



Palaeoenvironmental and faunal inferences based on the avian fossil record of Patagonia and Pampa: what works and what does not

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Analysing the effect of climatic/environmental changes on bird communities during the South American Cenozoic is quite complicated. Taking into consideration the extremely complex evolution of such environmental conditions and the incomplete and episodic fossil bird record in this part of the continent, any generalization should be considered with caution. However, some aspects may be noted: (1) certain typically South American bird groups evolved in total isolation, i.e. terrestrial or poorly flying birds, incapable of crossing important water barriers (Rheiformes, Tinamiformes, Phorusrhacidae, Brontornithidae, Anhimidae); (2) other good flyers did not cross until immediately before the definitive connection between both Americas (Teratornithidae, Passeriformes Suboscines); (3) most of the families established important intercontinental relationships (Anhingidae, Pelecanidae, Ciconiidae, Anatidae, Presbyornithidae, Rallidae, Falconidae and Accipitridae); (4) several taxa that are presently important members of the rich South American bird fauna are unknown for certain geological time periods (Throchilidae); and (5) there is a high prevalence of carnivorous birds over all other trophic habits, regardless of the association or age analysed. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 458–474.

ADDITIONAL KEYWORDS: Aves – biogeography – Cenozoic – faunal associations – palaeoenvironments.

Analizar el efecto que los cambios climáticos y ambientales tuvieron en las comunidades de aves durante el Cenozoico sudamericano es complicado y cualquier generalización debe tomarse con cautela. Sin embargo pueden señalarse algunos aspectos: (1) algunos grupos de aves típicamente sudamericanas evolucionaron en total aislamiento (Rheiformes, Tinamiformes, Phorusrhacidae, Brontornithidae, Anhimidae); (2) otros grupos buenos voladores no cruzaron a América del Norte hasta establecido el puente Panameño entre las dos Américas (Teratornithidae, Passeriformes Suboscines); (3) la mayoría de las familias establecieron importantes relaciones intercontinentales (Anhingidae, Pelecanidae, Ciconiidae, Anatidae, Presbyornithidae, Rallidae, Falconidae, Accipitridae); (4) importantes miembros de la avifauna sudamericana actual son desconocidos en el registro fósil (Throchilidae); (5) hay una prevalencia de aves carnívoras en todas las asociaciones cualquiera fuere su antigüedad.

PALABRAS CLAVE: Aves – biogeografía – Cenozoico – Asociaciones faunísticas – palaeoambientes.

INTRODUCTION

The country remains the same: terribly uninteresting. The great similarity in productions is a very striking feature in all Patagonia. The level plains of arid shingle support the same

stunted and dwarf plants; in the valleys the same thorn-bearing bushes grow. Everywhere we see the same birds and insects []. The curse of sterility is on the land.

Charles Darwin's Diary of the Voyage of H.M.S. Beagle,
April 22nd, 1834

Patagonia is currently an arid (yearly precipitations under 300 mm), cold (mean annual temperature,

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12 °C) and windy territory with low-growing, steppe-adapted shrub vegetation. Only towards the west, in the vicinity of the Andean mountain range, do precipitations become more abundant and allow the development of forests with dense undergrowth (Barreda & Palazzesi, 2007) and more abundant and varied vegetation. According to phytogeographical and ecological criteria, Argentina can be divided into 18 eco-regions, seven of which are represented in Patagonia and in the marine coastal sectors and neighbouring islands (Fig. 1). Each of these eco-regions is also characterized by the presence of certain bird species, both residents and visitors. Taken as a whole, Patagonia currently hosts about 40 nonpasseriform and 14 passeriform bird families (Narovsky & Babarskas, 2000) with heterogeneous concentration in each eco-region, with the prevalence of marine birds near the Atlantic Ocean coast, low bird diversity on the steppe and highest diversity in the mountain forests.

Modern-day Patagonia has been moulded by a transformation process resulting from the interaction of global tectonics, with palaeogeographical and palaeoclimatic changes. Two events are key and may be considered as iconic for this transformation: first, the opening of the Drake Passage at some point during the Eocene–Oligocene transition (c. 28 Ma ago; Madden *et al.*, 2010) isolated Antarctica from Patagonia, bringing about a trend towards cooler conditions (Reguero & Marensi, 2010), and, second, the rise of the Andes mountain range during the Miocene, which blocked the passage of the humid East winds, induced a process of desertification. The trend towards global cooling, which was already evident after the Mid-Eocene Climate Optimum, became more marked towards the Miocene, although with some interspersed warmer periods, such as the event known as the Middle Miocene Climate Optimum (Zachos *et al.*, 2001; Madden *et al.*, 2010, and references cited therein). According to Pascual & Odreman Rivas (1971), two areas can be recognized in Patagonia: to the north, the San Jorge Gulf Basin extends between the Somun Curá massif and the Deseado massif (Fig. 1B), and the Austral Basin to the south of the Deseado massif (Tonni & Carlini, 2008). This scheme provides a useful basis for the arrangement of the bird records discussed here.

Although the San Jorge Gulf Basin is dominated by Palaeogene sediments (Palaeocene–Oligocene, approximately between 65 and 23 Ma, which comprises the first part of the Cenozoic era, according to Gradstein, Ogg & Smith, 2004), the Austral Basin comprises mostly sediments from the initial part of the Neogene (Tonni & Carlini, 2008). The wonderful exposures of the Santa Cruz Formation (late early Miocene) have undoubtedly provided the best repre-

sentatives of the earliest Neogene. These exposures are emblematic as they have been known since the late 19th century thanks to the work of the brothers Carlos and Florentino Ameghino, the former recognized by his essential field work and the latter by his vast written production (Ameghino, 1891, 1895, 1906, 1908).

Accordingly, the oldest Neornithes (or modern) birds from Patagonia (and the whole of Argentina) come from the San Jorge Gulf Basin (Chubut and Santa Cruz Provinces), corresponding fundamentally to the Riochican (middle to late Palaeocene), Casamayoran (late Eocene) and Deseadan (late Oligocene) periods (Fig. 1A), whereas the Neogene records originate from the Santacruzian (late early Miocene) of the Austral Basin, up to the most modern Huayquerian (late Miocene), located on the northern San Jorge Gulf Basin, in Chubut Province (Dozo *et al.*, 2010), as well as north of Patagonia, in La Pampa Province (Montalvo *et al.*, 2008; M. N. Cenizo, C. P. Tambussi & C. Montalvo, unpubl. data). The vertebrate fossil record in Patagonia is very scarce from the end of the Miocene to the present. Information for this period thus needs to be complemented with extra-Patagonian (Pampasian) records to better understand the macro-events in the Patagonian region (Tonni & Carlini, 2008).

