Diversity and paleobiology of the Santacrucian birds

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Abstract

This chapter presents the state of knowledge of the avian diversity recorded in Santacrucian beds (late Early Miocene) with an updated systematic summary of all taxa. Phorusrhacids outnumber seriemas, rheas, and basal faliconiforms in diversity and abundance. More fragmentary occurrences are reported of pelecaniforms, anseriforms, gruiforms, and ciconiforms. Body masses of fossil forms are inferred from the dimensions of their hindlimb bones (i.e. femur, tibiotarsus) based on logarithmic equations previously modeled from living analogs. In some cases, body sizes of the extinct species are also inferred from the relative sizes of other bones of similar extant species. Inferences about diet and foraging strategies are based on the size and shape of the limb elements and structural details of the cranial elements, by analogy with extant birds. The predator niche is represented by falconids, four species of phorusrhacids and a seriemid. Phorusrhacids and seriemids probably lived in open areas because of their cursorial capabilities. However, birds such as the waterfowls, limpkins, spoonbills, and darters indicate the presence of temporarily flooded savannas or permanent water bodies in forested areas. Habitat preferences of extant seriemas, rheas, tinamous, and the falconid Herpetotheres are consistent with Chacoan-like conditions, and they are useful to infer by extrapolation similar Santacrucian paleoenvironments for their extinct analogs. Santacrucian environments were probably characterized by seasonality in temperature and rainfall and the presence of alternating areas of herbaceous vegetation with shrubby or wooded areas.

Resumen

Este capítulo contiene una síntesis actualizada del conocimiento sobre el registro paleontológico de las aves del Santacrucense (Mioceno Temprano tardío). Los fororra- cos superan a las chuñas, ñandúes y faliconiformes en diversidad y abundancia. Especímenes fragmentarios de pelecaniformes, anseriformes, gruiformes y ciconiformes son también reportados. Las estimaciones de las masas corporales de taxones fósiles aquí presentadas, a partir de las dimensiones de los huesos de sus miembros posteriores (fémur, tibiotarso), están basadas en ecuaciones logarítmicas previamente modeladas en análogos vivientes. En algunos casos, el tamaño corporal de las especies extinguidas es inferido a partir del tamaño relativo de otros huesos en las especies actuales análogas. Las interpretaciones sobre dietas y estrategias de alimentación están basadas en el tamaño y la forma de los elementos de los miembros y los detalles estructurales del cráneo y mandíbula, por analogía con las aves actuales. El nicho de los depredadores se encuentra representado por los fal- cónidos, cuatro especies de fororacas y una chuña, los cuales habrían habitado ambientes abiertos debido a sus capacidades locomotoras cursoriales. Sin embargo, aves como patos, carajás, espárrulas y anhingas indican la presencia de sabanas temporalmente inundadas o de cuerpos de agua permanentes en áreas más forestadas. Las preferencias de hábitat de las actuales chuñas, ñandúes, perdices y Herpetotheres son consistentes con condiciones de tipo chacoey que son útiles para inferir similares paleoambientes santacrucenses al extrapolarse a sus análogos fósiles. Los escenarios santacrucenses habrían estado caracterizados por la estacionalidad en las temperaturas y las lluvias, así como por la presencia de áreas de vegetación herbácea alterando con zonas arbustivas o incluso boscosas.

9.1 Introduction

The late Early Miocene vertebrate fauna of the Santa Cruz Formation along the Atlantic coast of southern Patagonia (see Vizcaíno et al., Chapter 1, Figs. 1.1 and 1.2) comprises one of the richest fossil assemblages known in the continent (Hatcher, 1903; Tauber, 1997a, b; Vizcaíno et al., 2006; Vizcaíno et al., 2010). The collection of avian fossils began in the nineteenth century with Carlos Ameghino. Some of his specimens were originally deposited at the Museo de La Plata and Museo Argentino de Ciencias Naturales “B. Rivadavia” (Argentina), but some were later sold to the British Museum of Natural History (England), as is evident through the analysis of Ameghino’s catalog at the latter institution. Florentino Ameghino described several new taxa based on these specimens. In the 1890s, John B. Hatcher made extensive collections for Princeton University, and this was followed by Elmer S. Riggs’ expeditions in the 1920s for the Field Museum of Natural History in Chicago. These collections included numerous well-preserved bird remains. Some of these older collections have been revised recently (Alvarenga and

Scattered bird remains were also reported from localities farther northwest in Santa Cruz Province, in sediments of the Pinturas Formation (Chiappe, 1991; Noriega and Chiappe, 1993; Bertelli and Chiappe, 2005). The Pinturas Formation (Early Miocene) is regarded as slightly older than the Santa Cruz Formation (Ameghino, 1906; Frenguellí, 1931; Barrio et al., 1984; Fleagle et al., 1995). The distinctiveness of the Pinturas fauna from the Santacrucian fauna has been questioned, with some authors referring the former to the Santa Cruz Formation (Pascual and Odremán Rivas, 1971; Marshall, 1976), but recent radiometric dates for a Pinturan fauna at Gran Barranca show that the Pinturas Formation is definitely older than the coastal Santa Cruz rocks (Ré et al., 2010).

