the Laboratório de Paleontologia of MCN PUC at Gruta dos Brejões, in Morro do Chapéu, Bahia. The material consists of three carpometacarpi, two humeri, and a coracoid, representing six individuals, deposited in the MCN PUC Minas paleontology collection.

## Caprimulgiformes

### Caprimulgidae

#### 168. Caprimulgidae indet. 1

Quaternary - Minas Gerais

- *Caprimulgus* [?] - Gervais 1844a: 294.
- “les Engoulevents” [?] - Liais 1872: 303.
- *Caprimulgus* - Lund (in Winge 1887): 42.
- G. sp. indet., forte *Hydropsalis forcipata* - Winge 1887: 42–43.
- cfr. *Hydropsalis forcipata* - Lambrecht 1933: 773.
- *Cypselus ? affinis* (“*Cypselus* und *Caprimulgus* nach Lund in den Knochenhöhlen Brasiliens”) [?; in part] - Lambrecht 1933: 774.
- *Hydropsalis brasiliana* [in part] - Brodkorb 1971: 235.
- *Hydropsalis* [in part?] - Sick 1984a: 336.
- *Hydropsalis brasiliana* [in part?] - Mones 1986: 96.
- *Hydropsalis* [in part?] - Sick 1993: 303.
- *Hydropsalis* [in part?] - Sick 1997: 412.
- Caprimulgidae indet. 1 - Nascimento & Silveira 2020: 493.

Winge (1887: 42, 43) reported a humerus (determined as “*Caprimulgus*” in Lund’s catalog) from a cave near Mocambo, quite similar to *Hydropsalis torquata*, but much larger, with dimensions that correspond well to *Macropsalis forcipata*. Winge noted that the similarity with *Nyctidromus* is significant, but no species with these dimensions are known. The humerus of *Anrostomus rufus* is much smaller and different in shape. There is also a certain similarity with *Chordeiles* in the small differences observed compared to *Hydropsalis torquata*, and it is much smaller than in *Chordeiles nacunda*.

#### 169. Caprimulgidae indet. 2

Quaternary - Minas Gerais

- G. sp. indet. (*Antrostomus*, sp. e parvis, ?) - Winge 1887: 43.
- cfr. *Antrostomus* - Lambrecht 1933: 773.
- Caprimulgidae indet. 2 - Nascimento & Silveira 2020: 493.

Winge (1887: 43) reported humeri in considerable number from Lapa da Escrivânia V. He noted they are generally smaller than in *Hydropsalis torquata*, from which a clear boundary could not be defined, but some fragments must belong to a different species, with some differences between the bones existing. Two of these humeri are quite peculiar in their morphology. There is less similarity with *Antrostomus rufus* than with *H. torquata* and *Nyctidromus albicollis*, but the bones may belong to a smaller species of *Antrostomus*. Winge used the contemporary definition of the genus and noted that, of these smaller species, *Antrostomus ocellatus* (= *Nyctiphrynus ocellatus*) lives today in the region, and they could hardly belong to *Chordeiles minor* and *C. nacunda* due to morphological differences.

### **170. *Nyctidromus albicollis* (Gmelin)**

Quaternary - Minas Gerais

- *Nyctidromus albicollis* - Winge 1887: 42.
- *Nyctidromus albicollis* - Lambrecht 1933: 773.
- *Nyctidromus albicollis* - Brodkorb 1971: 235.
- *Nyctidromus* - Sick 1984a: 336.
- *Nyctidromus albicollis* - Mones 1986: 96.
- *Nyctidromus albicollis* - Cuello 1988: 57.
- *Nyctidromus* - Sick 1993: 303.
- *Nyctidromus* - Sick 1997: 412.
- *Nyctidromus albicollis* - Nascimento & Silveira 2020: 493.

Winge (1887: 42) reported the occurrence of several humeri from Lapa da Escrivânia V, well-differentiated from each other.

### **171. cf. *Hydropsalis* sp.**

Quaternary - Piauí

- cf. *Hydropsalis* - Guérin *et al.* 1996: 84.
- cf. *Hydropsalis* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material comparable with the genus from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **172. *Hydropsalis anomala* (Gould)**

Quaternary - Minas Gerais

- *Eleothreptus anomalus* - Winge 1887: 42.
- *Eleothreptus anomalus* - Lambrecht 1933: 773.
- *Eleothreptus anomalus* - Brodkorb 1971: 235.
- *Eleothreptus anomalus* - Mones 1986: 96.
- *Eleothreptus anomalus* - Cuello 1988: 58.
- *Hydropsalis anomala* - Nascimento & Silveira 2020: 494.

Winge (1887: 42) reported two humeri from Lapa da Escrivânia V, one left and one right, noting they are slightly smaller than the observed in a fresh skeleton.

### **173. *Hydropsalis torquata* (Gmelin)**

Quaternary - Minas Gerais

- *Hydropsalis torquata* - Winge 1887: 43.
- *Hydropsalis torquata* - Lambrecht 1933: 773.
- *Hydropsalis brasiliana* [in part] - Brodkorb 1971: 235.
- *Hydropsalis* [in part?] - Sick 1984a: 336.
- *Hydropsalis brasiliana* (“*Hydropsalis torquata*”) [in part?] - Mones 1986: 96.
- *Hydropsalis brasiliana* - Cuello 1988: 57.
- *Hydropsalis* [in part?] - Sick 1993: 303.
- *Hydropsalis* [in part?] - Sick 1997: 412.
- *Hydropsalis torquata* - Nascimento & Silveira 2020: 494.

Winge (1887: 43) reported several humeri from Lapa da Escrivânia V, and several bones of recent age<sup>20</sup> - mandible, sternum, scapula, ulna, and femur—that can be attributed to the species, although they show some differences. Winge also noted that *Nyctidromus albicollis* is bigger and more different. Besides the description of this material and the remains that he defined as *G. sp. indet.* (*Antrostomus*, sp. e parvis, ?) (see Caprimulgidae indet. 2), Winge reported the existence of several bones from the same cave (Lapa da Escrivânia V) in addition to the humeri, represented by the

coracoid, ulna, femur, and tibiotarsus. Part of these correspond with *H. torquata* and part is very small and slightly different, without clear boundaries.

## Apodiformes

### Apodidae

#### 174. *Streptoprocne zonalis* (Shaw)

Quaternary - Minas Gerais, Piauí

- *Cypsellus collaris* [in part] - Lund 1841d: 18.
- “une autre [espèce] de celui des hirondelles” [?; in part] - Liais 1872: 303.
- *Cypsellus* aff. *collari* [in part] - Lund (in Winge 1887): 44.
- *Chaetura zonalis* - Winge 1887: 44.
- *Chaetura zonalis* - Lambrecht 1933: 773.
- *Cypselus* ? *affinis* (“*Cypselus* und *Caprimulgus* nach Lund in den Knochenhöhlen Brasiliens”) [in part] - Lambrecht 1933: 774.
- *Streptoprocne zonalis* - Brodkorb 1971: 240.
- *Streptoprocne zonalis* - Sick 1984a: 345.
- *Streptoprocne zonalis* (“*Chaetura zonalis*”) - Mones 1986: 97.
- *Streptoprocne zonalis* - Cuello 1988: 58.
- *Streptoprocne zonalis* - Nascimento & Silveira 2020: 494.

Winge (1887: 44) reported several individuals from Lapa da Escrivânia V, some very young, two bones from “various caves”<sup>18</sup>, and some bones from an unknown locality, including four humeri determined as “*Cypsellus* aff. *collari*” in Lund’s catalog. The total material is represented by the coracoid, sternum (anterior part), humerus (in great number), ulna, radius, carpometacarpus, the first phalanx of the second digit of the wing, femur, tibiotarsus, and tarsometatarsus.

- Apodidae - Guérin *et al.* 1993a: 198.
- Apodidae - Guérin *et al.* 1993b: 328.
- *Streptoprocne zonalis* - Guérin *et al.* 1996: 85.
- *Streptoprocne zonalis* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.



## Trochilidae

### 175. Trochilidae indet. 1

Quaternary - Minas Gerais

- "Oiseau-mouche dépassant à peine la dimension du *Trochilus minimus* de Linné" - Liais 1872: 303.
- Trochilidae indet. 1 - Nascimento & Silveira 2020: 494.

While living in Brazil, the French scientist Emmanuel Liais (1826–1900) found a well-preserved sternum among the bones of Lapa do Gambá in the Lagoa Santa region during his first voyage. He believed it belonged to a hummingbird slightly larger than *Trochilus minimus* (= *Mellisuga minima*) due to its size and shape (Liais 1872: 303). Ruschi (1979: 32), on the possible identity of the specimen, commented: “as in this locality some species of slightly larger size still live today, such as: *Calliphlox a. amethystina* Boddaert 1831; *Heliactin cornuta* Wied, 1821; *Chlorostilbon aureoventris pucherani* Bourcier and Mulsant, 1848 and *Amazilia versicolor kubitschecki* Ruschi, 1959, it is difficult to determine the fragment without a comparative examination”. The staff of the Muséum Emmanuel Liais, in Cherbourg-en-Cotentin, France, was contacted about the possible whereabouts of this material, but it could not be located.

### 176. Trochilidae indet. 2

Quaternary - Minas Gerais

- G. sp. indet. e majoribus - Winge 1887: 44.
- sp. indet. größere Formen - Lambrecht 1933: 774.
- *Clytolaema rubricauda* - Brodkorb 1971: 243.
- *Clytolaema rubricauda* - Mones 1986: 97.
- *Clytolaema rubricauda* - Cuello 1988: 58.
- Trochilidae indet. 2 - Nascimento & Silveira 2020: 494.

Winge (1887: 44) reported a carpometacarpus from Lapa da Escrivânia V, of a species slightly larger than that observed in *Clytolaema rubricauda*. Brodkorb (1971: 243), most likely following Winge’s comment, listed the material under this name, associating it with the locality “Lapa da Escrivânia?”.

### **177. *Phaethornis pretrei* (Lesson & Delattre)?**

Quaternary - Minas Gerais

- *Phaëthornis pretrei?* - Winge 1887: 50.
- *Phaethornis pretrei?* - Nascimento & Silveira 2020: 494.

Winge (1887: 50) reported a carpometacarpus and a fragment of the anterior part of a sternum, both of recent age, without attributing them to a specific cave. They belong to a smaller form than the indeterminate trochilid<sup>23</sup> from Lapa da Escrivânia V (see above). The size and shape correspond to *Phaethornis pretrei*, but whether it belongs to this species could not be defined.

### **178. *Phaethornis pretrei* (Lesson & Delattre)**

Quaternary - Minas Gerais

- *Phaethornis pretrei* sp. - Sales 2003: 214.

Sales (2003: 214) also reported a specimen of this species appearing among the material composed of bones and mummified carcasses found in Zona II of Lapa do Rezar, Minas Gerais.

### **179. *Chlorestes notata* (Reich)**

Quaternary - Minas Gerais

- *Chlorestes notatus* sp. - Sales 2003: 214.

Sales (2003: 214) reported a specimen among the material composed of bones and mummified carcasses found in Zona II of Lapa do Rezar, Minas Gerais.

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<sup>23</sup> In the appendix that lists the species that had recent age remains found in the caves, Winge (1887: 50, 51) appears to have confused (or did not revise them after adding) the numbers of the species in his main list that he referenced in the description of the materials of “*Phaëthornis pretrei?*”, in which it mentions the other trochilid discovered as No. 91 and not No. 92, and in “Picid. g. sp., and minimis”, which references “*Picus (Campias) maculifrons*” as No. 107 and not No. 108.

## Opisthocomiformes

### Opisthocomidae

#### 180. †*Hoazinavis lacustris* Alvarenga, Mayr & Mourer-Chauviré

Late Oligocene/Early Miocene - São Paulo

Fig. 13.A

*Type locality:* Tremembé Formation, Taubaté Basin, state of São Paulo, Brazil.

*Etymology:* *Hoazinavis*, a portmanteau of “hoatzin”, a common name of the species (as in English and German languages) and the Latin *avis* (“bird”), and the Latin *lacustris* referencing the lake deposits of the Tremembé Formation.

- *Hoazinavis lacustris* - Mayr *et al.* 2011b: 961–966, fig. 1D, E, H, I, M, N.

From material found in 2008 by Herculano Alvarenga (Pivetta 2011: 51) in the Tremembé Formation, Mayr *et al.* (2011b) described the (then) unmistakably oldest and smallest member of the Opisthocomiformes, erecting the new genus and species *Hoazinavis lacustris*.

The material (MHNT-VT 5332, holotype) is a complete right humerus, the omal end of a right coracoid and the cranial end of a right scapula, all from a same adult individual, deposited in the Museu de História Natural de Taubaté (Mayr *et al.* 2011b: 962).

In the same study, Mayr *et al.* (2011b: 963, 964) reclassified *Namibiavis senutae*, a species from the early Miocene of Namibia (Mourer-Chauviré 2003), from an Idiornithidae to an Opisthocomiformes, and through phylogenetic analysis placed it as the sister of a clade formed by *Hoazinavis* and *Opisthocomus*.

The remains of both species indicate they were weak distance flyers, just like the living *Opisthocomus hoazin*, which, due to the proportionally large crop, developed a modified sternal keel and pectoral musculature to accommodate it (Mayr *et al.* 2011b: 964). Whether and to what degree the two fossil species were already folivorous cannot be stated, but a large crop considerably affects the morphology of the pectoral girdle’s bones. Due to the similarities of the known elements with those of *O. hoazin*, Mayr *et*

*al.* (2011b: 965) believed it is likely that at least *H. lacustris* had already evolved a large crop and folivory at some level, whose development in the only living species suggests a very long evolutionary history of specialized feeding.

The discovery of *Namibiavis* in Africa shows that the current distribution of hoazins is relictual and implies that the distribution of stem Opisthocomiformes was the result of dispersion and not vicariance, given the fact that South America and Africa separated during the Cretaceous, before the appearance of crown Neornithes in the fossil record (Mayr *et al.* 2011: 965). Because of this, Mayr *et al.* (2011: 965) believed that, even if the Miocene hoazins had better flight capabilities than the living ones and the existence of islands in the South Atlantic during the beginning of the Cenozoic is considered, the dispersion by the ocean (minimum distance of 1000 km in a straight line during that time) through floating vegetation rafts is the most plausible explanation, and their folivorous diet would favor these birds in these rafts, which come off the mouth of large rivers and can reach considerable sizes. Therefore, an African origin is more likely, as was the case with caviomorph rodents, platyrrhinous primates, and some South American amphibians and geckos, favored by paleocurrents and paleowinds, but additional fossils and a better understanding of the phylogenetic relationships of Opisthocomiformes are needed to the establishment of a hypothesis of dispersion direction (Mayr *et al.* 2011: 965). Additionally, Mayr (2014: 56, 58, 59) reported a middle Miocene tarsometatarsus from Kenya (Maboko Formation) assigned to *?Namibiavis* sp., which has an essentially modern morphology and indicates arboreal habits consistent with a folivorous diet.

The theory of hoazins origin in the Old World and their current relictual distribution were corroborated with the description of European fossils. Mayr & De Pietri (2014: 144, 145, 146, 147) described *Protoazin parisiensis* from the late Eocene of France, the group's oldest known representative and the first found in the Northern Hemisphere. The material shows greater affinity with *Opisthocomus* and *Hoazinavis* than with *Namibiavis*. However, Mayr & De Pietri (2014: 147) noted that the theory of an alternative route of dispersion through the Northern Hemisphere lacks support with the absence of known fossils of the group in North America.

From South America, the only other known fossil opisthocomiform is *Hoazinoides magdalenae* (Miller 1953), from the middle Miocene of Colombia (Villavieja Formation), which represents a species slightly larger than the living hoazin, and along with *Hoazinavis lacustris* point South American records outside the group's current geographical distribution (Mayr *et al.* 2011b: 964).

## Gruiformes

### Rallidae

#### 181. Rallidae indet. 1

Quaternary - Minas Gerais

- G. sp. indet. (similis praecedenti [*Rallus nigricans*]) - Winge 1887: 26.
- *Rallus nigricans* (?) [in part] - Lambrecht 1933: 760.
- *Ortygonax nigricans* (?) [in part] - Brodkorb 1967: 133.
- *Rallus nigricans* [in part] - Cuello 1988: 42.
- Rallidae indet. 1 - Nascimento & Silveira 2020: 491.

Winge (1887: 26) reported as indeterminate a humerus from Lapa do Capão Seco, similar to the largest specimens of the species [*Pardirallus nigricans*] he presented just before this record in his list, which has a very large internal condyle.

#### 182. Rallidae indet. 2

Quaternary - Minas Gerais

- *Crex minuta* [in part] - Lund 1841d: 18.
- “les Rallus” [in part] - Liais 1872: 303.
- *Rallus minutus* [in part] - Lund (in Winge 1887): 26.
- *Porzana* sp. e minimis, non *P. flaviventris* - Winge 1887: 26–27.
- *Porzana* sp. - Lambrecht 1933: 761.
- “other species” - Brodkorb 1967: 134.
- *Porzana flaviventris* - Mones 1986: 86.
- *Porzana flaviventer* - Cuello 1988: 42.
- Rallidae indet. 2 - Nascimento & Silveira 2020: 492.

Winge (1887: 26, 27) reported several bones from Lapa da Escrivânia V, noting that this is perhaps the most numerous bird in the cave, a single bone from Lapa da

Escrivânia III, several bones from Lapa da Lagoa do Sumidouro, some bones from an unknown locality, and material of recent age<sup>20</sup> in large volume (including a humerus that Lund determined as “*Rallus minutus*”). It shows that, apparently, it is one of the most common birds in the region, and the fact that neither Lund nor Reinhardt found it alive may be a consequence of its secretive habits. The material is represented by several head parts, scapula, coracoid, furcula, sternum, humerus, ulna, radius, carpometacarpus, pelvis, femur, tibiotarsus, and tarsometatarsus. Winge noted that bones do not belong to *Porzana* (= *Hapalocrex*) *flaviventer*, which he defines as the only small species of the genus known in the region. The tarsometatarsus is slightly smaller than that of the species mentioned above, but the forearm bones are much larger, and, on them, Winge remarked that it is necessary to consider the great individual variation observed in the tarsometatarsi and ulnae from the caves. Among the variations present in the tarsometatarsi, one of them, unusually short, is similar to that of *Porphyriops*, but it was not possible to define whether it is an individual variation or another species. Mones (1986: 86) listed the record as *Porzana flaviventris*, noting that he followed Brodkorb (1967: 134), who, nevertheless, said that such materials belong to another species.

### **183. Rallidae indet. 3**

Quaternary - Minas Gerais

- G. sp. indet. (generi *Porphyriopi*, ut videtur, affinis vel saltem similis) - Winge 1887: 27.
- Rallidae indet. 3 - Nascimento & Silveira 2020: 492.

Winge (1887: 27) reported several humeri from Lapa da Escrivânia V, relatively short and robust (providing the length of seven of them), among which the difference in size could indicate two species. The longer ones have the same length and general shape as *Porphyriops melanops* but are more robust, with wider ends. They are quite different from *Porphyrio flavirostris*. Winge further noted that there is also a tarsometatarsus very similar to that of *P. melanops* - and different from all the others he could compare, but smaller.

### **184. Rallidae indet. 4**

Quaternary - Minas Gerais

- Rallid. indet. (s. Tillæg til Rallidæ) - Winge 1887: 13.
- “mindre Rallide” - Winge 1887: 27.
- Rallidae indet. 4 - Nascimento & Silveira 2020: 492.

Winge (1887: 27) reported a tarsometatarsus of a small rallid from Lapa da Lagoa do Sumidouro, which hardly belongs to the other rallids he mentioned in his study.

### **185. Rallidae indet. 5**

Quaternary - Piauí

- Rallidae [in part] - Guérin *et al.* 1993a: 198.
- Rallidae [in part] - Guérin *et al.* 1993b: 328.
- cf. *Porphyryla* - Guérin *et al.* 1996: 84.
- cf. *Porphyryla* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material comparable with the genus *Porphyryla* (= *Porphyrio*?) from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **186. Rallidae indet. 6**

Quaternary - Piauí

- Rallidae [in part] - Guérin *et al.* 1993a: 198.
- Rallidae [in part] - Guérin *et al.* 1993b: 328.
- cf. *Gallinule* [sic] - Guérin *et al.* 1996: 84.
- cf. *Gallinule* [sic] - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material comparable with the genus “*Gallinule*” (= *Gallinula*?) from Toca da Janela da Barra do Antonião.

### **187. Rallidae indet. 7**

Quaternary - Goiás

- Rallidae indet - Paulo 2009: 142.

Paulo (2009: 142) reported an indeterminate record of the family to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

## 188. †*Rallus* sp.

Holocene - Pernambuco

Fig. 16.C

- Rallidae - Olson 1977: 357.
- Rallidae - Olson 1981: 483.
- “saracura fóssil” - Sick 1984a: 250.
- Rallidae - Alvarenga 1992: 254.
- Rallidae - Alvarenga 1993a: 63-64.
- “sub-fossil rail” - Sick 1993: 211.
- Rallidae - Alvarenga 1997: 123.
- “saracura fóssil” - Sick 1997: 296.
- *Rallus* sp. - Carleton & Olson 1999: 55.
- ?*Atlantisia* sp. - Hume 2017: 116–117.

The existence of a rallid species exterminated by man-introduced mammals into the Fernando de Noronha Archipelago (Fig. 2.12) or in the Trindade Island was speculated by Olson (1973: 29), when he theorized on the absence *Atlantisia* species or of another genus in South Atlantic islands, noting that a search for subfossil remains in these territories could provide interesting results. During an expedition in Fernando de Noronha Island in 1973, Olson (1977: 357; 1981: 483) found the remains of a medium-sized rallid in a dune area at the base of the Santo Antônio peninsula, in addition to the remains of other vertebrates, gastropods, and land crabs, with an estimated age in the late Holocene. Most of the dune material was scattered and many specimens were well mineralized (Olson 1981: 483; Carleton & Olson 1999: 2).

Most parts of the skeleton were found, associated with several individuals. The bird was probably flightless, showing reduced wings, but to a lesser extent than other species in this category (Olson 1981: 483). Olson (1977: 357) initially postulated that the remains did not seem to be related to the genera found in mainland Brazil, believing that it was a form of *Atlantisia*, a genus now represented only by *Atlantisia rogersi* from Inaccessible Island in the archipelago of Tristan da Cunha (Taylor 1996). Later he associated the remains with the genus *Rallus* (Carleton & Olson 1999: 55). Today the geographically closer species to the archipelago of Fernando de Noronha is *Rallus longirostris*, occurring in almost the entire Brazilian coastline (Taylor & Christie 1996).



The complete description of the material, deposited at the Smithsonian Institution (Washington, D.C.) (Hume 2017: 116), is still pending.

The first mention of the archipelago's fauna is found in the account of the disputed fourth voyage of explorer Amerigo Vespucci (1454–1512) - “*Lettera di Amerigo Vespucci delle Isole Nuovamente in Quattro Suoi Viaggi*” (1504), written in 1503, the year in which the discovery of the islands is generally attributed (Olson 1981: 481, 482; Carleton & Olson 1999: 2, 44, 47). Vespucci described birds occurring in large numbers, both terrestrial and marine, “so tame that it was possible to catch them by hand”, having “filled an entire boat with them”. He also cited reptiles and “large rats” (Carleton & Olson 1999: 47), the latter likely being representatives of the now-extinct *Noronhomys vespucci*, described by Carleton & Olson (1999) from material discovered by Olson on his expedition. After Vespucci's account, no biological survey on the islands would be made until the arrival of naturalists J.C. Branner in 1876 and H.N. Ridley in 1887 (Carleton & Olson 1999: 48). If the rail was among the terrestrial birds observed by Vespucci, the action of man in direct hunting, in the alteration of the habitat, or in the introduction of predatory species of both eggs and adults (*Noronhomys vespucci* was described as predominantly herbivore [Carleton & Olson 1999 : 52]) had a devastating effect on this bird that evolved in isolation, leading to its extinction shortly afterward, as happened with several other rallids on islands across the planet.

### **189. *Porphyrio martinica* (Linnaeus)?**

Quaternary - Minas Gerais

- *Porphyrio martinicus?* - Winge 1887: 27.
- *Porphyrio* sp. (“(?) *martinicus*”) - Lambrecht 1933: 761.
- *Porphyryula martinica* (?) - Brodkorb 1967: 135.
- *Porphyryula martinica* (“*Porphyrio martinicus?*”) - Mones 1986: 86.
- *Porphyryula martinica* - Cuello 1988: 43.
- *Porphyrio martinicus?* - Nascimento & Silveira 2020: 492.

Winge (1887: 27) associated to this species two humeri from Lapa da Escrivânia V, with uncertainty.

### **190. *Laterallus melanophaius* (Vieillot)?**

Quaternary - Minas Gerais

- *Porzana melanophæa?* - Winge 1887: 26.
- *Porzana* sp. (“(?) *melanocephala*”) - Lambrecht 1933: 761.
- *Porzana melanophaius* - Brodkorb 1967: 134.
- *Porzana melanophaius?* - Mones 1986: 86.
- *Laterallus melanophaius* - Cuello 1988: 43.
- *Laterallus melanophaius?* - Nascimento & Silveira 2020: 492.

Winge (1887: 26) reported two tibiotarsi and two tarsometatarsi from Lapa da Escrivânia V, and one tarsometatarsus of recent age<sup>20</sup>, similar to the remains he described as “*Porzana* sp. and *minimis*, non *P. flaviventris*” but larger and slenderer. Of the species that live in the region, he believed they could only belong to *Laterallus melanophaius*, of which the tarsometatarsus of a taxidermized specimen corresponds in size. Additionally, several humeri from Lapa da Escrivânia V probably belong to this species, similar in size to *Porphyrio flavirostris* but different in shape. Winge noted they are perhaps quite large regarding the other bones, but this does not prevent them from belonging to the same species.

### **191. *Mustelirallus albicollis* (Vieillot)**

Quaternary - Minas Gerais

- *Porzana albicollis* - Winge 1887: 26.
- *Porzana albicollis* - Lambrecht 1933: 761.
- *Porzana albicollis* - Brodkorb 1967: 134.
- *Porzana albicollis* - Mones 1986: 86.
- *Porzana albicollis* - Cuello 1988: 42.
- *Mustelirallus albicollis* - Nascimento & Silveira 2020: 492.

Winge (1887: 26) associated with this species bones from several individuals from Lapa da Escrivânia V, noting that they are very similar to *Pardirallus nigricans* and that there may be some doubt about some bones being from a small representative of this species or a large *Porzana albicollis*.

### **192. *Pardirallus nigricans* (Vieillot)**

Quaternary - Minas Gerais

- *Rallus nigricans* (et. aff.) - Winge 1887: 26.
- *Rallus nigricans* (?) [in part] - Lambrecht 1933: 760.

- *Ortygonax nigricans* [in part] - Brodkorb 1967: 133.
- *Ortygonax nigricans* (“*Rallus nigricans*”) - Mones 1986: 86.
- *Rallus nigricans* [in part] - Cuello 1988: 42.
- *Pardirallus nigricans* - Nascimento & Silveira 2020: 492.

Winge (1887: 26) associated with this species the bones of several individuals from Lapa da Escrivânia V, noting that some larger ones may belong to other species. Additionally, he reported a single bone of recent age<sup>20</sup>.

### **193. *Aramides* sp. 1**

Quaternary - Minas Gerais

- *Aramides* sp. (*cayennensis* v. *serracura*) - Winge 1887: 25–26.
- *Aramides cayanea* (“oder *A. serracura*”) - Lambrecht 1933: 760.
- *Aramides cajanea* - Brodkorb 1967: 133.
- *Aramides cajanea* - Mones 1986: 86.
- *Aramides cajanea* - Cuello 1988: 42.
- *Aramides* sp. - Nascimento & Silveira 2020: 492.

Winge (1887: 25, 26) reported a humerus from “various caves”<sup>18</sup> and a femur from an unknown location as classifiable under *Aramides cayennensis* (= *cajaneus*). However, he noted that due to their significant similarity to *Aramides saracura* and the lack of a significant number of specimens for comparison, it was not possible to reach a definition at the species level.

Brodkorb (1967: 133; and, following him, Cuello 1988: 42) listed the material under the locality “Lapa da Escrivania?”, probably due to Winge (1887: 12) having listed the taxon under “I Lapa da Escrivania Nr. 5 mangle blot følgende” (“In Lapa da Escrivânia V only the following are missing”).

### **194. *Aramides* sp. 2**

Early Holocene - Goiás

- *Aramides* sp. - Dias 2004: 255.

Dias (2004) reported the genus among avian remains from the early Holocene of GO-JA-01 shelter in Serranópolis, Goiás.

### **195. *Aramides saracura* (Spix)**

Holocene - Rio de Janeiro

- *Aramides saracura* - Vogel 1987: 231, 237, fig. 2.

A complete skull from the sambaqui Zé Espinho “A”, in Guaratiba, Rio de Janeiro, was reported by Vogel (1987: 231, 237). In addition to this determined material, Vogel (1987: 231, 237, 244) also commented that other fragmented remains, including bones of the limbs and scapular girdle, associated with wading birds, were found. Of the total material, in sambaqui “A”, three remains were found in layer I, five in II, and fourteen in III, and in sambaqui “D” eight in I, seventeen in II, and five in III.

### **196. *Porzana carolina* (Linnaeus)**

Quaternary - Piauí

- Rallidae [in part] - Guérin *et al.* 1993a: 198.
- Rallidae [in part] - Guérin *et al.* 1993b: 328.
- *Porzana carolina* - Guérin *et al.* 1996: 84.
- *Porzana carolina* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material. This species, which breeds in North America and winters in Central and northern South America, was previously unknown reaching Brazil today, until the first authentic record was published by Camacho & Accorsi (2016) for Rio de Janeiro.

### **197. *Gallinula galeata* (Lichtenstein)**

Quaternary - Minas Gerais

- *Gallinula galeata* - Winge 1887: 27.
- *Gallinula galeata* - Lambrecht 1933: 761.
- *Gallinula chloropus* - Brodkorb 1967: 135.
- *Gallinula chloropus* (“*Gallinula galeata*”) - Mones 1986: 86.
- *Gallinula chloropus* - Cuello 1988: 43.
- *Gallinula galeata* - Nascimento & Silveira 2020: 492.

Winge (1887: 27) associated to the species a humerus and a tarsometatarsus from Lapa da Escrivânia V.

## Charadriiformes

### Charadriidae

#### 198. *Vanellus* sp.

Quaternary - Minas Gerais

Fig. 9.A–D

- *Vanellus* aff. *cayennensi*, forma magna; *Vanellus cayennensis* et aff. [“Knogler af en Art eller Form, der staar ganske nær ved *V. cayennensis* og *occidentalis*, men er større”] - Winge 1887: 13, 27–28.
- *Vanellus cayennensis* [in part] - Lambrecht 1933: 763.
- *Belonopterus chilensis* - Brodkorb 1967: 199.
- *Belonopterus chilensis* - Mones 1986: 92.
- *Vanellus chilensis* - Cuello 1988: 45.
- *Belonopterus chilensis* - Cenizo & Agnolin 2007: 41.
- *Vanellus* sp. - Nascimento & Silveira 2020: 492.

Winge (1887: 27, 28) reported an almost complete right humerus (in two pieces) from Lapa da Escrivânia V, which corresponds well to that of *Vanellus chilensis* (“*V. cayennensis* or *occidentalis*”) but is considerably larger, besides presenting a small variation in morphology. Additionally, he reported the proximal end of another right humerus from Lapa da Escrivânia XI, equivalent to the previous one.

#### 199. *Vanellus chilensis* (Molina)

Quaternary - Goiás, Minas Gerais

- *Vanellus cayennensis* et aff. [“Knogler af Størrelse som hos *V. cayennensis*”] - Winge 1887: 28.
- *Vanellus cayennensis* [in part] - Lambrecht 1933: 763.
- *Vanellus chilensis* - Nascimento & Silveira 2020: 492.

From Lapa da Escrivânia V, Winge (1887: 28) reported the distal end of a tibiotarsus, a coracoid, and a fragment of the frontal and medial parts of the sternum of a young individual. Despite small variations, these pieces correspond well in size to *Vanellus chilensis*.

- *Vanellus chilensis* - Paulo 2009: 142.

Paulo (2009: 142) reported the species to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

## **Scolopacidae**

### **200. Scolopacidae indet.**

Quaternary - Minas Gerais

- “*Totanus*- eller *Tringa*-agtig Fugl” - Winge 1887: 29.
- *Limicola* sp. - Lambrecht 1933: 764.
- Scolopacidae indet. - Nascimento & Silveira 2020: 492.

Winge (1887: 29) reported the upper part of an ulna of a bird similar to *Tringa* or the then valid *Totanus* from Lapa da Escrivânia V, insignificantly smaller and slightly different than that of a *Tringa melanoleuca*, noting that it may be due to individual variation.

### **201. *Calidris cf. melanotos* (Vieillot)**

Quaternary - Minas Gerais

- *Tringa maculata* (fere certe) - Winge 1887: 28.
- *Tringa maculata* - Lambrecht 1933: 763.
- *Erolia melanotos* - Brodkorb 1967: 196.
- *Erolia melanotos* (“*Tringa maculata*?”) - Mones 1986: 91.
- *Calidris melanotos* - Cuello 1988: 48.
- *Calidris cf. melanotos* - Nascimento & Silveira 2020: 492.

Winge (1887: 28) associated a humerus from Lapa da Escrivânia V with this species, noting that for comparison there was a fresh humerus that lacked the proximal part—necessary for the diagnosis, but that even so the similarity between the two bones was so pronounced that they almost certainly belong to the same species.

### **202. *Calidris cf. pusilla* (Linnaeus)**

Quaternary - Minas Gerais

- *Ereunetes pusillus* (fere certe) - Winge 1887: 28.
- *Ereunetes pusillus* - Lambrecht 1933: 764.
- *Ereunetes pusillus* - Brodkorb 1967: 196.

- *Ereunetes pusillus?* - Mones 1986: 91.
- *Calidris pusilla* - Cuello 1988: 48.
- *Calidris cf. pusilla* - Nascimento & Silveira 2020: 492.

Winge (1887: 28) associated a humerus from Lapa da Escrivânia V with almost certainty with the species. He noted that what he said about the material associated with *Calidris melanotos* also applies to this one. The fresh bone available for comparison was only slightly more incomplete. Winge described the humerus as larger than in *Calidris minuta* and even larger than in *Calidris temminckii*, but much smaller than in *Calidris bairdii* and quite different from *Actitis macularius*.

### **203. *Gallinago cf. paraguaiae* (Vieillot)**

Quaternary - Minas Gerais

- *Gallinago frenata* (v. sp. aff.) - Winge 1887: 28.
- *Gallinago frenata* (?) - Lambrecht 1933: 764.
- *Capella paraguaiae* - Brodkorb 1967: 197.
- *Capella paraguaiae* (“*Gallinago frenata*”) - Mones 1986: 91.
- *Gallinago gallinago paraguaiae* - Cuello 1988: 47.
- *Gallinago cf. paraguaiae* - Nascimento & Silveira 2020: 492.

Winge (1887: 28) reported bones of several individuals from Lapa da Escrivânia V, represented by the frontal part of the sternum, humerus, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. In addition to small morphological differences, most of the bones are slightly larger than in a specimen of *Gallinago paraguaiae*, but, in general, they belong to a very similar form, which like it has shorter legs and weaker wings than in *Gallinago gallinago*. There is also marked individual difference between the bones of the cave, particularly in the humeri. Winge also noted that *Thinocorus* is quite similar to *Gallinago* in some bones but distinct enough. There is also a coracoid from Lapa da Lagoa do Sumidouro.

### **204. *Tringa solitaria* Wilson**

Quaternary - Minas Gerais

- *Totanus solitarius* - Winge 1887: 28.
- *Totanus solitarius* - Lambrecht 1933: 764.
- *Tringa solitaria* - Brodkorb 1967: 195.

- *Tringa solitaria* (“*Totanus solitarius*”) - Mones 1986: 91.
- *Tringa solitaria* - Cuello 1988: 46.
- *Tringa solitaria* - Nascimento & Silveira 2020: 492.