At least two marine transgressions affected the entire South American continent along different corridors during the Miocene. The first transgression took place between 15 and 13 Ma and was dominated by eustatic and tectonic factors. The second transgression took place between 10 and 5 Ma and resulted mainly from tectonic events (Hernandez *et al.*, 2005). Thus, the continental sediments of the Palaeogene and Neogene are interdigitated with highly fossiliferous sediments of marine origin containing both vertebrates and invertebrates. Among birds, penguins are the most frequent (Acosta Hospitaleche *et al.*, 2007, 2008). Marine sediments are represented in the San Julián, Monte León and Gaiman Formations (late Eocene to early Miocene) and the more modern Puerto Madryn Formation (middle to late Miocene) outcropping in the Valdés Peninsula (Dozo *et al.*, 2010). The greatest of the Miocene transgressions is known as the Paranaensean; it began in the latest Oligocene and ended during the early middle Miocene (15–13 Ma). The final phases of this transgression are coincident with the Neogene Climatic Optimum. The Paranaensean covered much of the Chaco-Paranaensean lowlands and eastern Patagonia, affecting the current territories of Argentina, Uruguay, parts of Brazil and Paraguay, southern Bolivia, Venezuela, Colombia and Ecuador.

Although the fossil record of birds in the Cenozoic is incomplete, scarce and consisting mostly of isolated

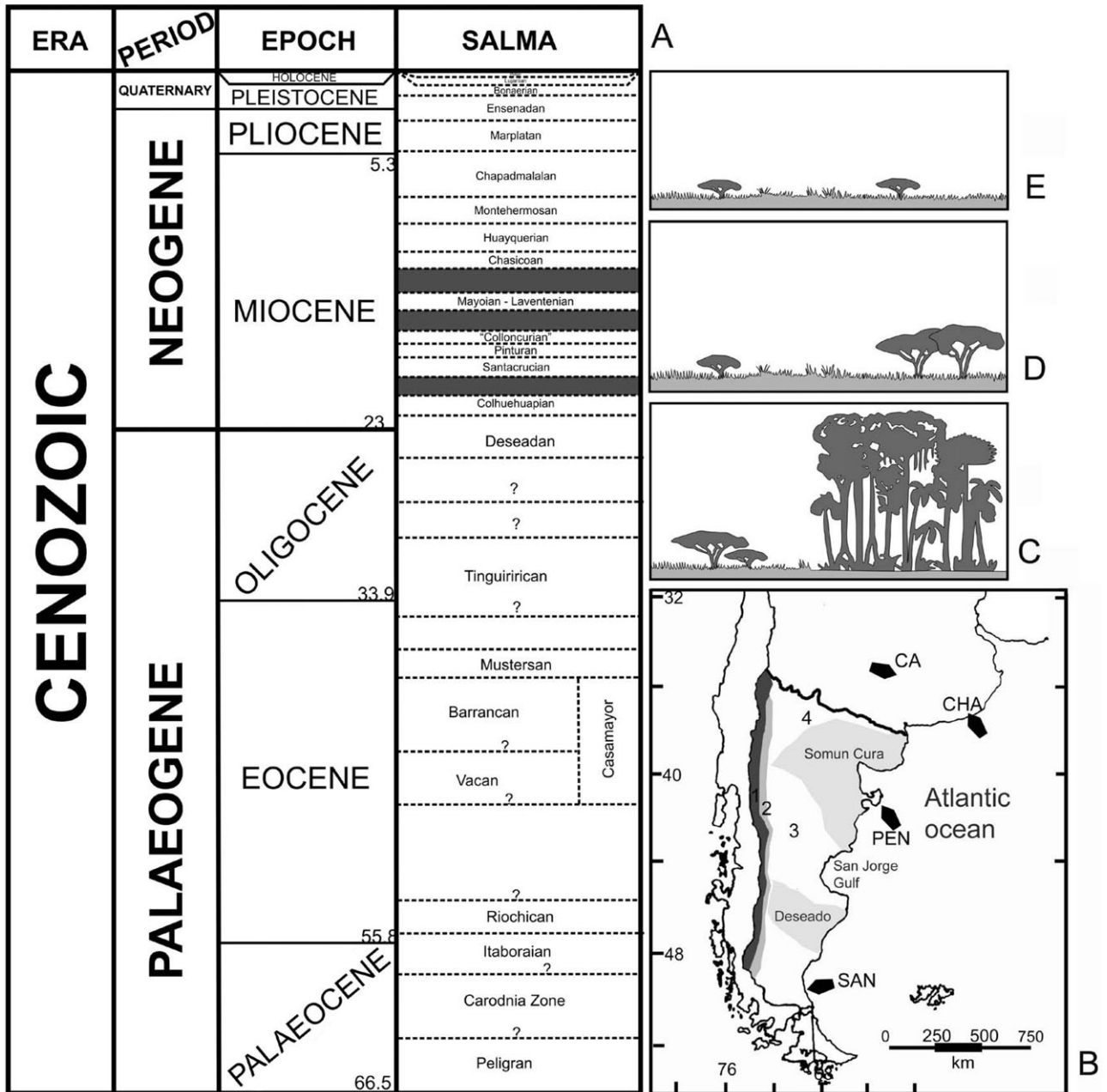


Figure 1. A, Palaeocene to Recent time scale following Gradstein *et al.* (2004) including time scale for Cenozoic mammalian faunas of South America (SALMA). B, Map of Patagonia showing the present-day major ecosystems (1, High Andes; 2, Araucanian Forest; 3, Steppe; 4, Shrub) and four important fossil localities used in the text (SAN, Santa Cruz Formation at Santa Cruz Province; PEN, Puerto Madryn Formation at Península Valdés; CA, Cerro Azul Formation at La Pampa Province; CHA, Chapadmalal at Buenos Aires Province). C–E, Vegetation-type physiognomies under increasingly drier and/or more markedly seasonal climates (modified from Barreda & Palazzesi, 2007): C, late Oligocene–early Miocene; D, middle late Miocene; E, late Miocene.

bones (very exceptionally complete skeletons have been exhumed; Tambussi & Noriega, 1996; Acosta Hospitaleche *et al.*, 2007), it is sufficient to suggest that many of the orders of living birds were present around 33 Ma (Oligocene) and that nearly all families

with extant species were already represented at about 20 Ma (Miocene). The bird fossil record in Patagonia provides the basis for support of this scenario of first appearances of the major groups of Neornithes birds (the clade that includes all modern birds), the analy-

sis of which is the focus of this work. Many of the records, especially those from the Palaeogene, however, correspond to collections made during the late 19th and early 20th centuries, and they lack reliable provenance information. Inferences made from these materials thus have a restricted value.

In spite of their small sample sizes and incomplete preservation, fossil birds may be a source of valuable palaeoecological and palaeoenvironmental information, especially when they form assemblages and are analysed in a general context. The focus of this study is to interpret the palaeoenvironmental, palaeoecological and faunal conditions of the Cenozoic using the four best bird assemblages recovered from Neogene sediments of Patagonia and Pampa.