9.2 The fossil record

The record of Santacrucian birds comprises at least 18 species included in 15 genera and nine families. Most holotypes are very fragmentary and eroded. Brief descriptions and poor illustrations make the reassessment of the known taxa challenging (Olson, 1981, 1985; Tonni, 1980; Tambussi and Noriega, 1996). What follows is a commentary about the material. The main localities where all these remains were recovered are shown in Vizcaíno et al. (Chapter 1, Figs. 1.1 and 1.2).

Rheiformes Rheids are represented by Opisthodactylus patagonicus Ameghino, 1891 (Fig. 9.1a), a taxon initially placed in its own family, Opisthodactylidae (Ameghino, 1895; Brodkorb, 1963), but transferred to Rheidae because of its strong resemblance to living rheas (Patterson and Kraglievich, 1960; Tonni and Tambussi, 1986; Tambussi, 1995).

Tinamiformes At least two species coming from the localities of Monte Obsesión (= Cerro Observatorio), Monte León, and Cañadón de Las Vacas are recognized (Bertelli and Chiappe, 2005). They represent two distinct morphotypes of Nothurinae, but they cannot be assigned to any known taxon or described as new taxa because of their fragmentary state.

“Gruiformes” A distal end of tarsometatarsus (Fig. 9.1b) described as Anisolorinus excavatus Ameghino, 1891 was originally assigned to the “Pelecyornidae” (= Phorusrhacidae Psilopterinae). Later it was tentatively assigned to the Phasianidae (Galliformes) by Ameghino (1895). Alternatively, it has been considered a seriema or a tinamou (Brodkorb, 1964), a gruiform of the family Aramidae (Cracraft, 1973), or closely related to the Psophiidae (Olson, 1985; see Tambussi and Noriega, 1996).

Anseriformes Two species of waterfowl (Anatidae) have been described: Eutelornis patagonicus Ameghino, 1891 (based on a distal end of a humerus and a proximal end of a tibiotarsus, Fig. 9.1c) and Eoneornis australis Ameghino, 1891 (represented by a distal end of radius, Fig. 9.1d) (Ameghino, 1895). Recently, Worthy (2008) considered both taxa as incertae sedis, but Cenizo and Agnolín (2010) stated that Eoneornis australis is similar to basal screamers (Anhimidae) and that Eutelornis patagonicus also belongs to a basal anseriform clade. Ankonetta larriestrai Cenizo and Agnolín (2010) was recently described as a basal anatid on the basis of an incomplete tarsometatarsus.

The anseriform Brontornis burmeisteri Moreno and Mercerat, 1891 is represented by a mandibular symphysis, a quadrate, fragmentary remains of a femur, tibiotarsus, tarsometatarsus (Fig. 9.2a–c), and several phalanges. This taxon was considered a phorusrhacid (Brodkorb, 1967; Mourer-Chauvire, 1981; Alvarenga and Höfling, 2003; Alvarenga et al., 2011), or related to the Anseriformes (Moreno and Mercerat, 1891; Agnolín, 2007). The hindlimb of Brontornis Moreno and Mercerat, 1891 resembles that of Cygnus (Anatidae), and Dolgopol de Sáez (1927) even created a separate order for the genera Brontornis and Rostrornis Moreno and Mercerat, 1891 (synonym of the first sensu Alvarenga and Höfling, 2003) based on features of the tarsometatarsus and phalax.

Pelecaniformes Liptornis hesternus Ameghino, 1895 was originally described, with doubt, as a pelecaniform based on a cervical vertebra (Fig. 9.1e). Our study of a cast and photographs of the type specimen allowed us to confirm that L. hesternus is an anhingid. Cenizo and Agnolín (2010) reported the presence of an indeterminate species of the extinct genus Macranhinda Noriega, 1992 at Río Bandurrias from the Santa Cruz Formation in the homonymous Argentinian province. Santacrucian anhingids are also known from sediments of the Curá Mallín Formation (Early to Middle Miocene) in Chile (Alvarenga, 1995). These records are the oldest for the family in South America, earlier than the important radiation that took place in the Middle to Late Miocene at northern latitudes in Argentina, Uruguay, Brazil, Colombia, and Peru (Rasmussen and Kay, 1992; Noriega, 1995, 2002; Campbell, 1996; Rinderknecht and Noriega, 2002; Areta et al., 2007; Noriega and Agnolín, 2008).

Ciconiiformes Proditis cuneialis Ameghino, 1891, based on a distal end of tibiotarsus (Fig. 9.1f), has been considered a plataleid (Threskiornithidae). The lack of cranial or complete appendicular remains referred to this purported spoonbill species makes its systematic assignment highly speculative.
Falconiformes The birds of prey are known by three species of the family Falconidae: *Badiostes patagonicus* Ameghino, 1895, *Thegornis musculus* Ameghino, 1895, and *T. debilis* Ameghino, 1895. The first was described on the basis of a very damaged and fragmentary specimen (Fig. 9.3a) from the La Cueva locality and it was referred with doubt to the family Strigidae. However, Brodkorb (1964) assigned *B. patagonicus* to the Falconidae, a view also shared by Olson (1985). The type material belonging to this taxon is currently under review (J. Noriega and H. Alvarenga, unpublished data, 2011). The species of *Thegornis* were both erected on fragments of distal tarsometatarsi (*T. debilis*, Fig. 9.3b, and *T. musculus*, Fig. 9.3c) and referred to the Falconidae. The holotype of *T. musculus* was collected at the locality Yegua Quebrada, whereas *T. debilis* came from the Corriguen Aike (= Puesto Estancia La Costa) locality. The recent find of a very well-preserved, complete specimen (Fig. 9.3d–i) referable to *T. musculus* at Puesto Estancia La Costa reconfirms Ameghino’s placement of this.
taxon within the Falconidae (Noriega et al., 2008; Noriega et al., 2011). A cladistic analysis places *T. musculus* as the sister-group of the Laughing Falcon, *Herpetotheres cachinnans*, within the basal clade of the Herpetotherinae (Noriega et al., 2011).