From Lapa da Escrivânia V, Winge (1887: 28) associated with this species a humerus, in addition to possibly an ulna.

## Jacanidae

### 205. *Jacana jacana* (Linnaeus)

Quaternary - Minas Gerais

- *Parra jacana* - Winge 1887: 29.
- *Jacana jacana* - Lambrecht 1933: 762.
- *Jacana spinosa* - Storer 1960: 74.
- *Jacana spinosa* - Brodkorb 1967: 202.
- *Jacana spinosa* - Olson 1976: 259.
- *Jacana spinosa* (“*Parra jacana*”) - Mones 1986: 91.
- *Jacana jacana* - Cuello 1988: 44.
- *Jacana jacana* - Nascimento & Silveira 2020: 492.

Winge (1887: 29) reported three humeri and a carpometacarpus from Lapa da Escrivânia V, and a carpometacarpus from Lapa da Lagoa do Sumidouro.

## Laridae

### 206. Laridae (*sensu lato*) indet.

Quaternary - Minas Gerais

- G. sp. indet. *Larus* (s. lat.) e minoribus, vel *Sterna* (s. lat.) e majoribus - Winge 1887: 29.
- *Larus* sp. (“kann auch *Sterna* sein”) - Lambrecht 1933: 766.
- *Pseudosterna degener* (?) - Mercerat 1897: 238.
- Laridae (*sensu lato*) indet. - Nascimento & Silveira 2020: 492.

Winge (1887: 29) reported a carpometacarpus lacking the inferior part from Lapa da Escrivânia V, which may have belonged to a large tern or a small gull, noting that it has a shape similar to that of *Rynchops niger*, but it is slightly smaller.



Mercerat (1897: 238) raised the possibility that this material belongs to *Pseudosterna degener* Mercerat (Mercerat 1897), genus and species that he erected for material of the Pleistocene of Argentina (Brodkorb 1967). However, his assumption was based on Winge's texts only. In addition to being represented by different skeletal elements than those known from the larid of the Lagoa Santa region, the type material of both *P. degener* and *P. pampeana* Mercerat, a second species described on the same occasion, were never illustrated and were subsequently lost (Olson 1985b; Mones 1986).

### **207. *Thalasseus* sp.**

Holocene - Rio de Janeiro

- *Thalasseus* sp - Kneip *et al.* 1975: 105.
- *Thalasseus* sp - Kneip 1977: 52.
- *Thalasseus* sp - Souza Cunha *et al.* 1977: 147.

Kneip *et al.* (1975) reported material associated with the genus from Sambaqui do Forte, in Cabo Frio, Rio de Janeiro. It consists of some long bones of the leg and others from the wing.

### **208. *Thalasseus aculavidus eurygnathus* (Saunders)**

Holocene - Rio de Janeiro

- *Sterna eurygnatha* - Kneip *et al.* 1994: 51.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui Moa II (3 pieces of at least one individual), in Saquarema, Rio de Janeiro.

## **Sphenisciformes**

### **Spheniscidae**

### **209. *Spheniscus magellanicus* (Forster)**

Holocene - Rio de Janeiro, Rio Grande do Sul, Santa Catarina

- *Spheniscus magellanicus* - Jacobus *et al.* 1988: 465.
- “Penguin bones” [in part?] - Sick 1993: 119–120.
- “Ossos de pingüins” [in part?] - Sick 1997: 186.

Remains from archeological sites in the country’s southern region were reported by Jacobus *et al.* (1988: 465). At Praia das Laranjeiras site, in Balneário do Camboriú, Santa Catarina, 116 fragments were identified, represented by the front and hind limbs, coracoid, and synsacrum belonging to at least 19 individuals with an age of approximately 1,000 years. At Itapeva site, in Torres, Rio Grande do Sul, 22 fragments were identified, represented by the same bone elements found in Santa Catarina, belonging to at least five individuals, with an approximate age of 4,000 years. Jacobus *et al.* also suggested that, because they are associated with traces of invertebrates and other vertebrates, and there are no traces of skull, these bones are probably the result of human consumption.

Sick (1993: 119, 120; 1997: 186) referenced this study, but mentioning (in Sick 1997) the provenance of the finds as Rio de Janeiro and Santa Catarina (possibly an error?).

- *Spheniscus magellanicus* - Kneip *et al.* 1994: 48.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Beirada II (4 pieces of at least one individual) and Moa I (1 piece), in Saquarema, Rio de Janeiro.

## **Procellariiformes**

### **Diomedeidae**

#### **210. *Thalassarche cf. chlororhynchos* (Gmelin)**

Holocene - Rio de Janeiro

- *Diomedea cf. chlororhynchos* - Kneip *et al.* 1994: 48.
- Diomedeidae (“albatroz”) [*sic*] [in part] - Kneip *et al.* 1995: 7.
- Diomedeidae (“albatroz”) [*sic*] [in part] - Kneip *et al.* 1997: 19, 37.
- Diomedeidae [*sic*] [in part] - Kneip 2001: 7.
- Diomedeidae (“albatroz”) [*sic*] [in part] - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material comparable with the species from the sambaqui of Beirada II (1 piece), in Saquarema, Rio de Janeiro.

## **211. *Thalassarche cf. melanophrys* (Temminck)**

Quaternary - Rio de Janeiro, Rio Grande do Sul

- *Diomedea cf. melanophrys* - Kneip *et al.* 1994: 48.
- Diomadeidae (“albatroz”) [*sic*] [in part] - Kneip *et al.* 1995: 7.
- Diomadeidae (“albatroz”) [*sic*] [in part] - Kneip *et al.* 1997: 19, 37.
- Diomadeidae [*sic*] [in part] - Kneip 2001: 7.
- Diomadeidae (“albatroz”) [*sic*] [in part] - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material comparable with the species from the sambaquis of Beirada I (3 pieces of at least one individual), Beirada II (5 pieces of at least three individual), Beirada III (2 pieces of at least one individual), Beirada IV (2 pieces of at least one individual), and Moa II (6 pieces of at least one individual), in Saquarema, Rio de Janeiro.

- [cf.] *Diomedea melanophrys* [*lapsus*] - Lopes *et al.* 2006a: 45.
- [cf.] *Thalassarche melanophrys* [*lapsus*] - Lopes *et al.* 2006b: 648–650, figs. 2A–C.

Fossils attributable to this species from submerged fossiliferous deposits of late Pleistocene age along the internal continental shelf of the state of Rio Grande do Sul were first described by Lopes *et al.* (2006a) and later with further details by Lopes *et al.* (2006b).

The material consists of the middle part of the diaphysis of a left tibiotarsus LGP-A0002 collected at concheiros, the cervical vertebrae LGP-A0001 collected at farolete da Verga, and LGP-A0003 collected at farol Sarita, all three between 1999 and 2000 during fieldwork in the coastline south of Laguna dos Patos, and the cervical vertebra LGP-A0004 collected in front of Balneário do Cassino in 2003.

The material’s good condition indicates that no significant reworking had taken place from their source sites to the beach and suggests that the submerged deposits are located near the present shoreline. In addition, remains of terrestrial mammalian megafauna, cetaceans, elasmobranchs, teleosts, crustaceans, echinoderms, and mollusks were also found in the same deposits.

## Procellariidae

### 212. *Macronectes giganteus* (Gmelin)

Holocene - Rio de Janeiro

- “Procellariid remains” [in part?] - Sick 1993: 114.
- *Macronectes giganteus* - Kneip *et al.* 1994: 48.
- “Restos de procelarídeos” [in part?] - Sick 1997: 178.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Moa I (1 piece), in Saquarema, Rio de Janeiro.

### 213. *Procellaria aequinoctialis* Linnaeus

Holocene - Rio de Janeiro

- “Procellariid remains” [in part?] - Sick 1993: 114.
- *Procellaria aequinoctialis* [*sic*] - Kneip *et al.* 1994: 48.
- “Restos de procelarídeos” [in part?] - Sick 1997: 178.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Beirada I (3 pieces of at least one individual), Beirada II (2 pieces of at least one individual), Beirada III (5 pieces of at least two individuals), Moa I (1 piece), and Moa II (6 pieces of at least one individual), in Saquarema, Rio de Janeiro.

### 214. *Ardenna grisea* (Gmelin)

Holocene - Rio de Janeiro

- “Procellariid remains” [in part?] - Sick 1993: 114.
- *Puffinus griseus* - Kneip *et al.* 1994: 49.
- “Restos de procelarídeos” [in part?] - Sick 1997: 178.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Beirada II (5 pieces of at least two individuals), in Saquarema, Rio de Janeiro.

### 215. *Ardenna gravis* (O’Reilly)

Holocene - Rio de Janeiro

- “Procellariid remains” [in part?] - Sick 1993: 114.
- *Puffinus gravis* - Kneip *et al.* 1994: 49.
- “Restos de procelarídeos” [in part?] - Sick 1997: 178.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Moa I (1 piece) and Moa II (5 pieces of at least two individuals), in Saquarema, Rio de Janeiro.

## **216. *Puffinus puffinus* (Brünnich)**

Holocene - Rio de Janeiro

- “Procellariid remains” [in part?] - Sick 1993: 114.
- *Puffinus puffinus* - Kneip *et al.* 1994: 49.
- “Restos de procelarídeos” [in part?] - Sick 1997: 178.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui Beirada II (3 pieces of at least one individual), in Saquarema, Rio de Janeiro.

## **Ciconiiformes**

### **Ciconiidae**

#### **217. Ciconiidae indet.**

Quaternary - Bahia

- Ciconiidae - Cartelle & Santos 1985: 140.

Cartelle & Santos (1985) reported a complete ciconiid skeleton among the numerous bird remains of quaternary age from Gruta dos Brejões, in Morro do Chapéu, Bahia.

#### **218. *Ciconia* sp.**

Late Pleistocene - Rio Grande do Sul

- *Ciconia* sp. - Lopes *et al.* 2019: 199–216, figs. 3, 6.

Lopes *et al.* (2019) reported a large ciconiid fossil cervical vertebra from the assemblage of mammalian remains of Santa Vitória Formation, Rio Grande do Sul.

The specimen (MCTFM-PV1090) is similar to that of *Ciconia maguari*, but its larger dimensions suggest that it could be a morphotype of that taxon or represent another extinct one.

## **219. *Ciconia maguari* (Gmelin)**

Holocene - Rio de Janeiro

- *Euxenura maguari* - Kneip *et al.* 1994: 49.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Beirada II (3 pieces of at least one individual), Beirada III (6 pieces of at least 2 individuals), and Pontinha III (2 pieces of at least one individual), in Saquarema, Rio de Janeiro.

## **220. †*Ciconia lydekkeri* (Ameghino)**

Late Pleistocene - Minas Gerais

Figs. 10, 15.B

*Type locality:* The assigned localities are “South America” (Lydekker 1891: 65) and “Brazilian caves” (Ameghino 1891: 445).

*Etymology:* *lydekkeri* honoring British naturalist Richard Lydekker (British Museum (Natural History)).

- *Palaeociconia australis* (Moreno) - Lydekker 1891: 64–65.
- ***Prociconia Lydekkeri*** - Ameghino 1891: 445.
- *Palaeociconia australis* - Lambrecht 1930: 24–25.
- *Palaeociconia australis* (Moreno) - Lambrecht 1933: 321, 735.
- *Jabiru lydekkeri* - Patterson & Kraglievich 1960: 8, footnote.
- *Prociconia lydekkeri* - Brodkorb 1963: 290–291.
- “Lydekker’s stork, *Prociconia lydekkeri*” - HRH The Prince Philip, Duke of Edinburgh & J. Fisher 1970: 193.
- *Prociconia lydekkeri* - Mones 1986: 80.
- *Prociconia lydekkeri* - Cuello 1988: 9.
- *Jabiru lydekkeri* - Alvarenga 1993a: 62.
- *Prociconia lidekkeri* [*lapsus*] - Alvarenga 1993b: 21.
- *Jabiru lydekkeri* - Alvarenga 1997: 21.
- *Ciconia lydekkeri* - Agnolin 2009a: 53–58.
- *Ciconia lydekkeri* - Nascimento & Silveira 2020: 490, fig. 4.

Lydekker (1891) described some fossils from the Lagoa Santa region in the British Museum (Natural History) collection, which were sold to the institution by Peter Claussen. Two fragments, the proximal end of a right tarsometatarsus (NHMUK PV OR 18878; acquired in 1842) and the distal end of a left tarsometatarsus (NHMUK PV OR 18879), were associated with *Palaeociconia australis* Moreno, an Argentinean species described by the paleontologist Francisco Moreno (1889) from a fragmented tarsometatarsus from Monte Hermoso, Buenos Aires, of pliocenic age. Ameghino (1891) did not consider *P. australis* to be a ciconiid (being, in fact, a phorusrhacid [Agnolin 2009a]), from figures of the fossil later published by Moreno & Mercerat (1891) and erected the new genus and species *Prociconia lydekkeri* for the Brazilian material. He also provisionally classified under this name bones of a large fossil bird from the Pampean Formation of Buenos Aires mentioned by Burmeister.

Lambrecht (1930; 1933), who considered this taxon one of the most problematic forms of South American fossil birds, used the name *Palaeociconia australis* and treated *Prociconia lydekkeri* as a synonym. He had no access to Moreno's description of *P. australis*, and therefore believed he described the tarsometatarsi from Lagoa Santa in the British Museum, with Lydekker only depicting one of them. He noted that this material is not identical to that figured later by Moreno & Mercerat, which he thought should be classified in the phorusrhacids.

Patterson & Kraglievich (1960) followed the specific name given by Ameghino, considering the name given by Moreno in 1889 a *nomen nudum* but associated it with the genus *Jabiru* after an examination of the type. However, Brodkorb (1963) used *Prociconia lydekkeri* and found no evidence to place the species in the genus *Jabiru*.

Harrison (1975) proposed that Lydekker's publication constituted validity for the name *Palaeociconia australis* attributed to the material of the Lagoa Santa region, with *Prociconia lydekkeri* being a synonym. Harrison did not seem to have consulted Moreno (1889) (although he included the study in his references) and, like Lambrecht, understood that he described the material from Brazil. According to him, this name given by Moreno in 1889 is a *nomen nudum*, and the date of publication of Lydekker's study precedes that of Moreno & Mercerat (April 25 or "before May 2" versus "May to August 5"). Furthermore, he mentioned that Brodkorb also supported this proposal after reviewing the data. Harrison also referred to this species the distal end of a left femur

(NHMUK PV OR 12878<sup>24</sup>) from the same deposits and collection in the British Museum, pointing affinity to the genus *Mycteria*. This bone and the two others mentioned above are possibly referable to the same specimen (Agnolin 2009a).

Agnolin (2009a) transferred the species to the genus *Ciconia*, considering the description of Ameghino as valid and creating the combination *Ciconia lydekkeri*. During comparison with other fossil storks, he associated with *C. lydekkeri* the distal end of a right humerus of late Pleistocene age present in the collection of the Museo Municipal in Monte Hermoso. He also synonymized *Ciconia maltha* Miller to this species—a comparison already suggested by Brodkorb (1963), originally described in 1910 from a left tarsometatarsus from the late Pleistocene of Rancho La Brea, California, United States. After Miller's description, several other specimens originally associated with *C. maltha* were found, including complete skeletons, with a high degree of variation, in the United States, in Idaho (late Pliocene, middle and late Pleistocene), California and Florida (late Pleistocene), and isolated fragments in Cuba (late Pleistocene of Cienfuegos province) and Bolivia (early–middle Pleistocene of the municipality of Tarija) (Brodkorb 1963; Agnolin 2006b).

The synonymization of the stork of Rancho La Brea with the bird of Lagoa Santa allows us to have a clearer picture of this component of the Brazilian prehistoric avifauna. Agnolin (2006) suggested, when describing the material collected in Bolivia, that, given the age of the fossils, it is likely that the stork came from North to South America during the Great American Interchange. Furthermore, numerous remains of anatids and rallids from the Tarija Formation indicates that the locality was dotted with numerous water bodies.

## **221. *Jabiru mycteria* (Lichtenstein)**

Holocene - Rio de Janeiro

- *Jabiru mycteria* - Kneip *et al.* 1994: 50.
- Ciconidae (“jaburu”) [*sic*] - Kneip *et al.* 1995: 7.
- Ciconiidae (“jaburu”) - Kneip *et al.* 1997: 19, 37.
- Ciconidae (“jaburu”) [*sic*] - Magalhães *et al.* 2001: 59.

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<sup>24</sup> Specimen number given as 12878 by Harrison (1975), but as 18878 by Agnolin (2009a), the same as the proximal end of the right tarsometatarsus.



Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Moa II (3 pieces of at least one individual), in Saquarema, Rio de Janeiro.

## **222. *Mycteria cf. americana* Linnaeus**

Late Pleistocene - Rio Grande do Sul

- Ciconiidae indet. - Ribeiro *et al.* 1995: 107.
- cf. *Ciconia* sp. - Oliveira 1999: 67.
- Ciconiiformes indet. - Hsiou 2007: 23.
- Ciconiiformes indet. - Kerber & Oliveira 2008a: 50, 62.
- *Mycteria cf. M. americana* - Hsiou 2009a: 145–146, fig. 4.
- “ave ciconiforme” - Hsiou 2009b: 335–337, figs. 15–16.
- *Mycteria cf. M. americana* - Kerber *et al.* 2014: 254.

The species is known from a fragment of tarsometatarsus (MCN-PV 1845) lacking the proximal end found in the Barranca Grande locality (Kerber & Oliveira 2008a: 50) of the Touro Passo Formation in the municipality of Uruguaiana, Rio Grande do Sul. It is the state’s first late Pleistocene bird record (Ribeiro *et al.* 1995: 107; Kerber *et al.* 2014: 250).

The fragment was first determined as close to the ciconiids by Ribeiro *et al.* (1995: 107), attributed to cf. *Ciconia* sp. by Oliveira (1999: 67). According to Hsiou (2007: 23; 2009a: 146), it is quite similar to *Mycteria americana*, but due to the poor state of conservation and the absence of more skeleton elements for comparison, a definitive association was not possible.

In the same formation several species of mammals were also found, including large ones, and reptiles, fishes, mollusks, and phytoliths (Kerber & Oliveira 2008a; Kerber *et al.* 2014).

## **Suliformes**

### **Fregatidae**

## **223. Fregatidae indet.**

Holocene - Pernambuco

- “Frigatebirds” - Olson 1981: 483.
- Fregatidae - Alvarenga 1992: 254.

Well-mineralized seabird bones were frequent during collection on dunes on the Santo Antônio peninsula in Fernando de Noronha during Olson’s expedition (1981: 483) in 1973, with an estimated age in the late Holocene (Carleton & Olson 1999: 2). The proximal end of a humerus appears to belong to a small species, comparable in size to that of *Fregata ariel*, which is currently found only in the Atlantic Ocean in the Trindade and Martin Vaz Archipelago (Orta *et al.* 2016), although Olson (1975: 22, 23) noted that subfossils of similar size were found on the island of Santa Helena.

## **Sulidae**

### **224. Sulidae indet.**

Holocene - Pernambuco

- “Boobies” - Olson 1981: 483.

Sulid bones are among the material found by Olson (1981: 483). They possibly belong to the genus *Sula* and the species found today in the islands: *Sula sula*, *Sula leucogaster*, and *Sula dactylatra*.

### **225. *Sula* sp.**

Holocene - Rio de Janeiro

- *Sula* sp - Kneip *et al.* 1975: 105.
- *Sula* sp - Kneip 1977: 52.
- *Sula* sp - Souza Cunha *et al.* 1977: 146.

Kneip *et al.* (1975) reported material associated with the genus from Sambaqui do Forte, in Cabo Frio, Rio de Janeiro. It consists of a distal portion of a femur and a fragment of carpometacarpus, of a bird more robust than the living *Sula* members.

### **226. *Sula leucogaster* (Boddaert)**

Holocene - Rio de Janeiro

- *Sula leucogaster* - Kneip *et al.* 1994: 49.
- Sulidae (“atobá”) - Kneip *et al.* 1995: 7.

- Sulidae (“atobá”) - Kneip *et al.* 1997: 19, 37.
- Sulidae - Kneip 2001: 7.
- Sulidae (“atobá”) - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Beirada II (2 pieces of at least one individual), in Saquarema, Rio de Janeiro.

## Anhingidae

### 227. †Anhingidae indet.

Late Miocene - Amazonas

- Anhingidae - Souza-Filho & Guilherme 2015: 152.
- “birds” [?] - Bissaro-Júnior *et al.* 2019: 65.

Souza-Filho & Guilherme (2015) mentioned anhingid material from the Talismã locality of Solimões Formation in Amazonas, without developing further. Bissaro-Júnior *et al.* (2019) mention bird material from the Talismã locality, though they cite Alvarenga & Guilherme (2003) as the source.

### 228. †Anhinga sp.

Late Miocene - Acre

- *Anhinga* indet. - Bandeira *et al.* 2015: 115.

Bandeira *et al.* (2015) reported a fragmented right tarsometatarsus (DGM 1297-R) from the Cachoeira do Bandeira locality, attributing it to an indeterminate *Anhinga*.

### 229. *Anhinga anhinga* (Linnaeus)

Holocene - Rio de Janeiro

- *Anhinga anhinga* - Kneip *et al.* 1994: 49.
- Phalacrocoracidae (“biguá, biguatinga”) [in part] - Kneip *et al.* 1995: 7.
- Phalacrocoracidae (“biguá, biguatinga”) [in part] - Kneip *et al.* 1997: 19, 37.
- Phalacrocoracidae (“biguá, biguatinga”) [in part] - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Pontinha I (1 piece), in Saquarema, Rio de Janeiro.

### 230. †*cf. Anhinga minuta* Alvarenga & Guilherme

Late Miocene - Acre

- *Anhinga cf. A. minuta* - *Bandeira et al.* 2015: 115.

*Bandeira et al.* (2015) reported a fragmented right humerus (DGM 1168-R) from the Cachoeira do Bandeira locality, referring to it as *Anhinga cf. A. minuta*.

### 231. †*Anhinga minuta* Alvarenga & Guilherme

Late Miocene - Acre

Fig. 16.D

*Type locality:* Cachoeira do Bandeira site, between the Brazilian municipalities of Brasiléia and Assis Brasil, left margin of the Rio Acre, state of Acre, Brazil (about 69° 20' W, 11° 26' S).

*Etymology:* *minuta*, Latin for “small”, referring to its small size.

- “Fósiles de anades” [?; in part?] - *Wall et al.* 1991: 397.
- “Anhingidae extinto” [?; in part?] - *Alvarenga* 1992: 254.
- *Anhinga* sp. [?; in part?] - *Bocquentin & Silva* 1998: 154.
- *Anhinga minuta* - *Alvarenga & Guilherme* 2003: 617-618, figs. 7A, 8A, 9D, 10A.
- *Anhinga minuta* - *Alvarenga & Höfling* 2011: 127.
- *Anhinga minuta* - *Diederle* 2015: 100-101, pl. 1.

This little anhingid, the smallest known member of the family, was described by *Alvarenga & Guilherme* (2003) from fossils from the Cachoeira do Bandeira site (LACM 5158 [*Negri et al.* 2010: 257]).

The material consists of an almost complete left tibiotarsus (UFAC-4720, holotype) and an almost complete left humerus (UFAC-4719) (*Alvarenga & Guilherme* 2003: 617), which show signs of advanced ontogenetic states (*Diederle* 2015: 100).

An estimated height of about 50 cm was mentioned by *Pivetta* (2003: 53). *Diederle* (2015: 207, 210) estimated its body mass at 0.9 kg and wingspan at 91.3 cm. Later, *Diederle* (2016: 290, 291, 294) estimated them at 729 g and 0.958 m, respectively. He used these parameters and others (wing area and load), along with the reconstruction of its musculature, to infer a capacity of flapping flight, alternated with moments of thermal soaring, in addition to the capacity of fast flights in forest areas. The bird would be able to dive efficiently, climb the vegetation and take off from the

water to outwit predators quickly. Their food would mainly consist of small fishes, complemented with invertebrates, amphibians and small reptiles, and their nesting area would be the same as in the living species, on trees (Diederle 2015: 234).

Noriega (1995: 144) reported six isolated humeri in various states of preservation from the “Mesopotamiense”, Ituzangó Formation (late Miocene), in the province of Entre Ríos, Argentina, noting that perhaps they would represent a new species of probably flightless *Anhinga*. Noriega & Agnolin (2008: 277, 278) observed similarities between this material and the referred humerus of *Anhinga minuta*, but, because they have a similar size to that observed in the living *Anhinga anhinga*, they remarked that additional and more complete material would be necessary to a better systematic association of the Argentinean material (which they determined as cf. *Anhinga minuta*) and increase the knowledge about *A. minuta*. Cenizo & Agnolin (2010: 498), in a preliminary reanalysis of this material, found enough differences not to group it with *A. minuta*, preferring to provisionally refer to it as Anhingidae gen. et sp. indet., as proposed by Noriega (1995: 144).

### 232. †*Macranhinga* sp. 1

Late Miocene - Acre

- “undescribed gigantic anhinga from the Miocene of Brazil” [?; in part?] - Campbell (in Mourer-Chauviré 1989): 7.
- “Fósiles de ánaes” [?; in part?] - Wall *et al.* 1991: 397.
- “Anhingidae extinto” [?; in part?] - Alvarenga 1992: 254.
- *Macranhinga* [?; in part?] - Alvarenga 1993b: 21.
- *Anhinga* sp. [?; in part?] - Bocquentin & Silva 1998: 154.
- *Anhinga* cf. *grandis* - Alvarenga & Guilherme 2003: 618, fig. 9E.
- *Anhinga grandis* [in part?] - Alvarenga & Höfling 2011: 127.
- *Macranhinga* sp. [in part] - Diederle 2015: 131–132, pl. 9 (9–11).

Alvarenga & Guilherme (2003) described several anhingid remains from the Solimões Formation (late Miocene) from two localities in the state of Acre.

The well-preserved distal end with the axis of a right humerus (UFAC-4721) was reported from the Cachoeira do Bandeira site (LACM 5158 [Alvarenga & Guilherme 2003: 618; Negri *et al.* 2010: 257]), of which Alvarenga & Guilherme noted

to be larger than the specimen they attributed to *Anhinga* cf. *fraileyi* (see below) and match in size and almost completely in morphology with a replica of the *Anhinga grandis* holotype, a species described from the late Miocene of Nebraska (United States) (Martin & Mengel 1975), with records in Florida (Becker 1987) and a disputed from the middle Miocene of Colombia (Rasmussen & Kay 1992; referred to as Anhingidae gen. et sp. indet. by Cenizo & Agnolin [2010: 499]). Diederle (2015: 131, 132) reexamined the humerus and associated it with the genus *Macranhinga*.

### 233. †*Macranhinga* sp. 2

Late Miocene - Acre

- “nova espécie de *Anhinga*” - Bocquentin & Janoo 1997: 111.
- *Anhinga* sp. [?; in part?] - Bocquentin & Silva 1998: 154.
- *Anhinga* sp. nov. - Kellner 1998: 654, 659.
- *Anhinga* cf. *fraileyi* - Alvarenga & Guilherme 2003: 618, figs. 9C, 10B.
- *Anhinga fraileyi* - Bocquentin & Melo 2006: 188.
- *Macranhinga fraileyi* [in part] - Cenizo & Agnolin 2010: 498.
- *M.* sp. cf. *M. fraileyi* - Cenizo & Agnolin 2010: 506.
- *Anhinga fraileyi* [in part?] - Alvarenga & Höfling 2011: 127.
- *Anhinga fraileyi* - Kachniasz & Silva-Caminha 2013: 128.
- *Macranhinga* sp. [in part] - Diederle 2015: 131–132, pl. 9 (14–15).

Alvarenga & Guilherme (2003: 618) reported a left humerus lacking part of the distal end (UFAC-4562) from the Cachoeira do Bandeira site (LACM 5158 [Negri *et al.* 2010: 257]), most likely the same<sup>25</sup> found in 1996 in a very compact conglomerate on the left bank of the Rio Acre and mentioned by Bocquentin & Janoo (1997: 111) as representing a new species of *Anhinga*.

The specimen has a size and aspect consistent with a humerus referred to as *Anhinga fraileyi* by Campbell (1996), but Alvarenga & Guilherme (2003: 618) noted that the attribution of any of these humeri to the same species as the *A. fraileyi* holotype tarsometatarsus is not recommended due to the number of anhingid species present in this outcrop.

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<sup>25</sup> Based on the fact that it is a humerus from the same locality, with the proximal end present and larger than that observed in *Anhinga anhinga* (the provided measurements are approximate). Several mentions of fossil anhingids from Acre have been made in the literature prior to Alvarenga & Guilherme (2003), but without specifications. These mentions are present, with question marks, in the synonyms of the records reported here.

Campbell (1996) described this large form (represented by the tarsometatarsus, humerus, ulna, tibiotarsus, and cervical vertebrae) from the late Miocene of the Peruvian Amazon, preferring not to erect a new genus. Noriega & Alvarenga (2002: 47), through phylogenetic analysis, raised the possibility that *A. fraileyi* belonged to the genus *Macranhinga*, preferring to maintain its current status until new, more preserved fossils are discovered. This possibility was also reinforced by Noriega & Agnolin (2008: 275), and Cenizo & Agnolin (2010: 494, 498) mentioned it as *Macranhinga fraileyi*, including the Brazilian material. Diederle (2015: 106, 107, 148, 149; 2017: 344, 345, 346) re-examined the *A. fraileyi* material, suggesting that the species is a junior synonym of *Macranhinga paranensis* (and part of the associated elements as an indeterminate anhingid), expanding its geographic distribution significantly. As for the Brazilian material, he associated it with the genus *Macranhinga* (Diederle 2015: 131, 132).

### 234. †*Macranhinga ranzii* Alvarenga & Guilherme

Late Miocene - Acre, Amazonas

Fig. 16.E

*Type locality*: Niterói site, about 20 km south of the municipality of Rio Branco, right margin of Rio Acre, state of Acre, Brazil (about 68° W, 10° 30' S).

*Etymology*: *Macranhinga*, with the Greek *makros*, “large anhinga”, and *ranzii* honoring Alceu Ranzi, for his dedication to the paleontology in the state of Acre.

- “undescribed gigantic anhinga from the Miocene of Brazil” [?; in part?] - Campbell (in Mourer-Chauviré 1989): 7.
- “Fósiles de ánaes” [?; in part?] - Wall *et al.* 1991: 397.
- “Anhingidae extinto” [?; in part?] - Alvarenga 1992: 254.
- “dos formas muy grandes de Brasil (K. E. Campbell, com. pers.) y Chile (Alvarenga, 1992)” [?; in part] - Noriega 1992: 218.
- *Macranhinga* [in part?] - Alvarenga 1997: 122.
- *Anhinga* sp. [?; in part?] - Latrubesse *et al.* 1997: 112.
- *Anhinga* sp. [?; in part?] - Bocquentin & Silva 1998: 154.
- *Macranhinga ranzii* - Alvarenga & Guilherme 2003: 614–616, figs. 2A, 2C, 3A, 4A, 5A, 6A.
- *Macranhinga ranzi* [*sic*] - Alvarenga & Höfling 2011: 127.
- *Macranhinga ranzii* [in part] - Diederle 2015: 113–114, pl. 4.
- Anhingidae indet [in part] - Diederle 2015: 122–126, pl. 7 (3–6, 11–12, 21–22).
- ?Anhingidae [in part] - Diederle 2015: 130, pl. 8.

Alvarenga & Guilherme (2003: 614, 615, 616) described this large species from the Niterói site (LACM 5954 [Negri *et al.* 2010: 258]).

The material consists of a left femur lacking the distal end (UFAC-3640, holotype), a deformed right femur lacking the distal end (UFAC-4034, paratype), a well-preserved right femur (UFAC-4860, paratype), the distal end of a right tarsometatarsus lacking the lateral trochlea (UFAC-3523) and four vertebrae representing the ninth cervical (UFAC-4108), the fourteenth (UFAC-2212), the fifteenth (UFAC-3522), and the twentieth (UFAC-2235) (Alvarenga & Guilherme 2003: 614). The association of the referred material was questioned by Diederle (2015: 114, 122, 124, 125, 130), who considered the vertebrae to be an indeterminate anhingid and the tarsometatarsus as of doubtful attribution to the Anhingidae family.

When described, this taxon received the title of the largest known anhinga until then (Alvarenga & Guilherme 2003: 614), a title currently belonging to cf. *Giganhinga*, from the late Miocene of Argentina (Areta *et al.* 2007; Mayr 2016: 183). In any case, the fossils indicate a very large anhingid, with an estimated weight of 7.8 kg (Areta *et al.* 2007: 344) or 8.8 kg (Diederle 2015: 207, 209), and size between 20 and 25% larger than the giant *Macranhinga paranensis* (Alvarenga & Guilherme 2003: 614; or 34% larger in mass, according to Diederle [2015: 209]), genus and species described from the Ituzaingó Formation (late Miocene) in the province of Entre Ríos, Argentina (Noriega 1992). A height estimate of 1.5 m was mentioned by Pivetta (2003: 53). A third, smaller species, *Macranhinga ameghinoi*, was described from the middle Miocene of the province of Río Negro (Diederle & Agnolin 2017: 1058), and remains attributed to the genus were reported from the early/middle Miocene of the province of Santa Cruz, Argentina (Cenizo & Agnolin 2010).

Diederle (2015: 234, 290) suggested that its large size allowed prolonged dives in greater depths, with stronger strokes (but not more than the phalacrocoracids) and capturing larger prey than the living aningas do, competing for these resources with gharials or cetaceans. The bird would inhabit both the upper and lower parts of large rivers basins and possibly nest in the ground on small islands or islets, safe from predators.



Noriega & Agnolin (2008: 277) associated with *M. ranzii* the proximal end of a left femur (MACN PV 14371), from the “Mesopotamiense”, Ituzangó Formation (late Miocene) in the province of Entre Ríos, Argentina, being the first record of the species outside Brazil.

A close relationship between the genera *Macranhinga*, *Meganhinga* (with *Meganhinga chilensis* of the early Miocene of Chile [Alvarenga 1995a]) and *Giganhinga* (with *Giganhinga kiyuensis* of the Pliocene/Pleistocene of Uruguay [Rinderknecht & Noriega 2002]) was suggested by Diederle & Agnolin (2017: 1062; see also Agnolin 2016b: 166). Guilherme *et al.* (2020) found two equally probable evolutionary hypotheses, none of them with a monophyletic *Macranhinga*, as *G. kiyuensis* was recovered as a sister species of *M. ranzii*. In one of these scenarios, *M. chilensis* was recovered as the sister species of the (*Macranhinga* + *Giganhinga*) clade.

- Aves - Loboda *et al.* 2019: 136.
- *Macranhinga ranzii* - Guilherme *et al.* 2020: 3091–3100, figs. 2–5.

Guilherme *et al.* (2020) tentatively attributed to this taxon new material from the Cajueiro locality, municipality of Boca do Acre, Amazonas. It consists of a virtually complete pelvic girdle articulated with the synsacrum (UFAC-6471), with a surprisingly well-preserved surface. Such elements were unknown for the species. The fossil was recovered in two pieces, with the cranial portion free from the rock over the sediments and the other half in situ partially exposed within the rock, and were then glued together in the laboratory. With this new element, a mean weight of 8.6 kg was inferred for the species, making the species the second heaviest anhingid known from South America, after *G. kiyuensis* with 25.7 kg. Behavioral information was also inferred, with morphological and myological data indicating the taxon was a proficient swimmer and diver.

## **Phalacrocoracidae**

### **235. Phalacrocoracidae indet.**

Late Oligocene/Early Miocene - São Paulo

- Phalacrocoracidae - Alvarenga (in Castro *et al.* 1988b): 2360.
- Phalacrocoracidae - Alvarenga 1993a: 63.

- *Phalacrocoracidae* - Alvarenga 1993b: 24.
- *Phalacrocoracidae* - Alvarenga 1997: 123.

Among the remains of poorly preserved birds from the Taubaté Basin, which await the discovery of new specimens for further study, are the remains of phalacrocoracids (Alvarenga [in Castro *et al.* 1988b: 2360]; Alvarenga 1993b: 24; 1997: 123).