THE PALAEOGENE BIRDS OF PATAGONIA

Very little is known about the Palaeogene birds of Patagonia: in all cases they are poorly represented. With isolated fossil material, their phylogenetic affinities are uncertain or their relationships are in need of exhaustive revision (Tambussi & Noriega, 1996; Mayr, 2009). Indeed, for the Palaeocene, the only known records are feather imprints collected from fluvial levels of the Salamanca Formation (the Danian–Selandian boundary, *c.* 61 Ma, early Palaeocene; Degrange *et al.*, 2006). This is the oldest evidence of Neornithes birds for Patagonia and also for all of South America. However, an isolated phalanx from the foot of a member of Rheiformes, the taxon that includes the living rheas or South American ostrich-like birds (Tambussi, 1995), was collected in the Río Chico Formation (middle Palaeocene). Both records come from the San Jorge Gulf Basin (see Appendix).

From the same area, but exhumed from Eocene sediments, a few birds from the Casamayor Formation and probably middle Eocene (Casamayoran) in age have been described (Tonni, 1980; Tambussi & Noriega, 1996; Mayr, 2009; see also Agnolin, 2004, 2006a, b, 2007a, b) as well as some from the Sarmiento Formation (late Eocene, Mustersan; Tambussi & Acosta Hospitaleche, 2005).

The Eocene of Patagonia holds the first record of the Presbyornithidae, a very particular family of aquatic or semi-aquatic Anseriformes birds with a duck-like head and a body reminiscent of that of flamingos (Tambussi & Noriega, 1999). The affinity of these birds with the Anseriformes has been recognized since the 1970s (Olson & Feduccia, 1980), and currently they are considered as a sister group of the Anatidae (swans and ducks) (Ericson, 1997; Livezey, 1997).

Penguins constitute a second group with first Patagonian records during the Eocene (see Appendix). At that time, their species' diversity was much higher

than at present (for a synthesis of the fossil record of penguins in Patagonia, see Acosta Hospitaleche & Tambussi, 2008).

The record of Phorusrhacidae also begins during the Eocene. In particular, Psilopterines from the late Eocene (Mustersan) were reported by Tambussi & Acosta Hospitaleche (2005). The Phorusrhacidae are an extinct group of predatory terrestrial birds (Andrews, 1899; Sinclair & Farr, 1932; Tonni, 1980; Tambussi & Noriega, 1996; Alvarenga & Höfling, 2003; Bertelli, Chiappe & Tambussi, 2007; Degrange *et al.*, 2010). Traditional studies of phorusrhacids classify them into five subgroups; in order of increasing size and body mass, these are the psilopterines, mesembriornithines, patagornithines, phorusrhacines and brontornithines. This subject is described in detail below in the section on birds found in the Patagonian Miocene.

According to Agnolin (2006b), the diurnal birds of prey (Accipitridae, buzzards and hawks) also have their first records in the Patagonian Eocene. (See Appendix for other Eocene records.)

The Oligocene bird record is fragmentary and little progress has been made since Ameghino's original assignments. As far as I know, there have been no new records of this age. Agnolin (2004) attempted a review, but the existing record is highly fragmentary and of dubious affinities (see Appendix for a synthesis). Only the appearance of new and more complete records would allow appropriate reconstruction of the continental scenarios of the Oligocene in Patagonia.

Psilopterus affinis (Ameghino), a species that seems to be the smallest among phorusrhacid species, is safely recorded in the late Oligocene of the San Jorge Gulf Basin. The first records of the middle-sized phorusrhacids, Patagornithinae (*Andrewsornis abbotti* Patterson) and the giant Brontornithinae (*Physornis fortis* Ameghino) also occur in the Oligocene.

With regard to the marine sediments from the San Julián area, in Santa Cruz Province (late Eocene–early Oligocene), the remains of two mid- to large-sized penguins have been exhumed: *Paraptendytes robustus* (Ameghino) and *Arthrodytes andrewsi* (Ameghino) (Acosta Hospitaleche & Tambussi, 2008) (see Appendix).

THE NEOGENE OF PATAGONIA: THE SANTACRUCIAN BIRDS

It is not possible to refer to the Patagonian or South American Neogene without mentioning the birds from the late early Miocene of the Santa Cruz Formation (Santacrucian). Known since the times of Ameghino, the Santa Cruz Formation occurs in southern Patagonia and is the most widespread and most richly fossiliferous of all Patagonian nonmarine Tertiary