**Cariamiformes** The seriemas (Cariamidae) are represented only by *Cariama santacrucensis* Noriega et al., 2009, which is based on an incomplete cranium (Fig. 9.2d, e) and two unassociated fragments of tibiotarsi, all from Puesto Estancia La Costa (= Corriguen Aike).

The “terror birds” (Phorusrhacidae) are the world’s largest known terrestrial carnivorous birds. Their biological and morphological design represents an extreme of terrestrial vertebrate evolution. They are a very interesting group not only for this reason, but also for the presence of an enormous and rigid skull, with a high and narrow beak, which is a peculiar, unique morphology among birds (Degrange et al., 2010a).
The fossil record of phorusrhacids extends from the Middle Paleocene (Alvarenga, 1985) to the Late Pleistocene (Alvarenga et al., 2010). Their greatest diversity occurred during the late Early Miocene (Santacrucian).

Among the several systematic proposals for the subdivision of the Phorusrhacidae (Dolgopol de Sáez, 1927; Patterson and Kraglievich, 1960; Brodkorb, 1967; Alvarenga and Höfling, 2003; Agnolin, 2009), we recognize four of the five subfamilies proposed by Alvarenga and Höfling (2003): Mesembriornithinae, Phorusrhacinae, Patagornithinae, and Psilopterinae, of which only the latter three are represented in the Santacrucian.

1. Phorusrhacinae: *Phorusrhacos longissimus* Ameghino, 1887 (Fig. 9.2f–i) is known for the Santacrucian and represented by fragments of skulls, jaws, femora, tibiotarsi, tarsometatarsi, and phalanges. Most of these
materials were widely, although ambiguously, described by F. Ameghino (1887, 1889, 1895).

2. Patagornithinae: *Patagornis marshi* Moreno and Mercerat, 1891 is known by a abundant and well-preserved fossil remains (Figs. 9.4a, 9.5a). A very extensive description of *P. marshi* can be found in Andrews (1899).

3. Psilopterinae: two species of psilopterines come from Santacrucian sediments: *Psilopterus lemoinei* (Moreno and Mercerat, 1891) (Fig. 9.4b) and *P. bachmanni* (Moreno and Mercerat, 1891) (Figs. 9.4c, 9.5b), both widely, but ambiguously, described by Sinclair and Farr (1932). *Psilopterus lemoinei* is one of the best-known phorusrhacids, being represented by several specimens, including skulls.

9.3 Materials and methods

9.3.1 Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA.

FMNH, Field Museum of Natural History, Chicago, USA.

MLP, Museo de La Plata, La Plata, Argentina.

MPM-PV, Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Santa Cruz Province, Argentina.

YPM-VPPU, Yale Peabody Museum, Princeton University Collection, New Haven, USA.

The material studied is listed in Appendix 9.1.

9.3.2 Body mass estimation

Campbell and Marcus (1992) developed a method to estimate body masses of extinct birds based on regression equations derived from the minimum shaft circumferences of the femur (LFC) and tibiotarsus (LTC) of extant birds of known body mass representing 89 families and spanning several ecologically (and morphologically) distinct subgroups (Campbell and Marcus, 1992: 397); data available in Campbell and Marcus (1992: 405; Table 1). The femur and tibiotarsus dimensions are better estimators of body masses than the tarsometatarsus, evidently because the former have a more direct role in body support whereas the tarsometatarsus tends to be more associated with feeding and locomotor styles than with body support (Campbell and Marcus, 1992).

In most cases, for body mass estimates we employed Campbell and Marcus data for “long-legged” birds because phorusrhacids, seriema, and rheas had relatively long legs. We used Campbell and Marcus “predatory” flying birds to estimate the body mass of *Thegornis musculosus*.

The logarithmic estimating equation is as follows:

\[
\log_{10}(\text{mean mass for subgroup})/\log_{10}(\text{LFC or LTC for subgroup}) = \log_{10}(\text{mass for fossil})/\log_{10}(\text{LFC or LTC of fossil})
\]

(Eq. 9.1)

Several Santacrucian bird taxa are not represented by femora or tibiotarsi. In such cases, we used measurements taken from other bones and body masses of living analogs to predict the body weight of fossil forms, assuming constant proportions (i.e. isometry). Geometric similarity between a fossil species and its living analog implies that the length of homologous parts will be proportional to linear dimensions, and the surface will increase to the square and the volume to the cube.

The isometric weight estimation is thus calculated as:

\[
\text{mass (fossil)}/\text{mass (living analog)} = (L \text{ fossil} / L \text{ living analog})^3
\]

(Eq. 9.2)

where \( L \) is a linear dimension.