### **236. *Nannopterum* sp.**

Quaternary - Goiás

- *Phalacrocorax* indet - Paulo 2009: 142.

Paulo (2009: 142) reported the genus *Phalacrocorax* [= *Nannopterum*] to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

### **237. *Nannopterum brasilianum* (Gmelin)**

Quaternary - Minas Gerais, Rio de Janeiro

- *Phalacrocorax brasilianus* - Winge 1887: 31.
- *Phalacrocorax brasilianus* - Lambrecht 1933: 733.
- *Phalacrocorax olivaceus* - Brodkorb 1963: 255.
- *Phalacrocorax olivaceus* (“*Phalacrocorax brasilianus*”) - Mones 1986: 78.
- *Phalacrocorax olivaceus* - Cuello 1988: 30.
- *Nannopterum brasilianus* - Nascimento & Silveira 2020: 491.

Winge (1887: 31) reported the distal end of a humerus and remains of a pelvis from Lapa da Lagoa do Sumidouro, and part from another pelvis from Lapa da Escrivânia V, noting that these two specimens present some differences between them and a fresh specimen, being most likely individual variations.

- *Phalacrocorax olivaceus* - Kneip *et al.* 1994: 49.
- *Phalacrocoracidae* (“biguá, biguatinga”) [in part] - Kneip *et al.* 1995: 7.
- *Phalacrocoracidae* (“biguá, biguatinga”) [in part] - Kneip *et al.* 1997: 19, 37.
- *Phalacrocoracidae* - Kneip 2001: 7.
- *Phalacrocoracidae* (“biguá, biguatinga”) [in part] - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Beirada I (5 pieces of at least two individual), in Saquarema, Rio de Janeiro.

## **Pelecaniformes**

### **Ardeidae**

#### **238. Ardeidae indet.**

Late Oligocene/Early Miocene - São Paulo

- Ardeidae - Castro *et al.* 1988b: 2362.

Castro *et al.* (1988b: 2362) mentioned the occurrence of the Ardeidae family among the paleofauna of the Tremembé Formation. However, the summary of bird records from the Formation provided in the same publication (Castro *et al.* 1988b: 2360), derived from the literature and information provided by Herculano Alvarenga, does not include mention of this family.

#### **239. *Ixobrychus exilis erythromelas* (Vieillot)**

Quaternary - Minas Gerais

- *Ardetta erythromelas* et aff. - Winge 1887: 30–31.
- *Ardetta erythromelas* - Lambrecht 1933: 734.
- *Ixobrychus exilis* - Brodkorb 1963: 285.
- *Ixobrychus exilis* (“*Ardetta erythromelas*”) - Mones 1986: 80.
- *Ixobrychus exilis* - Cuello 1988: 32.
- *Ixobrychus exilis erythromelas* - Nascimento & Silveira 2020: 491.

Winge (1887: 30, 31) reported two tarsometatarsi from Lapa da Escrivânia V, one of them corresponds well with that of *Ixobrychus exilis erythromelas*, being slightly more robust, and the other is somewhat smaller and markedly different. He also reported a first phalanx of the left hallux, slightly shorter than in *I. e. erythromelas*, but with the proximal end a little more robust; two tibiotarsi, of which one is slightly smaller and different when compared to that of *I. e. erythromelas*; an incomplete humerus, but which corresponds well to that of *I. e. erythromelas*; two cervical vertebrae, much smaller than in *Butorides striata*, being most likely from *Ixobrychus*; a coracoid, similar to that of *Butorides*, but smaller and relatively longer and slender; a femur, longer and thinner and different in several aspects from that of *B. striata*; and the proximal end of another femur, not much smaller than in *B. striata*, which may belong to another species

than the other bones, perhaps even *B. striata*. Winge noted that *Ixobrychus exilis* and *Ixobrychus (exilis) erythromelas* bones from skins were available for comparison.

## Threskiornithidae

### 240. *Theristicus* sp.

Quaternary - Minas Gerais

- *Ibis (Theristicus)* sp.; *melanopsis* v. *caudata*?; *coerulescens*? - Winge 1887: 29–30.
- *Ibis (Theristicus)* sp. (“*melanopsis* var. *caudata* oder *coerulescens*”) - Lambrecht 1933: 735.
- *Theristicus caudatus* - Brodkorb 1963: 279.
- *Theristicus caudatus* (“*Ibis (Theristicus)* sp.”) - Mones 1986: 80.
- *Theristicus caudatus* - Cuello 1988: 33.
- *Theristicus* sp. - Nascimento & Silveira 2020: 491.

Winge (1887: 29, 30) reported several bones of a considerable number of individuals from Lapa da Escrivânia V, most of them young birds—indicating that they probably nested in the area—from fully formed bones to fragments of difficult recognition, which he considered to belong to this taxon with a certain degree of uncertainty. The material is represented by the scapula, coracoid, humerus, ulna, radius, carpometacarpus, first phalanx of the second digit of the wing, femur, tibiotarsus, and tarsometatarsus. There is also the coracoid of an adult individual from Lapa da Escrivânia XI.

Winge noted the bones are different in many ways from *Plegadis chihi*, *Platalea leucorodia*, and *Platalea ajaja*. They are very similar to *Phimosus infuscatus* but much larger and somewhat smaller than in an exceptionally large young specimen of *Theristicus melanopsis*, but, besides this, almost completely the same. However, the humerus in *T. melanopsis* is slightly different from the cave material and *P. infuscatus* (of which two specimens showed variations between them).

From the size, Winge considered that the material could belong to *Theristicus melanopsis*, *Theristicus caudatus*, *Theristicus caerulescens*, or *Cercibis oxycerca*, and hardly to *Mesembrinibis cayennensis*. Due to the morphological differences between the material and *T. melanopsis*, *T. caerulescens* was considered, but this species, like *T. melanopsis* and *C. oxycerca*, does not occur (at least nowadays) in the region (Matheu *et*

al. 2017a; 2017b; 2017c), and, probably due to this, Brodkorb (1963: 279) listed the record as *T. caudatus*.

## **241. *Theristicus caudatus* (Boddaert)**

Quaternary - Piauí

- Plataleidae (*Ibis*) - Guérin *et al.* 1993a: 198.
- Plataleidae (*Ibis*) - Guérin *et al.* 1993b: 328.
- *Theristicus caudatus* - Guérin *et al.* 1996: 84.
- *Theristicus caudatus* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material. This is one of the taxa that the authors highlighted as no longer living in the region today.

## **Cathartiformes**

### **Cathartidae**

## **242. Cathartidae indet. 1**

Quaternary - Minas Gerais

Fig. 9.G–I

- “un *Cathartes* plus grand que les espèces actuelles” [?] - Gervais 1844a: 294.
- “des *Urubus* (*Cathartes* d’Illiger)” [?] - Liais 1872: 303.
- *Cathartes* aff. *papa* [in part] - Lund (in Winge 1887): 32.
- *Gyparchus* sp. forma magna; *Gyparchus papa* et aff. (v. sim.) [”Knogler af en Form, der er meget større end *Gyparchus papa* og maaske er en egen Art”] - Winge 1887: 14, 32.
- *Gypagus papa* [in part] - Lambrecht 1933: 744.
- *Sarcoramphus papa* (?) [in part] - Brodkorb 1964: 257.
- *Sarcoramphus papa* (“*Gyparchus papa*”) [in part] - Mones 1986: 83.
- *Sarcoramphus papa* [in part] - Cuello 1988: 37.
- Cathartidae indet. 1 - Nascimento & Silveira 2020: 491.

Along with the description of remains that he associated with *Sarcoramphus papa*, Winge (1887: 32) described in detail three quite altered fragments in a way that could represent a distinct species or even genus, much larger than *S. papa*, but smaller than

*Vultur gryphus*. The bones, coming from Lapa da Escrivânia I, seem to belong to the same individual. They are the proximal end of a right humerus that is quite incomplete and partially covered with incrustations (“*Cathartes* aff. *papa*” in Lund’s catalog), the proximal end of an ulna, also quite incomplete and partially covered with hardened sediment, and a coracoid in two parts, relatively shorter and more robust than in *S. papa*, of which the finding site was not informed, but apparently has the same origin.

Winge (1887: 32) noted that he was not sure whether these bones belong to an exceptionally large *S. papa*, a large extinct race, or a vanished species, but that several factors point to the latter, and, in this case, it would represent a genus of cathartid other than *Sarcoramphus*. Alvarenga *et al.* (2008: 617) commented that the bones found in Lapa da Escrivânia were cleaned and re-prepared by Storrs Olson and Steven Emslie, but that they do not show structures preserved enough for a taxonomic diagnosis, and they may belong to the genus *Pleistovultur*, found in the same region.

These fossils were also mentioned by Lönnberg (1902) when he described a tarsometatarsus and an incomplete femur of a fossil cathartid from the Pleistocene of Tarija valley, Bolivia under the name *Sarcoramphus patruus* Lönnberg (*Sarcoramphus* here as a synonym of *Vultur*). Regarding the possible relation between the remains from Brazil with the ones from Bolivia, he commented (1902: 8): “Whether this can be identical to the fossil condor of Tarija, or not, it cannot be decided, since unfortunately only remains of the bones of the Brazilian bird’s wing, such as the Inspector H. Winge kindly told me. The size seems, he said, however, to match up considerably well. But if the Brazilian bird was a real *Gyparchus* [= *Sarcoramphus*], as I suppose it was, when that judgment was pronounced by an ornithologist as capable as Mr. [Oluf] Winge, it could not, for the reasons mentioned above [differences of morphology and size], be identical with the fossil condor of Tarija”. In the face of the association of a fossil ulna from the Lagoa Santa region to *S. papa* by Lydekker (1891; see below), Lönnberg also commented that, although rather scanty, it is right to consider, based on these authorities, the bones from the caves of Brazil as true *Sarcoramphus*. Agnolin *et al.* (2017a) recently assessed the Bolivian material, considering it a valid taxon with an uncertain generic position.

## 243. †*Cathartidae* indet. 2

Quaternary - Bahia

- *Vulturidae* gen. et sp. indet. - Alvarenga *et al.* 2008: 613–618, fig. 3.

Alvarenga *et al.* (2008), in the same study *Pleistovultur nevesi* was presented, described the distal end of a left tibiotarsus found by Cástor Cartelle in Gruta dos Brejões, Morro do Chapéu, Bahia, the same site where *Wingegyps cartellei* type specimen was found.

Because the specimen's condyles were considerably damaged, an accurate diagnosis of its identity was not possible. After a comparative study, the possibility of the specimen belonging to *Vultur*, *Gymnogyps*, *Breagyps*, *Sarcoramphus*, *Geronogyps*, and *Pleistovultur* was excluded, despite the size being relatively close to the last, where Alvarenga *et al.* (2008: 617) believed that it does not belong to any known genus in the family. However, a new name was not raised in favor of the surfacing of better material for study. The specimen, identified as MCL-A-1795, is deposited in the collection of the Museu de Ciências da Pontifícia Universidade Católica de Minas Gerais.

## 244. *Sarcoramphus papa* (Linnaeus)

Quaternary - Minas Gerais

Fig. 8.G–L, 9.E–F

- *Cathartes* aff. *papa* [in part] - Lund (in Winge 1887): 32.
- *Gyparchus papa*, typicus; *Gyparchus papa* et aff. (v. sim.) [”Knogler, der passe til *Gyparchus papa*”] - Winge 1887: 14, 32–33.
- *Gypagus papa* [in part] - Lambrecht 1933: 744.
- *Sarcoramphus papa* [in part] - Brodkorb 1964: 257.
- *Sarcoramphus papa* (“*Gyparchus papa*”) [in part] - Mones 1986: 83.
- *Sarcoramphus papa* [in part] - Cuello 1988: 37.
- *Sarcoramphus papa* - Nascimento & Silveira 2020: 491.

Winge (1887: 32, 33) reported remains of two individuals from Lapa do Baú. One of them, of which most elements were identified as “*Cathartes* aff. *papa*” in Lund's catalog, the maxilla, jugal arches, tip of the mandible, part of the anterior portion of the sternum, scapula, humerus, ulna, radius, and carpometacarpus were found. They correspond well with fresh bones of the species, presenting only small variations, of which the most notable is the more robust ulna. Of the other individual, only the

fragmented remains of the proximal end of left humerus and the distal end of the right tibiotarsus were found, slightly larger than in fresh bones, where the humerus also presents some variations, especially in the much thicker head.

- *Gypagus papa* - Lydekker 1891: 34.

Lydekker (1891: 34) associated with this species the proximal end of a left ulna (NHMUK PV OR 18887), indistinguishable from that of fresh skeletons. It came from the Lagoa Santa region and was acquired by the British Museum (Natural History) in 1848 as part of the Claussen Collection.

## **245. *Coragyps atratus* (Bechstein)**

Quaternary - Minas Gerais

- *Catharistes atratus* - Winge 1887: 31, fig. 8.
- *Catharistes urubu* [in part] - Lambrecht 1933: 744.
- *Coragyps atratus* [in part] - Brodkorb 1964: 257.
- *Coragyps atratus* (“*Catharistes atratus*”) - Mones 1986: 82–83.
- *Coragyps atratus* - Cuello 1988: 36–37.
- *Coragyps atratus* - Nascimento & Silveira 2020: 491.

Winge reported bones of several individuals from Lapa da Escrivânia V, young and adults, and more bones from Lapa da Lagoa do Sumidouro, apparently from a single individual. The material is represented by the quadrate, coracoid, humerus, ulna, carpometacarpus, first phalanx of the second digit of the wing, femur, tibiotarsus, tarsometatarsus, and first phalanx of the third digit of the foot. Winge noted that *Coragyps atratus* and *Cathartes aura* could be easily distinguished in most bones.

## **246. *Cathartes aura* (Linnaeus)**

Quaternary - Minas Gerais, Rio de Janeiro

- *Cathartes aura* - Winge 1887: 31.
- *Cathartes aura* - Lambrecht 1933 : 744.
- *Cathartes aura* - Brodkorb 1964: 257.
- *Cathartes aura* - Mones 1986: 82.
- *Cathartes aura* - Cuello 1988: 36.
- *Cathartes aura* - Nascimento & Silveira 2020: 491.



Winge (1887: 31) reported some apparently related bones from Lapa da Escrivânia V, some bones (possibly from the same individual) from Lapa da Escrivânia XI, and two tarsometatarsi from Lapa da Lagoa do Sumidouro, from an adult and a young specimen. The total material is represented by the scapula, coracoid, humerus, ulna, carpal<sup>19</sup>, tibiotarsus, and tarsometatarsus.

- *Cathartes aura* - Kneip *et al.* 1994: 50.

Kneip *et al.* (1994) reported material associated with the species from the sambaqui of Beirada II (2 pieces of at least one individual), in Saquarema, Rio de Janeiro.

## **247. *Vultur gryphus* Linnaeus**

Early Holocene - Minas Gerais

- “Condor remains” - Alvarenga (in Sick 1993): 150.
- “restos do condor” - Alvarenga (in Sick 1997): 223.
- *Vultur gryphus* - Alvarenga 1998: 60–63, figs. 2–3.
- *Vultur gryphus* - Nascimento & Silveira 2020: 491.

Alvarenga (1998) associated a premaxilla (MNRJ-A-LV-82) discovered by the Franco-Brazilian Archeological Mission (1971–1976) in Lapa Vermelha IV, in Confins, Minas Gerais with *Vultur gryphus*, a species never positively recorded in Brazil (Pacheco *et al.* 2021). He previously alluded to it briefly in Sick (1993: 150; 1997: 223).

Alvarenga commented that the presence of *V. gryphus* at the beginning of the Holocene in Minas Gerais might indicate that the region’s climate was colder, with strong wind currents that would facilitate its takeoff and flight maintenance, or even that its distribution during this time reached the east coast of the continent broadly. The sediments where the bone was found are 10,220–11,680 years old.

Agnolin (2016b), Agnolin *et al.* (2016), and Agnolin *et al.* (2017), reviewing the fossil records associated with *V. gryphus*, restricted their occurrence to the late Pleistocene of northwestern Peru and southern Chile. They noted that, although the Brazilian specimen is similar to the species, its fragmentary nature and the lack of knowledge on the morphology of the beak in most South American fossil condors

prevent its determination, and it is not unlikely that it may belong to *Pleistovultur nevesi*, found in a nearby site (see below).

## 248. †*Brasilogyys faustoi* Alvarenga

Late Oligocene/Early Miocene - São Paulo

Fig. 13.C

*Type locality*: Sedimentary Taubaté Basin: municipality of Tremembé, state of São Paulo, Brazil.

*Etymology*: *Brasilogyys*, with the Greek *gyys*, “Brazilian vulture”, and *faustoi* honoring the Brazilian paleontologist Fausto Luiz de Souza Cunha (1926–2000) (MN), for his work done in the Taubaté Basin and support given to the author’s research.

- *Brasilogyys faustoi* - Alvarenga 1985b: 349–357, figs. 1–2, 3A, 4, 5A, 6C, 7A.
- *Brasilogyys faustoi* - Mones 1986: 82.
- *Brasilogyys faustoi* - Cuello 1988: 11.
- *Brasilogyys faustoi* - Alvarenga 1993a: 62.
- *Brasilogyys faustoi* - Alvarenga 1997: 123.
- *Brasilogyys faustoi* - Kellner 1998: 654, 659.
- *Brasilogyys faustoi* - Alvarenga & Höfling 2000: 589.
- *Brasilogyys faustoi* - Alvarenga & Höfling 2004: 827.
- *Brasilogyys faustoi* - Alvarenga & Höfling 2011: 127.

Alvarenga (1985b) described the genus and species *Brasilogyys faustoi* from two associated bone fragments collected in January 1978, in the montmorillonite clay layer of Fazenda Santa Fé, in Tremembé.

The material (MNRJ-4045-V, holotype) comprises the distal end of a right tibiotarsus with a significantly worn extremity and the proximal end of a right tarsometatarsus. The study of this material showed that it is related to the genus *Coragyys*, being slightly larger and more robust than *Coragyys occidentalis*, from the Quaternary of North America, which was larger than the living *Coragyys atratus* (Alvarenga 1985b: 350, 355; Brodkorb 1964: 254, 255).

Its age and geographical origin are valuable for understanding the evolution of cathartids (Alvarenga 1985b: 350). It is the oldest known cathartid for South America (Alvarenga 1993b: 22; 1997: 123; Alvarenga *et al.* 2008: 613; Tambussi & Degrange 2013: 43; Mayr 2016: 200), or even in the Americas as a whole, if *Phasmagyys patritus*,

from the Eocene of Colorado is, in fact, not a member of the family, as noted by Olson (1985b: 191) about its problematic systematic position.

## 249. †*Wingegyps cartellei* Alvarenga & Olson

Quaternary - Bahia, Minas Gerais

Figs. 9.J–M, 15.C

*Type locality*: Brazil, Bahia State, Município de Morro do Chapéu, Gruta dos Brejões (11°00'30''S, 41°26'07''W), elevation ca. 600m.

*Etymology*: *Wingegyps*, with the Greek *gyps*, “Winge’s vulture”, honoring Oluf Winge for his perspicacity in recognizing the distinctiveness of the fossils, and *cartellei* honoring the Spanish-Brazilian paleontologist Cástor Cartelle (Universidade Federal de Minas Gerais), in recognition of his excavations at Gruta dos Brejões and his contributions to Brazilian paleontology.

- *Cathartes* - Lund (in Winge 1887): 33.
- G. sp. indet. magnitudine *Catharistæ atrati* - Winge 1887: 33–34, fig. 7.
- *Cathartidarum* gen. sp. indet. - Lambrecht 1933: 397.
- Gen. sp. indet. - Lambrecht 1933: 744.
- *Catharistes urubu* (?) [in part] - Lambrecht 1933: 744.
- *Cathartidarum* - Fisher 1944: 294.
- *Coragyps atratus* (?) [in part] - Brodkorb 1964: 257.
- *Wingegyps cartellei* [in part] - Alvarenga & Olson 2004: 1–9, figs. 3–4.
- *Wingegyps cartellei* [in part] - Alvarenga & Höfling 2011: 127.
- “*Wingegyps* (Amazonian Vulture)” - Campbell 2016: 120–121.
- *Wingegyps cartellei* - Nascimento & Silveira 2020: 491, figs. 5A–C.

Winge (1887: 33, 34) described in detail two fragments of similar aspect (determined as “*Cathartes*” in Lund’s catalog), the distal end of a right humerus (ZMUC 1116), and the proximal end of a right ulna (ZMUC 1118) from Lapa do Tiú<sup>26</sup>. They are different from the known living cathartids, but Winge did not attribute them to a new genus or species, referring to them just as a bird of similar size to *Coragyps atratus*. An illustration of the humerus was included, in which it was compared with a fossil humerus of *C. atratus* also found by Lund.

Before the description by Alvarenga & Olson (see below), there was some confusion regarding how this material was referred to. Lambrecht (1933: 397)

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<sup>26</sup> We were not able to find this site’s location. It is not the site with the same name in the municipality of Lassance, Minas Gerais, about 260 km from Lagoa Santa.

mentioned the humerus fragment from Lapa to Tiú described by Winge as “Cathartidarum gen. sp. indet.” (“undetermined cathartid genus and species”) and even listed unrelated material from France with a similar provisional term (“Cathartidarum gen. inc.”). Posteriorly, the same material from the Lagoa Santa region was mentioned as “Gen. sp. indet.” of Cathartidae in the same study (Lambrecht 1933: 744). The first term, however, was used as a genus by Fisher (1944: 294), who wrote “*Cathartidarum* is the genus erected for a Pleistocene humerus from Lagoa Santa, Brazil, by Winge (1888)” and “It is about the size of ‘*Cathartes atratus*’”. Although he did not cite Lambrecht’s study, the mentioned information is the same found in it. He also noted (Fisher 1944: 295) that, if it is a valid genus, “it is the oldest member of the King Vulture group, and is probably a close relative of *S. papa*”. Fisher based his assumption of affinity on Miller (1931: 71), who only noted that one species close to the king vulture was found in Brazilian Pleistocene cave deposits. Miller did not specify which cathartid remains Winge described he was referring to, but it was likely the fossils determined as *Gyparchus papa* et aff. (v. sim.) and not to the material mentioned by Lambrecht. Tordoff (1959) kept the name used by Fisher, maintaining the same interpretation of Miller’s text, although he noted that he did not consult Winge’s work. The name was also kept in publications (Wing 1956: 157; Stager 1964: 6) that reused the phylogenetic tree presented by Fisher. Despite predating *Wingegyps*, the circumstances in which Fisher used the name as a genus for the humerus found in Minas Gerais are not valid according to the norms of the International Commission on Zoological Nomenclature (2000: Art. 13.3). Emslie (1988: 223) mentioned “*Cathartidarum*” as a “species” that is no longer considered a member of the family when commenting on the use of fossil species in systematics analysis of Cathartidae (including Fisher’s).

- *Wingegyps cartellei* [in part] - Alvarenga & Olson 2004: 1–9, figs. 1–4.
- *Wingegyps cartellei* [in part] - Alvarenga & Höfling 2011: 127.

Alvarenga & Olson (2004), while identifying bird bones from Gruta dos Brejões, municipality of Morro do Chapéu, Bahia, noticed an ovoid-shaped skull similar to that of *Gymnogyps*, but much smaller, and two humeri, probably belonging to the same species as the skull, of which a well-preserved distal fragment appeared to be identical to the specimen illustrated in Winge’s study. The reanalysis of the bones discovered by

Lund confirmed that this is indeed a new genus and species, and, with the inclusion of the material from Bahia, the genus and species *Wingegyps cartellei* Alvarenga & Olson were erected. The age of the material from Bahia was estimated at about 12,200 years BP based on that of a giant sloth coprolite found in the same locality and associated mammalian megafauna found in the caves of Bahia and Minas Gerais (Alvarenga & Olson, 2004: 3).

The material found in Bahia comprises an incomplete neurocranium (MCL CLA782, holotype), a complete but much worn left humerus (MCL CLA670), and one third of a distal end of another left humerus (MCL CLA1678).

The species is closer to condors, especially *Gymnogyps*, than to the smaller genera of the family (i.e., *Cathartes* and *Coragyps*), which are basically differentiated by skull morphology (Alvarenga & Olson 2004). However, it is much smaller than any known condor and slightly smaller than the smallest living species of the family, the vulture *Cathartes burrovianus* Cassin (Alvarenga & Olson 2004: 4), with length from the tip of the beak to the end of the tail estimated in 50 cm and wingspan in 130 cm (Pivetta, 2003: 54). Its description attests to the greater diversity of condor sizes in the past (Alvarenga & Olson 2004: 6).

Its distribution range was probably much wider than the extent of the two geographical points from where its remains are known. If its remains were collected in any other deposit, possibly they were treated as *Cathartes* or *Coragyps* due to its reduced size (Alvarenga & Olson 2004: 6). Three complete coracoids, two incomplete humeri, and one complete humerus of an undescribed species of the genus *Wingegyps* were mentioned by Steadman *et al.* (2015) from the late Pleistocene of the asphalt deposit of Mene de Inciarte, municipality of Mara, in Zulia, northwestern Venezuela.

Alvarenga & Olson postulated that *W. cartellei* could hardly process most of the carcasses or compete for them with other vulture species because of its small size. If, like other condors, it did not possess the olfactory capabilities of the *Cathartes* species, it would also have had difficulty competing with them for smaller carcasses. It could, however, have harvested the fruits of palm trees, a niche best exploited in the Old World by the accipitrid *Gypohierax angolensis* (Gmelin) in Africa, which consumes the fruits of the African oil palm *Elaeis guineensis*. This niche is also present in Brazil

through the consumption of the fruits of this same species (which was introduced) by *Cathartes aura* (Linnaeus), that also feeds on the macaúba palm *Acrocomia aculeata*, a native species whose broad geographical distribution coincides with the known past range of *W. cartellei*. The authors added that, although this small condor may have occupied this niche, its habits may have been similar to those of the accipitrid *Neophron percnopterus* (Linnaeus), which consumes scraps of carcasses left by larger vultures. This behavior could explain its extinction since many New World scavenging birds have disappeared along with the mammalian megafauna.

## 250. †*Pleistovultur nevesi* Alvarenga, Brito, Migotto, Hubbe & Höfling

Quaternary - Minas Gerais

Fig. 15.D

*Type locality*: Brazil, state of Minas Gerais, municipality of Matozinhos, Gruta Cuvieri (19°28'36''S, 44°00'41''W), elevation of ca. 812m.

*Etymology*: *Pleistovultur* “Pleistocene condor”, and *nevesi* honoring the Brazilian anthropologist Walter Neves, of Laboratório de Estudos Evolutivos Humanos of Departamento de Genética e Biologia Evolutiva da Universidade de São Paulo, responsible for the team that collected the fossil and the forwarding of the material to the authors.

- “new extinct genus” - Migotto & Alvarenga 2007: 29R.
- *Pleistovultur nevesi* - Alvarenga *et al.* 2008: 613–618, fig. 2.
- *Pleistovultur nevesi* - Alvarenga & Höfling 2011: 127.
- *Pleistovultur nevesi* - Nascimento & Silveira 2020: 491, figs. 5D–E.

This large condor was described by Alvarenga *et al.* (2008) from a right tibiotarsus (MHNT-VT-5238) found by Alex Hubbe around July 2005 in the Locus 1 of Gruta Cuvieri (Hubbe, personal communication), in the municipality of Matozinhos, Minas Gerais. The bone is well-preserved and apparently belongs to an adult individual, 25% larger than in *Sarcoramphus* and 11% smaller than in *Vultur*. The existence of this bone was firstly mentioned by Migotto & Alvarenga (2007).

The material's assignment to the late Pleistocene or the early Holocene was defined based on associated faunal remains present in the same cave (two *Scelidodon* ground sloths were dated at around 9,990 and 12,510 years BP) and adjacent ones previously dated, since the taphonomic conditions of the specimen could not be adequately determined due to previous work carried out on the site.

Its discovery, along with material already described in the literature, attests to the great diversity of cathartids in South America during the Pleistocene. The disappearance of the megafauna has certainly led many of these species to extinction (Alvarenga *et al.* 2008: 617).

## †Teratornithidae

### 251. †*Taubatornis campbelli* Olson & Alvarenga

Late Oligocene/Early Miocene - São Paulo

Fig. 13.D

*Type locality:* Brazil, State of São Paulo, 2 km NE of Tremembé, Fazenda Santa Fé (22°30'S, 45°32'W).

*Etymology:* *Taubatornis*, with Greek *ornis*, “Bird of Taubaté”, referring to the Taubaté Basin, and *campbelli* honoring American paleontologist Kenneth E. Campbell, Jr., of the Natural History Museum of Los Angeles County, in recognition of his contributions to the knowledge of the teratornithids.

- *Taubatornis campbelli* - Olson & Alvarenga 2002: 701–705, figs. 1–2.
- *Taubatornis campbelli* - Alvarenga & Höfling 2011: 127.

Olson & Alvarenga (2002) described the genus and species *Taubatornis campbelli* from two fragments found in the montmorillonite clay of the Tremembé Formation, about 4 m below the most superficial level of the shales, at Fazenda Santa Fé. It is the smallest member of the family known so far (with an estimated wingspan of 1,9 m [Pivetta 2003: 54]), but still a large bird and the only one described for the Brazilian territory.

The material consists of the distal end of a right tibiotarsus (holotype, MHNT-VT 5154) and the proximal end of a left ulna lacking part of the olecranon (paratype, MHNT-VT 5155).

Like other teratornithids, *T. campbelli* was found syntopic with cathartid fossils (*Brasilogyps faustoi*). The shales of the lacustrine environment of the Tremembé Formation suggest that there was an alternation between wet and dry seasons, resulting in the periodic death of a large number of small fish, as the fossils indicate, possibly responsible for the presence of these birds (Olson & Alvarenga, 2002: 704).

Its fossils are the oldest record for the family, about 25 million years older than the next oldest member, the gigantic *Argentavis magnificens* of the Miocene of

Argentina, around 6 million years old. The age of Brazilian fossils corroborates the theory that the family originated in South America (Olson & Alvarenga 2002: 704; Agnolin 2016b).

## Accipitriformes

### Accipitridae

#### 252. Accipitridae indet. 1

Quaternary - Minas Gerais

- *Thrasaëtus?* sp. - Winge 1887: 35–36.
- *Thrasaëtus* sp. - Lambrecht 1933: 747.
- *Harpia harpyja* - Brodkorb 1964: 283.
- *Harpia harpyja* (“*Thrasaëtus?* sp.”) - Mones 1986: 84.
- *Harpia harpyja* - Cuello 1988: 39.
- *Harpia harpyja* - Penido *et al.* 2012: 8.
- *Harpia harpyja* - Penido *et al.* 2013: 117.
- Accipitridae indet. 1 - Nascimento & Silveira 2020: 491.

Winge (1887: 35, 36) reported the distal end of an ulna of unknown origin. He noted that it is larger than in *Haliaeetus albicilla*, *Aquila chrysaetos*, and *Trigonoceps occipitalis*, smaller than in *Gyps fulvus*, and close to *Gypaetus barbatus*. Its shape is very close to that of *Buteo* and even more so to *Spizaetus* (*S. ornatus* and *S. tyrannus*), concluding that of the living South American species, one can think of *Harpia harpyja* and *Buteogallus coronatus*, although only the first was known from the Lagoa Santa region.

#### 253. Accipitridae indet. 2

Quaternary - Minas Gerais

- Buteonin. indet., s. Tillæg til Buteoninæ [“Løb (nederste Ende) og Mellemlhaand (øverste Ende); en god Del større end hos *Buteo* (*Asturina*) *nattereri*”] - Winge 1887: 15, 36.
- *Buteo* sp. [in part] - Lambrecht 1933: 748.
- *Accipiter* sp. [?; in part?] - Mones 1986: 83.
- Accipitridae indet. 2 - Nascimento & Silveira 2020: 491.



Winge (1887: 36) reported the distal end of a tarsometatarsus and the proximal end of a carpometacarpus from “various caves”<sup>18</sup>. He noted that they are significantly larger than in *Rupornis magnirostris nattereri*.

### **254. Accipitridae indet. 3**

Quaternary - Minas Gerais

- Buteonin. sp. indet., s. Anm. til Buteoninæ [“Et Albueben (Stump) og et Taaled af en Art af lignende Størrelse som foregaaende”] - Winge 1887: 13, 36.
- *Buteo* sp. [in part] - Lambrecht 1933: 748.
- *Accipiter* sp. [?; in part?] - Mones 1986: 83.
- Accipitridae indet. 3 - Nascimento & Silveira 2020: 491.

Winge (1887: 36) reported the fragment of an ulna and part of a toe of a bird of similar size to the previous one from Lapa da Lagoa do Sumidouro.

### **255. Accipitridae indet. 4**

Quaternary - Minas Gerais

- “Bækken og Ravenæbsben. Størrelse nogenlunde svarende til de foregaaende” - Winge 1887: 37.
- *Buteo* sp. [in part] - Lambrecht 1933: 748.
- *Accipiter* sp. [?; in part?] - Mones 1986: 83.
- Accipitridae indet. 4 - Nascimento & Silveira 2020: 491.

Winge (1887: 37) reported a pelvis and a coracoid from Lapa da Escrivânia V, roughly equivalent in size to the previous bird. Besides these three indeterminate accipitrids that he described along with the other remains of the family, he reported the existence of several other fragments.

### **256. Accipitridae indet. 5**

Quaternary - Bahia

- Accipitridae - Silva & Cozzuol 2010: 111.

An incomplete tarsometatarsus lacking the proximal epiphysis was associated with the family by Silva & Cozzuol (2010: 111), from material found in the 1980s at Toca da Boa Vista, in Campo Formoso, Bahia. The fossil is deposited in the MHNJB/UFMG collection.

## 257. *Accipitridae* indet. 6

Pleistocene - Ceará

Fig. 11

- “Neornithes: indeterminadas” [in part] - Souza Cunha 1961: 5.
- “Neornithes, Ordens e gêneros indeterminados” [in part] - Paula Couto 1961: 8.
- “aves (indeterminadas)” [?; in part] - Paula Couto 1962: XIX.
- “Neognathae, Undetermined” [?; in part] - Paula Couto 1980: 145.
- Neognathae indet. [?; in part] - Ximenes 2009: 472.
- Neognathae indet. [?; in part] - Souto & Carvalho 2010: 116.
- “gavião fóssil” - Metello & Araújo Júnior 2013: 69–70.
- Acciptriformes indet. [sic] - Araújo Júnior 2015: 193.
- Acciptriformes indet. [sic] - Araújo Júnior 2016: 150, fig. 2B.
- “bird remains” - Patusco *et al.* 2016: 190.
- Acciptriformes indet. [sic] - Waldherr *et al.* 2017: 471.
- Acciptriformes indet. [sic] - Waldherr *et al.* 2019: 115.

Remains of pleistocenic age found in a tank in the João Cativo locality, in Itapipoca, Ceará, were associated with a fossil hawk by Metello & Araújo Junior (2012). The material, attributed to a single individual, consists of four well-preserved vertebrae (MN 3326-V), the distal end of a tarsometatarsus (MN 3275-V), a complete ungual phalanx (MN 3263-V, figured in Araújo Júnior 2016), a hallux (MN 3265-V<sup>27</sup>), and still-indeterminate fragments (3270-V, MN 3271-V, MN 3272-V, MN 3273-V, MN 3293-V, and MN 3294-V), all deposited in the MNRJ collection and likely collected by the institution’s expedition of 1961 (see Paula Couto 1962; 1980). This record suggests an association between forest environments and open areas for the Itapipoca region during the Pleistocene.

## 258. *Chondrohierax uncinatus* (Temminck)

Quaternary - Minas Gerais

- *Cymindis uncinatus* - Winge 1887: 35.
- *Cymindis (Regerhinus) uncinnatus* - Lambrecht 1933: 751.
- *Chondrohierax uncinatus* - Brodkorb 1964: 288.

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<sup>27</sup> Metello & Araújo Júnior (2013) mentioned the code MN 3265-V two times, for the hallux and indeterminate fragment.