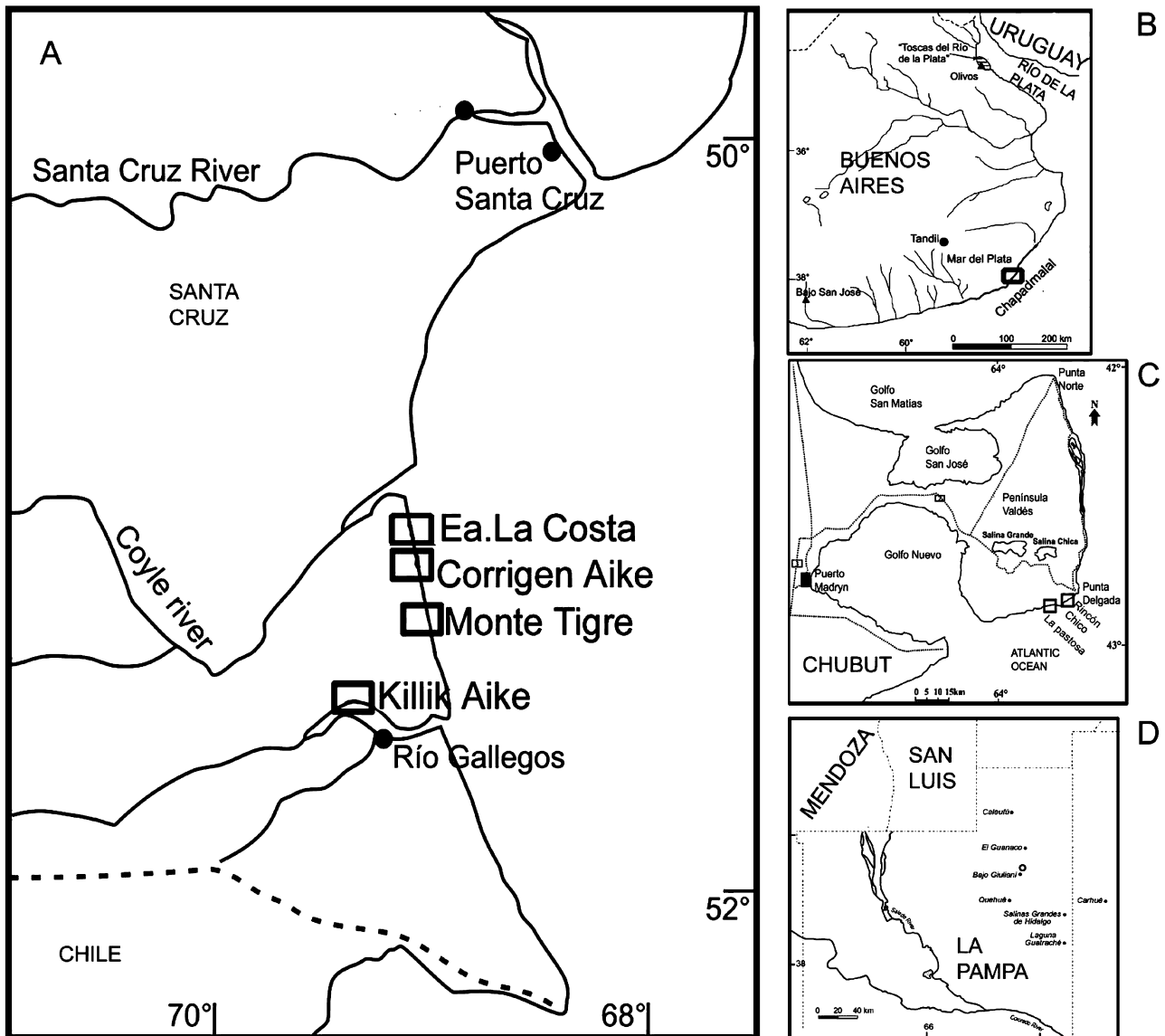


Figure 2. Location maps of the fossil localities used in the text. A, Late early Miocene localities of Santa Cruz Formation at Santa Cruz Province. B, Late Pliocene Chapadmalal locality at Buenos Aires Province. C, Late Miocene localities of Puerto Madryn Formation at Peninsula Valdés, Chubut Province. D, Late Miocene localities of Cerro Azul Formation of La Pampa Province.

formations of southern Argentina (Tauber, 1994, 1997a, b; Tejedor *et al.*, 2006; Vizcaíno *et al.*, 2006, and references cited therein). This formation outcropping at the Atlantic Ocean coast represents the continental facies after the regression of the Patagonian Sea (Tonni & Carlini, 2008). The richest fossil localities lie along the Atlantic Ocean coast of southern Patagonia from Monte León to Río Gallegos and along the valleys of the Chico, Coyle, Chalia, Santa Cruz and Gallegos streams (Fig. 2A). Its lower levels are dated as 19.33 and 20.18 Ma, whereas the upper levels are in the 16.18–20.61 Ma range (Tejedor *et al.*, 2006). Tauber (1997b)

recognized two biozones within the Santa Cruz Formation, stratigraphically represented by the lower Estancia La Costa Member and the upper Estancia La Angelina Member (see also Croft, 2001).

By the late Oligocene–early Miocene, forest elements are gradually replaced by other shrubby and herbaceous forms (Fig. 1B–D), signalling the beginning of the expansion of xerophytic environments determined by a cooling and drying trend manifested in areas to the east of the Andes (Barreda & Palazzesi, 2007), and Patagonia begins to acquire its modern appearance. Some evidence supports the existence of

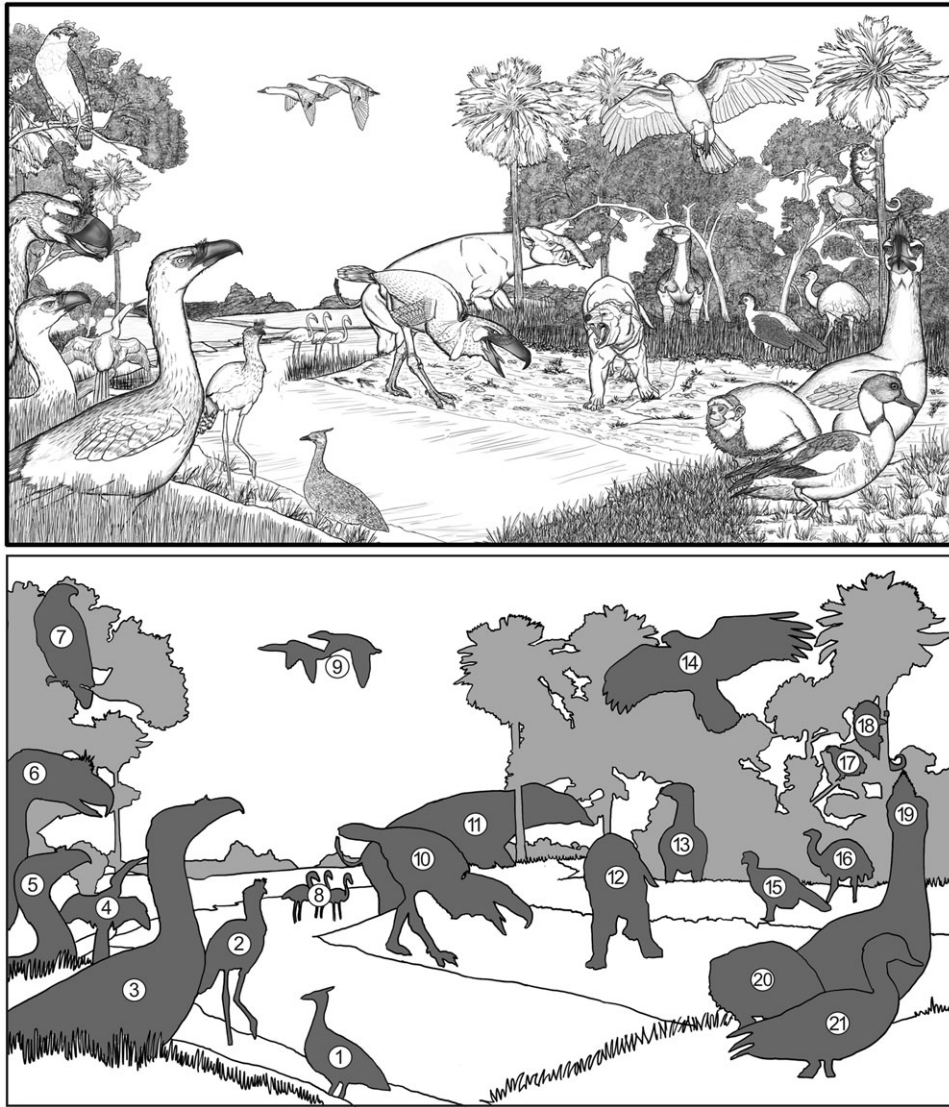


Figure 3. Top: climatic scenario during the late early Miocene (Santacrucian stage) of Patagonia. Birds and some landmark mammals are included. Bottom: explanation of the figure: 1, Tinamidae; 2, *Cariama santacrucensis*; 3, *Psilopterus lemoini*; 4, Anhingidae indet.; 5, *Psilopterus bachmanni*; 6, *Phorusrhacos longissimus*; 7, *Thegornis debilis*; 8, *Protibis cnemialis*; 9, *Eutelornis patagonicus*; 10, *Kelenken guillermoi*; 11, *Astrapotherium magnum* (Astrapotheriidae); 12, *Arctodictis muñizi* (Borhyaenidae); 13, *Brontornis burmeisteri*; 14, *Badiostes patagonicus*; 15, Cracidae indet.; 16, *Opistodactylus patagonicus*; 17, *Thegornis musculosus*; 18, *Steiromys* sp. (Erethizontidae); 19, *Patagornis marshi*; 20, *Soriacebus* sp. (Atelidae); 21, *Ankonetta larriestrai*. Drawings by Marcos Cenizo.

both open and closed environments (see Vizcaíno *et al.*, 2010, and references cited therein). Birds also reflect this process.