Accuracy of estimations using this method depends directly on the presence of allometric differences or similarities along the evolutionary lineages involved in each case.

9.3.3 Bite force estimation

Published *in vivo* bite force data for birds is largely restricted to passerines (van der Meij and Bout,
2004, 2006). These studies show that bite force is related to skull morphology and geometry, as well as to the capacity of contraction of the jaw muscles (van der Meij and Bout, 2004; Herrel et al., 2005a, b). It has been demonstrated that in Galápagos finches, beak size, and especially head width, are strongly correlated with bite force, and head size closely correlates with jaw muscle dimensions (Herrel et al., 2001, 2002). However, passerines are a poor model for the estimation of bite force in phorusrhacids because of differences in phylogeny, skull size, and morphology. Instead, we use the linear model presented by Degrange et al. (2010a) to estimate bite force of the Santacruzian phorusrhacids, Brontornis, and Thegornis. This model considers the relationship between bite force and body mass as follows:

$$\log_{10} BF = 1.3988 + 0.4541 \log_{10} BM$$  \hspace{1cm} (Eq. 9.3)

where BF is the bite force (in newtons) and BM is the body mass (in kilograms).
Table 9.1. Allometric and isometric body mass and bite force estimations for selected Santacrucian birds

<table>
<thead>
<tr>
<th>Species</th>
<th>Allometric calculation</th>
<th>Isometric calculation</th>
<th>Bite force (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Opisthodactylus patagonicus</td>
<td>–</td>
<td>56.95</td>
<td>–</td>
</tr>
<tr>
<td>Anisolornis excavatus</td>
<td>–</td>
<td>1.43</td>
<td>–</td>
</tr>
<tr>
<td>Brontornis burmeisteri</td>
<td>319</td>
<td>–</td>
<td>343</td>
</tr>
<tr>
<td>Liptornis hesternus</td>
<td>–</td>
<td>0.97</td>
<td>–</td>
</tr>
<tr>
<td>Protibis enemialis</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Thegornis musculusos</td>
<td>1.9</td>
<td>–</td>
<td>33.6</td>
</tr>
<tr>
<td>Badiostes patagonicus</td>
<td>–</td>
<td>0.217</td>
<td>–</td>
</tr>
<tr>
<td>Phorusrhacos longissimus</td>
<td>93</td>
<td>–</td>
<td>196</td>
</tr>
<tr>
<td>Patagornis marshi</td>
<td>26</td>
<td>–</td>
<td>110</td>
</tr>
<tr>
<td>Psilopterus lemoinei</td>
<td>8</td>
<td>–</td>
<td>64</td>
</tr>
<tr>
<td>Psilopterus bachmanni</td>
<td>4.5</td>
<td>–</td>
<td>49.5</td>
</tr>
<tr>
<td>Cariama santacruicensis</td>
<td>–</td>
<td>1.5</td>
<td>–</td>
</tr>
</tbody>
</table>

9.4 Results

9.4.1 Body mass estimations

Table 9.1 lists the body mass estimates of the taxa analyzed. The body mass predictions using Campbell and Marcus (1992) model revealed that phorusrhacids show a wide variation in body size. The Santacrucan species range from 4.5 kg in *Psilopterus bachmanni* (Psilopterinae) to 93 kg in *Phorusrhacos longissimus* (Phorusrhacinae), with intermediate weights of 26 kg exhibited by *Patagornis marshi* (Patagornithinae).

The estimations obtained by means of ratios between linear dimensions and body masses in extant analog forms are also presented in Table 9.1. We used the lengths of the tenth vertebral body (from *facies articularis cranialis* through *facies articularis caudalis*) as a scaling variable for *Liptornis hesternus* based on the extant *Anhinga anhinga* (21.5 mm; Alvarenga and Guilherme, 2003) and the average mass of *A. anhinga* (1.2 kg; Ovre, 1967). In a similar way, the values of the greatest distal tarsometatarsal widths through trochleae and mean body weights in living *Rhea americana* and *Aramus guarauna* were used to estimate the body mass of *Opisthodactylus patagonicus* and *Anisolornis excavatus*. Likewise, the greatest width of the proximal end of the tarsometatarsus (5.75 mm) and the average body mass (0.125 kg) in the extant American Kestrel (*Falco sparverius*), together with the tarsometatarsal proximal end width (10 mm) of *Badiostes patagonicus*, allowed us to estimate the mass of the latter. Finally, the cranial width through the postorbital apophyses of *Cariama santacruicensis* (c. 50 mm), which is nearly identical to the same measurement in *Cariama cristata*, and the average weight of the latter (1.5 kg; Jutglar, 1992: 239) were employed to estimate the body mass of the former. The material belonging to fossil waterfowl is too fragmentary and eroded to be useful in scaling. The same is true for *Thegornis debilis*.

9.4.2 Bite force estimations

Bite force estimations are summarized in Table 9.1. These forces were estimated based solely on the mass predictions using the femur.