- *Chondrohierax uncinatus* - Mones 1986: 84.
- *Chondrohierax uncinatus* - Cuello 1988: 37.
- *Cymindis uncinatus* - Penido *et al.* 2012: 8.
- *Cymindis uncinatus* - Penido *et al.* 2013: 117.
- *Chondrohierax uncinatus* - Nascimento & Silveira 2020: 491.

Winge (1887: 35) reported a right femur and a left tibiotarsus of unknown origin. The tibiotarsus corresponds well to *Chondrohierax uncinatus*, presenting an insignificantly larger size and small morphological variation, probably individual, when compared to a corresponding fresh bone. *Leptodon cayanensis* has a similar but larger tibiotarsus. The femur, of which there was no comparative correspondent of *C. uncinatus*, is very similar to that of *L. cayanensis*, except for the much smaller size. Winge also noted that the tibiotarsus of *Elanoides forficatus* is different but still close, and *Elanus* and *Ictinia* are very different from the mentioned species.

## **259. *Accipiter* sp.**

Quaternary - Minas Gerais

- *Accipiter* sp., magnitudine *A. nisi* ♀, forte *A. pileatus* ♂ - Winge 1887: 36.
- *Accipiter* sp. - Lambrecht 1933: 749.
- *Accipiter* sp. [in part?] - Mones 1986: 83.
- *Accipiter bicolor* - Penido *et al.* 2012: 8.
- *Accipiter bicolor* - Penido *et al.* 2013: 117.
- *Accipiter* sp. - Nascimento & Silveira 2020: 491.

Winge (1887: 36) determined the proximal and distal ends of a right tarsometatarsus of unknown origin as belonging to a bird of this genus, of size comparable to that of a female *Accipiter nisus*, probably belonging to a male *Accipiter bicolor pileatus*.

## **260. *Accipiter bicolor* (Vieillot)**

Quaternary - Piauí

- Accipitridae [in part] - Guérin *et al.* 1993a: 198.
- Accipitridae [in part] - Guérin *et al.* 1993b: 328.
- *Accipiter bicolor* - Guérin *et al.* 1996: 84.
- *Accipiter bicolor* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **261. *Geranospiza caerulescens* (Vieillot)**

Quaternary - Bahia

- *Geranospiza caerulescens* - Penido *et al.* 2012: 8.
- *Geranospiza caerulescens* - Penido *et al.* 2013: 116–117.

Penido *et al.* (2012: 8; 2013: 116, 117) reported a right tarsometatarsus, a fragmented left tarsometatarsus, and a synsacrum among material collected in 1980 and 1984 by the team of the Laboratório de Paleontologia of MCN PUC Minas at Gruta dos Brejões, in Morro do Chapéu, Bahia. The material was associated with the species by the MHNT team.

### **262. *Heterospizias meridionalis* (Latham)**

Holocene - Rio de Janeiro

- *Heterospizias meridionalis* - Kneip *et al.* 1994: 50.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis Beirada I (3 pieces of at least one individual), Beirada II (2 pieces of at least one individual), and Beirada IV (5 pieces of at least one individual), in Saquarema, Rio de Janeiro.

### **263. *Urubitinga urubitinga* (Gmelin)**

Holocene - Rio de Janeiro

- *Buteogallus urubitinga* - Kneip *et al.* 1994: 50.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis Beirada II (1 piece) and Beirada IV (1 piece), in Saquarema, Rio de Janeiro.

### **264. *Rupornis magnirostris nattereri* (Sclater & Salvin)**

Quaternary - Minas Gerais

- *Buteo (Asturina) nattereri* - Winge 1887: 36.
- *Buteo (Asturina) Nattereri* - Lambrecht 1933: 748.

- *Buteo magnirostris* - Brodkorb 1964: 283.
- *Buteo magnirostris* (“*Buteo (Asturina) nattereri*”) - Mones 1986: 84.
- *Buteo magnirostris* - Cuello 1988: 38.
- *Buteo natteri* [sic] - Penido *et al.* 2012: 8.
- *Buteo natteri* [sic] - Penido *et al.* 2013: 117.
- *Rupornis magnirostris nattereri* - Nascimento & Silveira 2020: 491.

Winge (1887: 36) reported a humerus and a tibiotarsus from Lapa da Escrivânia V, a coracoid (that almost certainly belongs to this species) from Lapa da Escrivânia XI, a radius from Lapa da Lagoa do Sumidouro, and a tibiotarsus (of a very young individual) of recent age<sup>20</sup>.

## **265. *Geranoaetus albicaudatus* (Vieillot)**

Holocene - Rio de Janeiro

- *Buteo albicaudatus* - Kneip *et al.* 1994: 50.

Kneip *et al.* (1994) reported material associated with the species from a sambaqui in Saquarema, Rio de Janeiro.

## **266. *Geranoaetus melanoleucus* (Vieillot)**

Quaternary - Minas Gerais

- *Buteo* sp., *melanoleucus* v. aff., s. under *B. melanoleucus* [in part] - Winge 1887: 14.
- *Buteo melanoleucus* - Winge 1887: 36.
- *Buteo melanoleucus* - Lambrecht 1933: 748.
- *Buteo fuscescens* - Brodkorb 1964: 281.
- *Buteo fuscescens* (“*Buteo melanoleucus*”) - Mones 1986: 83–84.
- *Geranoaetus melanoleucus* - Cuello 1988: 38.
- *Geranoaetus melanoleucus* - Penido *et al.* 2012: 8.
- *Geranoaetus melanoleucus* - Penido *et al.* 2013: 117.
- *Geranoaetus melanoleucus* - Nascimento & Silveira 2020: 491.

Winge (1887: 36) reported several bones of an individual from Lapa da Escrivânia V, which correspond precisely to the skeleton of a Chilean specimen of *Geranoaetus melanoleucus* and are larger and different from that observed in *Geranoaetus albicaudatus*, represented by the skull, mandibular branch, thoracic vertebra, part of the synsacrum and pelvis, scapula, humerus, ulna, radius, carpal<sup>19</sup>, carpometacarpus, femur,

tibiotarsus, first phalanx of the hallux, second phalanx of the second digit of the foot, and ungual phalanx. There is also a femur and a tibiotarsus of two individuals, one of them slightly larger than in a fresh skeleton, and a third phalanx of the third digit, somewhat small for this species. The proximal end of a humerus from Lapa da Escrivânia XI fits well into this species. A radius and several phalanges of the feet (including the second phalanx of the second right and left digits) from Lapa da Escrivânia III possibly belong to this or a close species, being smaller than in *G. melanoleucus* and larger than in *G. albicaudatus*, with which there is a certain correspondence. Winge also noted that *Spizaetus ornatus* and *Spizaetus tyrannus*, of similar size, are different in several ways.

### **267. *Buteo* sp.**

Quaternary - Goiás

- *Buteo* indet - Paulo 2009: 141.

Paulo (2009: 141) reported the genus to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

## **Strigiformes**

### **268. Strigiformes indet.**

Holocene - Rio Grande do Norte

- Strigidiformes [*sic*] - Silva 2014: 133.

Silva (2014: 133) reported strigiform material among zooarcheological remains of holocenic age collected by the team of NEA-UFPE starting in the 1990s in rock shelters of Pedra do Alexandre site, in Carnaúba dos Dantas, Rio Grande do Norte.

## **Tytonidae**

### **269. *Tyto furcata* (Temminck)**

Quaternary - Minas Gerais, Piauí

- *Strix perlata* [in part] - Lund 1837: 247–248.
- *Strix* [?] - Gervais 1844a: 294.

- “les Strix” [?] - Liais 1872: 303.
- *Strix flammea (perlata)* [in part?] - Winge 1887: 37.
- *Strix flammea (perlata)* [in part?] - Lambrecht 1933: 770.
- *Tyto alba* [in part?] - Brodkorb 1971: 232.
- *Tyto alba* (“*Strix flammea*”) [in part?] - Mones 1986: 96.
- *Tyto alba* [in part?] - Cuello 1988: 55.
- *Tyto furcata* [in part?] - Nascimento & Silveira 2020: 493.

Winge (1887: 37) reported bones in large number from Lapa da Escrivânia V, from many individuals ranging from very young to adults, two bones from Lapa da Escrivânia XI, a bone from Lapa da Lagoa do Sumidouro, several from an unknown origin, and another number of bones of recent age<sup>20</sup>. The material is represented by various skull parts, scapula, coracoid, humerus, ulna, radius, carpometacarpus, first phalanx of the second digit of the wing, pelvis, femur, tibiotarsus, fibula, tarsometatarsus, and several phalanges of the feet, with individual variation present.

Lund (1837: 242, 247, 248/1950a: 89, 92, 93) reported the presence of bones of varying ages, and traces of its predatory activity, from Lapa Nova de Maquiné. Perhaps they are among the material of unknown origin and of recent age mentioned by Winge. He also mentioned (Lund 1841a) their activity as the authors of mounds of remains of small mammals and birds, of varying ages, from the very first cave he studied, near the village of Cachoeira do Campo. Remains of the owls’ feeding activities in the caves were mentioned by Lund several times in subsequent works (1839; 1841b; 1841c; 1846).

- *Tyto alba* - Guérin *et al.* 1993a: 198.
- *Tyto alba* - Guérin *et al.* 1993b: 328.
- *Tyto alba* - Guérin *et al.* 1996: 84.
- *Tyto alba* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1993a; 1993b; 1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least three adults and one young individual are present in the material.

## Strigidae

### 270. Strigidae indet. 1

Quaternary - Minas Gerais

- *Syrnium* sp. e minoribus - Winge 1887: 38.
- *Syrnium* sp. (“Mehrere Formen”) [in part] - Lambrecht 1933: 771.
- *Syrnium* sp. [in part] - Mones 1986: 96.
- Strigidae indet. 1 - Nascimento & Silveira 2020: 493.

Winge (1887: 38) reported a tarsometatarsus lacking the proximal end from Lapa da Escrivânia N° 11. He noted it is very close to the tarsometatarsus of the skeleton of an indeterminate “*Syrnium*” from the Lagoa Santa region, which may be “*Syrnium melanotum*” (= *Pulsatrix melanota* or *Pulsatrix koenigswaldiana*?<sup>28</sup>) and especially “*Syrnium huhula*” (= *Ciccaba huhula*) or “*Syrnium suinda*” (= *Asio flammeus suinda*).

### 271. Strigidae indet. 2

Quaternary - Minas Gerais

- *Syrnium?* sp. e majoribus - Winge 1887: 38.
- *Syrnium* sp. (“Mehrere Formen”) [in part] - Lambrecht 1933: 771.
- *Syrnium* sp. [in part] - Mones 1986: 96.
- Strigidae indet. 1 - Nascimento & Silveira 2020: 493.

Winge (1887: 38) reported a humerus from an unknown origin which he defined as “*Syrnium?* sp.”, somewhat larger and slightly different than the above record, noting that it is slightly larger and considerably different from that observed in *Asio clamator* and slightly larger than in a female *Strix aluco* (“*Syrnium aluco*”).

### 272. Strigidae indet. 3

Quaternary - Piauí

- Strigidae [in part] - Guérin *et al.* 1993a: 198.
- Strigidae [in part] - Guérin *et al.* 1993b: 328.

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<sup>28</sup> *Pulsatrix koenigswaldiana* M.S. Bertoni & A.W. Bertoni was thought to be close to *Pulsatrix melanota* (Tschudi), sometimes being treated as specific. Because of this, it may be that Winge elected *P. melanota* as a possibility, even though the species, strictly speaking, is found only in Colombia, Ecuador, Peru and Bolivia (Holt *et al.* 2017).



- *Rhinoptynx clamator* [ou] *Ciccaba huhula* - Guérin *et al.* 1996: 84.
- *Rhinoptynx clamator* ou *Ciccaba huhula* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material associable with *Asio clamator* or *Strix huhula* from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material. This is one of the taxa that the authors highlighted as no longer living in the region today.

### **273. *Megascops choliba* (Vieillot)**

Quaternary - Piauí

- Strigidae [in part] - Guérin *et al.* 1993a: 198.
- Strigidae [in part] - Guérin *et al.* 1993b: 328.
- *Otus choliba* - Guérin *et al.* 1996: 84.
- *Otus choliba* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least two adults and one young individual are present in the material.

### **274. *Strix virgata* (Cassin)**

Quaternary - Piauí

- Strigidae [in part] - Guérin *et al.* 1993a: 198.
- Strigidae [in part] - Guérin *et al.* 1993b: 328.
- *Ciccaba virgata* - Guérin *et al.* 1996: 84.
- *Ciccaba virgata* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material. This is one of the taxa that the authors highlighted as no longer living in the region today.

### **275. *Glaucidium minutissimum* (Wied)**

Quaternary - Piauí

- Strigidae [in part] - Guérin *et al.* 1993a: 198.
- Strigidae [in part] - Guérin *et al.* 1993b: 328.

- *Glaucidium minutissimum* - Guérin *et al.* 1996: 84.
- *Glaucidium minutissimum* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material. This is one of the taxa that the authors highlighted as no longer living in the region today.

## **276. *Glaucidium brasilianum* (Gmelin)**

Quaternary - Minas Gerais, Piauí

- *Scops brasilianus* - Winge 1887: 37.
- *Scops brasilianus* - Lambrecht 1933: 771.
- *Glaucidium brasilianum* [in part] - Brodkorb 1971: 225.
- *Glaucidium brasilianum* (“*Scops brasilianus*”) - Mones 1986: 96.
- *Glaucidium brasilianum* [in part?] - Cuello 1988: 56.
- *Glaucidium brasilianum* [in part] - Nascimento & Silveira 2020: 493.

Winge (1887: 37) reported bones of several individuals from Lapa da Escrivânia V, represented by the scapula, coracoid, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, and tarsometatarsus, with great individual variation. Additionally, there is an ulna and a tarsometatarsus from a “saltpeter cave near Escrivânia”, two coracoids and a tarsometatarsus from Lapa da Lagoa do Sumidouro, a humerus and a tibiotarsus from “various caves”<sup>18</sup>, a sternum, a scapula, and a femur of unknown origin, and a scapula, a humerus, and a tarsometatarsus of recent age<sup>20</sup>. Winge noted that only the ulna and tibiotarsus were determined by comparison with fresh bones. The others had the same size and matching characters, which were quite different from *Athene cunicularia*.

- *Glaucidium ferox* (et aff.) - Winge 1887: 38.
- *Glaucidium ferox* (?) - Lambrecht 1933: 771.
- *Glaucidium brasilianum* [in part] - Brodkorb 1971: 225.
- *Glaucidium ferox* - Mones 1986: 96.
- *Glaucidium brasilianum* [in part?] - Cuello 1988: 56.
- *Glaucidium brasilianum* [in part] - Nascimento & Silveira 2020: 493.

Winge (1887: 38) described remains other than the record above as “*Glaucidium ferox* (et aff.)”. The material consists of several bones from Lapa da Escrivânia V, represented by the scapula, coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus, and

tarsometatarsus, being most of the bones slightly smaller than the observed in two fresh skeletons. However, two left humeri are considerably smaller and slightly different, and Winge speculated that they might belong to *Glaucidium minutissimum*. Additionally, there are both coracoids of a very young individual from Lapa da Escrivânia III.

- Strigidae [in part] - Guérin *et al.* 1993a: 198.
- Strigidae [in part] - Guérin *et al.* 1993b: 328.
- *Glaucidium brasilianum* - Guérin *et al.* 1996: 84.
- *G. brasilianum* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **277. *Athene cunicularia* (Molina)**

Quaternary - Minas Gerais

- *Athene (Speotyto) cunicularia* - Winge 1887: 38.
- *Speotyto cunicularia* - Lambrecht 1933: 771.
- *Speotyto cunicularia* - Brodkorb 1971: 226.
- *Athene (Speotyto) cunicularia* - Mones 1986: 95.
- *Athene cunicularia* - Cuello 1988: 56.
- *Athene cunicularia* - Nascimento & Silveira 2020: 493.

Winge (1887: 38) reported two femora, one proximal end and one distal end, from Lapa da Escrivânia V, which correspond very well to this species.

### **278. *Asio stygius* (Wagler)**

Quaternary - Minas Gerais

- *Nyctalops stygius* - Winge 1887: 37.
- *Nyctalops stygius* - Lambrecht 1933: 773.
- *Asio stygius* - Brodkorb 1971: 227.
- *Asio stygius* (“*Nyctalops stygius*”) - Mones 1986: 95–96.
- *Asio stygius* - Cuello 1988: 56.
- *Asio stygius* - Nascimento & Silveira 2020: 493.

Winge (1887: 37) associated several bones from Lapa da Escrivânia V to at least two individuals, represented by the humerus (proximal and distal ends), carpometacarpus, femur, tibiotarsus (distal end), tarsometatarsus (almost complete), and the first phalanx

of one of the opposite fingers [hallux]. Winge noted that only the humeri and femora were determined by comparison, since of fresh bones he had in hands only the torso skeleton, femora, and the proximal ends of the humeri of the taxidermized specimen from Lagoa Santa. However, he did not doubt that the other bones belong to the same species, and that *Asio clamator*, of which there were two skeletons available, is quite distinct.

## Trogoniformes

### Trogonidae

#### 279. *Trogon* sp.

Quaternary - Minas Gerais

- *Trogon* sp. indet., præcedente [*Trogon aurantius*] et *Tr. viridi* major - Winge 1887: 44.
- *Trogon* sp. (“cfr. *viridus*”) - Lambrecht 1933: 774.
- *Trogon* sp. - Nascimento & Silveira 2020: 494.

Winge (1887: 44) reported the distal end of a tibiotarsus from an unknown location, possibly from Lapa da Escrivânia V. He noted it is much larger than that in *Trogon aurantius* and somewhat larger than in *Trogon viridis*, from which it also differs slightly in shape.

#### 280. *Trogon surrucura aurantius* Spix

Quaternary - Minas Gerais

- *Trogon* aff. *violaceo* - Lund (in Winge 1887): 44.
- *Trogon aurantius* - Winge 1887: 44.
- *Trogon aurantius* - Lambrecht 1933: 774.
- *Trogon surrucura* - Brodkorb 1971: 247.
- *Trogon surrucua* (“*Trogon aurantius*”) - Mones 1986: 97.
- *Trogon surrucua* - Cuello 1988: 58.
- *Trogon surrucura aurantius* - Nascimento & Silveira 2020: 494.

Winge (1887: 44) reported a humerus (“*Trogon* aff. *violaceo*” in Lund’s catalog) from “a cave near Sumidouro” other than Lapa da Lagoa do Sumidouro (erroneously attributed this way by Brodkorb [1971: 247] and [Sick, 1984a: 384; 1993: 352; 1997:

467]; this is present in Lambrecht (1933) in some entries as well and in Cuello [1988] too). He noted it corresponds well to several specimens of this species used in the comparison and that it is considerably smaller than in *Trogon viridis*.

## Coraciiformes

### Momotidae

#### 281. *Baryphthengus ruficapillus* (Vieillot)

Quaternary - Minas Gerais

- *Alcedo* aff. *amazonæ* [in part] - Lund (in Winge 1887): 45.
- *Momotus* sp. (næppe *M. ruficapillus*) [in part] - Winge 1887: 11.
- *Momotus* (*Baryphthongus*) *ruficapillus* (et aff.) - Winge 1887: 44–45.
- *Momotus* (*Baryphthongus*) *ruficapillus* - Lambrecht 1933: 774.
- *Baryphthengus ruficapillus* - Brodkorb 1971: 254.
- *Baryphthengus ruficapillus* - Mones 1986: 97.
- *Baryphthengus ruficapillus* - Cuello 1988: 59.
- *Baryphthengus ruficapillus* - Nascimento & Silveira 2020: 494.

Winge (1887: 44, 45) reported an ulna and the distal end of a tibiotarsus from Lapa da Escrivânia V, a humerus from Lapa da Escrivânia XI, a humerus of an old individual and the coracoid of a young one from Lapa do Marinho II, two ulnae of two individuals from “various caves”<sup>18</sup>, the proximal end of a humerus from “a cave near Sumidouro” (other than Lapa da Lagoa do Sumidouro; erroneously attributed this way by Brodkorb [1971: 254], Cuello [1988: 59] and Sick [1984a: 392; 1993: 359; 1997: 476]), determined as “*Alcedo* aff. *amazonæ*” in Lund’s catalog (about which Winge commented that it is very similar to the equivalent bone in *Chloroceryle amazona*), several bones of unknown origin, and fragments of recent age<sup>20</sup>. The total material is represented by the maxilla, coracoid, sternum, humerus, ulna, pelvis, femur, tibiotarsus, and tarsometatarsus. Winge also reported a carpometacarpus from Lapa do Capão Seco, which, due to morphological differences, may belong to another species.

#### 282. *Momotus momota* (Linnaeus)

Holocene - Mato Grosso

- *Momotus momota* - Figuti 2005: 156–157, fig. 1.

Figuti (2005: 156, 157) reported a mummified incomplete nestling from the superficial layer of the Santa Elina rock shelter in Jangada, Mato Grosso, less than eight thousand years old. In addition, indeterminate bird claws were found at the same site.

## **Alcedinidae**

### **283. *Chloroceryle amazona* (Latham)**

Quaternary - Minas Gerais

- *Ceryle amazona* - Winge 1887: 44.
- *Ceryle amazona* - Lambrecht 1933: 774.
- *Chloroceryle amazona* - Brodkorb 1971: 253.
- *Chloroceryle amazona* (“*Ceryle amazona*”) - Mones 1986: 97.
- *Chloroceryle amazona* - Cuello 1988: 59.
- *Chloroceryle amazona* - Nascimento & Silveira 2020: 494.

Winge (1887: 44) reported a rather incomplete but well-determined humerus from Lapa da Escrivânia V.

## **Galbuliformes**

### **Bucconidae**

### **284. *Malacoptila striata* (Spix)**

Quaternary - Minas Gerais

- *Malacoptila torqvata* - Winge 1887: 45.
- *Malacoptila torquata* - Lambrecht 1933: 775.
- *Malacoptila torquata* (= *M. striata*) - Storer 1960: 80.
- *Malacoptila striata* - Brodkorb 1971: 257.
- *Malacoptila striata* (“*Malacoptila torqvata*”) - Mones 1986: 97.
- *Malacoptila striata* - Cuello 1988: 60.
- *Malacoptila striata* - Nascimento & Silveira 2020: 494.

Winge (1887: 45) attributed a humerus from Lapa da Escrivânia V to this species.

## 285. *Nystalus chacuru* (Vieillot)

Quaternary - Minas Gerais

- *Capito melanotis* [in part] - Lund 1841d: 18.
- “un Tamatia (*Capito* de Temminck)” [in part] - Liais 1872: 303.
- *Bucco chacuru* - Winge 1887: 45–46.
- *Capito* sp. (“angeblich aus den Knochenhöhlen Brasiliens”) [in part] - Lambrecht 1933: 769.
- *Bucco chacuru* - Lambrecht 1933: 775.
- *Nystalus chacuru* - Brodkorb 1971: 257.
- *Nystalus chacuru* (“*Bucco chacuru*”) - Mones 1986: 97.
- *Nystalus chacuru* - Cuello 1988: 59.
- *Nystalus chacuru* - Nascimento & Silveira 2020: 494.

Winge (1887: 45, 46) reported bones of several individuals from Lapa da Escrivânia V, represented by the mandible, scapula, coracoid, humerus (in great number), ulna, radius, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. Additionally, there is a mandible from Lapa da Escrivânia III, two humeri (one left and one right) from a “saltpeter cave near Escrivânia”, some bones of unknown origin, and bones of several individuals of recent age<sup>20</sup>, of which Lund determined a humerus. Winge also noted that it is easily distinguished from *Malacoptila striata* by the humerus and other bones.

## ?Piciformes

### †Gracilitarsidae

## 286. †*Eutreptodactylus itaboraiensis* Baird & Vickers-Rich

Early Eocene - Rio de Janeiro

Fig. 12.B

*Type locality*: São José de Itaboraí, Brazil.

*Etymology*: *Eutreptodactylus*, Greek for “easily changeable toe”, and *itaboraiensis*, referring to the São José de Itaboraí Basin.

- “Aves, undetermined (small birds)” [in part?] - Rich 1979: 323, 324.
- *Eutreptodactylus itaboraiensis* sp. nov. - Baird & Vickers-Rich 1997: 123-127, figs. 1–2.
- *Eutreptodactylus itaboraiensis* - Bergqvist *et al.* 2006: 55.

Baird & Vickers-Rich (1997) described the genus and species *Eutreptodactylus itaboraiensis* from material collected by Ney Vidal in 1950 in the São José de Itaboraí Basin, with an estimated age in the early Eocene. The presence of small bird fossils (microfossils) in this location had already been mentioned by Rich eighteen years before this study (Rich 1979: 323, 324).

The material is an incomplete and slightly worn distal fragment of a right tarsometatarsus (MN 4083-V) with damage in the three trochleae, which was subsequently lost, on which the study and accompanying illustrations were based. Photographs, figures, and a replica of the original material were deposited in MN (Baird & Vickers-Rich 1997: 124). The fossil suggests facultative zygodactyly (Baird & Vickers-Rich 1997: 124, 126) or semizygodactyly (Mayr 2009: 203).

The species was initially attributed to the Cuculidae and then considered its oldest and most primitive representative, possibly belonging to a new subfamily (Baird & Vickers-Rich 1997: 123, 124, 126). Baird & Vickers-Rich (1997: 124) also noted that without the original fossil, its attribution to a higher taxon requires the discovery of more material. Mourer-Chauviré (1999: 88) noted that the fossil is quite similar to the genus *Sylphornis*, from the middle Eocene of France, suggesting that it should be included in the Sylphornithidae. Mayr (2001: 78, 82) contested the attribution to the Cuculidae and found similarities between *E. itaboraiensis* and *Gracilitarsus mirabilis* (Gracilitarsidae) of the middle Eocene of Messel deposits in Germany, raising the possibility that they are close relatives. Later, Mayr (2005) included *E. itaboraiensis* and *Neanis schucherti* from the early Eocene of the Green River Formation (United States) in the Gracilitarsidae. Mayr presented a phylogenetic analysis that resulted in a clade made up by Gracilitarsidae, Sylphornithidae, and the Piciformes crown group, although reiterated (Mayr 2009: 203; 2016: 230) that such a hypothesis is not yet properly established.

Mayer *et al.* (2011a: 682) mentioned the distal end of a left tibiotarsus (MN 4119-V) from the same locality, which may have belonged to this species (see Aves indet. 2).



## Piciformes

### Ramphastidae

#### **287. *Ramphastos toco*** Statius Müller

Quaternary - Minas Gerais

- *Rhamphastus toco* [sic] - Winge 1887: 46.
- *Rhamphastus toco* - Lambrecht 1933: 774.
- *Ramphastos toco* - Storer 1960: 81.
- *Ramphastos toco* - Brodkorb 1971: 260.
- *Ramphastos toco* - Sick 1984a: 406.
- *Ramphastos toco* - Mones 1986: 98.
- *Ramphastos toco* - Cuello 1988: 60.
- *Ramphastos toco* - Sick 1993: 372.
- *Ramphastos toco* - Sick 1997: 492.
- *Ramphastos toco* - Nascimento & Silveira 2020: 494.

Winge (1887: 46) reported the proximal part of an ulna and the distal part of a tarsometatarsus from Lapa da Escrivânia V, of which he noted that it is the only one comparable with fresh bones of the same species, having a similar-sized ulna.

#### **288. *Ramphastos cf. dicolorus*** Linnaeus

Quaternary - Minas Gerais

- *Rhamphastus discolor* vel sp. aff. [sic] - Winge 1887: 46.
- *Rhamphastus discolor* - Lambrecht 1933: 774.
- *Ramphastos discolor* [sic] - Storer 1960: 81.
- *Ramphastos dicolorus* [sic] - Brodkorb 1971: 260.
- *Ramphastos dicolorus* (“*Ramphastos discolor*”) - Mones 1986: 98.
- *Rhamphastos dicolorus* [sic] - Cuello 1988: 60.
- *Ramphastos cf. dicolorus* - Nascimento & Silveira 2020: 494.

Winge (1887: 46) reported an ulna from “various caves”<sup>18</sup>, slightly larger than in *Ramphastos dicolorus*. He reported another ulna, from an uncertain locality, slightly smaller than in *R. dicolorus* and insignificantly different, noting that it is quite different from that observed in *Pteroglossus aracari wiedii* and *Selenidera maculirostris*.

Brodkorb (1971: 260) erroneously listed it coming from “Lapa da Escrivania?”, which was followed by Cuello (1988: 60).

## **Picidae**

### **289. Picidae indet. 1**

Quaternary - Minas Gerais

- G. sp. indet., forte *Leuconerpes candidus* - Winge 1887: 46–47.
- cfr. *Leuconerpes candidus* - Lambrecht 1933: 775.
- *Leuconerpes candidus* - Brodkorb 1971: 265.
- cf. *Leuconerpes candidus* - Mones 1986: 98.
- *Melanerpes candidus* - Cuello 1988: 61.
- Picidae indet. 1 - Nascimento & Silveira 2020: 494.

Winge (1887: 46, 47) reported a humerus from Lapa da Escrivânia V, shorter and relatively more robust than in *Colaptes campestris*, insignificantly longer and much stronger than in *Colaptes melanochloros*, shorter and much stronger than in *Celeus flavescens*, and much smaller than in *Hylatomus lineatus* and *Campephilus robustus*. Winge speculated that it might be *Melanerpes candidus*, although he had only the distal end of a fresh humerus available for comparison, which is much more similar to the fossil than other species in the region. Still, there is a slight difference in shape (perhaps individual variation), and the fresh bone is somewhat smaller.

### **290. Picidae indet. 2**

Quaternary - Minas Gerais

- Picid. g. sp., e minimis - Winge 1887: 51.
- Picidae indet. 2 - Nascimento & Silveira 2020: 494.

Winge (1887: 51) reported a coracoid of recent age, without attribution of locality, of a species smaller than *Veniliornis maculifrons*<sup>23</sup>, perhaps being *V. mixtus (cancellatus)*.

### **291. Picidae indet. 3**

Quaternary - Piauí

- Piciformes [in part] - Guérin *et al.* 1993a: 198.
- Piciformes [in part] - Guérin *et al.* 1993b: 328.

- *Dryocopus lineatus* [ou] *Campephilus melanoleucos* - Guérin *et al.* 1996: 85.
- *Dryocopus lineatus* ou *Campephilus melanoleucos* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material associable with *Dryocopus lineatus* or *Campephilus melanoleucos* from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

## **292. *Melanerpes flavifrons* (Vieillot)**

Quaternary - Minas Gerais

- *Melanerpes flavifrons* - Winge 1887: 47.
- *Melanerpes flavifrons* - Lambrecht 1933: 775.
- *Melanerpes flavifrons* - Brodkorb 1971: 265.
- *Melanerpes flavifrons* - Mones 1986: 98.
- *Melanerpes flavifrons* - Cuello 1988: 60.
- *Melanerpes flavifrons* - Nascimento & Silveira 2020: 494.

Winge (1887: 47) reported a humerus from Lapa da Escrivânia V, which corresponds well to the species.

## **293. *Veniliornis maculifrons* (Spix)**

Quaternary - Minas Gerais

- *Picus (Campias) maculifrons* - Winge 1887: 47.
- *Picus (Campias) maculifrons* - Lambrecht 1933: 775.
- *Veniliornis maculifrons* - Brodkorb 1971: 265.
- *Veniliornis maculifrons* (“*Picus (Campias) maculifrons*”) - Mones 1986: 98.
- *Veniliornis maculifrons* - Cuello 1988: 61.
- *Veniliornis maculifrons* - Nascimento & Silveira 2020: 494.

Winge (1887: 47) reported three well-matched humeri (one slightly smaller) from Lapa da Escrivânia V.

## **294. *Colaptes* sp.**

Quaternary - Goiás

- *Colaptes* indet - Paulo 2009: 142.

Paulo (2009: 142) reported the genus to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

## **295. *Colaptes melanochloros* (Gmelin)**

Quaternary - Minas Gerais, Piauí

- *Chrysoptilus chlorozostus* - Winge 1887: 46.
- *Chrysoptilus chlorozostus* - Lambrecht 1933: 775.
- *Chrysoptilus melanochloros* - Brodkorb 1971: 264.
- *Chrysoptilus melanochloros* (“*Chrysoptilus chlorozostus*”) - Mones 1986: 98.
- *Colaptes melanochloros* - Cuello 1988: 61.
- *Colaptes melanochloros* - Nascimento & Silveira 2020: 494.

Winge (1887: 46) reported a femur from Lapa da Escrivânia V, which corresponds well to the species and is quite different in size from that of the other species that were available for comparison, noting that the same can be said of an incomplete quadrate and the anterior part of a scapula.

- Piciformes [in part] - Guérin *et al.* 1993a: 198.
- Piciformes [in part] - Guérin *et al.* 1993b: 328.
- *Colaptes melanochloros* - Guérin *et al.* 1996: 85.
- *Colaptes melanochloros* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

## **296. *Colaptes campestris* (Vieillot)**

Quaternary - Minas Gerais

- *Colaptes campester* [*sic*] - Winge 1887: 46.
- *Colaptes campester* - Lambrecht 1933: 775.
- *Colaptes campestris* - Brodkorb 1971: 264.
- *Colaptes campestris* - Mones 1986: 98.
- *Colaptes campestris* - Cuello 1988: 61.
- *Colaptes campestris* - Nascimento & Silveira 2020: 494.

Winge (1887: 46) reported bones of many individuals from Lapa da Escrivânia V, a humerus from Lapa da Escrivânia XI, and an ulna from “various caves”<sup>18</sup>. The total material is represented by the scapula, coracoid, humerus (in large number), ulna,

carpometacarpus, femur, tibiotarsus, and tarsometatarsus. Winge noted that there is much difference between these bones and that they are also quite distinct from *Campephilus robustus*, *Hylatomus lineatus*, *Colaptes melanochloros*, and *Celeus flavescens*. However, some tarsometatarsi, somewhat smaller, may belong to *Melanerpes candidus*.

## **Cariamiformes**

### **297. †Cariamiformes indet.**

Early Eocene - Rio de Janeiro

- Ralliformes - Taranto & Bergqvist 2009: 51R.
- Ralliformes - Taranto *et al.* 2009a: 287.
- Ralliformes - Taranto & Bergqvist 2010: 118.

Taranto & Bergqvist (2009: 51R), Taranto *et al.* (2009a: 287), and Taranto & Bergqvist (2010: 118) associated with Ralliformes (=Cariamiformes?) the distal end of a right femur (UFRJ 01-AV) from the early Eocene of São José de Itaboraí, which was for a long time stored in the collection of the Departamento de Geologia at UFRJ. Taranto & Bergqvist (2010: 118) described the material with a similar size to the corresponding in a pigeon, a comparison associated with a tibiotarsus (UFRJ 02-AV) in the two previous publications.

### **298. †Paleopsilopterus itaboraiensis Alvarenga**

Early Eocene - Rio de Janeiro

Fig. 12.D

*Type locality:* Holotype collected in the calcareous basin of the São José village, district of Cabuçu, municipality of Itaboraí, state of Rio de Janeiro, Brazil, among the marl that fills the limestone galleries.

*Etymology:* *Paleopsilopterus*, with the Greek “*palaeos*” (ancient), following the proposal to it was an older and perhaps ancestral form of *Psilopterus*, and *itaboraiensis* referring to the municipality of Itaboraí.

- Aves [“Ainda por determinar”; in part?] - Paula Couto 1958: 11.
- Aves [“Diversas, não identificadas”; in part?] - Paula Couto 1970: 909.
- Aves [“fragmentos de ossos longos”; in part?] - Palma 1973: 40.
- Aves [“fragmentos de ossos longos”; in part?] - Palma & Brito 1974: 400.