The Aves remains of the Santa Cruz Formation are spectacular because of their diversity and morphological disparity (Tonni, 1980; Olson, 1985; Tambussi & Noriega, 1996; Alvarenga & Höfling, 2003; Agnolin, 2004, 2006a, b, 2007a, b, 2009; Noriega, Vizcaíno & Bargo, 2009; Cenizo & Agnolin, 2010). These materials were beautifully illustrated and reasonably well

described in the Reports of the Princeton University Expeditions to Patagonia (Sinclair & Farr, 1932). However, most specimens are fragmentary. Some have recently been reanalysed (Alvarenga & Höfling, 2003; Agnolin, 2004, 2006a, b, 2007b, 2009), but a thorough review is still pending (Noriega *et al.*, 2009). The Appendix summarizes all known records to date, which, although from different localities within the Santa Cruz Formation, are considered jointly in the present paper (Fig. 3).

Rheiformes are herbivorous/omnivorous ground birds, inhabitants of open grasslands. They are magnificent runners and their long necks and excellent vision provide them with an effective monitoring system. *Opisthodactylus patagonicus* Ameghino, the only Santacrucian record for this family, does not differ greatly from that of the living Rheidae (Tambussi, 1995).

Records of Santacrucian tinamous (Tinamidae) from the fossil localities of Monte Observación, Monte León and Cañadón de las Vacas have been reported (Chiappe, 1991; Bertelli & Chiappe, 2002). At present, the tinamous are a Neotropical group of palaeognaths. They are basically ground birds and poor fliers.

Modern Neotropical faunas are highly diverse in anseriforms, particularly anatids, but fossil ducks are poorly known in Patagonia and South America. Their fossil record is characterized by isolated and poorly informative specimens, with most species known from their original diagnosis. The list of Patagonian anseriforms includes *Eoneornis australis* Ameghino (Anhimidae *sensu* Cenizo & Agnolin, 2010), *Eutelornis patagonicus* Ameghino (a basal anseriform) and *Ankoneta larriestrai* Cenizo & Agnolin, a mid-sized anatid considered to have superficial similarities with the whistling ducks (i.e. *Dendrocygna*) (see Appendix).

The idea originally suggested by Moreno & Mercerat (1891) and recently revived by Agnolin (2007b), that *Brontornis burmeisteri* is a basal anseriform, is quite reasonable. *Brontornis* was traditionally placed within phorusrhacids, as a representative of the 'graviportal' habit in the family. Systematic issues aside, *Brontornis* was undoubtedly the giant beast of the Patagonian Miocene, reaching a standing height of over 2 m and 380 kg (body mass estimation according to Jones, 2010). Alvarenga & Höfling (2003) hypothesized that brontornithines may have been scavengers/kleptoparasites, but Agnolin (2007b) considered them to be herbivorous. Further studies are needed, especially focused on the mandible, to corroborate any of these hypotheses.

During the late early Miocene, phorusrhacids experienced the greatest diversification ever recorded (at least four species) and were common inhabitants of coastal localities. They include *Phorusrhacos longissimus* Ameghino, *Patagornis marshi* Moreno & Mercerat, *Psilopterus bachmanni* (Moreno & Mercerat) and *Psilopterus lemoinei* (Moreno & Mercerat). The seriema-like *Cariama santacrucensis* Noriega, Vizcaíno & Bargo was also present. *Cariama* is the oldest South American genus with living representatives.

Phorusrhacids show considerable variation in body size, including the small psilopterines, three or four times larger than the living seriemas of 1.5 kg (body mass from Dunning, 2008), and the giant *Phorusrhacos longissimus* at approximately 160 kg (body mass

estimation according to Jones, 2010). All phorusrhacids, whose larger forms are popularly known as 'terror birds', are characterized by a very large and compressed skull, raptor-like beak and elongate leg bones. The wings seem to be greatly reduced in all species, ranging from marked reductions in the largest forms that would not have allowed them to fly, to more moderate reduction in which flight might have been possible (e.g. Psilopterinae; Tonni & Tambussi, 1988; Tambussi & Acosta Hospitaleche, 2005; for an alternative view, see Alvarenga & Höfling, 2003). With or without flight capability, all phorusrhacids were large terrestrial, swift cursorial birds, and it is generally assumed that they were among the top predators of the Patagonian Cenozoic scenarios. A carnivorous lifestyle was recently tested from a biomechanical point of view (Degrange *et al.*, 2010) using the skull of the medium-sized Patagornithinae *Andalgalornis steulleti* Kraglievich from the Pliocene of northwestern Argentina. Because terror birds have no close analogues among modern-day birds, this study was essential to understand the biology of this extinguished group. In a broad sense, we may assume that the skulls of other large phorusrhacids, characterized by high and compressed beaks, would respond similarly to that of *Andalgalornis* (body mass, 40 kg). Phorusrhacids chased and killed their prey using their huge beaks as a hatchet (Degrange *et al.*, 2010). They probably could have swallowed small prey whole or, at least in some cases, dismembered large prey with the help of their strong neck muscles and the claw on digit II of the foot. For most of the existence of phorusrhacids, South America was isolated (like a large island?) and inhabited by a peculiar fauna: the nonavian predators were represented by marsupials and reptiles, whereas herbivores (as in the rest of the world) were placental mammals. The marsupials tended to be heavily limbed forms (e.g. borhyaenids) and the predaceous reptiles were terrestrial crocodiles: both probably inhabited forests, whereas the large phorusrhacids tended to prefer more open plains. However, there is no contrary evidence to support that the smaller psilopterines foraged in the woods. The Americas were connected at about 3 Ma, the Panamanian bridge was completed, and this resulted in the interchange of faunas to and from South America. The phorusrhacids are one example of south to north movement. An array of modern placentals, such as modern carnivores, arrived to the south. It is not easy to understand whether the phorusrhacids were the losers in the direct competition with these carnivores and/or whether their diversity was already in decline because their disappearance had already begun. The truth is that the last record of phorusrhacids in South America dates from the early Pleistocene (Tambussi, Ubilla & Perea, 1999; see also Alvarenga, Jones & Rinderknecht, 2010, and later in this article).

The latest South American species recorded in Uruguay was among the largest phorusrhacids ever, suggesting that it coexisted with the large carnivorous immigrants from North America with which it could have competed.

Other carnivorous birds from the Santa Cruz Formation include Accipitridae (eagles, hawks) and Falconidae (caracaras, falcons). Both families have a sharply hooked beak, strong legs, feet with raptorial claws and diurnal habits. Again, Ameghino described three species: *Badiostes patagonicus* Ameghino, *Thegornis debilis* Ameghino and *T. musculosus* Ameghino. Apparently, they all have falconid affinities; furthermore, new findings would have established that *Thegornis* is neither a Falconinae nor a Polyborinae, but has similarities with the living forest falcons and laughing falcon (Noriega *et al.*, 2008).