While the results presented here show that bite force is correlated with body mass in birds (*R = 0.77912, R² = 0.607, P < 0.0001*), the extrapolations based on body mass for the phorusrhacids produced relatively low values. The lower values are found among the psilopterines and the higher values occur among phorusrhacines. The Santacrucan psilopterines show values between 49 (*P. bachmanni*) and 64 N (*P. lemoinei*). *Patagornis marshi* had a bite force of 110 N and *Phorusrhacos longissimus* had a bite force of 196 N. The bite of *Brontornis* (343 N) is difficult to interpret in the absence of more cranial data.

*Thegornis musculus* (33.6 N) had a stronger bite than extant accipitrids, but weaker than extant falconids (Sustaita and Hertel, 2010).

9.5 Discussion

9.5.1 Paleobiology of the Santacrucian birds

Rheiformes *Opisthodactylus patagonicus* had proportions similar to modern rheas, although it was almost twice as heavy. It is probable that they were mainly grazers, roaming open grasslands, scrub forest, or chaparral in search of different vegetation items, as well as feeding on insects and small animals in the same fashion as living rheas (Folch, 1992).
**Tinamiformes** The Santacrucian tinamous appear to be related to the extant nothurine forms of open habitats (Bertelli and Chiappe, 2005). Tinamous are exclusively ground foragers, feeding on seeds, buds, roots, and insects. They prefer to run rapidly when threatened, but they can fly for up to 100 m when alarmed (Feduccia, 1996; Cabot, 1992; Davies, 2002).

“Gruiformes” *Anisolornis excavatus* represents a most interesting record from paleobiological and paleoenvironmental perspectives. This taxon has been considered to be a trumpeter (Psophiidae) or a limpkin (Aramidae) by different authors. Trumpeters, a relictual Amazonian family of medium-sized terrestrial birds, comprise five living species in the genus *Psophia* (Oppenheimer and Silveira, 2009). They have fairly long necks and legs, short, stout bills, and a hump-backed appearance. They are inhabitants of dense areas of tropical forest, feeding on fallen fruits and insects (Sherman, 1996). On the other hand, the living limpkin (*Aramus guarauna*) is the sole member of the family Aramidae, and it is thought to represent a primitive crane-like form (Olson, 1985; Feduccia, 1996). It is a medium to large wading bird about 70 cm in height, intermediate in size between true cranes and rails. Limpkins generally live in wetlands, preferring marshy wooded areas (Bryan, 1996). They are resident in open freshwater marshes, swamp forests bordering slow-moving rivers, lake or pond shores, and mangroves. They feed mainly on large freshwater snails that they obtain by walking in shallow water, rarely in deeper water.

Notwithstanding the controversy about the family allocation of *A. excavatus*, it is clear that the holotypical distal tarsometatarsus corresponds to a basal gruiform that was a medium-sized, long-legged bird with terrestrial habits, but perhaps with facultative wading abilities as well.

**Anseriformes** *Brontornis burmeisteri* is a bulky-bodied bird that surpassed 2 m in height (Fig. 9.6). It is characterized by its short, wide, and deep mandibular symphysis, and its short but wide tarsometatarsus which barely reaches half the length of the tibiotarsus (Alvarenga and Höfling, 2003). This feature and its heavy body were interpreted as characterizing a slow bird of scavenging habits (Tonni, 1977; Tambussi, 1997). However, based on the morphology of its jaw and its relationship with the anseriforms, Agnolin (2007) proposed that *B. burmeisteri* was herbivorous. A similar diet was also proposed for the giant Holartic *Diatryma gigantea* Cope (Watson, 1976; Andors, 1988, 1992). Unfortunately, cranial remains of *Brontornis* are scarce and very fragmentary, making all assumptions of dietary habits speculative.

Santacrucian waterfowl are either of highly dubious identity or known only through very fragmentary material that does not provide any paleobiological information.

**Pelecaniformes** The size and predicted body mass of *Liptornis hesternus* are similar to those of extant *Anhinga anhinga*. Modern anhingas are freshwater birds that live and breed in forested borders of lakes, lagoons, or rivers, feeding exclusively on fish. All members of this family are...
foot-propelled swimmers, with very good diving capabilities. They dart their prey underwater with the beak. This mode of seizing prey is related to an adaptive specialization of the vertebral anatomy of their long necks. Despite its uncertain taxonomic status, there is no reason to suppose that *L. hesternus* was biologically different from extant species of darters when one considers the striking resemblance between the morphology of their vertebrae.

**Ciconiformes** *Proctis cnemialis* could be classified as a wading bird owing to its affinities with plataeids (spoonbills) and its long and slender tibiotarsus. It is known that spoonbills feed mainly on aquatic insects and larvae, but also eat molluscs, crustaceans, small fish, tadpoles, and frogs. Although inferring the diet of *P. cnemialis* in detail without knowing its skull morphology is highly speculative, it is probable that *P. cnemialis* was a carnivorous predator on small prey items, as are most wading birds.

**Falconiformes** *Thegornis musculus* and *Thegornis debilis* are medium-sized herpetotherines (Fig. 9.6), closely related to the living Laughing Falcon (*Herpetotheres cachinans*), a snake-specialist predator (Skutch, 1999; DuVal et al., 2006). Stout tarsi and short toes, typical features of snake-eating raptors (Bierregard, 1994), are present in *T. musculus*. Given the anatomical similarities between *H. cachinans* and *T. musculus*, we might infer that the latter also could have fed preferentially upon snakes. Morphotype resemblance and a close phylogenetic relationship lead us to suspect a similar biology for both species. In the case of *Badiostes patagonicus*, a small falcon with a generalized raptorial morphotype, it is not possible to infer precise dietary habits.