- “restos de diversas aves, metatarsais, vértebras, pré-maxilas, etc.” [in part?] - Price (*in lit.* 1977 in Sick 1984a): 65.
- Aves [“representadas por ossos longos”; in part?] - Francisco & Cunha 1978: 390, 402, 408.
- *Paleopsilopterus itaboraiensis* sp. n. - Alvarenga 1985a: 17–20, figs. 1–4.
- *Palaepsilopterus itaboraiensis* [sic] - Mones 1986: 89.
- *Paleopsilopterus itaboraiensis* - Cuello 1988: 18.
- “fragmentos de ossos longos de aves” [in part?] - Brito 1989: 60.
- *Paleopsilopterus itaboraiensis* - Alvarenga 1993a: 62.
- *Paleopsilopterus itaboraiensis* - Alvarenga 1997: 123.
- *Paleopsilopterus itaboraiensis* - Kellner 1998: 654, 659.
- *Paleopsilopterus* - Alvarenga & Höfling 2000: 590.
- *Paleopsilopterus itaboraiensis* - Alvarenga & Höfling 2003: 84–85, figs. 29, 34.
- *Paleopsilopterus* - Alvarenga & Höfling 2004: 828.
- *Paleopsilopterus itaboraiensis* - Bergqvist *et al.* 2006: 55, fig. 61.
- *Paleopsilopterus itaboraiensis* - Agnolin 2009b: 21, fig. 18.
- *Paleopsilopterus itaboraiensis* [in part] - Alvarenga *et al.* 2011: 191–192, fig. 7.2.
- *Paleopsilopterus* - Alvarenga & Höfling 2011: 128.

The genus and species *Paleopsilopterus itaboraiensis* were raised by Alvarenga (1985a) from a tibiotarsus and two tarsometatarsi collected in the late 1940s in the São José de Itaboraí Basin, of early Eocene age.

The holotype is the proximal end of a right tarsometatarsus with the upper extremity of the hypotarsus partially damaged (MN 4040-V), collected by Ney Vidal in 1948. The paratypes are the two tibiotarsi of the same individual (DGM 1431-R), incomplete in the proximal end, very deformed and encrusted with limestone, collected by Júlio de Carvalho in 1949 in the same locality of the holotype and deposited, after thorough restoration, in the collection of the Seção de Paleontologia of the Departamento Nacional de Produção Mineral. Although the condyles of the right tibiotarsus articulate perfectly with the holotype tarsometatarsus, they are likely to belong to different individuals, due to the different collection date and state of conservation, in addition to the lack of more accurate data on the collection site (Alvarenga 1985a).

Its body mass was estimated at 4.198 kg, being one of the lightest phorusrhacids, most of which weighs more than 10 kg (Taranto & Bergqvist 2010: 118).

Its systematic placement was widely debated. Alvarenga (1985a: 17, 20) initially included it in the Psilopteridae. In favor of a position close to the Phorusrhacidae (possibly even much closer to a common ancestor of the phorusrhacoids), he highlighted the greater size and robustness of the bones when compared to *Psilopterus* (middle Oligocene to the late Miocene of Argentina), and the great similarity with the tarsometatarsus of *Paraphysornis brasiliensis*, resembling a miniaturized version of it. Later, Alvarenga & Höfling (2003: 84) included it in the Psilopterinae subfamily within Phorusrhacidae, highlighting the similarity with *Procarriama simplex* (late Miocene and early Pliocene of Argentina). Mayr (2009: 140) commented that the assignment to that subfamily was based on general similarities, and verification from new specimens is necessary. Agnolin (2009b: 21, 37) excluded the taxon from the Phorusrhacoidea in favor of a placement with the European Cariamoidea Idiornithidae. Tambussi & Degrange (2013: 31, 32) also disagreed with the placement within the Phorusrhacidae Psilopterinae. However, not convinced of the arguments used by Agnolin (2009b) for its inclusion in the Idiornithidae, they considered it a *Cariamiformes incerti familiae* due to its fragmentary nature and a set of characters that it shares with other *Cariamiformes*. Alvarenga *et al.* (2011: 192, 199) maintained the tentative classification within the Phorusrhacidae Psilopterinae, according to the characteristics indicated in Alvarenga & Höfling (2003). Agnolin (2013: 49, 50), rebutting Alvarenga *et al.*, kept his arguments previously presented (Agnolin 2009b). Mayr (2016: 190) pointed out that additional specimens are needed to clarify its classification.

*Paleopsilopterus itaboraiensis* was considered the oldest known member of the Phorusrhacidae (Alvarenga 1985a: 20; Alvarenga & Höfling 2003: 85; Mayr 2009: 140; Alvarenga *et al.* 2011: 187, 188, 201; Mayr 2016: 190). If excluded from Phorusrhacoidea, the best-documented record of Phorusrhacidae in South America would come from the late Eocene of Chubut, Argentina (Tonni & Tambussi 1986 *apud* Angst & Buffetaut 2017: 141, 144). There is also, from a slightly older age (middle Eocene), the material of the Guabirota Formation, state of Paraná, Brazil, pending a more detailed description (see Phorusrhacidae indet. 1; Angst & Buffetaut 2017: 141).

The proximal end of a tarsometatarsus from the late Eocene of the Sarmiento Formation, in Gran Hondonada (province of Chubut, Argentina), was assigned to the genus *Paleopsilopterus* by Acosta Hospitaleche & Tambussi (2005: 129, 130). Agnolin

(2009b: 21, 22) considered it a member of the Idiornithidae, representing a new genus and species. Tambussi & Degrange (2013: 33), mentioning Degrange (2012 *apud* Tambussi & Degrange, 2013: 33), who indicated that the material is not a Phorusrhacidae, noted that it is not possible to verify its systematic position without any additional material.

- Phorusrhacidae - Taranto & Bergqvist 2009: 51R.
- Phorusrhacidae - Taranto *et al.* 2009a: 287.
- *Paleopsilopterus itaboraiensis* - Taranto & Bergqvist 2010: 118.
- *Paleopsilopterus itaboraiensis* [in part?] - Metello *et al.* 2014: 84.
- *Paleopsilopterus itaboraiensis* [in part?] - Metello & Bergqvist 2014: 151.

An unguis phalanx (UFRJ 03-AV), present among material long stored in the collection of the Departamento de Geologia of UFRJ, approximately half the length of that of *Phorusrhacos longissimus*, was first associated with the Phorusrhacidae by Taranto & Bergqvist (2009: 51R) and Taranto *et al.* (2009a: 287), and then to this species by Taranto & Bergqvist (2010: 118). Metello & Bergqvist (2014: 151) mentioned two unguis phalanges associated with this species, possibly listing this material as MCT 1837-R.

- *Paleopsilopterus itaboraiensis* [in part] - Alvarenga *et al.* 2011: 191-192, fig. 7.2.

Alvarenga *et al.* (2011: 191) tentatively attributed to this species five unguis phalanges collected by Rubens da Silva Santos during the 1970s in the same locality as the type material. They are assigned to digits I (MHNT-5320), II (MHNT-5316), III (MHNT-5317 and MHNT-5319) and IV (MHNT-5318).

- *Paleopsilopterus itaboraiensis* - Metello *et al.* 2012b: 140.
- *Paleopsilopterus itaboraiensis* [in part?] - Metello *et al.* 2014: 84.
- *Paleopsilopterus itaboraiensis* [in part] - Metello & Bergqvist 2014: 151.

Another unguis phalanx (MCT 1836-R), attributed to the digit IV, was associated with this species by Metello *et al.* (2012b: 140)—which, strangely, marked it as the first avian unguis phalanx described for the Paleocene [=early Eocene following Woodburne *et al.* 2014b] of South America—and Metello & Bergqvist (2014: 151). Assessing the curvature of the phalanges, Metello & Bergqvist (2014: 151) found support for the assumption of terrestrial habits, reinforcing the theory that the Phorusrhacidae attacked



their prey with their massive skull, but not excluding the possibility of use in their raptorial habits.

## 299. †*Itaboravis elaphrocnemoides* Mayr, Alvarenga & Clarke

Early Eocene - Rio de Janeiro

Fig. 12.C

*Type locality:* São José de Itaboraí, Rio de Janeiro, Southeast Brazil.

*Etymology:* *Itaboravis*, with the Latin *avis*, “Bird of Itaboraí”, and *elaphrocnemoides* referring to the similarity with the genus *Elaphrocnemus*.

- “Une forme très proche du genre *Elaphrocnemus*” [in part?] - Alvarenga (in Mourer-Chauviré 1999): 87.
- “idiornithid-like birds” [in part?] - Mayr 2009: 142.
- “Idiornithidae indeterminado” [in part?] - Agnolin 2009b: 20.
- “unpublished Cariamae, closely related to the European Idiornithidae” [in part?] – Alvarenga *et al.* 2011: 201.
- ***Itaboravis elaphrocnemoides*, gen. et sp. nov.** - Mayr *et al.* 2011a: 679–684, fig. 1.
- *Itaboraves elaphrocnemoides* [lapsus] - Taranto 2012: 11, 51.

The occurrence of a form very similar to *Elaphrocnemus*, a European genus of the late Eocene and Oligocene with three known species (Mayr 2016: 196), for the early Eocene of the São José de Itaboraí Basin was first mentioned by Mourer-Chauviré (1999: 87), through information provided by Herculano Alvarenga. Mayr *et al.* (2011a) described this form as new the genus and species *Itaboravis elaphrocnemoides*.

The fossils are a left coracoid (MN 4114-V, holotype), a right humerus (MN 4113-V), and the distal end of a left humerus (MN 4121-V). Alvarenga, one of the study’s authors, was informed by Fausto Cunha in 1985 that specimens MN 4113-V and MN 4114-V come from the same calcareous matrix block of approximately 1.4 kg, which also contained many small bones not belonging to birds. Furthermore, both bones share the same color, have equivalent sizes, and are similar to those of the genus *Elaphrocnemus*, leading the authors to believe that they belonged to the same individual (Mayr *et al.* 2011a: 680).

The coracoid has the size of a bird the size of *Crypturellus tataupa*. The humerus also has a certain affinity to the Tinamidae (Mayr *et al.* 2011a: 680) and indicates a poor flight capacity, comparable to that of the living tinamids (Mayr *et al.* 2011a: 684).

Mayr *et al.* (2011a: 680) considered the affinity with *Elaphrocnemus* the best supported in the face of the evidence available then, tentatively attributing the material from Itaboraí to the Cariamae (*sensu* Mayr 2009). They noted, however, that such a classification is based on general similarities, and that if the indeterminate carpometacarpus MN 4115-V (see Aves indet. 1) belongs to this taxon, *Itaboravis* may represent the trunk group of Tinamidae with a coracoid of different morphology.

*Elaphrocnemus* was for a long time (including the time of *Itaboravis* description) placed within the Idiornithidae, a stem group of European Cariamiformes. Their phylogenetic affinities are not convincingly resolved, showing similarities to both Cariamiformes and Opisthocomiformes, and, in any case, likely they do not belong to a clade comprising the Idiornithidae, Phorusrhacidae, and Cariamidae (Mayr 2016: 195, 196). Accordingly, Mayr (2016: 196) also noted that *Itaboravis* kinship is equally uncertain. Regardless of its classification, *I. elaphrocnemoides* supports the evidence that the avifaunas of the beginning of the Cenozoic were already diversified (Mayr *et al.* 2011a: 684).

## **Cariamidae**

### **300. *Cariama cristata* (Linnaeus)**

Quaternary - Minas Gerais

- *Dicholophus cristatus* - Winge 1887: 31.
- *Cariama cristata* - Lambrecht 1933: 761.
- *Cariama cristata* - Brodkorb 1967: 173.
- *Cariama cristata* (“*Dicholophus cristatus*”) - Mones 1986: 89.
- *Cariama cristata* - Cuello 1988: 44.
- *Cariama cristata* - Nascimento & Silveira 2020: 494.

Winge (1887: 31) reported part of the proximal end of a slightly rolled tarsometatarsus from Lapa da Lagoa do Sumidouro.

## †Phorusrhacidae

### 301. †Phorusrhacidae indet. 1

Middle Eocene - Paraná

- Phorusrhacidae - Sedor *et al.* 2014a: 614.
- Aves - Cunha *et al.* 2014: 691.
- Phorusrhacidae - Sedor *et al.* 2014b: 807.
- Phorusrhacidae - Cunha 2016: 68.
- Phorusrhacidae - Sedor *et al.* 2016: 40.

Sedor *et al.* (2014b: 807) reported phorusrhacid remains from the Guabirota Formation (Fig. 2.4), in the Curitiba Basin, Paraná, with an estimated age at the end of the middle Eocene (Barrancan SALMA [Sedor *et al.* 2016: 50, 51, 52]). The fossils were found on an outcrop at the border of the municipalities of Curitiba and Araucária (Sedor *et al.* 2014a: 614).

The material consists of a large isolated cervical vertebra, corresponding to the most caudal part of the neck (C7 to C10), and the distal end of a tarsometatarsus, deposited in the paleontological collection of the Museu de Ciências Naturais da Universidade Federal do Paraná (Sedor *et al.* 2014b: 807).

The bird lived in floodplains, in predominantly humid climatic conditions alternating with drier periods, and the region's fauna was also composed of gastropods and other invertebrates, bony fishes, anurans, testudines, sebecosuchian crocodylians and cingulates, notoungulates, astrapotheres, and metatherians (Sedor *et al.* 2014a: 614; Sedor *et al.* 2016: 39, 40, 52).

### 302. †Phorusrhacidae indet. 2

Late Miocene - Acre

- Phorusrhacidae - Alvarenga 1992: 254.
- [might be referred to the] Phorusrhacinae - Tambussi & Noriega 1996: 252.
- Phorusrhacinae indet. - Latrubesse *et al.* 1997: 112.
- Phorusrhacidae indet - Bocquentin & Silva 1998: 154.
- Phorusrhacinae gen. et sp. indet. - Negri & Ferigolo 1999: 18.
- “Género y especie indeterminados” - Agnolin 2009b: 56.

Phorusrhacid remains from Acre were first reported by Alvarenga (1992: 254), who mentioned “several bones of a gigantic bird (Phorusrhacidae), not yet studied” collected by researchers at the Natural History Museum of Los Angeles County, through personal communication with Kenneth E. Campbell. Tambussi & Noriega (1996) commented that the fragmentary remains might be referred to the Phorusrhacinae, which, if confirmed based on additional material, would be the first member of the subfamily in Brazil. They were later listed by Latrubesse *et al.* (1997: 112), Bocquentin & Silva (1998: 154), Negri & Ferigolo (1999: 18) and Agnolin (2009b: 56).

The material comes from Niterói site (Negri & Ferigolo 1999: 18) and is composed of pedal phalanges, deposited without number in the collection of the Laboratório de Pesquisas Paleontológicas of Universidade Federal do Acre (Bocquentin & Silva 1998: 154; Agnolin 2009b: 56). Agnolin (2009b: 56) commented that, despite being incomplete, they could be attributed to the subfamily Phorusrhacinae (*sensu* Agnolin 2009b) for its large size and for presenting a higher than wide proximal articular face, a character shared with the genera *Devincenzia*, *Paraphysornis*, and *Physornis*.

### 303. †*Paraphysornis brasiliensis* (Alvarenga)

Late Oligocene/Early Miocene - São Paulo

Figs. 4.A–B, 13.B

*Type locality*: Municipality of Tremembé, district of Padre Eterno, near the right bank of the river Paraíba do Sul, state of São Paulo.

*Etymology*: *Paraphysornis*, with the Greek “*para*” (close to), alluding to the related genus *Physornis*, and *brasiliensis*, referring to Brazil.

- *Physornis brasiliensis* - Alvarenga 1982: 697–712, figs. 1–16.
- “ave gigante” - Sick 1984a: 65.
- *Physornis brasiliensis* - Mones 1986: 88.
- *Physornis brasiliensis* - Cuello 1988: 16.
- *Physornis brasiliensis* - Alvarenga 1993a: 62, fig. 34.
- *Paraphysornis brasiliensis* - Alvarenga 1993c: 403–406, figs. 1–2.
- *Paraphysornis brasiliensis* - Alvarenga 1997: 123, fig. 34.
- *Paraphysornis brasiliensis* - Kellner 1998: 654, 659.
- *Paraphysornis brasiliensis* - Alvarenga & Höfling 2000: 590, fig. 31.9.
- *Paraphysornis brasiliensis* - Alvarenga & Höfling 2003: 70, figs. 1–4, 6, 15–17, 34.

- *Paraphysornis brasiliensis* - Alvarenga & Höfling 2004: 828, fig. 44.9.
- *Paraphysornis brasiliensis* - Agnolin 2009b: 53-54, figs. 1–2, 23, 29, 32, 42, 52.
- *Paraphysornis brasiliensis* - Jones 2010: 10, figs. 2.4–2.5, 2.8, 4.4–4.9, E.6–E.7.
- *Paraphysornis brasiliensis* - Alvarenga *et al.* 2011: 201, figs. 7.1, 7.3–7.6, 7.8–7.10.
- *Paraphysornis brasiliensis* - Alvarenga & Höfling 2011: 128, fig. 7.11.
- *Paraphysornis brasiliensis* - Angst & Buffetaut 2017: 137, figs. 5.1, 5.9–5.10.

Alvarenga (1982) described the species from well-preserved and sparse fragments found in the bentonite clay, two or three meters below the pyrobituminous shales, collected during several months between 1977 and 1978 in the Taubaté Basin, in Tremembé, São Paulo.

The holotype is an incomplete skeleton (DGM 1418-R), which lacks most of the skull and premaxilla, pelvis, and sternum, with the other bones being well represented and some even complete—about 70% of the total is present (Alvarenga *et al.* 2011: 195). Alvarenga (1982: 697) further mentioned many bone fragments accompanying the specimen, which may provide new information about its anatomy. In the original description, the figured elements were the mandible lacking the right branch, left quadrate, left pterygoid, left supraorbital, skullcap fragment, premaxilla extremity fragment, cervical vertebrae (C-1 [atlas], C-2 [axis]), C-3, C-10, and C-11, out of a total of thirteen), thoracic vertebrae (T-1, T-2, T-3, T-4, and T-5; a sixth is said to appear to be attached to the pelvis) and caudal vertebrae (one more anterior and one more posterior), the anterosuperior portion of the pelvis, fragments of dorsal ribs (seven pieces) and sternal ribs (two fragmented and one complete), left coracoid (which indicates, along with the sternal ribs, the presence of a well-developed sternum), left and right humerus, left ulna, proximal half of the left radius, left and right carpometacarpi, proximal and distal phalanges of the left second digit of the wing, left and right femora (both lacking a segment of the diaphysis), left and right tibiotarsi, left and right fibulae, left and right tarsometatarsi, metatarsal bone of the left hallux, nine phalanges of the left foot (second and unguis of the digit II, third and unguis of the digit III and first, second, third, fourth, and unguis of the digit IV), and the fourth phalanx of the digit IV of the right foot. A partial reconstruction of the skeleton was presented, with the posture in life, in addition to a life reconstruction of the bird. Alvarenga *et al.* (2011: 194, 196, 197, 198, 199) figured a fragment that appears to belong to the cranial end of the left

clavicle and fragments of the pelvis<sup>29</sup> that preserved the cranial parts of the ischium and the caudal projections of the two pubes, all not originally described by Alvarenga (1982). There are also figured three cervical vertebrae (third and possibly the tenth and eleventh), one thoracic vertebra, the reconstructed first pre-synsacral thoracic vertebrae, and remains of the cranial end of the iliac dorsal crest.

The bird had a large head, with a strong jaw approximately half a meter long (Alvarenga 1982: 698, 712). Alvarenga (1982: 710, 712), after restoring the skeleton, initially calculated that it reached around 2 m in height, being able to reach 3 m at the tip of the beak when keeping the legs and spine stretched. Later, Alvarenga & Höfling (2003: 59, 70) estimated 140 cm of height on the back, reaching 240 cm with the head stretched, and a weight of approximately 180 kg, being perhaps the smallest of the Brontornithinae (*sensu* Alvarenga & Höfling, 2003). The wings were quite small, and the ulna has no marks of remige insertions (Alvarenga 1982: 702, 703). The second toe has a very wide, curved, and strong claw, probably important for holding prey (Alvarenga 1982: 709).

Alvarenga (1982: 707, 712) proposed that due to the relatively short and thick tarsometatarsus (a little longer than half the length of the tibiotarsus), the bird seems to have been slower and unfit to run when compared to other species of the family, perhaps having been a scavenger. Alvarenga & Höfling (2003: 60) supported this theory of graviportality (applying it also to the other Brontornithinae) through the fact that the Tremembé Formation, of lacustrine nature, presented periods of drought, with a high fish mortality rate, and the only known skeleton of the species may have come from an individual who succumbed to this swampy land when looking for these fish and other dead animals. This same food source possibly also attracted the Cathartiformes (*Brasilogyps* and *Taubatornis*) found in the same place. The attribution of necrophagy as the main dietary form of the larger species, while the smaller ones would be active predators, was also mentioned by other authors (Tonni 1977 and Tambussi & Hoffmann 1998 *apud* Agnolin 2009b: 43). Jones (2005 *apud* Jones 2010: 129) reported that the conformation of the tibiotarsus of *Paraphysornis* (as well as that of *Brontornis*) could

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<sup>29</sup> In the body of the text in Alvarenga *et al.* (2011: 198), the associated identification is DGM-1014, but in the figures, it is that of the holotype skeleton, DGM-1418-R.

be associated with the ability to break bones proposed to other species by Blanco & Jones (2005: 1771, 1772), relating with inferences about possible scavenging habits.

Jones (2010: 29) proposed that *Paraphysornis* and *Brontornis* could have horny sheaths in the curveless ungual phalanges, especially in digit III, as in the large living running birds (e.g., struthionids, rheids, and otidids). However, he also noted (Jones 2005 *apud* Jones 2010: 128, 129; Jones 2010: 129) that from the ungual phalanges of Brontornithinae (*sensu* Alvarenga & Höfling 2003), the graviportal condition can only be expressed due to its robust character and lateral expansion of the pedal phalanges, and, added to the study of the proportions of the bones of the legs, they would not present prominent cursorial habits.

Tambussi & Degrange (2013: 43), noting that the tarsometatarsus of *Paraphysornis* is similar in general to that of *Dromornis stirtoni* (late Miocene of Australia), pointed out the contrast of Alvarenga's theory (1982) with that of Murray & Vickers-Rich (2004), who argued that high masses would not limit the cursorial skills of the dromornithids and that even those estimated at 500 kg were able to run. However, the pelvis, an important element for establishing locomotor and postural habits (Degrange 2012 *apud* Tambussi & Degrange 2013: 43), was not found complete. Tambussi & Degrange (2013: 89) also noted that the known cranial remains of *Paraphysornis* include the mandible and the quadrate of which the morphology itself is not indicative of trophic habits, and care should be taken when associating it with any.

Angst *et al.* (2016: 219, 221; see also Angst & Chinsamy-Turan 2016: 3) also pointed to *Paraphysornis* as a bird with relatively slow graviportal locomotion, possibly due to the biomechanical limitations of its size and body mass. However, they noted, keeping in mind that its skull clearly demonstrates adaptation to a carnivorous diet, the bird may have used a specific hunting method, having been an ambush predator or, as already mentioned in its original description (Alvarenga 1982), a scavenger. Angst & Buffetaut (2017: 153) added the possibility that the more robust phorusrhacids attacked large and slow prey, such as astrapotheres and pyrotheres, also found in the Tremembé Formation.

In the original description, the taxon was provisionally attributed to the genus *Physornis* (originally from the Oligocene of the province of Santa Cruz, Argentina), in

the subfamily Brontornithinae (Alvarenga 1982: 710). Subsequently, Alvarenga (1993c: 403, 404), aiming to review the family, examined the referred material in museums in Argentina, the United States, England, and France, focusing on his comparisons with the specimen from the Taubaté Basin. He concluded that the Brazilian species is significantly different from *Brontornis burmeisteri* and *Physornis fortis*, although closer to the latter, and erected the new genus *Paraphysornis*.

Alvarenga & Höfling (2003: 64, 70) kept the taxon within the Brontornithinae, as perhaps the smallest of their representatives. Agnolin (2007: 21), excluding *Brontornis* from the Phorusrhacidae in favor of a basal position in the Anseriformes<sup>30</sup>, coined the subfamily Physornithinae to include *Physornis* and *Paraphysornis*. Later, Agnolin (2009b: 51, 52) included *Paraphysornis* in the Phorusrhacinae Physornitini, along with *Physornis* and *Devincenzia*. Alvarenga *et al.* (2011: 200, 201), not supporting Agnolin's theory, kept *Paraphysornis* along with *Brontornis* and *Physornis* in the Phorusrhacidae Brontornithinae, with *Devincenzia* in the Phorusrhacinae. Angst & Buffetaut (2017: 136, 137) followed Agnolin for *Brontornis* and kept *Paraphysornis* in the Phorusrhacinae, not mentioning any tribes.

## **Falconiformes**

### **304. Falconiformes (*sensu lato?*) indet.**

Holocene - Rio Grande do Norte

- Falconiformes - Silva 2014: 133.

Silva (2014: 133) reported Falconiformes (*sensu lato?*) material among zooarcheological remains of holocenic age collected by the team of NEA-UFPE starting in the 1990s in rock shelters of Pedra do Alexandre site, in Carnaúba dos Dantas, Rio Grande do Norte.

## **Falconidae**

### **305. *Micrastur* sp.**

Quaternary - Minas Gerais

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<sup>30</sup> Its classification is debated, varying according to the author (Angst & Buffetaut 2017: 161).



- *Micrastur* sp. e majoribus (*M. melanoleucus?*) - Winge 1887: 34.
- *M. cfr. melanoleucus* (?) - Lambrecht 1933: 751.
- *Micrastur semitorquatus* - Brodkorb 1964: 296.
- *Micrastur semitorquatus* - Mones 1986: 85.
- *Micrastur semitorquatus* – Cuello 1988: 39.
- *Micrastur* sp. - Nascimento & Silveira 2020: 495.

Winge (1887: 34) reported the distal ends of a humerus and a tibiotarsus of unknown origin. The length is greater than in *Micrastur ruficollis*, and the shape is equal to that of *Micrastur semitorquatus*, but it is somewhat shorter than the specimen used for comparison, which is large, probably a female, and the bones of the cave possibly being a small male. Winge also noted that it differs considerably from *Milvago* and *Polyborus*, and that from *Herpetotheres* there was no material available for comparison.

### **306. *Micrastur ruficollis* (Vieillot)**

Quaternary - Minas Gerais

- *Micrastur ruficollis* - Winge 1887: 34.
- *Micrastur ruficollis* - Lambrecht 1933: 751.
- *Micrastur ruficollis* - Brodkorb 1964: 296.
- *Micrastur ruficollis* - Mones 1986: 85.
- *Micrastur ruficollis* - Cuello 1988: 39.
- *Micrastur ruficollis* - Nascimento & Silveira 2020: 495.

From Lapa da Escrivânia V, Winge (1887: 34) reported two left humeri.

### **307. *Caracara plancus* (Miller)**

Quaternary - Minas Gerais, Piauí

- *Polyborus tharus* - Winge 1887: 34.
- *Polyborus tharus* - Lambrecht 1933: 750.
- *Caracara plancus* - Brodkorb 1964: 296.
- *Caracara plancus* (“*Polyborus tharus*”) - Mones 1986: 85.
- *Polyborus plancus* - Cuello 1988: 39.
- *Caracara plancus* - Nascimento & Silveira 2020: 494.

Winge (1887: 34) reported bones of several individuals from Lapa da Escrivânia V, young or very young, listing the coracoid, humerus, ulna, femur, tibiotarsus, and

tarsometatarsus, all slightly smaller than that observed in two fresh skeletons. He also reported the tarsometatarsus of a very young individual from Lapa da Escrivânia XI.

- Accipitridae [?] [in part] - Guérin *et al.* 1993a: 198.
- Falconidae [?] [in part?] - Guérin *et al.* 1993a: 198.
- Accipitridae [?] [in part] - Guérin *et al.* 1993b: 328.
- Falconidae [?] [in part?] - Guérin *et al.* 1993b: 328.
- *Polyborus plancus* - Guérin *et al.* 1996: 84.
- *Polyborus plancus* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **308. *Milvago chimachima* (Vieillot)**

Quaternary - Minas Gerais

- *Milvago chimachima* - Winge 1887: 34.
- *Milvago chima chima* [sic] - Lambrecht 1933: 749.
- *Milvago chimachima* - Brodkorb 1964: 296.
- *Milvago chimachima* - Mones 1986: 85.
- *Polyborus chimachima* - Cuello 1988: 39.
- *Milvago chimachima* - Nascimento & Silveira 2020: 494.

Winge (1887: 34) reported a tarsometatarsus among the aforementioned large number of bones from Lapa da Escrivânia V.

### **309. *Milvago chimango* (Vieillot)**

Quaternary - Minas Gerais

- *Milvago chimango* - Winge 1887: 34.
- *Milvago chimango* - Brodkorb 1964: 296.
- *Polyborus chimango* - Cuello 1988: 39.
- *Milvago chimango* - Nascimento & Silveira 2020: 494.

Winge (1887: 34) associated with this species a tarsometatarsus and two tibiotarsi out of some bones which he determined as *Milvago* (which then included *Milvago chimango*) from Lapa da Escrivânia V, including young specimens. Most of the bones probably belong to *Phalcoboenus chimango* instead of *Milvago chimachima*, but it was not possible to determine with certainty. Winge also noted that, unlike *M. chimachima*,

which is quite common in the area, *P. chimango* was known to live in the Lagoa Santa region.

### **310. *Falco sparverius* Linnaeus**

Quaternary - Minas Gerais, Piauí

- *Falco (Tinnunculus) sparverius* - Winge 1887: 34–35.
- *Falco sparverius* - Lambrecht 1933: 750.
- *Falco sparverius* - Brodkorb 1964: 296.
- *Falco sparverius* - Mones 1986: 85.
- *Falco sparverius* - Cuello 1988: 40.
- *Falco sparverius* - Nascimento & Silveira 2020: 495.

Winge (1887: 34, 35) reported remains of several individuals from Lapa da Escrivânia V, both adult and young, a coracoid from Lapa da Escrivânia XI, and several bones of recent age<sup>20</sup>, two of which were determined by Lund. The total material is represented by the thoracic vertebra, scapula, coracoid, sternum, humerus (in large number), ulna, carpometacarpus, pelvis, femur, tibiotarsus, and tarsometatarsus, showing considerable individual variation, especially in the material from Lapa da Escrivânia V, with individuals larger than a female *Falco sparverius*. However, Winge noted that it was not possible to establish a division between smaller and larger sets of bones.

- Accipitridae [?] [in part] - Guérin *et al.* 1993a: 198.
- Falconidae [?] [in part?] - Guérin *et al.* 1993a: 198.
- Accipitridae [?] [in part] - Guérin *et al.* 1993b: 328.
- Falconidae [?] [in part?] - Guérin *et al.* 1993b: 328.
- *Falco sparverius* - Guérin *et al.* 1996: 84.
- *F. sparverius* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material.

### **311. *Falco ruficularis* Daudin**

Quaternary - Piauí

- Accipitridae [?] [in part] - Guérin *et al.* 1993a: 198.
- Falconidae [?] [in part?] - Guérin *et al.* 1993a: 198.
- Accipitridae [?] [in part] - Guérin *et al.* 1993b: 328.

- Falconidae [?] [in part?] - Guérin *et al.* 1993b: 328.
- *Falco rufigularis* - Guérin *et al.* 1996: 84.
- *Falco rufigularis* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least one adult individual is present in the material. This is one of the taxa that the authors highlighted as no longer living in the region today.

### **312. *Falco cf. femoralis* Temminck**

Quaternary - Minas Gerais

- *Falco femoralis* (fere certe) - Winge 1887: 35.
- *Falco femoralis* - Lambrecht 1933: 750.
- *Falco femoralis* - Brodkorb 1964: 294.
- *Falco femoralis* - Mones 1986: 85.
- *Falco femoralis* - Cuello 1988: 40.
- *Falco cf. femoralis* - Nascimento & Silveira 2020: 495.

Winge (1887: 35) reported remains of several individuals from Lapa da Escrivânia V, adult and young, represented by the coracoid, humerus, ulna, femur, and tarsometatarsus. The bones closely match *Falco rufigularis* but are larger and almost certainly belong to *Falco femoralis*, being close in shape, although smaller than in the fresh bones of a female used in the comparison. There is a marked variation in size among the bones found in the caves, but this is also observable in *F. femoralis*, with the female being larger than the male. Winge noted that even the smaller bones are slightly larger than the equivalent in a female *F. rufigularis* and that *Falco deiroleucus*, which does not live in the region, was not compared.

## **Psittaciformes**

### **Psittacidae**

#### **313. Psittacidae indet. 1 (spp.?)**

Quaternary - Minas Gerais

- Psittaciformes - Souza-Cunha & Magalhães 1986: 122.
- Psittacidae indet (spp.?) - Nascimento & Silveira 2020: 495.

Souza-Cunha & Magalhães (1986) noted that psittacids may figure among the avian remains from Cerca Grande, municipality of Matozinhos, Minas Gerais.

### **314. Psittacidae indet. 2**

Quaternary - Goiás

- Psittacidae [*sic*] - Paulo 2009: 142.

Paulo (2009: 142) reported material associated with the family, including beaks and other fragments, to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

### **315. Psittacidae indet. 3**

Holocene - Rio Grande do Norte

- Psittaciformes [*sic*] - Silva 2014: 133.

Silva (2014: 133) reported Psittaciformes material among zooarcheological remains of holocenic age collected by the team of NEA-UFPE starting in the 1990s in rock shelters of Pedra do Alexandre site, in Carnaúba dos Dantas, Rio Grande do Norte.

### **316. Arinae indet. 1**

Quaternary - Minas Gerais

- *Ara* sp. e minoribus, præcedente [*Ara maracana* et aff.] major - Winge 1887: 41.
- *Sittace* sp. [in part] - Goeldi 1894: 129.
- *Ara* sp. (“kleinere und größere Formen”) [in part] - Lambrecht 1933: 770.
- “undetermined macaws” [in part] - Boles 2017: 10.
- Arini indet. 1 - Nascimento & Silveira 2020: 495.

Winge (1887: 41) reported the distal end of a humerus from Lapa da Escrivânia V, larger than in *Primolius maracana*, but smaller than in the specimen labeled here as *Ara* sp. (“*Ara* sp. e majoribus”). He noted morphological differences between this humerus and that of a recent *P. maracana*, but also similarities between it and the two smaller humeri determined as fossil *P. maracana*. He added that the mentioned forms are very distinctive from *Cyanoliseus patagonus*.

### 317. *Arinae* indet. 2

Quaternary - Minas Gerais

- *Ara chloroptera* (et forte *A. hyacinthina*) [in part] - Winge 1887: 42.
- *Sittace hyacinthina* (?) - Goeldi 1894: 129.
- *Ara chloroptera* [in part] - Lambrecht 1933: 770.
- *Ara chloroptera* [in part] - Brodkorb 1971: 212.
- *Ara chloroptera* [in part] - Mones 1986: 94.
- *Ara chloroptera* [in part] - Cuello 1988: 53.
- *Ara chloropterus* [in part] - Boles 2017: 10.
- Arini indet. 2 - Nascimento & Silveira 2020: 495.

Winge (1887: 42) reported some bones under “*Ara chloroptera* (et forte *A. hyacinthina*)” from Lapa da Lagoa do Sumidouro, represented by the coracoid, ulna, and femur. He noted that they are similar in size to the remains determined as *Ara chloropterus*, but bear some differences in shape, being likely other species than *Ara ararauna*, possibly *Anodorhynchus hyacinthinus*, of which he had no bones available for comparison.

### 318. *Brotogeris chiriri* (Vieillot)

Quaternary - Minas Gerais

- *Brotogeris xanthoptera* - Winge 1887: 40.
- *Brotogeris xanthoptera* - Lambrecht 1933: 770.
- *Forpus coelestis* - Brodkorb 1971: 213.
- *Forpus coelestis* (“*Brotogeris xanthoptera*”) - Mones 1986: 95.
- *Forpus coelestis* (“alguna forma de *Forpus xanthopterygius*”) - Cuello 1988: 53.
- *Brotogeris chiriri* - Boles 2017: 10.
- *Brotogeris chiriri* - Nascimento & Silveira 2020: 495.