Darters (Pelecaniformes Anhingidae) are flying, foot-propelled diving and fish-eating waterbirds. They are mostly tropical and common in freshwater environments, but also occur in marshes and marine coasts. There are four living species, all placed in the genus *Anhinga*. Their fossil record is rather abundant (Noriega, 1992, 1995; Alvarenga & Guilherme, 2003; Areta, Noriega & Agnolin, 2007; Cenizo & Agnolin, 2010) and began during the early Miocene. Fossil anhingids in South America include species similar to those living today, as well as some very large forms with a marked tendency to becoming flightless. The Santacrucian anhingids include *Macranhinga* Noriega, recovered far from the ocean coast in Santa Cruz Province, and *Liptornis hesternus* Ameghino, which may also be a darter (Cenizo & Agnolin, 2010).

Another species recorded at the Santa Cruz Formation is *Protibis cnemialis* Ameghino, a species belonging to the Threskiornithidae (Brodkorb, 1963; Pelecaniformes *sensu* Hackett *et al.*, 2008). Living members of the family are large terrestrial birds that prey on invertebrates and small vertebrates; they occur near slow-flowing freshwater or brackish water areas.

Finally, *Anisolornis excavatus* Ameghino (?Cracidae), another species recognized by Ameghino from the Santa Cruz Formation, is of uncertain affinities (see Brodkorb, 1964, Cracraft, 1973 and Olson, 1985 for different proposals).

This overview of the Santacrucian avifauna allows some inferences. Various lines of evidence suggest the presence of open vegetation and dry conditions for the Santacrucian environments, although others are contradictory. At present, seriemas occupy semi-open and dry landscapes, but *Cariama cristata*, at least, does not appear to be a climatic indicator (Tambussi *et al.*, 2005). There is a clear predominance of ground and pedestrian birds in the records known so far for this age: rheids, giant anseriforms or large phorusrhacids.

These forms can only be associated with open habitats. This does not exactly agree with the presence of cebine monkeys (Tejedor *et al.*, 2006) or anhingids (Cenizo & Agnolin, 2010). If anything, these latter records suggest that the area was more humid and less open, perhaps agreeing with Croft (2001). Diurnal raptors and psilopterines are compatible with the presence of environments with alternating grasslands and woodlands, as suggested from the floras (Barreda & Palazzesi, 2007). Considering only the unquestionable records, medium- to large-sized carnivorous species markedly predominate within the Santacrucian avifauna: phorusrhacids, diurnal raptors, ibises and anhingids (Fig. 3).

BIRDS FROM THE LATE MIOCENE: TWO HUAYQUERIAN ASSOCIATIONS AS EXAMPLES

The Cerro Azul Formation of La Pampa Province (central Argentina) has yielded numerous and varied bird remains recovered from the Salinas Grandes de Hidalgo classical area, and several new localities that correspond to the most complete South American avian association of Huayquerian Age (late Miocene) (Fig. 2D) (M. N. Cenizo, C. P. Tambussi & C. Montalvo, unpubl. data). The Formation seems to have been deposited under a semi-arid, probably warm and seasonal climate (Montalvo *et al.*, 2008, and references cited therein). This avian assemblage includes nine taxa representing at least six families, two of which do not have living representatives (Fig. 4): teratorns, at least two genera of tinamids with modern representatives (*Eudromia* and *Nothura*), phorushacids, the falconid *Milvago* and an undetermined Passeriformes Tyraniidae (M. N. Cenizo, C. P. Tambussi & C. Montalvo, unpubl. data). Other than passerines, all families had been recorded in previous times.

Undoubtedly, the most impressive is *Argentavis magnificens* Campbell & Tonni (Teratornithidae), the world's largest flying bird of all times (80 kg; wingspan, 6.5–7.0 m). Teratorns are well known for complete late Pleistocene skeletons preserved in the Rancho La Brea tar pits (California) and were related to storks (Ciconiidae) or New World vultures (Vulturidae). Their wing bones are pneumatic, elongated and robust. The ulna exhibits large and widely spaced nodes for the attachment of the feathers and, altogether, the wing bones resemble those of large soaring birds. *Argentavis* probably used a thermal soaring mode over the open Pampas, a nonflapping style of flight energetically inexpensive (Chatterjee, Templin & Campbell, 2007). Nowadays, it is thought to have been a diurnal predator (see also Palmqvist & Vizaín, 2003) dependent on thermals for flying.