**Cariamiformes** Living seriemas range over a variety of semi-open and dry landscapes in South America, such as the thorny scrub and other semi-arid woodland areas of the Brazilian “caatinga,” the grassy savanna-like “cerrados,” and the “monte” and “chaco” forests in Bolivia, Paraguay, and Argentina (Gonzaga, 1996). They are capable of performing occasional, but not sustained flights. Seriemas have diets consisting of a variety of invertebrates and small vertebrates. The skull, leg bone morphology, and body mass of *Cariama santacruzensis* (Fig. 9.6) are very similar to that of the extant forms, which would have allowed them to step on similar prey items while tearing them into pieces with the bill (Noriega et al., 2009).

Phorusrhacids, together with marsupial carnivores, have been considered as the top predators of the Santacrucian fauna (Alvarenga and Höfling, 2003; Blanco and Jones, 2005; Chiappe and Bertelli, 2006; Bertelli et al., 2007), dominating the Tertiary stages of South America in the absence of placental mammalian carnivores. This conclusion was reached primarily on the basis of skull morphology (especially the shape of the beak), large body size, reduced forelimbs, and slender hindlimbs.

Their bizarre skull morphology is characterized by the presence of a very developed lacrimal bone; the occipital region is very expanded and vertically oriented, providing an insertion area for strong neck muscles; the temporal fossae are large, deep, and approach the mid-sagittal plane of the skull, producing a sagittal crest. However, the most outstanding feature is their huge beak. Contrary to the vast majority of extant birds, the beaks of phorusrhacids are long, high, very mediolaterally compressed, completely hollow (Degrange et al., 2010a), and endowed with a projecting hook as in raptors. The lower jaws of phorusrhacids are relatively narrow and slender, describing a slight sigmoid wave longitudinally, and with a very well-developed medial process. Phorusrhacids are characterized by the loss of cranial kinesis, an interpretation based on the absence (by secondary loss) of permissive linkages, or an intracranial *zonae flexoria* (Degrange et al., 2010a). The absence of zones of flexibility indicates that the palate was immobile in all the subfamilies. These features, together with the intimate contact between a descending branch of the lacrimal bone and the jugal, convert the skull of the larger phorusrhacids into a very rigid structure (Degrange et al., 2010a, b).

Traditionally, two functional groups of phorusrhacids have been recognized: non-volant cursorial predators (Phorusrhacinae, Mesembrinomithinae, and Patagornithinae), and predators with some flying capability (Psilopterinae) (Tonni, 1977; Tambussi, 1997).

In the gigantic phorusrhacines and the slimmer medium-sized patagornithines (Fig. 9.6), the tarsometatarsus is gracile and its length reaches 70% of the tibiotarsus length (Alvarenga and Höfling, 2003). The elongated tibiotarsus and tarsometatarsus (relative to body size and femur length), the highly developed *crisae cnemialis*, and toes of moderate to short length are all features related to cursoriality (Engels, 1938; Storer, 1971; Coombs, 1978) present in the terror birds. They seem to indicate a great capability for running at high velocities and with high maneuverability, as proposed for *Andalgalornis steulleti* (Kraglievich, 1931) and *Patagornis marshi* which are very similar to those abilities observed in ostriches (*Struthionidae*) (Tambussi, 1997; Blanco and Jones, 2005). Moreover, the pelvis of patagornithines is narrow and has very elongated post- and preacetabular portions which give a mechanical advantage associated with a more effective origin and stronger development of the femoral retractor and protractor muscles. In addition, their ungual phalanges are robust, allowing them to restrain struggling prey with their feet (Jones, 2010). Collectively, the morphology of the leg and pelvis in phorusrhacids can be interpreted as adaptations for chasing and subduing prey.
The psilopterines are the smallest and most gracile phorusrhacids (Fig. 9.6). *Psilopterus lemoinei* only reached 90 cm in height and *P. bachmani* 70 cm (Alvarenga and Höfling, 2003), and their hind limbs are more gracile than other phorusrhacids (Tambussi and Noriega, 1996). *Psilopterus lemoinei* had a skull with a deep maxilla, whereas that of *P. bachmani* is shallower. Notably, the long and slim tarsometatarsus reaches 70 to 75% of the tibiotarsal length. Compared with the pelvis of *Patagornis marshi*, the pelvis of psilopterines are relatively wide, suggesting that they were somewhat less adapted for sustained and fast running than were the patagornithines.

Two predatory styles are traditionally proposed for the phorusrhacids. Some phorusrhacids might have used only their beak to subdue prey whereas others might have used their hind limbs to also destabilize their prey during capture, killing, and dismemberment, or to gain access to brains and bone marrow (Blanco and Jones, 2005).