Winge (1887: 40) reported several individuals from Lapa da Escrivânia V, represented by the coracoid, humerus, ulna, and femur (this being the most uncertain), a humerus from Lapa da Lagoa do Sumidouro, and several bones linked by soft tissues of recent age<sup>20</sup>, including a humerus still attached to the scapula and the coracoid.

Brodkorb (1971: 213) associated the record with *Forpus coelestis*. Regarding this, Cuello (1988: 53) noted that, since this species was never recorded in Brazil, “it is

likely that Winge's designation may be referred to some form of *Forpus xanthopterygius*".

The names *Brotogerys xanthoptera* (Spix) of Winge (1887: 6) and the one which he probably guided himself, *Conurus xanthopterus* (Spix) of Reinhardt (1870: 83) (originally *Aratinga xanthopterus* Spix [1824: 31], not *Psittaculus xanthopterygius* Spix [1824: 38]) are synonyms with *Brotogeris chiriri* (Hellmayr 1906: 580). Krabbe (2007: 339), while reviewing the skins collected by Lund and Reinhardt, associated the name *Conurus xanthopterus* of Reinhardt with *Brotogeris chiriri chiriri*, while *Forpus xanthopterygius* was associated with *Psittacula passerina* (L.) (= *Forpus passerinus*) of Reinhardt (1870: 86).

### **319. cf. *Amazona* sp.**

Quaternary - Minas Gerais

- “un Perroquet (*Psittacus*)” [?; in part] - Gervais 1844a: 294.
- “une espèce du groupe des perroquets” [?; in part] - Liais 1872: 303.
- *Psittacus* aff. *guyanensi* [in part] - Lund (in Winge 1887): 40.
- *Chrysotis* sp. e minor., vel g. aff. - Winge 1887: 40.
- *Chrysotis* sp. (“mehrere Arten”) [in part] - Lambrecht 1933: 770.
- *Psittacus* sp. [?; in part] - Lambrecht 1933: 770.
- *Chrysotis* sp. [in part] - Mones 1986: 95.
- “undetermined amazons” [in part] - Boles 2017: 10.
- cf. *Amazona* sp. - Nascimento & Silveira 2020: 495.

Winge (1887: 40) reported a humerus and a tarsometatarsus that match well to the next species in shape (but are smaller) from Lapa da Escrivânia V, besides an ulna, too big for this humerus, but too small to the smallest humerus of the previous species. From Lapa da Escrivânia XI, material represented by the coracoid, humerus, and carpometacarpus, equivalent to the bones found in Lapa da Escrivânia V. From a “saltpeter cave near Escrivânia”, a humerus. Finally, from an unknown locality, the distal end of a humerus (“*Psittacus* aff. *guyanensi*” in Lund's catalog), very similar to the first humerus mentioned.

### **320. *Amazona* sp.**

Quaternary - Minas Gerais

- *Chrysotis* sp., magnitude *Ch. amazonicæ* etc. - Winge 1887: 40.
- *Chrysotis* sp. (“mehrere Arten”) [in part] - Lambrecht 1933: 770.
- *Amazona amazonica* - Brodkorb 1971: 213.
- *Amazona amazonica* (“*Chrysotis* sp.” [in part]) - Mones 1986: 94–95.
- *Amazona amazonica* - Cuello 1988: 53.
- “undetermined amazons” [in part] - Boles 2017: 10.
- *Amazona* sp. - Nascimento & Silveira 2020: 495.

Winge (1887: 40) reported bones in general comparable in size with *Amazona amazonica*. From Lapa da Escrivânia V, several individuals, varying in size, represented by the coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus, and from Lapa da Escrivânia XI, a coracoid and an ulna.

### **321. *Amazona* cf. *aestiva* (Linnaeus)**

Quaternary - Piauí

- Psittacidae [in part] - Guérin *et al.* 1993a: 198.
- Psittacidae [in part] - Guérin *et al.* 1993b: 328.
- cf. *Amazona aestiva* - Guérin *et al.* 1996: 84.
- cf. *Amazona aestiva* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material comparable with the species from Toca da Janela da Barra do Antonião. At least one adult and one young individuals are present in the material.

### **322. *Pyrrhura frontalis* (Vieillot)**

Quaternary - Minas Gerais

- *Pyrrhura vittata* - Winge 1887: 41.
- *Pyrrhura vittata* - Lambrecht 1933: 770.
- *Pyrrhura frontalis* - Brodkorb 1971: 213.
- *Pyrrhura frontalis* (“*Pyrrhura vittata*”) - Mones 1986: 95.
- *Pyrrhura frontalis* - Cuello 1988: 52.
- *Pyrrhura frontalis* - Boles 2017: 10.
- *Pyrrhura frontalis* - Nascimento & Silveira 2020: 495.

Winge (1887: 41) reported four humeri and two carpometacarpi from Lapa da Escrivânia V.



### **323. *Anodorhynchus* sp.**

Quaternary - Minas Gerais

- Psittacidae - Cunha & Guimarães 1978: 219, fig. 11.
- “extinct undescribed *Anodorhynchus*” - Alvarenga (in Yamashita 1997): 181.
- *Anodorhynchus glaucus* ou *A. leari* - Alvarenga 2007b: 427–432, figs. 2–3.
- *Anodorhynchus* sp. - Nascimento & Silveira 2020: 495.

Alvarenga (2007b) determined as *Anodorhynchus glaucus* (Vieillot) or *A. leari* Bonaparte an almost complete maxilla (MNRJ-A-LV 81) discovered by the Franco-Brazilian archeological mission (1971–1976) in Lapa Vermelha IV, in Confins, Minas Gerais, briefly mentioned and figured by Souza Cunha & Guimarães (1978; 1981–1982).

The estimated age for the sediments in which the bone was found is 9,000 years BP. The identical size and shape of the specimen compared to *A. glaucus* or *A. leari* and the geographical location between the known distribution areas of these two species do not allow for a more precise determination. However, Alvarenga found that it is quite unlikely to represent a still-unknown species, despite an earlier mention as such in Yamashita (1997). Based on the data obtained from the remains found in Bahia (see below) and Minas Gerais, and by comparing the skins and skeletons of these two species, Alvarenga reinforced the interpretation that they represent geographic races or subspecies, suggesting a contiguous geographic distribution and clinal variation of the plumage at least 10,000 years in age.

### **324. *Anodorhynchus leari* Bonaparte**

Late Pleistocene - Bahia

- *Anodorhynchus leari* - Alvarenga 2007b: 427–432, figs. 4–7.

In addition to the material from Minas Gerais, Alvarenga (2007b) described bones collected by the paleontologist Cástor Cartelle in Gruta dos Brejões, Morro do Chapéu, Bahia, which he associated with *Anodorhynchus leari*, considering its geographical origin. Besides other bird bones (such as from *Wingegyps cartellei*), megafauna remains have also been found at the same site.

The material, estimated to be approximately 12,000 years old, consists of an incomplete mandible (CLA 821) and complete and well-preserved post-cranial bones, which possibly belong to a single individual, a right (CLA 1693) and a left (CLA 1709) coracoids, a left tibiotarsus (CLA 1707), and a right tarsometatarsus (CLA 1769).

### **325. *Eupsittula aurea* (Gmelin)**

Quaternary - Minas Gerais

- *Conurus aureus* - Winge 1887: 41.
- *Conurus aureus* - Lambrecht 1933: 770.
- *Aratinga aurea* - Brodkorb 1971: 213.
- *Aratinga aurea* (“*Conurus aureus*”) - Mones 1986: 95.
- *Aratinga aurea* - Cuello 1988: 53.
- *Eupsittula aurea* - Boles 2017: 10.
- *Eupsittula aurea* - Nascimento & Silveira 2020: 495.

Winge (1887: 41) reported bones of several individuals from Lapa da Escrivânia V, including the coracoid (rather dubious), humerus, ulna, carpometacarpus, tibiotarsus, and tarsometatarsus. This material also had its provenance erroneously listed as Lapa da Escrivânia XI by Lambrecht (1933: 770) and as “Salpeterhule” by Brodkorb (1971: 213).

### **326. *Eupsittula cf. cactorum* (Kuhl)**

Quaternary - Piauí

- Psittacidae [in part] - Guérin *et al.* 1993a: 198.
- Psittacidae [in part] - Guérin *et al.* 1993b: 328.
- cf. *Aratinga cactorum* - Guérin *et al.* 1996: 84.
- cf. *A. cactorum* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported archeofaunal material comparable with the species from Toca da Janela da Barra do Antonião. At least two adult individuals are present in the material.

### **327. *Primolius maracana* (Vieillot)**

Quaternary - Minas Gerais

- *Ara maracana* et aff. - Winge 1887: 41.
- *Sittace maracanã* [sic] - Goeldi 1894: 129.
- *Ara maracana* - Lambrecht 1933: 770.
- *Ara maracana* - Brodkorb 1971: 212.
- *Ara maracana* - Mones 1986: 94.
- *Ara maracana* - Cuello 1988: 53.
- *Primolius maracana* - Boles 2017: 10.
- *Primolius maracana* - Nascimento & Silveira 2020: 495.

Winge (1887: 41) reported, from Lapa da Escrivânia V, the distal end of a humerus that is similar to that of *Primolius maracana*, and an ulna, slightly different, but that he also considered belonging to the species. There are possibly two other humeri that show possible individual variations from the same site. Additionally, he reported an incomplete humerus from Lapa da Escrivânia XI.

### **328. *Ara* sp.**

Quaternary - Minas Gerais

- *Ara* sp. e majoribus - Winge 1887: 41.
- *Sittace* sp. [in part] - Goeldi 1894: 129.
- *Ara* sp. (“kleinere und größere Formen”) [in part] - Lambrecht 1933: 770.
- “undetermined macaws” [in part] - Boles 2017: 10.

Winge (1887: 41) reported a humerus from Lapa da Escrivânia V, shorter than in the compared specimens of *Ara ararauna*, *Ara macao*, and *Ara chloropterus*, but larger than in *Primolius maracana*. Additionally, there is the distal end of a femur from “various caves”<sup>18</sup>, matching in size the humerus from Lapa da Escrivânia, on which Winge commented that the femur of *A. ararauna* is about the same size.

### **329. *Ara chloropterus* Gray**

Quaternary - Minas Gerais, Rio de Janeiro, Piauí

- *Ara chloroptera* (et forte *A. hyacinthina*) [in part] - Winge 1887: 42.
- *Sittace chloroptera* - Goeldi 1894: 129.
- *Ara chloroptera* [in part] - Lambrecht 1933: 770.
- *Ara chloroptera* [in part] - Brodkorb 1971: 212.
- *Ara chloroptera* [in part] - Mones 1986: 94.

- *Ara chloroptera* [in part] - Cuello 1988: 53.
- *Ara chloropterus* [in part] - Boles 2017: 10.

Winge (1887: 42) reported some bones of two individuals from Lapa da Escrivânia V, represented by the scapula, humerus, ulna, carpometacarpus, first phalanx of the second digit of the wing, femur, and tarsometatarsus. This material is insignificantly smaller than in the compared specimen of *Ara chloropterus* and much bigger than two of *Ara macao*, in addition to showing somewhat more marked differences in size and shape than *Ara ararauna*. He also reported some bones belonging to at least three individuals from Lapa da Escrivânia XI, represented by the coracoid, humerus, ulna, radio, carpometacarpus, first phalanx of the second digit of the wing, pelvis, femur, tibiotarsus, and tarsometatarsus, all slightly larger than the material of Lapa da Escrivânia V and about the same size as in *A. chloropterus*.

- Psittacidae [in part] - Guérin *et al.* 1993a: 198.
- Psittacidae [in part] - Guérin *et al.* 1993b: 328.
- *Ara chloroptera* - Guérin *et al.* 1996: 84.
- *Ara chloroptera* - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. The species is represented by very numerous remains of at least four adult and two young individuals, possibly indicating that it was selectively hunted by the ancient inhabitants of the site. It also must have been rather abundant in the area in past times, while today it is restricted to a very small population.

- “a macaw (probably *A. chloroptera*)” - Alvarenga (in Sick 1993): 261.
- *Ara chloroptera* - Kneip *et al.* 1994: 51.
- Psittacidae (“arara-vermelha”) - Kneip *et al.* 1995: 7.
- “uma arara (provavelmente *A. chloroptera*)” - Alvarenga (in Sick 1997): 362.
- Psittacidae (“arara-vermelha”) - Kneip *et al.* 1997: 19.
- Psittacidae (“arara-vermelha”) - Magalhães *et al.* 2001: 59.

Kneip *et al.* (1994) reported material associated with the species from the sambaquis of Moa I (1 piece) and Moa II (1 piece), in Saquarema, Rio de Janeiro. This is a species that no longer occurs in the region today.

### **330. *Psittacara leucophthalmus* (Statius Müller)**

Quaternary - Minas Gerais, Piauí

- *Conurus pavua* - Winge 1887: 41.
- *Conurus pavua* - Lambrecht 1933: 770.
- *Aratinga leucophthalmus* - Brodkorb 1971: 212.
- *Aratinga leucophthalmus* (“*Conurus pavua*”) - Mones 1986: 95.
- *Aratinga leucophthalmus* - Cuello 1988: 52.
- *Psittacara leucophthalmus* - Boles 2017: 10.
- *Psittacara leucophthalmus* - Nascimento & Silveira 2020: 495.

Winge (1887: 41) reported two humeri and an ulna from Lapa da Escrivânia V, a humerus from Lapa da Escrivânia XI, a carpometacarpus from a “saltpeter cave near Escrivânia”, a humerus from “various caves”<sup>18</sup>, and a maxilla, a humerus, and a tibiotarsus of recent age<sup>20</sup>. Regarding the humeri, he noted that the difference is not small between them and partly between them and fresh bones, but that also three fresh skeletons show similar mutual differences between them.

- Psittacidae [in part] - Guérin *et al.* 1993a: 198.
- Psittacidae [in part] - Guérin *et al.* 1993b: 328.
- *Aratinga leucophthalmus* [sic] - Guérin *et al.* 1996: 84.
- *Aratinga leucophthalmus* [sic] - Guérin *et al.* 2002: 136.

Guérin *et al.* (1996) reported the species among archeofaunal remains from Toca da Janela da Barra do Antonião. At least three adults and one young individual are present in the material.

## **Passeriformes**

### **331. Passeriformes indet. 1 (spp.)**

Quaternary - Minas Gerais

- ”en hel Del Spurvefugle, saa godt som alle mesomyode; af de acromyode, de egenlige Sangfugle, der ellers ere de talrigste i Hulerne (smaa Finker o. s. v.), findes der netop Spor” [Lapa do Capão Seco] - Winge 1887: 11.
- ”Ikke faa ubestemte Spurvefugle, mesomyode og acromyode” [Lapa da Escrivânia XI] - Winge 1887: 13.
- ”Adskillige ubestemte Spurvefugle, mesomyode og acromyode” [Lapa da Lagoa do Sumidouro] -

Winge 1887: 13.

- "Nogle faa Spurvefugle, mesomyode og acromyode" [Lapa da Cerca Grande] - Winge 1887: 14.
- "Enkelte Knogler af acromyode Spurvefugle" [Lapa da Escrivânia III] - Winge 1887: 14.
- "Nogle faa Spurvefugle, mesomyode og acromyode" [Lapa da Escrivânia IX] - Winge 1887: 14.
- "En Del ubestemte Spurvefugle, mesomyode og acromyode" ["Saltpeter cave near Escrivânia"] - Winge 1887: 14.
- "Flere Spurvefugle; acromyode, i alt Fald de fleste" [Lapa do Marinho II] - Winge 1887: 14.
- "En Del Spurvefugle, mesomyode og acromyode" [Lapa da Pedra dos Índios] - Winge 1887: 14.
- "To Knogler af to Arter Spurvefugle" [Lapa do Periperi I] - Winge 1887: 14.
- "En Del ubestemte Spurvefugle" ["cavernas diversas"] - Winge 1887: 15.
- *Passeres* ["Arternes store Tal"] [in part?] - Winge 1887: 47.
- Passeriformes indet. 1 (spp.) - Nascimento & Silveira 2020: 495.

Winge (1887: 47) reported indeterminate passeriforms, the majority coming from Lapa da Escrivânia V, but also "Mesomyodes" and "Acromyodes"<sup>31</sup> coming from Lapa da Escrivânia IX and XI, Lapa da Lagoa do Sumidouro, Lapa of Cerca Grande, Lapa da Pedra dos Índios, Lapa do Capão Seco (mostly "Mesomyodes"), and a "saltpeter cave near Escrivânia", "Acromyodes" from Lapa da Escrivânia III and Lapa do Marinho II (at least the majority), two bones of two species from Lapa do Periperi I, and an amount coming from "various caves"<sup>18</sup> (Winge 1887: 11, 13, 14, 15). Winge noted that the large number of species and the uniformity of most bones make it difficult to determine them and that even a much larger collection of fresh, well-determined skeletons than what was available would allow a better diagnosis of many of these specimens. In addition, this material may contain representatives of groups that have not been determined among the fossils collected by Lund, such as Pipridae, Parulidae, and Coerebinae (Winge 1887: 9).

### **332. Passeriformes indet. 2 (spp.)**

Quaternary - Minas Gerais

- "En Mængde ubestemte Spurvefugle, mesomyode og acromyode" - Winge 1887: 51.
- Passeriformes indet. 2 (spp.) - Nascimento & Silveira 2020: 495.

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<sup>31</sup> Mesomyodes (or Clamatores), according to Mayr & Amadon (1951: 10): Suboscines passeriforms in which the intrinsic muscles of the syringe, if present, are attached to one end or the middle of the bronchial semirings, as opposed to the Acromyodes, in which these muscles are stuck at both ends. Passeri/Tyranni? [Sick 1997: 78; 520]

Winge (1887: 51) reported indeterminate “Mesomyodes” and “Acromyodes” passeriforms in a considerable number of recent age, without attribution to a locality.

### **333. Passeriformes indet. 3 (spp.?)**

Holocene - Rio de Janeiro

- “passeriformes (Sabiá?)” - Kneip *et al.* 1975: 105.
- “passeriformes” - Kneip 1977: 51–52.
- “passeriformes (sabiá?)” - Souza Cunha *et al.* 1977: 147.

Kneip *et al.* (1975) reported material associated with the order (hinting a possible association with turdids) from Sambaqui do Forte, in Cabo Frio, Rio de Janeiro. They noted that the bones are fragmented and consist of a few individuals.

### **334. Passeriformes indet. 4 (spp.)**

Quaternary - Minas Gerais

- Passeriformes - Cunha & Guimarães 1978: 219.
- Passeriformes indet. 3 (spp.) - Nascimento & Silveira 2020: 495.

Cunha & Guimarães (1978: 219) reported numerous bones representing passeriforms among the material collected by the team of archeologist Anette Laming-Amperaire in Lapa Vermelha (of Pedro Leopoldo) during the 1970s. The material includes mandibles, maxillae and several long bones, deposited in the MN collection. More accurate determination was not possible due to the poor state of conservation of the bones, which fall apart easily.

### **335. Passeriformes indet. 5 (spp.?)**

Quaternary - Minas Gerais

- Passeriformes - Souza-Cunha & Magalhães 1986: 122.
- Passeriformes indet. 4 (spp.?) - Nascimento & Silveira 2020: 495.

Souza-Cunha & Magalhães (1986) noted that passeriforms may figure among the avian remains from Cerca Grande, municipality of Matozinhos, Minas Gerais.

### **336. Passeriformes indet. 6 (spp.)**

Quaternary - Piauí

- Passeriformes - Guérin *et al.* 1993a: 198.
- Passeriformes - Guérin *et al.* 1993b: 328.
- Passeriformes - Guérin *et al.* 1996: 85.
- Passériformes indet. - Guérin *et al.* 2002: 136.

Guérin *et al.* (1993a; 1993b; 1996) reported indeterminate small to medium-sized Passeriformes among archeofaunal remains from Toca da Janela da Barra do Antonião.

### **337. Passeriformes indet. 7**

Quaternary - Minas Gerais

- Passeriforme - Ferreira *et al.* 2005: 156.
- Passeriforme - Oliveira 2008: 26, 78, 81, fig. 13A.

Parts of the indeterminate passeriform skeletons were mentioned by Ferreira *et al.* (2005: 156) from Lapa do Carlúcio, at Parque Nacional Cavernas do Peruaçu, Minas Gerais. The material was present among many fossils that originated from incrustation, permineralization, and substitution processes associated with stalagmitic floors, including representatives of mollusks, amphibians, and mammals. Oliveira (2008: 78, 81) reported the almost complete subfossil skeleton of a passeriform in observations in the same cave, but it is not clear whether it is the same material reported by Ferreira *et al.*

### **338. Passeriformes indet. 8 (3 spp.)**

Quaternary - Bahia

- “três espécies ainda não determinadas [Passeriformes]” - Silva & Cozzuol 2010: 111.

Silva & Cozzuol (2010: 111) reported eight humeri representing three indeterminate passeriforms from material collected in the 1980s at Toca da Boa Vista, in Campo Formoso, Bahia. The material is deposited in the MHNJB/UFMG collection.

### **339. Passeriformes indet. 9**

Holocene - Rio Grande do Norte

- Passeriformes - Silva 2014: 133.



Silva (2014: 133) reported Passeriformes material among zooarcheological remains of holocenic age collected by the team of NEA-UFPE starting in the 1990s in rock shelters of Pedra do Alexandre site, in Carnaúba dos Dantas, Rio Grande do Norte.

## **Thamnophilidae**

### **340. *Dysithamnus* sp.**

Quaternary - Tocantins

- *Desithamnus* [sic] sp. - Salum *et al.* 2016: 153.

Salum *et al.* (2016: 153) reported incomplete post-cranial materials of Thamnophilidae from Gruta do Urso, in the municipality of Aurora do Tocantins, aged between 22,000 and 3,800 years BP. The material, represented by the humeri (the most abundant, with four specimens), tibiotarsi, tarsometatarsi, and femora, was associated with the family, with possible greater taxonomic diversity, with five genera being attributed, one of which is *Dysithamnus*. Such assignments are the preliminary results of a research program that seeks to reveal the diversity of fossil birds in Gruta do Urso, from which new data is expected due to the abundance of the collected material.

### **341. *Herpsilochmus* sp.**

Quaternary - Tocantins

- *Herpsilochmus* sp. - Salum *et al.* 2016: 153.

Salum *et al.* (2016: 153) reported post-cranial remains attributed to this genus from Gruta do Urso.

### **342. *Thamnophilus* sp.**

Quaternary - Tocantins

- *Thamnophilus* sp. - Salum *et al.* 2016: 153.

The preliminary survey on bird material from Gruta do Urso reported by Salum *et al.* (2016: 153) includes this genus.

### **343. *Pyriglena* sp.**

Quaternary - Tocantins

- *Pyriglena* sp. - Salum *et al.* 2016: 153.

This genus appears in the material from Gruta do Urso reported by Salum *et al.* (2016: 153).

### **344. *Hypocnemis* sp.**

Quaternary - Tocantins

- *Hypocnemis* sp. - Salum *et al.* 2016: 153.

Salum *et al.* (2016: 153) attributed post-cranial material found in Gruta do Urso to this genus.

## **Formicariidae**

### **345. Formicariidae indet. (spp.)**

Quaternary - Minas Gerais

- *Formicariidae* [“Species non poucæ, indeterminatæ”] - Winge 1887: 8, 47.
- Formicariidae indet. (spp.) - Nascimento & Silveira 2020: 495.

Winge (1887: 8, 47) reported the occurrence of a good number of species, of which it was not possible to determine safely beyond the family level. On the bones, he commented that few fresh skeletons were available for comparison, no precise correspondents were found for the humeri of *Pyriglena leucoptera* and *Formicivora rufa* (*rufatra*)—thamnophilids then included in Formicariidae (indicating that the material under this determination may include more than one family)—and that two humeri from Lapa da Escrivânia V are somewhat thin and delicate even for this family. Although they have the same length as observed in *Troglodytes musculus*, the humerus of the last is relatively more robust.

### **346. *Chamaeza campanisona* (Lichtenstein)**

Quaternary - Minas Gerais

- *Chamaezosa brevicauda* (et aff.) - Winge 1887: 47.
- *Chamaezosa brevicauda* - Lambrecht 1933: 775.
- *Chamaeza* - Storer 1960: 81.
- *Chamaeza brevicauda* - Brodkorb 1978: 147.
- *Chamaeza brevicauda* - Mones 1986: 98.
- *Chamaeza brevicauda* - Cuello 1988: 62.
- *Chamaeza campanisona* - Nascimento & Silveira 2020: 496.

Winge (1887: 47) reported, from Lapa da Escrivânia V, five humeri, which looked the same as in fresh specimens, and two which were slightly smaller, with insignificant differences, and a coracoid from Lapa da Escrivânia XI. He noted that the shape is easily distinguishable among the other “*Mesomyodes*” passeriforms, but from the “*Grallaria* group”<sup>32</sup>, only this species is present among the fresh bones.

## Dendrocolaptidae

### 347. *Xiphocolaptes* spp.?

Quaternary - Brazil

- “*Xiphocolaptes* species” - Alvarenga (in Marantz *et al.* 2003): 358.

In addition to listing the records reported by Winge (1887) from the Lagoa Santa region, Marantz *et al.* (2003: 358), through the information of Herculano Alvarenga, noted that “specimens of *Xiphocolaptes* species have been found at another site in Brazil”, without further details. Perhaps this record may be the same reported by Sales (2003) (see below).

### 348. *Xiphocolaptes falcirostris franciscanus* Sneathlage

Quaternary - Minas Gerais

- *Xiphocolaptes franciscanus* sp. - Sales 2003: 214.

Among the bones and mummified carcasses from Zone II of Lapa do Rezar, Minas Gerais, Sales (2003: 214) reported this taxon, which had the largest number of specimens, with twelve.

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<sup>32</sup> *Grallaria* (Grallaridae) previously included in Formicariidae (see Rice 2005).

### **349. *Xiphocolaptes albicollis* (Vieillot)**

Quaternary - Minas Gerais

- *Xiphocolaptes albicollis* - Winge 1887: 48.
- *Xiphocolaptes albicollis* - Lambrecht 1933: 775.
- *Xiphocolaptes albicollis* - Brodkorb 1978: 146.
- *Xiphocolaptes albicollis* - Mones 1986: 98.
- *Xiphocolaptes albicollis* - Cuello 1988: 61.
- *Xiphocolaptes albicollis* - Marantz *et al.* 2003: 358.
- *Xiphocolaptes albicollis* - Nascimento & Silveira 2020: 496.

Winge (1887: 48) reported a tarsometatarsus from Lapa da Escrivânia V and a tibiotarsus of uncertain locality.

### **350. *Lepidocolaptes angustirostris* (Vieillot)**

Quaternary - Minas Gerais

- *Picolaptes bivittatus* - Winge 1887: 48.
- *Picolaptes bivittatus* - Lambrecht 1933: 775.
- *Lepidocolaptes angustirostris* - Brodkorb 1978: 146.
- *Lepidocolaptes angustirostris* (“*Picolaptes bivittatus*”) - Mones 1986: 98.
- *Lepidolaptes angustirostris* [*sic*] - Cuello 1988: 62.
- *Lepidocolaptes angustirostris* - Marantz *et al.* 2003: 358.
- *Lepidocolaptes angustirostris* - Nascimento & Silveira 2020: 496.

Winge (1887: 48) reported a tibiotarsus from Lapa da Escrivânia V, which corresponds well to this species, and a skull and most of the other bones of an individual of recent age<sup>20</sup>.

## **Furnariidae**

### **351. Furnariidae (*sensu lato*) indet. (spp.)**

Quaternary - Minas Gerais

- *Anabates* [?; in part] - Lund 1841d: 18.
- *Dendrocalaptes* [*sic*] [?; in part] - Lund 1841d: 18.
- *Opetiorrhynchus* [*sic*] [?; in part] - Lund 1841d: 18.
- *Anabates poliocephalus* [?; in part] - Lund 1841d: 18.
- “des Grimpar (Anabates de Temminck)” [?; in part] - Liais 1872: 303.

- “les Grimpereaux” [?; in part] - Liais 1872: 303.
- *Furnarius* [?; in part] - Reinhardt 1881: 142.
- *Dendrocolaptidæ* [“Species multæ, indeterminatæ, etiam affines Furnario etc.”] - Winge 1887: 8, 47–48.
- *Anabates* [?; in part] - Lambrecht 1933: 779.
- *Opetirhynchus* [sic] [?; in part] - Lambrecht 1933: 779.
- Dendrocolaptidae indet. (spp.) - Nascimento & Silveira 2020: 496.

Winge (1887: 47, 48) reported the occurrence of many indeterminate species. He noted that there were few fresh skeletons, and none of the most closely similar humeri found in the caves corresponds well to *Lochmias nematura*, *Synallaxis cinnamomea*, *Sittasomus griseicapillus* (*sylviellus*), and *Philydor rufum*. Many of them are quite similar to *Furnarius rufus* (*albogularis*), but they are a little more robust in length when compared to fresh specimens.

Brodkorb (1978: 146) associated with this indeterminate material the names *Anabates* (= *Synallaxis*), *Dendrocalptes* [sic], and *Opetiorrhynchus* [sic] (*Opetiorhynchus*; = *Furnarius*) used by Lund (1841d: 18).

### **352. *Furnarius rufus* (Gmelin)**

Quaternary - Minas Gerais

- *Furnarius rufus* - Sales 2003: 214.

Sales (2003: 214) reported a specimen among the bones and mummified carcasses from Zone II of Lapa do Rezar, Minas Gerais.

## **Tyrannidae**

### **353. Tyrannidae indet. (spp.)**

Quaternary - Minas Gerais

- *Tyrannidæ* (“Species multæ, indeterminatæ”) - Winge 1887: 8, 47.
- Tyrannidae (“mange arter”) - Lambrecht 1933: 775.
- Tyrannidae indet. (spp.) - Nascimento & Silveira 2020: 496.

Winge (1887: 8, 47) reported the occurrence of multiple species, of which it was not possible to determine beyond the family level, noting that the shape of the bones is very similar between them.

### **354. *Pitangus sulphuratus* (Linnaeus)**

Quaternary - Bahia, Goiás

- *Pitangus sulphuratus* - Paulo 2009: 142.

Paulo (2009: 142) reported the species to the Pleistocene/Holocene boundary of Serranópolis, Goiás.

- *Pitangus sulphuratus* - Silva & Cozzuol 2010: 111.

An incomplete tarsometatarsus lacking the proximal epiphysis was associated with the species by Silva & Cozzuol (2010: 111), from material found in the 1980s at Toca da Boa Vista, in Campo Formoso, Bahia. The fossil is deposited in the MHNJB/UFMG collection.

### **355. *Megarhynchus pitangua* (Linnaeus)**

Quaternary - Minas Gerais

- *Megarhynchus pitangua* [sic] - Winge 1887: 51.
- *Megarhynchus pitangua* - Nascimento & Silveira 2020: 496.

Winge (1887: 51) reported a skull of recent age, without assigning it to a locality.

### **356. *Myiozetetes similis* (Spix)**

Quaternary - Minas Gerais

- *Myiozetetes similis* sp. - Sales 2003: 214.

Sales (2003: 214) reported a specimen among the bones and mummified carcasses from Zone II of Lapa do Rezar, Minas Gerais.

## Vireonidae

### 357. Vireonidae indet.

Quaternary - Minas Gerais

- G. sp. indet. - Winge 1887: 49.
- Genus indet. - Lambrecht 1933: 780.
- Vireonidae indet. - Nascimento & Silveira 2020: 496.

Winge (1887: 49) reported a humerus from Lapa da Escrivânia V, considerably smaller than in the following species, and another similar humerus of recent age<sup>20</sup>.

### 358. *Cyclarhis* sp.

Quaternary - Minas Gerais

- *Cyclorhis?* sp. [sic] - Winge 1887: 49.
- *Cyclorhis* sp. (?) [sic] - Lambrecht 1933: 780.
- *Cyclarhis gujanensis* (?) - Brodkorb 1978: 195.
- *Cyclarhis* - Sick 1984b: 642.
- *Cyclarhis gujanensis* (“?Cyclorhis sp.”) - Mones 1986: 99–100.
- *Cyclarhis gujanensis* - Cuello 1988: 68.
- *Cyclarhis* - Sick 1993: 553.
- *Cyclarhis* - Sick 1997: 714.
- *Cyclarhis* sp. - Nascimento & Silveira 2020: 496.

Winge (1887: 49) reported three humeri from Lapa da Escrivânia V, all very similar but slightly smaller to *Cyclarhis gujanensis*. There is also a similar humerus from an uncertain location.

## Corvidae

### 359. *Cyanocorax cristatellus* (Temminck)

Quaternary - Minas Gerais

- *Dendrocalaptes* [sic] [?; in part] - Lund 1841d: 18.
- *Dendrocalaptes* aff. *gujanensi* [in part] - Lund (in Winge 1887): 48.
- *Cyanocorax cyanoleucus* - Winge 1887: 48.
- *Cyanocorax cyanoleucus* - Lambrecht 1933: 783.
- *Cyanocorax cristatella* - Brodkorb 1978: 161.

- *Cyanocorax cristatella* (“*Cyanocorax cyanoleucus*”) - Mones 1986: 99.
- *Cyanocorax cristatellus* - Cuello 1988: 69.
- *Cyanocorax cristatellus* - Nascimento & Silveira 2020: 496.

Winge (1887: 48) reported from Lapa da Escrivânia V the proximal end of a scapula, the distal end of a humerus and the first phalanx of the left hallux, which broke when the bird was alive and became slightly shorter after calcifying. From a “saltpeter cave near Escrivânia”, a tarsometatarsus, and from “various caves”<sup>18</sup> a maxilla and the distal end of a tibiotarsus, of which he noted to be well distinguished from *Pyroderus*, *Procnias*, and “*Cassicus*” (= *Psarocolius*?). There is also, from a “cave near Sumidouro” (other than Lapa da Lagoa do Sumidouro), the proximal end of a humerus of a *Cyanocorax* with an uncertain determination (“*Dendrocolaptes* aff. *gujanensi*” in Lund’s catalog; perhaps the material that Lund [1841d: 18] referred to as *Dendrocalaptes* [sic]), smaller than in *Cyanocorax cristatellus*, and larger and somewhat different than in *Cyanocorax cyanopogon*.

## Hirundinidae

### 360. Hirundinidae indet.

Quaternary - Minas Gerais

- *Hirundo* sp. 1 vel 2 e parvis (*cyanoleuca*, *leucorrhoea*) - Winge 1887: 49.
- *Hirundo* sp. [in part?] - Lambrecht 1933: 776.
- Hirundinidae indet. - Nascimento & Silveira 2020: 496.

Winge (1887: 49) reported bones of several individuals from Lapa da Escrivânia V, a humerus from Lapa da Escrivânia XI and bones from several individuals of recent age<sup>20</sup>. The total material is represented by the humerus, ulna, femur, and tibiotarsus, which perhaps represents two species, presenting a shape close to *Pygochelidon cyanoleuca* and *Tachycineta leucorrhoea*.

### 361. *Progne chalybea* (Gmelin)

Quaternary - Minas Gerais

- *Hirundo* (*Progne*) *domestica* - Winge 1887: 48.
- *Chelidon rustica* [in part?] - Lambrecht 1933: 776.
- *Progne chalybea* - Brodkorb 1978: 154.



- *Progne chalybea* (“*Hirundo (Progne) domestica*”) - Mones 1986: 98–99.
- *Progne chalibea* [*sic*] - Cuello 1988: 63.
- *Progne chalybea* - Nascimento & Silveira 2020: 496.

Winge (1887: 48) reported bones in good number from Lapa da Escrivânia V, a humerus from Lapa da Escrivânia XI and another humerus from Lapa da Lagoa do Sumidouro. The total material is represented by the humerus, ulna, carpometacarpus, first phalanx of the second digit of the wing, femur, and tarsometatarsus, with significant individual variations.