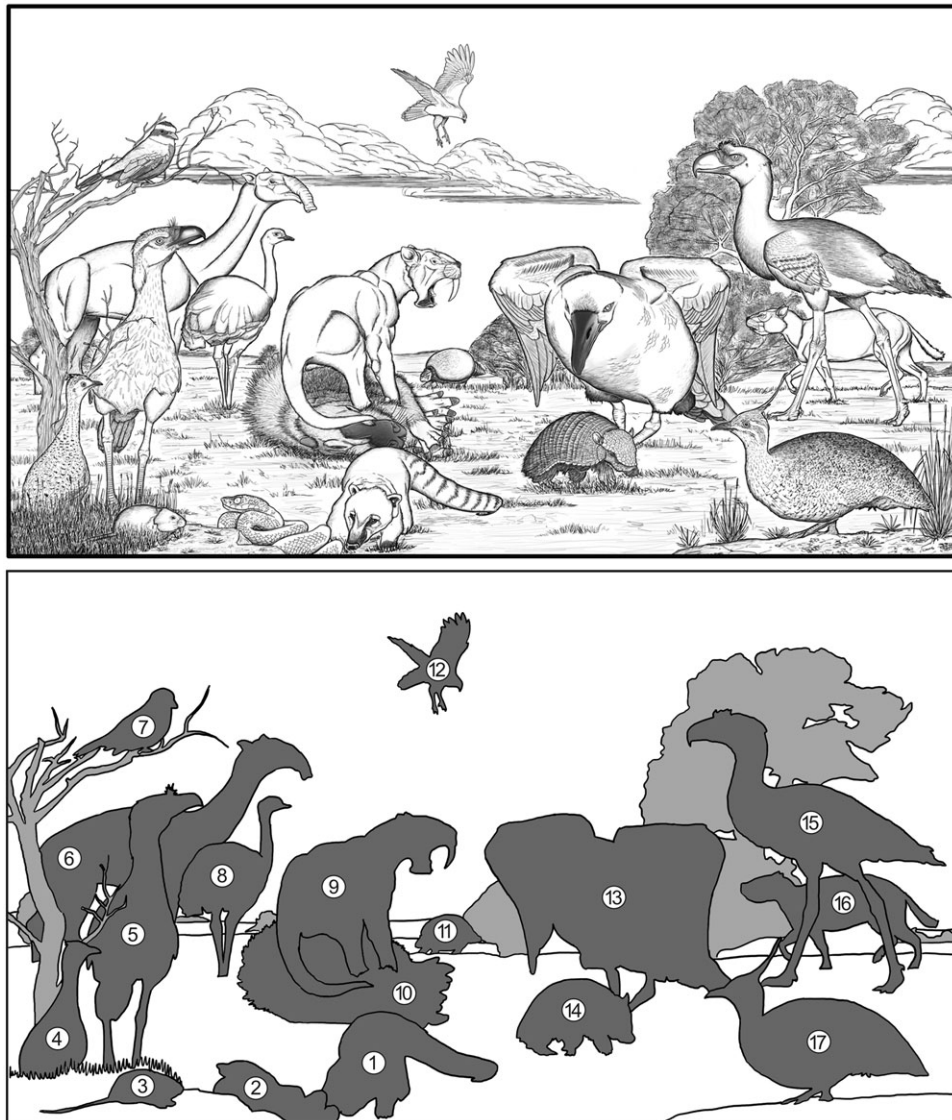


Figure 4. Top: climatic scenario during the late Miocene (Huayquerian stage) of La Pampa Province according to the Cerro Azul Formation record. Birds, some landmark mammals and reptiles are included. Bottom: explanation of the figure: 1, *Cyonasua* sp. (Procyonidae); 2, Viperidae; 3, Cricetidae; 4, *Nothura* sp.; 5, *Procariama simplex*; 6, Macraucheniiidae; 7, Tyrannidae; 8, *Pterocnemia* sp.; 9, Thylacosmilidae; 10, *Tetrastylus* sp. (Dinomyidae); 11, Glyptodontidae; 12, *Milvago* sp.; 13, *Argentavis magnificens*; 14, *Proeuphractus* sp. (Dasypodidae); 15, Phorusrhacidae indet.; 16, *Pseudototherium subinsigne* (Mesotheriidae); 17, *Eudromia* sp. Drawings by Marcos Cenizo.

Within Psilopterinae, *Procariama simplex* Rovereto has been recorded from the Cerro Azul Formation. This extinct monotypic genus was flightless, of medium to large size with a body mass of approximately 10 kg (Alvarenga & Höfling, 2003). It was originally described from the Miocene–Pliocene of northwestern Argentina (Huayquerian, Catamarca Province), representing the phorusrhacid with the widest geographical range.

Remains attributable to Passeriformes Tyrannidae are also present in the Cerro Azul Formation.

As pointed out in the Introduction, the climate deteriorated markedly at the end of the Miocene in northern Patagonia and open grassland areas, developed during dry periods, characterized the environment. Such environmental changes allowed the expansion of some faunal elements from northern localities to the southwest. This is the case for the Cerro Azul avian remains. These few but interesting remains are representatives of a typically Pampean bird fauna at the end of the late Miocene in central-south Argentina.

Another bird assemblage of Huayquerian age comes from the uppermost part of the late Miocene Puerto Madryn Formation at Península Valdés. These marine deposits crop out along the southwestern coast of the peninsula, near Punta Delgada (Fig. 2C). The climate during the accumulation of the late Miocene deposits in this region is inferred to have been warmer and seasonally drier than that of today. From terrestrial palynomorphic evidence, the Península Valdés Basin was characterized by the presence of low xerophytic open forests and several shrubs. In addition, the record of sedges and bur-reed would indicate permanently saturated soils with freshwater environments with algae and aquatic ferns (Dozo *et al.*, 2010). Eagles (Accipitridae), whistling ducks (Dendrocygninae) and phorusrhacid Psilopterae are recorded there. Birds are only a part of the exhumed vertebrate fauna that includes fishes (Loricariidae and Percomorpha) and abundant and varied mammals (Xenarthra, Rodentia and Litopterna) (Dozo *et al.*, 2010). Vertebrates come from two close sites of similar age and sedimentology: La Pastosa and Rincón Chico. In addition, a large species of marabou stork (*Leptotilus patagonicus* Noriega & Cladera) was recovered at the locality of Punta Buenos Aires (Noriega & Cladera, 2008). They represent the first assemblage of late Miocene continental vertebrates recorded in southern Río Negro Province.

Within birds, the most exquisite fossil remains is a fragment of the cranial roof for a large-sized adult eagle (Picasso, Tambussi & Dozo, 2009). Whistling ducks (Dendrocygninae) were also present. Some materials show considerable similarities with the living *Dendrocygna* (Dozo *et al.*, 2010). Dendrocygninae include herbivorous aquatic birds inhabiting lentic environments with dense surface vegetation. Within this continental assemblage, Psilopterae are also included. As mentioned, psilopterae are the smallest and most gracile phorusrhacids; some may even have retained their flying capability. Unlike the Cerro Azul Formation and other older sites, no large ground birds, such as rheids or Phorusrhacinae, have yet been registered in the Puerto Madryn Formation. The only carnivorous elements of these environments were psilopterae and eagles. Dendrocygninae records are consistent with the presence of freshwater environments. Large birds, such as Psilopterae or Accipitridae, are in agreement with the occurrence of open forest and shrubs.

BIRDS FROM THE PLIOCENE

The main Pliocene localities are situated on the Atlantic coast of Buenos Aires Province (Fig. 2B). The most recent sampling expeditions have not succeeded in collecting new data. Much of the following

discussion is based on information provided by the 1950s collections that had no rigorous provenance information. Chapadmalalan (late Pliocene, *c.* 4.0–3.0 Ma) was chosen to contrast with the previous scenarios in northern Patagonia. The Chapadmalalan age follows the Montehermosan and precedes the Uquian age. Records of this age belong to the families Rheidae, Tinamidae, Phorusrhacidae (Psilopterae and Mesembriornithinae), Cathartidae, Charadriidae, Scolopacidae and Furnariidae (Fig. 5, see Appendix).

Remains of the steppe tinamous *Nothura* and *Eudromia* are frequent. *Nothura parvula* Tambussi is the most common tinamous from the Chapadmalalan (Tambussi & Noriega, 1996). Another taxon recorded there is Darwin's *Nothura* (*Nothura darwini*), an extant species that currently inhabits arid steppes. *Eudromia elegans* inhabits Andean steppes and mountainsides from Patagonia to Buenos Aires Province and from central to northwestern Argentina. Echarri, Tambussi & Acosta Hospitaleche (2008) made a detailed bioclimatic analysis of the distribution of the elegant crested tinamou *E. elegans*, allowing a refinement of palaeoenvironmental reconstructions. Low precipitation areas (mean of 311.45 mm) were identified as suitable for *Eudromia elegans*. *Hinasuri nehuensis* Tambussi, 1995 is the sturdiest Rheidae ever recorded.

Two species of Phorusrhacidae have been described: *Mesembriornis australis* (Moreno & Mercerat) and *M. rapax* (Patterson & Kraglievich). These large ground birds, plus *Hinasuri nehuensis*, provide evidence of open environments.

Currently, condors (Vulturidae) do not live in the Pampas region, but their fossil record is abundant (Tonni & Noriega, 1998; Tambussi & Noriega, 1999), although there is no fossil record in Patagonia. This fact is used by several authors to support the North American origin of condors with a posterior shift to South America once the Panamanian bridge was established. It is well known that condors are soaring scavengers with high orographic affinity. For the Montehermosan/Chapadmalalan stages, arid or semi-arid conditions compatible with grasslands and forest patches have been inferred. Such conditions favour the presence of updrafts, such as those used by condors for soaring. Chapadmalalan condors were varied and exhibited different sizes. Their diversity appears to be concomitant with the decrease in phorusrhacids.