Regarding the manipulation of prey with the beak, previous reconstructions and biomechanical analyses of the jaw adductor musculature of *Andalgalornis steuelti* (Degrange, 2007, 2008) showed that the jaw apparatus of phorusrhacids was optimized for strength at the expense of speed. This is consistent with the loss of cranial kinesis, increased skull rigidity, and the increased area of attachment for the nuchal muscles that phorusrhacids experienced during their evolutionary history (Degrange et al., 2010a). Bite force will be increased with increasing stiffness of the jaw apparatus because muscle force is not attenuated at flexible areas (Wroe et al., 2007, 2008). Other factors being equal, any bird without cranial kinesis can bite with 1.3 times the force of those with cranial flexion (Bout and Zweers, 2001). However, a further consequence of the loss of flexibility is an increased potential for catastrophic failure when an organism bites into unexpectedly resistant materials (Wroe et al., 2007). In an akinsetic skull, more bone, or bone of greater density, will be needed to maintain effective safety margins. In akinsetic phorusrhacids such as patagornithines and phorusrhacines, the requisite increased bone mass was presumably tolerated because they were flightless and hence the advantages of ultra-light structures were lost (Degrange et al., 2010a). However, the tall, narrow beak of phorusrhacids would have been incapable of resisting great stress if they were to shake their head from side to side. A finite elements analysis of *Andalgalornis steuelti* showed that the skull was optimized to resist rostrocaudally and dorsoventrally directed loads, but it was less able to resist laterally directed loadings without failure (Degrange et al., 2010a). Taking into account that the morphology of the beak is very similar in the majority of phorusrhacids, it is probable that none of them could resist laterally directed loadings, especially the psilopterines with their very thin beak walls (Degrange and Tambussi, 2008, 2011). This fact is in agreement with the lower bite force values calculated for the group (Table 9.1) because with higher bite forces the beak is more sensitive to fracture. It seems reasonable to expect that if phorusrhacids used their beaks to dispatch relatively large prey, then the strike must have been applied with considerable precision in order to avoid sustaining high lateral loads. *Patagornis marshi* probably would have consumed prey of small size, but larger phorusrhacids such as *Phorusrhacos longissimus*, with their stronger bite force, probably were able to kill and ingest larger prey using a technique of multiple well-targeted strikes in a repetitive attack-and-retreat strategy. On the other hand, the psilopterines, with the lowest values for bite force and more fragile beaks, were probably restricted in their carnivorous diet to small vertebrates and invertebrates, as in living cairomids.

It has been proposed that the forelimb reduction and the lack of the processus acrocoroacodeus and procoracodeus of the coracoid in phorusrhacids (Alvarenga and Höfling, 2003) are related to the loss of flight (Alvarenga et al., 2011), whereas the species belonging to *Psilopterus* were able to fly (Tonni and Tambussi, 1988; F. Degrange and C. Tambussi, unpublished data, 2011; Degrange, 2012). The flight of the latter birds was probably brief and clumsy, as in extant seriemas.

### 9.5.2 Paleoenvironmental inferences

The Santacrucian fossil record of birds is relatively meager, which makes it difficult to reconstruct the avifauna from a paleoecological point of view and then to infer the paleoenvironment (Tambussi, 2011). However, we might suggest that the paleoenvironment was not unlike that found in the humid Chaco today. Vegetated open habitat dominated by shrubs or grasslands harbored cursorial predators (phorusrhacids and seriemas) and grazers (rheas and tinamous), while limpkins and spoonbills frequented flooded areas. Ecotonal margins between grasslands with seasonal water bodies and forest edges, ponds or marshes within the closed forest areas, as well as gallery forest along riversides, are appropriate habitats for anhingids.

The Laughing Falcon, *Herpetotheres cachinnans*, the living herptothere species considered to be the sister taxon of the Santacrucian *Thegornis muscosus*, is common in tropical and subtropical zones of South America at forest edges, open forests, and mixed palm savanna and forest habitats, always being observed near large clearings if nesting in closed primary forests (Noriega et al., 2011). Taking into account the habitat preferences mentioned above and the close phylogenetic relationship between both taxa, it is plausible to think that *Thegornis muscosus* was probably a forest dweller at the ecotonal margins of the gradually vanishing wet and humid Santacrucian forests that have been
Fig. 9.7. Life restoration of the Santacrucian birds. 1, Liptornis hesternus; 2, Eutelornis patagonicus; 3, Protibis enemialis; 4, Antisornis excavatus; 5, Psilopterus bachmanni; 6, Psilopterus lemoinei; 7, Thegornis musculosus; 8, Tinamidae; 9, Badiostes patagonicus; 10, Cariama santacrucensis; 11, Brontornis burmeisteri; 12, Phorusrhacos longissimus; 13, Patagornis marshi; 14, Opistodactylus patagonicus; 15, Eoneornis australis. Drawings by F. J. Degrange.

inferred from paleobotanical data (Barreda y Palazzesi, 2007; Noriega et al., 2011; Brea et al., Chapter 7).

In sum, the paleoenvironmental interpretation of a mixture of open and relatively closed vegetation in relatively dry conditions proposed by Tauber (1997a, b), and reinforced by Vizcaíno et al. (2006) based on the diversity of the Santacrucian armadillos, is consistent with the avian fossil record (Fig. 9.7).

### 9.6 Conclusions

1. In the absence of placentals, a number of birds represented by four species of phorusrhacids and a seriema, along with several groups of marsupials, occupied the large-predator niche in the Santacrucian paleocommunity. The avian small predator niche was occupied by falcons, darters, limpkins, and spoonbills. The first are
classified as terrestrial raptors, darters are exclusively freshwater predators, and the latter are included among the wading birds.