### **362. *Hirundo* sp.**

Quaternary - Minas Gerais

- *Hirundo* sp. indet., *Hirundine rustica paullo major* - Winge 1887: 48.
- *Chelidon rustica* [in part?] - Lambrecht 1933: 776.
- *Hirundo* sp. [in part?] - Lambrecht 1933: 776.
- *Hirundo rustica* (?) - Brodkorb 1978: 155.
- *Hirundo rustica* - Mones 1986: 98.
- *Hirundo rustica* - Cuello 1988: 63.
- *Hirundo* sp. - Nascimento & Silveira 2020: 496.

Winge (1887: 48) reported several bones from Lapa da Escrivânia V, represented by the humerus, ulna, and carpometacarpus, all slightly larger than in *Hirundo rustica*, from which they are a little different.

Lambrecht (1933: 776), as pointed out by Brodkorb (1978: 155), associated material from Lapa da Escrivânia V and XI and Lapa da Lagoa do Sumidouro to *Chelidon rustica*. Materials from these localities together were described by Winge as *Hirundo (Progne) domestica* (= *Progne chalybea*; see above).

## **Troglodytidae**

### **363. Troglodytidae indet.**

Quaternary - Minas Gerais

- G. sp. indet. e minimis - Winge 1887: 49.
- “anderen Arten” - Lambrecht 1933: 780.
- Troglodytidae indet. - Nascimento & Silveira 2020: 496.

Winge (1887: 49) reported a humerus from Lapa da Escrivânia V and another humerus of recent age<sup>20</sup>, of which a determination beyond the family level was not possible. Additionally, Winge noted that they are much smaller than in the following species.

### **364. *Troglodytes musculus* Naumann**

Quaternary - Minas Gerais

- *Troglodytes furvus* - Winge 1887: 49.
- *Troglodytes furvus* - Lambrecht 1933: 780.
- “*Troglodytes*” *furvus* - Mones 1986: 100.
- *Troglodytes aedon* - Cuello 1988: 63.
- *Troglodytes musculus* - Nascimento & Silveira 2020: 496.

Winge (1887: 49) reported some humeri from Lapa da Escrivânia V, and a single humerus of recent age<sup>20</sup>.

## **Turdidae**

### **365. *Turdus* sp. 1**

Quaternary - Minas Gerais

- *Turdus* sp. - Winge 1887: 49.
- *Turdus* sp. - Lambrecht 1933: 779.
- “*Turdus*” sp. - Mones 1986: 99.
- *Turdus* sp. 1 - Nascimento & Silveira 2020: 496.

Winge (1887: 49) associated with this genus some humeri found in Lapa da Escrivânia V.

### **366. *Turdus* sp. 2**

Quaternary - Minas Gerais

- *Turdus* sp. - Winge 1887: 51.
- *Turdus* sp. 2 - Nascimento & Silveira 2020: 496.

Winge (1887: 51) reported a skull of recent age without attributing it to a specific locality.

## Mimidae

### 367. *Mimus saturninus* (Lichtenstein)

Quaternary - Minas Gerais

- *Mimus saturninus* - Winge 1887: 49.
- *Mimus saturninus* - Lambrecht 1933: 777.
- *Mimus saturninus* - Brodkorb 1978: 179.
- *Mimus saturninus* - Mones 1986: 99.
- *Mimus saturninus* - Cuello 1988: 64.
- *Mimus saturninus* - Nascimento & Silveira 2020: 496.

Winge (1887: 49) reported several humeri from Lapa da Escrivânia V, a humerus from Lapa da Lagoa do Sumidouro, and two humeri of recent age<sup>20</sup>.

## Passerellidae

### 368. *Arremon flavirostris* Swainson

Quaternary - Minas Gerais

- *Arrhemon flavirostris* [sic] - Winge 1887: 51.
- *Arremon flavirostris* - Nascimento & Silveira 2020: 496.

Winge (1887: 51) reported a skull of recent age without attributing it to a specific locality.

## Icteridae

### 369. Icteridae indet. (spp.)

Quaternary - Minas Gerais

- *Tanagridae* (og *Coerebidae*), *Emberizidae* (med *Pitylinæ* o. s. v.) og *Icteridae* [“Familiæ characteribus ossium membrorum inter se non distinctæ. Species permultæ indeterminatæ.”] [in part] - Winge 1887: 8, 49–50.
- Icteridae indet. (spp.) - Nascimento & Silveira 2020: 496.

Winge (1887: 49, 50) reported many indeterminate passeriform bones of various species from Lapa da Escrivânia V and a good number from other caves. He noted that of skulls

and other more diagnostic parts, there was only the material of the caves, and, in general, the limb bones of Passeriformes are quite similar, being possible to determine only the easily recognizable forms.

### **370. *Psarocolius decumanus* (Pallas)**

Quaternary - Minas Gerais

- *Cassicus (Ostinops) cristatus* - Winge 1887: 50.
- *Cassicus (Ostinops) cristatus* - Lambrecht 1933: 785.
- *Psarocolius decumanus* - Brodkorb 1978: 200.
- *Psarocolius decumanus* (“*Cassicus (Ostinops) cristatus*”) - Mones 1986: 99.
- *Psarocolius decumanus* - Cuello 1988: 68.
- *Psarocolius decumanus* - Nascimento & Silveira 2020: 496.

Winge (1887: 50) reported the proximal end of a scapula from a “saltpeter cave near Escrivânia”, which fits well into this species. It differs in part from *Cyanocorax* scapula, being larger than in *Cyanocorax cristatellus*, and having a different aspect from the tarsometatarsus of this species found in the same cave. Additionally, it is different from the scapula of large cotingids such as *Pyroderus* and *Procnias*.

### **371. *Gnorimopsar chopi* (Vieillot)**

Quaternary - Minas Gerais

- *Aphobus chopi* - Winge 1887: 50.
- *Aphobus Chopi* [sic] - Lambrecht 1933: 790.
- *Gnorimopsar chopi* - Brodkorb 1978: 201.
- *Gnorimopsar chopi* (“*Aphobus chopi*”) - Mones 1986: 99.
- *Gnorimopsar chopi* - Cuello 1988: 69.
- *Gnorimopsar chopi* - Nascimento & Silveira 2020: 496.

Winge (1887: 50) reported a maxilla and humeri from Lapa da Escrivânia V.

### **372. *Pseudoleistes guirahuro* (Vieillot)**

Quaternary - Minas Gerais

- *Pseudoleistes viridis* - Winge 1887: 50.
- *Pseudoleistes viridis* - Lambrecht 1933: 790
- *Pseudoleistes guirahuro* - Brodkorb 1978: 201.

- *Pseudoleistes guirahuro* (“*Pseudoleistes viridis*”) - Mones 1986: 99.
- *Pseudoleistes guirahuro* - Cuello 1988: 69.
- *Pseudoleistes guirahuro* - Nascimento & Silveira 2020: 496.

Winge (1887: 50) associated humeri from Lapa da Escrivânia V to this species.

## Cardinalidae

### 373. *Piranga flava saira* (Spix)

Quaternary - Minas Gerais

- *Piranga saira* - Winge 1887: 51.
- *Piranga flava saira* - Nascimento & Silveira 2020: 497.

Winge (1887: 51) reported a maxilla of recent age without attributing it to a specific locality.

## Thraupidae

### 374. Thraupidae indet. 1 (spp.)

Quaternary - Minas Gerais

- *Tanagridæ* (og *Coerebidæ*), *Emberizidæ* (med *Pitylinæ* o. s. v.) og *Icteridæ* [“Familiæ characteribus ossium membrorum inter se non distinctæ. Species permultæ indeterminatæ.”] [in part] - Winge 1887: 8, 49-50.
- Thraupidae indet. 1 (spp.) - Nascimento & Silveira 2020: 496.

Winge (1887: 49, 50) reported indeterminate material of various species from Lapa da Escrivânia V and other caves.

### 375. Thraupidae indet. 2

Quaternary - Minas Gerais

- *Coerebid*. g. sp. indet. - Winge 1887: 51.
- Thraupidae indet. 2 - Nascimento & Silveira 2020: 497.

Winge (1887: 51) reported a skull, which he describes as somewhat different from *Coereba flaveola chloropyga*. The material is of recent age and was not attributed to a specific cave.

### **376. *Tersina viridis* (Illiger)?**

Quaternary - Minas Gerais

- *Procnias tersa?* - Winge 1887: 50.
- *Procnias tersa* (?) - Lambrecht 1933: 775.
- *Tersina viridis* - Storer 1960: 89.
- *Tersina viridis* - Brodkorb 1978: 198.
- *Tersina viridis* (“*Procnias tersa?*”) - Mones 1986: 99.
- *Tersina viridis* - Cuello 1988: 67.
- *Tersina viridis?* - Nascimento & Silveira 2020: 497.

Winge (1887: 50) associated, without complete certainty, the fragment of a maxilla from Lapa da Escrivânia V to this species. Although he mentioned (Winge 1887: 9) that no cotingid remains were found in the caves, Storer (1960: 89) commented that the original description of the material under the genus *Procnias* caused Lambrecht (1933: 775) and subsequent authors to erroneously list it as cotingid, arguing that the genus had been used for neotropical bellbirds since 1907. However, Lambrecht appears to have only listed the material as presented by Winge (as “*Procnias tersa* Auct.”), similarly to most other records in his study.

### **377. *Saltator similis* d’Orbigny & Lafresnaye**

Quaternary - Minas Gerais

- *Saltator similis* - Winge 1887: 50.
- *Saltator similis* - Lambrecht 1933: 790.
- *Saltator similis* - Brodkorb 1978: 198.
- *Saltator similis* - Mones 1986: 99.
- *Saltator similis* - Cuello 1988: 66.
- *Saltator similis* - Nascimento & Silveira 2020: 497.

Winge (1887: 50) reported a maxilla from Lapa da Escrivânia V.

### **378. *Thraupis sayaca* (Linnaeus)**

Quaternary - Minas Gerais

- *Tanagra sayaca* - Winge 1887: 51.
- *Tangara sayaca* - Nascimento & Silveira 2020: 497.

Winge (1887: 51) reported a maxilla of recent age without attributing it to a specific locality.

## **7. CONCLUSION**

A complete panorama of the avian fossil and subfossil diversity in Brazil is far from being reached, but herein we present a list with the most important records present in the literature. This present list is naturally biased by several factors of biological, geological, and political nature, but, to date, this is the most complete picture of Brazilian paleornithological studies ever compiled.

In general, the most complete fossil avifauna known for the country is the one from the Quaternary of Lagoa Santa Karst, which is also the first to be studied. The most complete from the Paleogene is that from Tremembé Formation. The most diverse known non-Quaternary avifauna is that from the Tremembé Formation. Of the 77 feather records, 70 are of Mesozoic age, all belonging to the Crato Formation, and cannot be assigned with security to avian dinosaur clades. Two fossil egg records have been published, with no ootaxa erected for them. Two ichnofossil records have been associated with birds, with one of them needing revision.

The following sections analyze this compilation from different points of view.

### **7. 1. Taxonomic representation**

The 378 taxa recorded can be divided into the following family or equivalent clades (from the most to the less numerous): Maniraptora (feathers) (70), Aves (23), Columbidae (20), Psittacidae (18), Rallidae (17), Accipitridae (16), Tinamidae (12), Cathartidae (9), Falconidae (9), Passeriformes (9), Strigidae (9), Anhingidae (8), Picidae (8), Anatidae (7), Cracidae (7), Caprimulgidae (6), Ciconiidae (6), Procellaridae (5), Scolopacidae (5), Thamnophilidae (5), Thraupidae (5), Trochilidae (5), Cuculidae (4), Dendrocolaptidae (4), Enantiornithes (4), Icteridae (4), Podicipedidae (4), Tyrannidae (4), Cariamiformes (3), Hirundinidae (3), Laridae (3), Phalacrocoracidae (3), Phorusrhacidae (3), Rheidae (3), Sulidae (3), Ardeidae (2), Bucconidae (2), Charadriidae (2), Diomedidae (2), Formicariidae (2), Furnariidae (2), Momotidae (2), Nyctibiidae (2), Palaeognathae (2), Quercymegapodiidae (2), Ramphastidae (2),

Threskiornithidae (2), Troglodytidae (2), Trogonidae (2), Turdidae (2), Vireonidae (2), Alcenididae (1), Anhimidae (1), Apodidae (1), Cardinalidae (1), Cariamidae (1), Corvidae (1), Fregatidae (1), Gracilitarsidae (1), Jacanidae (1), Mimidae (1), Neognathae (1), Odontophoridae (1), Opisthocomidae (1), Ornithuromorpha (1), Palaelodidae (1), Passerellidae (1), Pelagornithidae (1), Phoenicopteridae (1), Spheniscidae (1), Strigiformes (1), Teratornithidae (1), and Tytonidae (1). If we exclude Maniraptora and Aves, which comprises most indeterminate taxa, Columbidae is the clade with the best taxonomical representation in the fossil records of birds in Brazil.

Most records belong to living taxa (145). Extinct taxa are represented by 132 records, and 101 records do not have sufficient taxonomical determination to classify them into one of these categories. Two possibly recently, anthropically extinct taxa are present in the fossil record (*Anodorhynchus glaucus* and *Paraclaravis geoffroyi*), but here we considered them as living taxa.

The following orders of native Brazilian living avifauna (following Pacheco *et al.* 2021) do *not* have published fossil representatives found during this research: Steatornithiformes, Eurypygiformes, and Phaethontiformes. In the same category, the following families do not have fossil published fossil representatives: Steatornithidae, Aramidae, Psophiidae, Heliornithidae, Haematopodidae, Recurvirostridae, Burhinidae, Chionidae, Thinocoridae, Rostratulidae, Glareolidae, Stercorariidae, Eurypygidae, Phaethontidae, Oceanitidae, Hydrobatidae, Pelecanidae, Pandionidae, Galbulidae, Capitonidae, Melanopareidae, Conopophagidae, Grallaridae, Rhinocryptidae, Scleruridae, Xenopidae, Pipridae, Cotingidae, Tityridae, Oxyruncidae, Onychorhynchidae, Pipritidae, Platyrinchidae, Tachuridae, Rhynchocyclidae, Polioptilidae, Donacobiidae, Motacillidae, Fringillidae, Parulidae, and Mitrospingidae. The lack of known records of some taxa may be due to different taphonomic processes, paleontological fieldwork activities or simply because they were absent, as pointed out by Tambussi & Noriega (1996), and these factors must be considered when analyzing fossil bird communities.

No families with no living representatives in the country but living elsewhere have records published. Of the globally extinct families, the following have fossil



representatives in the country: Quercymegapodiidae (2), Pelagornithidae (dubious) (1), Palaelodidae (1), Teratornithidae (1), Gracilitarsidae (1), and Phorusrhacidae (3).

Sixteen new fossil genera and 21 species have been named, of seven extant and ten extinct families (equivalent clades): *Cratoavis cearensis*, *Kaririavis mater*, *Diogenornis fragilis*, *Chaunoides antiquus*, *Neochen pugil*, *Taubacrex granivora*, *Ameripodius silvasantosi*, *Pelagornis longirostris*, *Agnopterus sicki*, *Hoazinavis lacustris*, *Ciconia lydekkeri*, *Anhinga minuta*, *Macranhinga ranzii*, *Brasilogyys faustoi*, *Wingegyys cartellei*, *Pleistovultur nevesi*, *Taubatornis campbelli*, *Eutreptodactylus itaboraiensis*, *Paleopsilopterus itaboraiensis*, *Itaboravis elaphrocnemoides*, and *Paraphysornis brasiliensis*. The attribution of *Pelagornis longirostris* to Brazil is problematic. Additionally, two extinct species named from elsewhere have been found in the country, though one attribution is tentative: *Rhea fossilis* and *Palaelodus cf. ambiguus*.

Taxonomic uncertainty is present in 151 of the osteological records. However, even the positive records should not be taken without contestation due to the incomplete nature of the fossil record. Out of this number, 8 taxa have been determined to the subspecific level, all still living.

## 7. 2. Temporal representation

Most of South America's Paleogene and Neogene birds have been described from the southern part of the continent (Argentina in particular), which also holds most of the Mesozoic remains found in the continent (Rasmussen & Kay 1992; Agnolin 2016b). In Brazil, avian fossil material is known from the Early Cretaceous to the recent, holocenic record (extinct taxa are represented in temporal scale in Table 3), but there are still several temporal gaps to be filled.

Of the 378 taxa recorded, 74 are from Early Cretaceous, 7 from the Late Cretaceous, 14 from the Paleogene, 20 from the Paleogene–Neogene transition, 10 from the Neogene, and 253 from the Quaternary.

Fossil feathers are most numerous in the late Aptian (70 records of indeterminate maniraptoran affinities), followed by late Oligocene–early Miocene (7 records), and Eocene–Oligocene (indeterminate number of specimens).

Eggs have one record in the Mesozoic (Campanian–Maastrichtian) and one in the Cenozoic (Oligocene–Miocene). Coprolites have a single record from the late Oligocene–early Miocene. A dubious track ichnofossil record is attributed to the late Cretaceous.

In sum, most Brazilian avian prehistoric material is known from the Cenozoic during the Pleistocene–Holocene transition.

### **7. 3. Spatial representation**

The political territory defined as Brazil currently has twenty-six states and the Federal District distributed into five Regions (North, Northeast, Central-West, Southeast, and South). Avian fossil remains are known from all Regions.

There are no published records from Amapá, Rondônia (North), Maranhão, Paraíba, Sergipe (Northeast), Mato Grosso do Sul, Federal District (Central-West), and Espírito Santo (Southeast).

The 378 taxa recorded here can be assigned to the following states: North: Acre (8), Amazonas (1), Pará (1), Roraima (1), Tocantins (5); Northeast: Alagoas (1), Bahia (12), Ceará (77), Pernambuco (4), Piauí (35), Rio Grande do Norte (4); Central-West: Goiás (13), Mato Grosso (1); Southeast: Minas Gerais (174), Rio de Janeiro (38), São Paulo (22); South: Paraná (1), Rio Grande do Sul (5), and Santa Catarina (1).

Early Cretaceous records are restricted to Ceará (Northeast) and Late Cretaceous to São Paulo and Minas Gerais (Southeast). Most of the Paleogene records come from Rio de Janeiro (Southeast), with meager records from Paraná (South) and Minas Gerais (Southeast). With exception of some late Miocene records of Acre and Amazonas (North), the late Cenozoic records are virtually restricted to cave remains of Quaternary age, which occur predominantly in Minas Gerais (Southeast) and Bahia and Piauí (Northeast).

Two records of extinct species firstly described from elsewhere are present (Argentina and France), though one is uncertain.

#### **7. 4. Preservation**

Following the four categories of preservation established in this study (i.e., feathers, eggs, ichnofossil, and osteological remains), the 378 recorded taxa can be divided into: 77 feathers, 2 eggs, 2 ichnofossils, and 297 osteological remains (including mummifications). Regarding the number of records in the literature for a taxon, 348 include a single record, 22 include two, seven include 3, and one include 4.

Regarding the degree of preservation of these specimens, we can classify them in low, medium, and high preservations. This is naturally somewhat arbitrary (since we were not able to examine every record in hands and the literature is not complete) and applies almost exclusively to osteological remains. This classification follows how much of the total specimen was preserved, low being just a few bones, medium including a reasonably good number of elements, and high starting from an almost complete skeleton. The 297 osteologically represented records can then be divided into: 220 low, 41 medium, 8 high, and 28 data deficient. Although rarely stated in material descriptions, most records in the literature belong to seemingly adult individuals. Feathers show a mostly reasonable preservation degree, with some specimens keeping their original coloration scheme. The oological records include one with good preservation and the other lacking sufficient information for a definition. Ichnofossils are reasonably well preserved.

#### **7. 5. Final considerations**

As Bittencourt & Langer (2012) pointed out concerning the few non-avian dinosaur species described for Brazil, the small number of fossil bird species known is also incongruent in the face of the country's continental dimensions and its rich sedimentary deposits, even considering the fragile nature of avian bones. Several actions could help increase the number of paleornithological studies in Brazil, including, as for scientific studies in general, better investments leading to new field work campaigns and creating a more stimulating scenario for new researchers, reanalyzing museum collections (in which avian bones, generally poor preserved, go unnoticed), enforcing laws on fossil

traffic (which led valuable species into the scientific limbo of private collections), and geological sites preservation, and, as already pointed by Alvarenga (1992), expanding museum's osteological sections of ornithological collections.

Compiling and updating the knowledge on Brazilian bird remains gathered until the present is the first step for future studies to expand this knowledge, whether at a regional or national scale. Not only broadening the understanding of the taxonomic diversity and the evolution of birds, such expansion is important as a source of biogeographical and paleoecological information and may also help in future strategies for managing living species (Dietl & Flessa 2011).

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TABLE 1

Acronym	Institution	City and country
CAV	Centro Acadêmico de Vitória, Universidade Federal de Pernambuco	Vitória de Santo Antão, Brazil
CLA; MCL CLA; MCN PUC Minas	Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais	Belo Horizonte, Brazil
CPPLIP	Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Universidade Federal do Triângulo Mineiro	Uberaba, Brazil
DNPM	Departamento Nacional de Produção Mineral	Rio de Janeiro, Brazil
FUMDHAM	Fundação Museu do Homem Americano	São Raimundo Nonato, Brazil
IGc/USP; GP; 2E	Instituto de Geociências da Universidade de São Paulo, Geology and Paleontology, Vertebrates	São Paulo, Brazil
IGPA	Instituto Goiano de Pré-História e Antropologia, Universidade Católica de Goiás	Goiânia, Brazil
IPHAN	Instituto do Patrimônio Histórico e Artístico Nacional	Brasília, Brazil
LEIUG	Leicester University, Department of Geology	Leicester, United Kingdom
LGP	Laboratório de Geologia e Paleontologia, Universidade Federal do Rio Grande	Rio Grande, Brazil
LPRP-USP	Laboratório de Paleontologia, Universidade de São Paulo	Ribeirão Preto, Brazil
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”	Buenos Aires, Argentina
MCN-PV	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Paleovertebrados	Porto Alegre, Brazil
MCT	Museu Ciências da Terra, Departamento Nacional de Produção Mineral	Rio de Janeiro, Brazil
MHNJB/UFMG	Museu de História Natural e Jardim Botânico of Universidade Federal de Minas Gerais	Belo Horizonte, Brazil
MHNT	Museu de História Natural de Taubaté	Taubaté, Brazil
MN; MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro	Rio de Janeiro, Brazil

**Table 1.** Summary of the institutional abbreviations used in this study. Note: this is not a list of the institutions housing Brazilian bird fossil material.



TABLE 1. (Cont.)

<b>Acronym</b>	<b>Institution</b>	<b>City and country</b>
MPEG	Museu Paraense Emílio Goeldi	Belém, Brazil
MPM	Museu de Paleontologia de Marília	Marília, Brazil
MPSC	Museu de Paleontologia em Santana do Cariri	Santana do Cariri, Brazil
MUPHI	Museu de Pré-História de Itapipoca	Itapipoca, Brazil
MURJ	Private collection Masayuki Murata	Kyoto, Japan
MZUSP	Museu de Zoologia, Universidade de São Paulo	São Paulo, Brazil
NEA-UFPE	Núcleo de Estudos Arqueológicos, Universidade Federal de Pernambuco	Recife, Brazil
NHMUK	Natural History Museum, United Kingdom	London, United Kingdom
NSM	National Science Museum of Japan	Tokyo, Japan
PUC-MG	Pontifícia Universidade Católica de Minas Gerais	Belo Horizonte, Brazil
SGP-MHN-UFAL	Coleção de Paleovertebrados, Setor de Geologia e Paleontologia, Museu de História Natural da Universidade Federal de Alagoas	Maceió, Brazil
SMF	Senckenberg Museum, Frankfurt	Frankfurt, Germany
SMNK	Staatliches Museum für Naturkunde Karlsruhe	Karlsruhe, Germany
UCMG	Universidade Católica de Minas Gerais (now PUC Minas)	Belo Horizonte, Brazil
UFAC	Universidade Federal do Acre	Rio Branco, Brazil
UFC	Instituto de Paleontologia e Geologia do Cariri, Universidade Federal do Ceará	Crato, Brazil
UFRGS	Universidade Federal do Rio Grande do Sul	Porto Alegre, Brazil
UFRJ-DG	Universidade Federal do Rio de Janeiro, Departamento de Geologia	Rio de Janeiro, Brazil
UFRPE	Universidade Federal Rural de Pernambuco	Recife, Brazil
Unisinos	Universidade do Vale do Rio dos Sinos	São Leopoldo, Brazil
URCA	Universidade Regional do Cariri	Crato, Brazil
ZMUC	Zoological Museum, University of Copenhagen	Copenhagen, Denmark

Table 1. Continuation.

TABLE 2

Year	Event	Main reference
1836	First recorded occurrence of a fossil bird	Lund 1837
1841	Publication of the extract of Lund's treatise on the fossil birds of Lagoa Santa	Lund 1841d
1881	First investigative publication on the fossil birds of Lagoa Santa	Reinhardt 1881
1887	First thorough study on Brazilian bird fossils, with the description of the first fossil species <i>Chenalopex pugil</i>	Winge 1887
1891	Description of the new genus and species <i>Prociconia lydekkeri</i>	Ameghino 1891
1910	Description of the new species <i>Odontopteryx longirostris</i> , reportedly from Brazil	Spulski 1910
1916	First recorded occurrence of a fossil feather	Shufeldt 1916
1930	Description of the new genus <i>Pseudodontornis</i> for <i>Odontopteryx longirostris</i>	Lambrecht 1930
1977	First recorded occurrence of a subfossil extinct species	Olson 1977
1982	Description of the new species <i>Physornis brasiliensis</i>	Alvarenga 1982
1983	Description of the new genus and species <i>Diogenornis fragilis</i>	Alvarenga 1983
1985	Description of the new genus and species <i>Paleopterus itaboraiensis</i>	Alvarenga 1985a
1985	Description of the new genus and species <i>Brasilogyps faustoi</i>	Alvarenga 1985b
1988	Description of the new genus and species <i>Taubacrex granivora</i> , with the first occurrence of gastroliths associated with fossil birds	Alvarenga 1988
1988	First recorded occurrence of a coprolite	Castro <i>et al.</i> 1988b
1990	Description of the new species <i>Agnopterus sicki</i> and report of <i>Palaelodus cf. ambiguus</i>	Alvarenga 1990
1993	Description of the new genus <i>Paraphysornis</i> for <i>Physornis brasiliensis</i>	Alvarenga 1993c
1995	Description of the new genus and species <i>Ameripodius silvasantosi</i>	Alvarenga 1995

**Table 2.** Timeline containing the most important events in the history of paleornithology in Brazil.

TABLE 2 (Cont.)

Year	Event	Main reference
1997	Description of the new genus and species <i>Eutreptodactylus itaboraiensis</i>	Baird & Vickers-Rich 1997
1988	First recorded occurrence of a Mesozoic fossil feather	Martins-Neto & Kellner 1988
1998	First recorded occurrence of fossil eggshells	Azevedo & Carvalho 1988
1999	Description of the new genus and species <i>Chaunoides antiquus</i>	Alvarenga 1999
2002	Description of the new genus and species <i>Taubatornis campbelli</i>	Olson & Alvarenga 2002
2003	Description of the new species <i>Anhinga minuta</i> and <i>Macranhinga ranzii</i> and occurrence of <i>Anhinga</i> cf. <i>grandis</i> and <i>Anhinga</i> cf. <i>fraileyi</i>	Alvarenga & Guilherme 2003
2004	Description of the new genus and species <i>Wingegyps cartellei</i>	Alvarenga & Olson 2004
2004	Inauguration of MHNT, important center for avian osteological and paleontological studies in Brazil	-
2005	First recorded occurrence of Mesozoic osteological remains	Alvarenga & Nava 2005
2008	Description of the new genus and species <i>Pleistovultur nevesi</i>	Alvarenga <i>et al.</i> 2008
2008	First fossil feather showing unequivocally to have been preserved due to the presence of melanin	Vinther <i>et al.</i> 2008
2010	First record of <i>Rhea fossilis</i> for Brazil.	Faure <i>et al.</i> 2010
2011	Description of the new genus and species <i>Itaboravis elaphrocnemoides</i>	Alvarenga <i>et al.</i> 2011a
2011	Description of the new genus and species <i>Hoazinavis lacustris</i>	Alvarenga <i>et al.</i> 2011b
2012	First recorded occurrence of a Mesozoic fossil egg	Marsola <i>et al.</i> 2012
2015	Description of the new genus and species <i>Cratoavis cearensis</i> , first Mesozoic taxa named	Carvalho <i>et al.</i> 2015b
2021	Description of the new genus and species <i>Kaririavis mater</i> , first Mesozoic ornithuromorph taxa named, and the oldest member of the clade reported for Gondwana	Carvalho <i>et al.</i> 2021

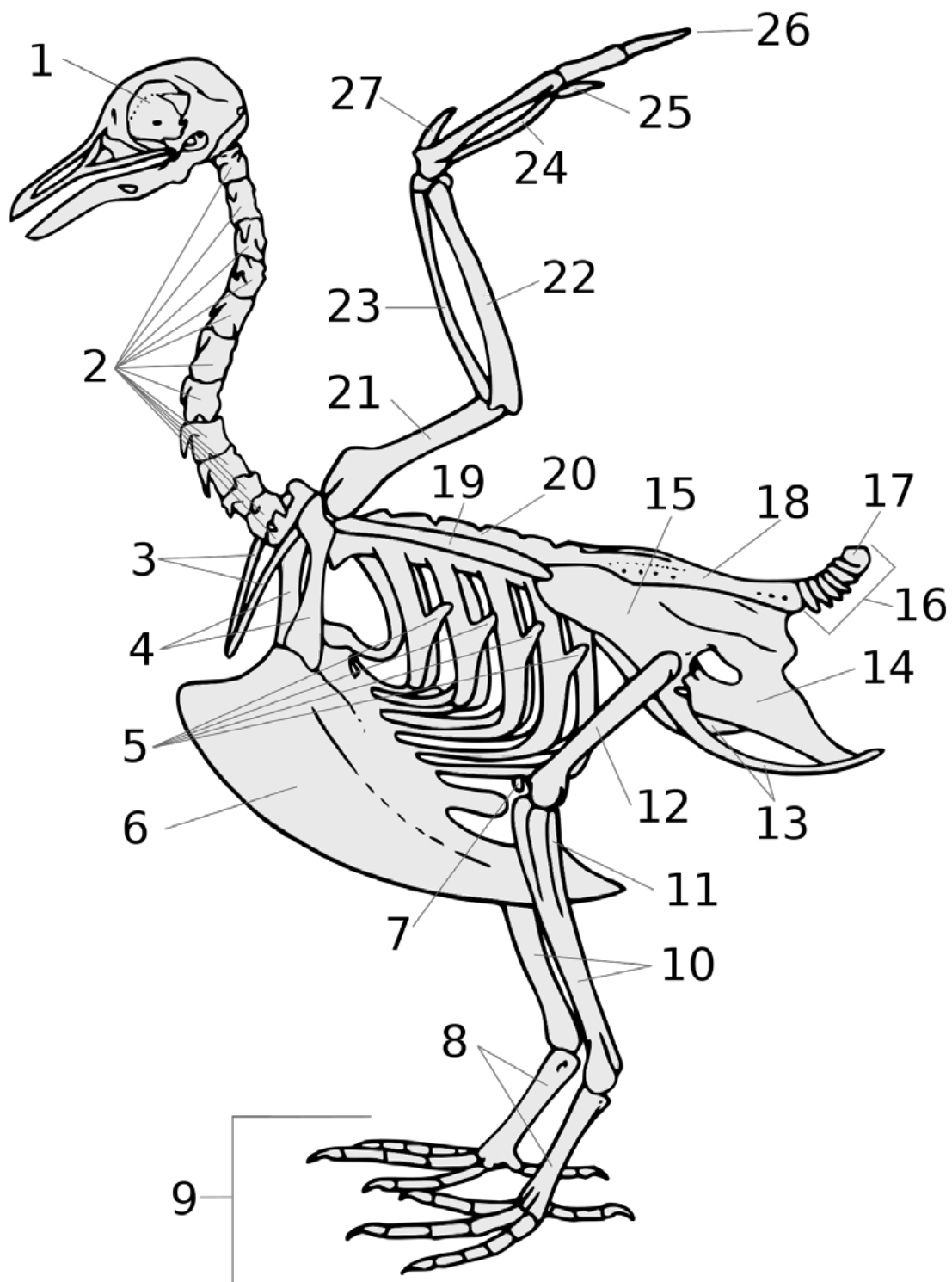
Table 2. Continuation.

TABLE 3

0	PHANEROZOIC	CENOZOIC	Quaternary	Holocene	<i>Rallus</i> sp.		
0.01				Pleistocene	<i>Neochen pugil</i> , <i>Ciconia lydekkeri</i> , <i>Wingegyps cartellei</i> , <i>Pleistovultur nevesi</i> , <i>Rhea fossilis</i>		
2.5			Tertiary	Neogene	Pliocene	-	
5.3					Miocene	<i>Anhinga minuta</i> , <i>Macranhinga ranzii</i> , <i>Anhinga</i> cf. <i>grandis</i> , <i>Anhinga</i> cf. <i>fraylei</i> , <i>Phorusrhacidae</i> indet., feather	
23				Paleogene	Oligocene	<i>Paraphysornis brasiliensis</i> , <i>Brasilogyps faustoi</i> , <i>Taubacrex granivora</i> , <i>Agnopterus sicki</i> , <i>Palaelodus</i> cf. <i>ambiguus</i> , <i>Ameripodius silvasantosi</i> , <i>Chaunoides antiquus</i> , <i>Taubatornis campbelli</i> , <i>Hoazinavis lacustris</i> , Aves indet., feathers, eggshells, coprolites	
33.9					Eocene	<i>Diogenornis fragilis</i> , <i>Paleopsilopterus itaboraiensis</i> , <i>Eutreptodactylus itaboraiensis</i> , <i>Itaboravis elaphrocnemoides</i> , <i>Phorusrhacidae</i> , Aves indet., feathers	
56					Paleocene	-	
66				MESOZOIC	Cretaceous	Late	Maastrichtian
72.1			Campanian				<i>Enantiornithes</i> indet., egg
83.3			Santonian				-
83.6	Coniacian	-					
89.8	Turonian	-					
93.9	Cenomanian	-					
100.5	Early	Albian	-				
113		Aptian	<i>Cratoavis cearensis</i> , <i>Kaririavis mater</i> , <i>Enantiornithes</i> indet., feathers				
125		Barremian	-				
129.4		Hauterivian	-				
132.6	Valanginian	-					
139.8	Berriasian	-					
145							

**Table 3.** Simplified geochronological table. Vertical axis scale in millions of years ago. Taxa with disputed distribution placed in the earlier proposed time unit (see main text).

FIG. 1



**Fig. 1.** Basic avian skeletal scheme. 1: Skull; 2. Cervical vertebrae; 3. Furcula; 4. Coracoid; 5. Uncinate process; 6. Keel; 7. Patella; 8. Tarsometatarsus; 9. Foot digits; 10–11. Tibiotarsus; 12. Femur; 13. Pubis; 14. Ischium; 15. Ilium; 16. Caudal vertebrae; 17. Pygostyle; 18. Synsacrum; 19. Scapula; 20. Lumbar vertebrae; 21. Humerus; 22. Ulna; 23. Radius; 24. Carpus; 25. Third digit of the wing; 26. Second digit of the wing; 27. Alula (Modified from Wikimedia Commons).