2. The omnivorous niche is represented by the rheid *Opisthodactylius*. Tinamous occupied the herbivorous niche, probably together with *Brontornis*.

3. Medium- to large-sized phorusrhacids (Phorusrhacinae and Patagornithinae) are thought to have preferred open habitats because of their cursorial mode of locomotion.

4. Waterfowl, limpkins, spoonbills, and darters indicate the presence of seasonally flooded areas, marshes, or permanent water bodies in more forested areas.

5. Habitat preferences of living seriemas, rheas, some tinamous, and *Herpetotheres*, all analogs of Santacrucian taxa discussed here, are consistent with the hypothesis of a Chacoan-like scenario for the Santacrucian paleoenvironment, the latter being characterized by open vegetation alternating with bushy or wooded areas.

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Appendix 9.1  List of the material studied

Anseriformes

**Incertae familiae**

*Brontornis burmeisteri*

MLP 20–88, left femur and tibiotarsus. Horizon and locality: Santa Cruz Formation, Lago Argentino, Santa Cruz Province.

MLP 20–91, left tarsometatarsus. Horizon and locality: Santa Cruz Formation, Lago Argentino, Santa Cruz Province.

*Eoneornis australis*

BMNH-A595, distal end of radius. Horizon and locality: Santa Cruz Formation, Santa Cruz Province.

*Eutelornis patagonicus*

BMNH-A596, distal end of humerus and a proximal tibiotarsus. Horizon and locality: Santa Cruz Formation, Santa Cruz Province.

Cariamiformes

Cariamidae

*Cariama santacrucensis*

MPM-PV 3511, incomplete cranium. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3, Puesto Estancia La Costa, Santa Cruz Province.

Cariaminae indet.

MPM-PV 3510 and 3512, two unassociated fragments of tibiotarsi. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Levels 6 (MPM-PV 3510) and 5.3 (MPM-PV 3512), Puesto Estancia La Costa, Santa Cruz Province.

Phorusracidae

*Patagornis marshi*

BMNH-A516, skull, mandible, right coracoid, right scapula, distal end of left humerus, right ulna, part of the right radius, both carpometacarpi, pelvis, both femur, right tibiotarsus, and right tarsometatarsus. Horizon and locality: Santa Cruz Formation, Santa Cruz Province; MPM-PV 4242, sternum. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 6, Puesto Estancia La Costa, Santa Cruz Province.

*Phorusrhacos longissimus*

MPM-PV 4241, mandible, left femur, tibiotarsus, and both fibulae. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Campo Barranca, Santa Cruz Province.

Psilopterus bachmanni

MPM-PV 4243, furcula and fragments of the left fore and hindlimb. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3, Puesto Estancia La Costa, Santa Cruz Province; YPM-VPPU 15904, an almost complete skeleton. Horizon and locality: Santa Cruz Formation, Lago Pueyrredón, Santa Cruz Province.

Psilopterus lemoinei

AMNH 9257, skull, humerus, vertebral column, pelvis and left hindlimb. Horizon and locality: Santa Cruz Formation, Estancia Halliday, Santa Cruz Province; MPM-PV 4240, left tibiotarsus. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Anfiteatro, Santa Cruz Province.

Ciconiiformes

**Incertae familiae**

*Protibis cyanus*

BMNH-A 598, distal end of right tibiotarsus. Horizon and locality: Santa Cruz Formation, Santa Cruz Province.

Falconiformes

Falconidae

*Badioestes patagonicus*

BMNH-A 602, very damaged and fragmentary specimen including ulna, femur and tarsometatarsus. Horizon and locality: Santa Cruz Formation, La Cueva, Santa Cruz Province.

*Thegornis debilis*

BMNH-A 601, distal end of a fragmentary right tarsometatarsus. Horizon and locality: Santa Cruz Formation, Corriguen Aike, Santa Cruz Province.

*Thegornis musculus*

BMNH-A 600, fragmentary right tarsometatarsus. Horizon and locality: Santa Cruz Formation, Yegua Quemada, Santa Cruz Province; MPM-PV 3433, an almost complete skeleton. Horizon and locality: Santa Cruz Formation, Estancia La Costa member, Fossiliferous Level 6, Puesto Estancia La Costa, Santa Cruz Province.

“Gruiformes”

**Incertae familiae**
**Anisolornis excavatus**

BMNH-A594, distal end of left tarsometatarsus. Horizon and locality: Santa Cruz Formation, Santa Cruz Province.

**Pelecaniformes**

Anhingidae

Liptornis hesternus

BMNH-A599, cervical vertebra. Horizon and locality: Santa Cruz Formation, Santa Cruz Province; FMNH-PA 22, cast of BMNH-A599.

**Rheiformes**

Rheidae

*Opisthodactylus patagonicus*

BMNH-A586, distal ends of both tarsometatarsi and phalanges. Horizon and locality: Santa Cruz Formation, Santa Cruz Province; BMNH-A587, mandibular symphysis, distal end of left tibiotarsus, fragmentary distal end of right tarsometatarsus. Horizon and locality: Santa Cruz Formation, Santa Cruz Province; BMNH-A588, fragments of distal tarsometatarsus. Horizon and locality: Santa Cruz Formation, Santa Cruz Province.

**REFERENCES**


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