FIG. 2

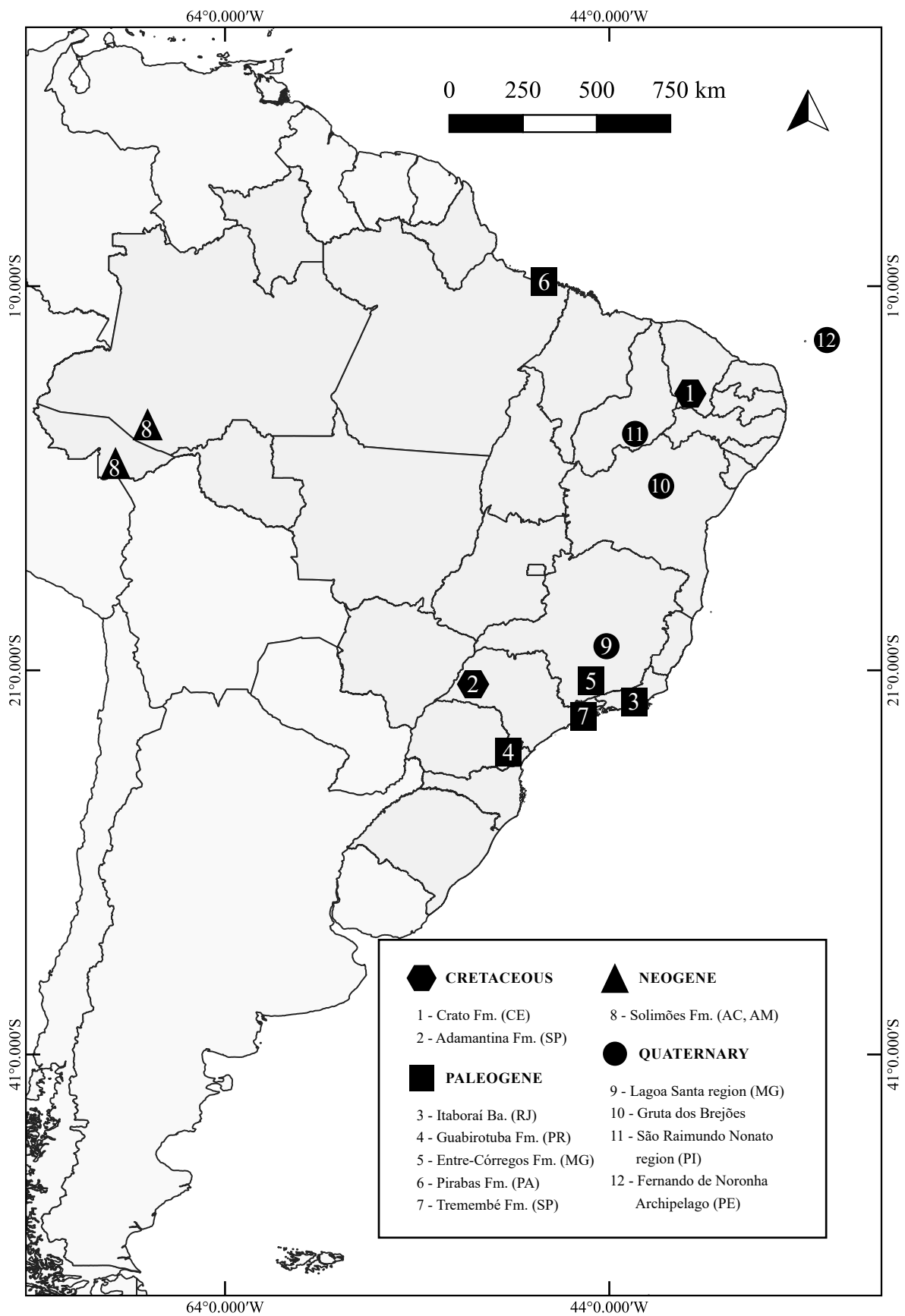
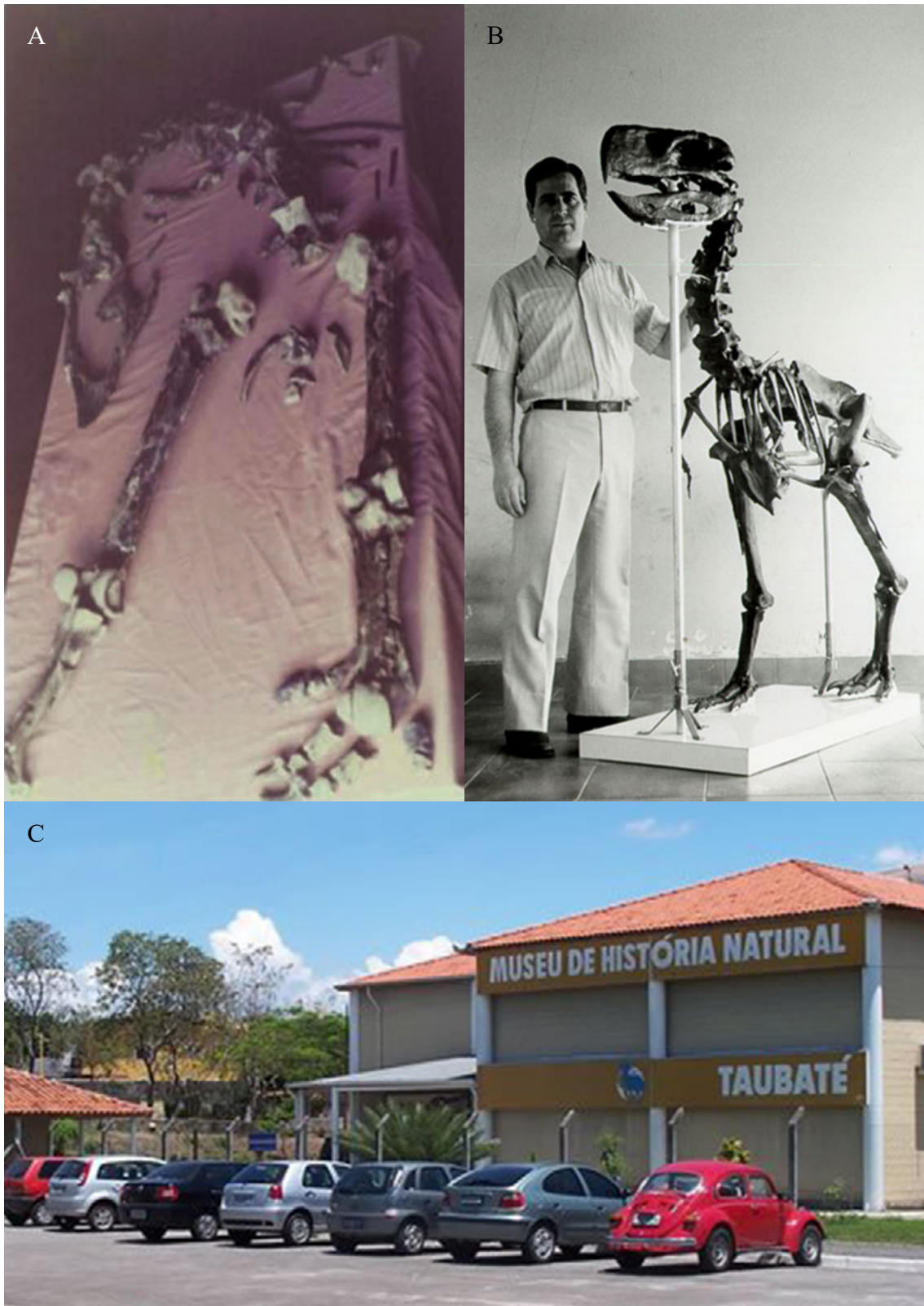


Fig. 2. Most important sites providing extinct taxa material. *Fm.*: Formation; *Ba.*: Basin.





**Fig. 3.** Lagoa Santa Karst. The Danish researchers responsible for the first studies on Brazilian fossil birds: A. Peter Wilhelm Lund (1801–1880); B. Johannes Theodor Reinhardt (1816–1882); C. The only known picture we can attribute to Gustav Oluf Bang Winge (1855–1889); D. One of the boxes used to transport the fossil material from Brazil To Denmark; E. Materials collected by Lund stored in ZMUC (A–C: Det Kongelige Bibliotek; D–E: K.L. Hansen).



**Fig. 4.** Tremembé Formation. The work of Herculano Alvarenga: A. First photo of *Paraphysornis brasiliensis* remains, when its restoration began (1977); B. Alvarenga with the reconstituted replica skeleton; C. Museu de História Natural de Taubaté (H.M.F. Alvarenga).





**Fig. 5.** *Neochen pugil* (Winge) ♂, Lapa da Escrivânia V. Holotype: proximal end of the left humerus (ZMUC 12017), cranial (A) and caudal (B) views; right coracoid (ZMUC 12115), ventral (C) and dorsal (D) views; right carpometacarpus (ZMUC 12044), ventral (E) and dorsal (F) views; left tibiotarsus lacking the proximal end (ZMUC 12122), cranial (G) and caudal (H) views; left tarsometatarsus (ZMUC 12084), dorsal (I) and plantar (J) views (K.L. Hansen).



**Fig. 6.** *Neochen pugil* (Winge) ♀, Lapa da Escrivânia XI. Ulnae (A, B); carpometacarpus (C); humeri (D, E, G?); femur (F). ♂ *Lapa dos Tatus*. Carpometacarpus (H), humerus (I?), foot phalanx (J) (K.L. Hansen).



**Fig. 7.** *Neochen pugil* (Winge) ♂, Lapa da Escrivânia V. Various elements. Carpometacarpi (A, B, C, G, H); rib (D); partial synsacrum and pelvis (E); wing phalanges (I, J); vertebrae (F, K, L, O, P); coracoids (M, N, V?); anterior part of the sternum (Q); ulnae (R, S?); tarsometatarsi (T, Aa, Ab); foot phalanx (U); radius (X); tibiotarsi (Y, Z, Ac); femora (W, Ad, Ae) (K.L. Hansen).

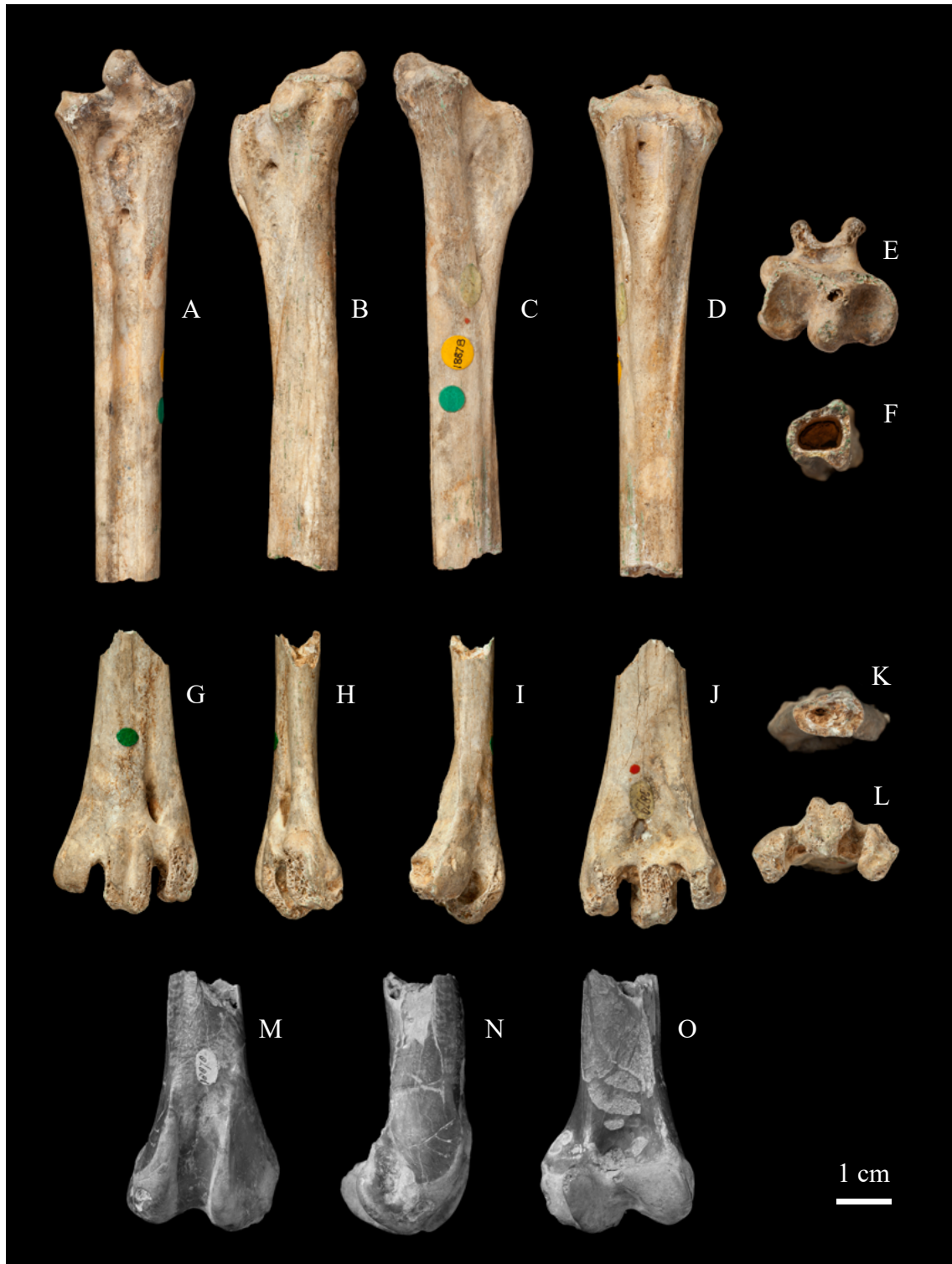




**Fig. 8.** *Neochen pugil* (Winge), *Lagoa Santa*. Referred material: right carpometacarpus (NHMUK PV OR 18906), cranial (A), ventral (B), dorsal (C), caudal (D), proximal (E), and distal (F) views. *Sarcoramphus papa* (Linnaeus), *Lagoa Santa*. Proximal end of the left ulna (NHMUK PV OR 18887), dorsal (G), caudal (H), cranial (I), ventral (J), proximal (K), and distal (L) views (S. Chapman).



**Fig. 9.** *Vanellus* sp., Lapa da Escrivânia XI. Proximal end of the right humerus, cranial (A) and caudal (B) views; Lapa da Escrivânia V. Right humerus, cranial (C) and caudal (D) views. *Sarcoramphus papa*, Lapa do Baú. Distal end of the right tibiotarsus (E) and fragment of the proximal end of the left humerus (F). **Cathartidae indet. 1**, Lapa da Escrivânia I. Proximal end of the right humerus (G), coracoid in two pieces (H), and proximal end of the ulna (I). *Wingegyps cartellei*, Lapa do Tiú. Paratypes: proximal end of the right ulna, (ZMUC 1118), dorsal (J) and ventral (K) views; distal end of the right humerus (ZMUC 1116), caudal (L) and cranial (M) views (K.L. Hansen).

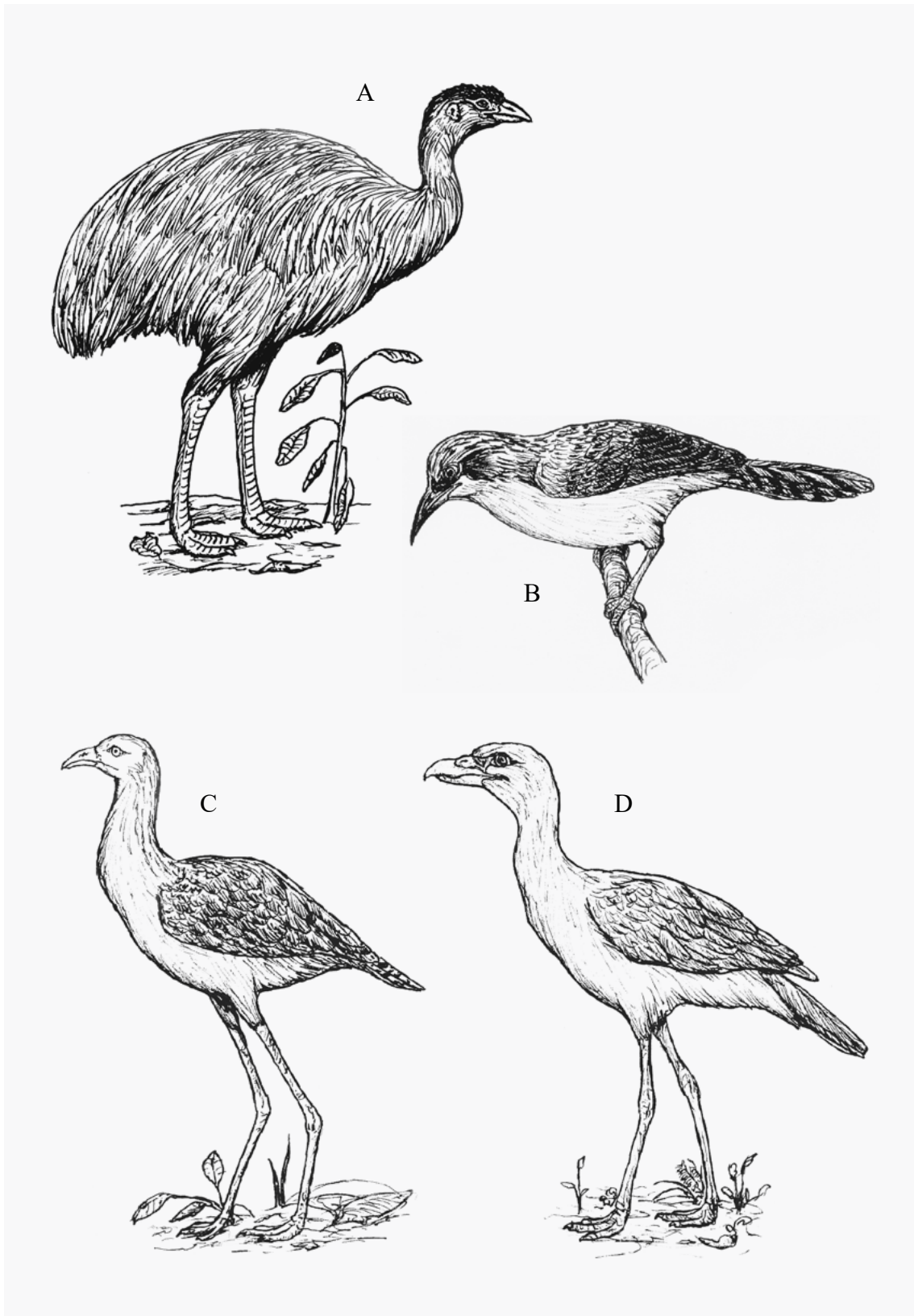


**Fig. 10.** *Ciconia lydekkeri* (Ameghino), Lagoa Santa. Holotype: proximal end of the right tarsometatarsus (NHMUK PV OR 18878), anterior (A), lateral (B), medial (C), posterior (D), proximal (E), and distal views; distal end of the left tarsometatarsus (NHMUK PV OR 1887), anterior (G), lateral (H), medial (I), posterior (J), proximal (K), and distal (L) views. Referred material: distal end of the left femur (NHMUK PV OR 12878), anterior (M), medial (N), and posterior (I) views (S. Chapman; F.L. Agnolin).



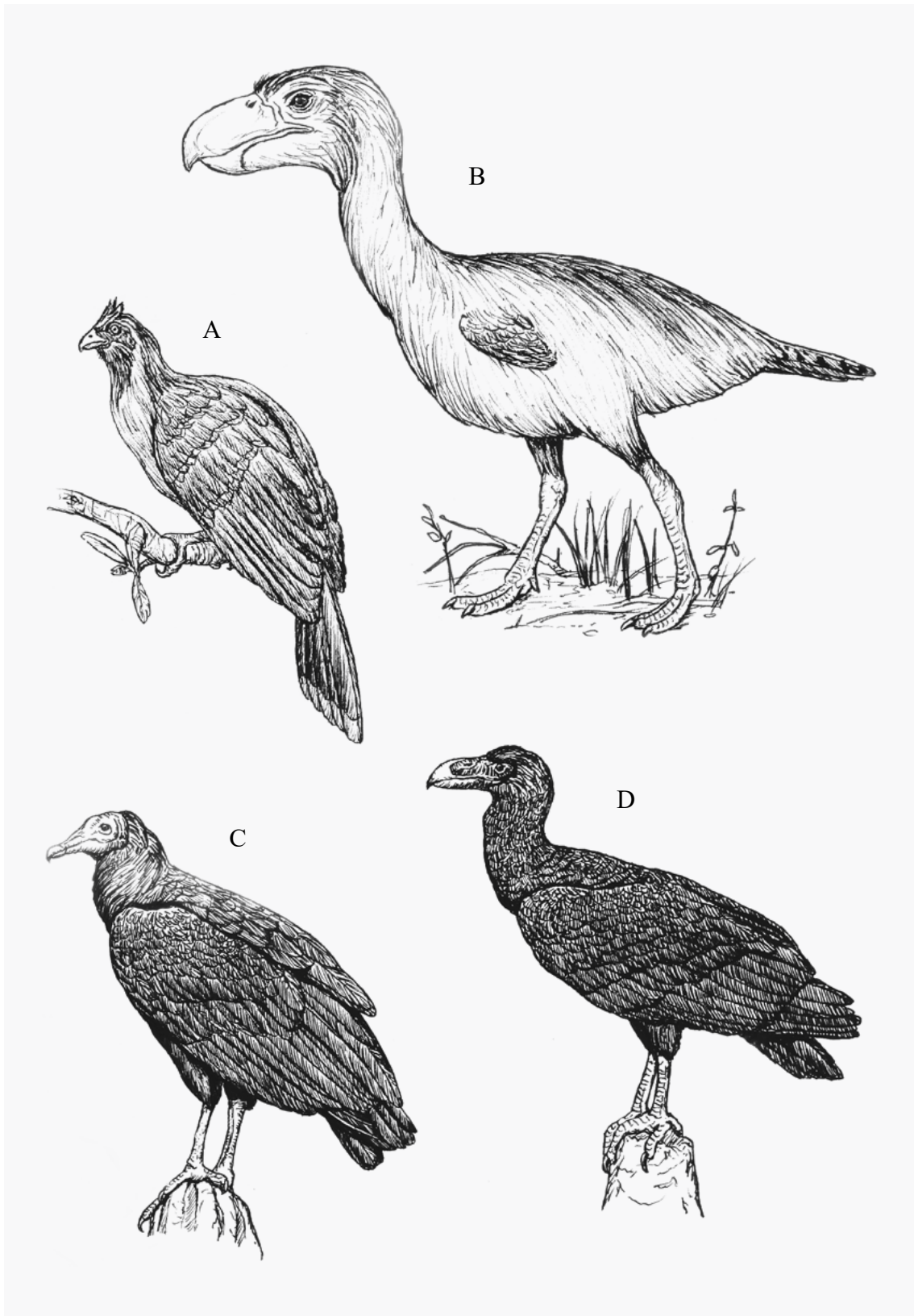


**Fig. 11. Accipitridae indet. 6, João Cativo.** Indeterminate fragments, presumably wing bones (MN 3270-V, MN 3271-V, MN 3272-V, MN 3273-V, MN 3293-V, and MN 3294-V), A and B (same specimen), C, D, E, F, G; ungueal phalanx (MN 3263-V), medial and lateral (H, I) and proximal view (J); distal end of the tarsometatarsus (MN 3275-V), anterior (K), caudal (L), and medial (M) views; hallux (MN 3265-V) (N, O, P); vertebrae (MN 3326-V), dorsal (Q, U, Y, Ac), ventral (R, V, Z, Ad), cranial (S, W, Aa, Ae), and caudal (T, X, Ab, Af) views (H.I. Araújo Júnior; C.L. Ximenes).

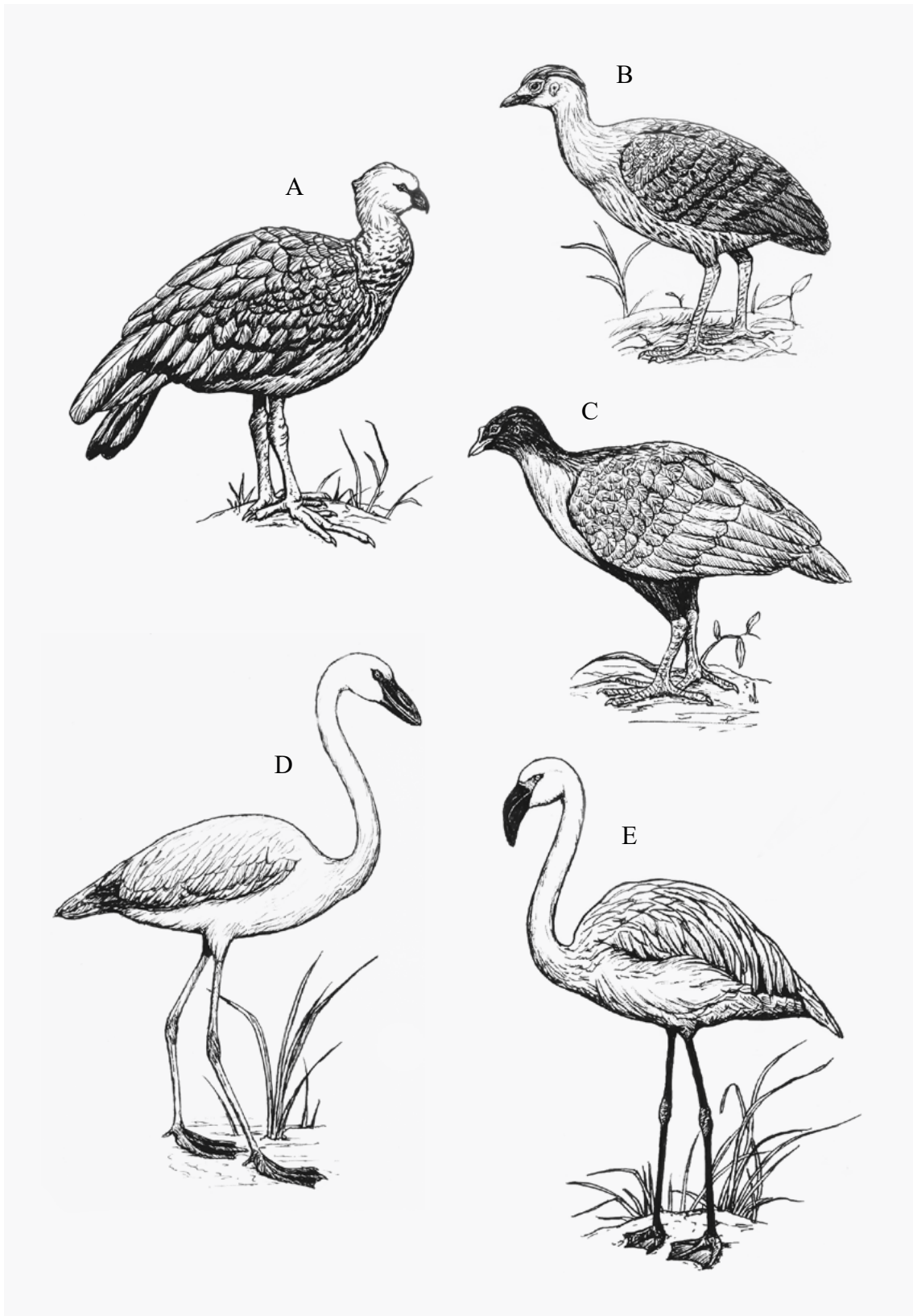


**Fig. 12. Life restoration of eocene taxa from the São José de Itaboraí Basin.** *Diogenornis fragilis* Alvarenga (A); *Eutreptodactylus itaboraiensis* Baird & Vickers-Rich (B); *Itaboravis elaphrocnemoides* Mayr et al. (C); and *Paleopsilopterus itaboraiensis* Alvarenga (D). Not to scale (R.S. Nascimento).

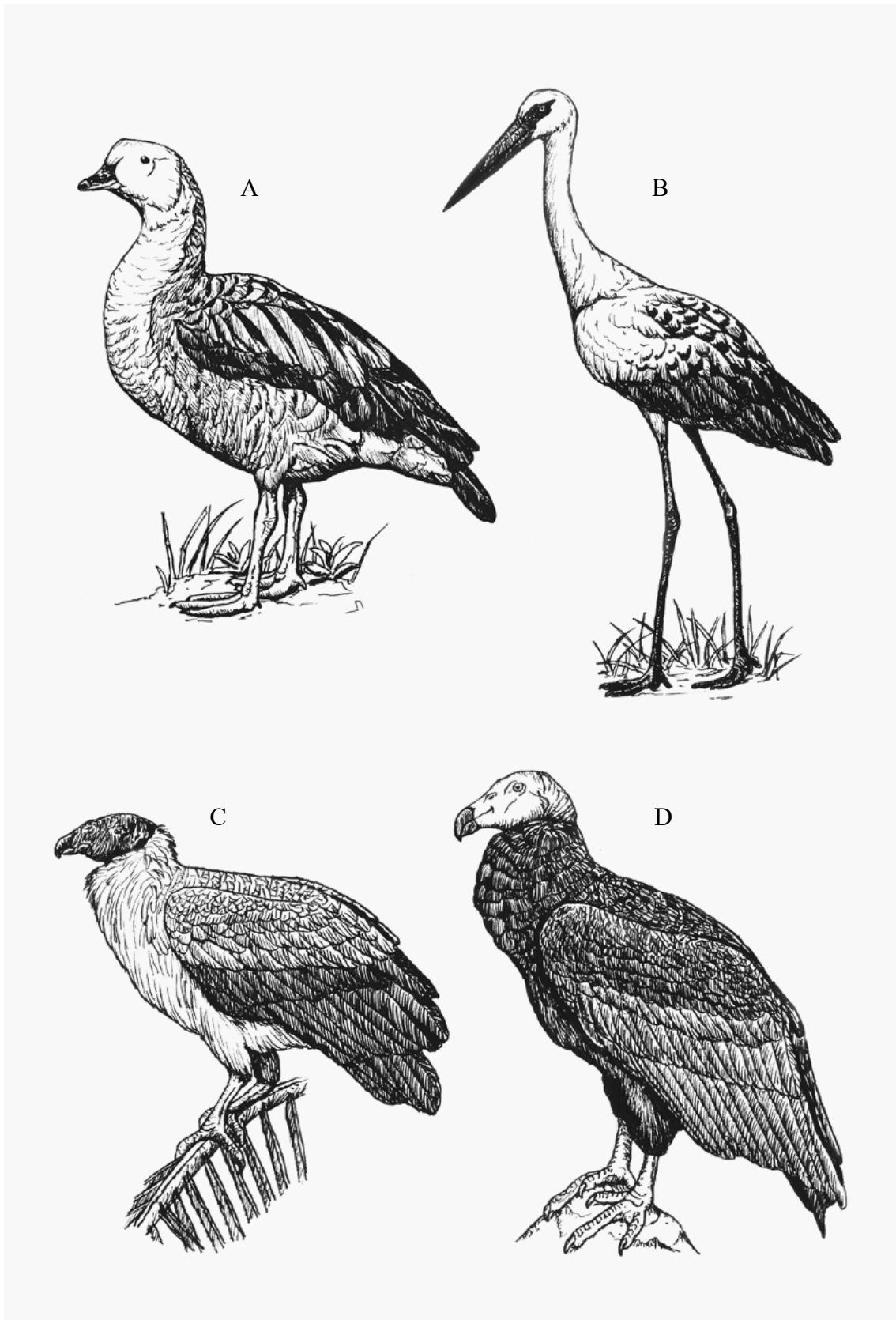




**Fig. 13. Life restoration of oligo-miocenic taxa from the Tremembé Formation.** *Hoazinavis lacustris* Alvarenga *et al.* (A); *Paraphysornis brasiliensis* (Alvarenga) (B); *Brasilogyps faustoi* Alvarenga (C); and *Taubatornis campbelli* Olson & Alvarenga (D). Not to scale (R.S. Nascimento).

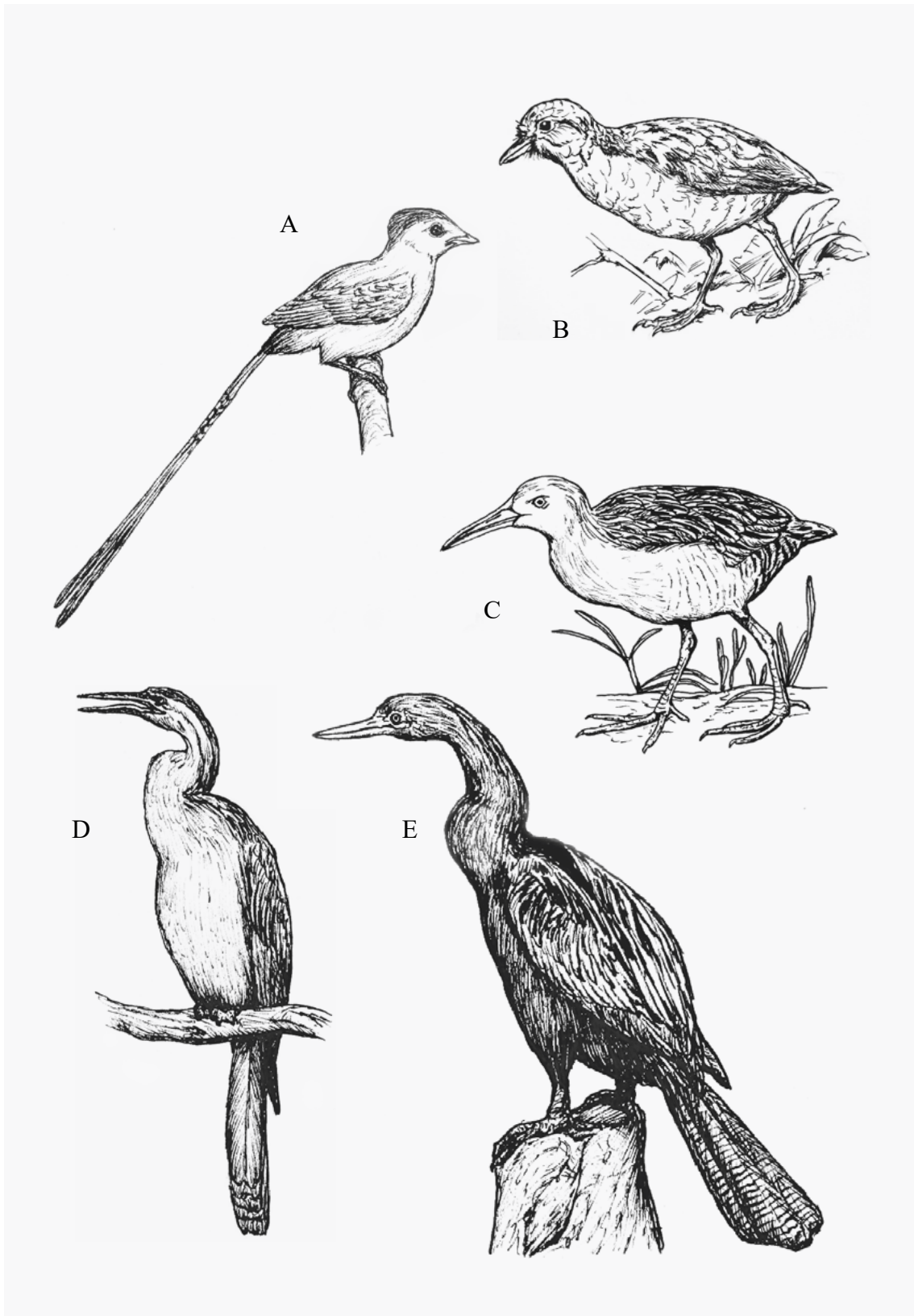


**Fig. 14. Life restoration of oligo-miocenic taxa from the Tremembé Formation.** *Chaunoides antiquus* Alvarenga (A); *Ameripodius silvasantosi* Alvarenga (B); *Taubacrex granivora* Alvarenga (C); *Palaelodus* cf. *ambiguus* Milne-Edwards (D); and *Agnopterus sicki* Alvarenga (E). Not to scale (R.S. Nascimento).



**Fig. 15. Life restoration of quaternary taxa from the Lagoa Santa region.** *Neochen pugil* (Winge) (A); *Ciconia lydekkeri* (Ameghino) (B); *Wingegyps cartellei* Alvarenga & Olson (C); and *Pleistovultur nevesi* Alvarenga et al. (D). Not to scale (R.S. Nascimento).





**Fig. 16. Life restoration of various mesozoic and cenozoic taxa.** *Cratoavis cearensis* Carvalho *et al.* (A); *Kaririavis mater* Carvalho *et al.* (B); *Rallus* sp. (Fernando de Noronha) (C); *Anhinga minuta* Alvarenga & Guilherme (D); and *Macranhinga ranzii* Alvarenga & Guilherme (E). Not to scale (R.S. Nascimento).