The waterbirds Charadriiformes *Calidris* and *Charadrius* indicate the presence of freshwater environments. Finally, the passerines are represented by the ovenbirds (Furnariidae). They are small- to medium-sized insectivores; most are forest birds, but some occur in more open habitats, such as savannah or grassland.

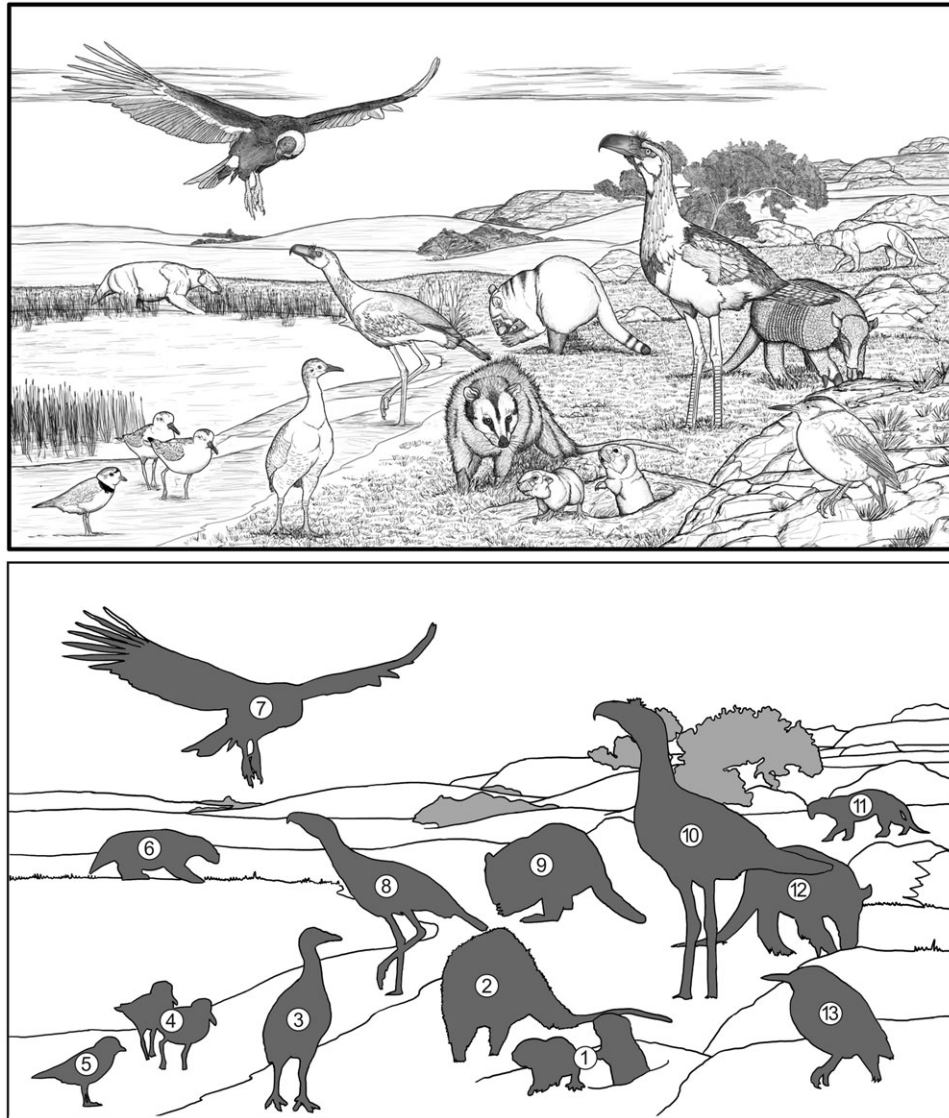


Figure 5. Top: climatic scenario during the late Pliocene (Chapadmalalan stage) of Buenos Aires Province. Birds and some landmark mammals are included. Bottom: explanation of the figure: 1, *Actenomys priscus* (Ctenomyidae); 2, *Thylophorops chapalmalensis* (Didelphidae); 3, Tinamidae; 4, *Calidris* sp.; 5, *Charadrius* sp.; 6, *Scelidodon* sp. (Mylodontidae); 7, Vulturidae indet.; 8, Phorusrhacidae indet.; 9, *Chapadmalania altaefrontis* (Procyonidae); 10, *Mesembriornis rapax*; 11, *Thylacosmilus atrox*; 12, *Ringueletia simpsoni* (Dasypodidae); 13, Furnariidae indet. Drawings by Marcos Cenizo.

The Chapadmalalan bird association (Fig. 5) shares the predominance of carnivores/scavengers with associations of the early Miocene. However, there are no Patagonian fossil condors and the phorusrhacids are smaller in the Chapadmalalan deposits.

WHAT WORKS AND WHAT DOES NOT

Although it is generally recognized that the Neornithes diversified explosively within 10 Ma following the Cretaceous–Palaeogene boundary, and that the

modern bird community began to be formed during the Oligocene–Miocene transition, South American bird fossil records are too fragmentary to allow the reconstruction of such a scenario.

The Cenozoic avian fossil record from Patagonia is still sparse – both geographically and temporally – and taxonomically poor, relative to the diverse contemporary avian fauna of South America. Palaeogene fossils do not provide a firm foundation to begin the reconstruction of the evolutionary and biogeographical history of the taxa of higher levels. It is not within

the scope of the present contribution to cover in detail the biogeographical patterns of the major lineages of Neornithes. I direct the reader to Cracraft (2001) and Mayr (2009) and the various references reviewed by them.

Although our knowledge on Patagonian (and South American) Neogene birds is characterized by many uncertainties, some biogeographical inferences are possible. Rheas belong to a family deeply rooted in South America. The fossil record for this family begins during the Palaeocene and is restricted to South America (Tambussi, 1995). There is evidence that Darwin's rhea, *Pterocnemia pennata*, a typically Patagonian arid–semi-arid element that nowadays inhabits areas with annual precipitations up to 300 mm (Tambussi & Acosta Hospitaleche, 2002), extended its distribution to the pampas during the Pleistocene (northeast of its current distribution) in accordance with environmental changes. Similarly, there is evidence indicating that a second extant species, the Greater Rhea, extended further south during the late Pleistocene, and this was facilitated by the more humid conditions prevailing at that time (Tambussi & Tonni, 1985).

The South American screamers (Anhimidae) constitute a basal lineage of Anseriformes with deep roots in South America. Their fossil record may go back into the late Oligocene–early Miocene of Brazil and, if the assignation of *Loxorhynchis clivus* to the Anhimidae is correct, they would have a record in the late Oligocene of Patagonia.

Gruiformes exhibit a clear Gondwanan distribution, but they also have a wide Laurasian Palaeogene record and the relationships of these taxa with those of South America are unclear. Presently, Gruiformes are not considered as a natural group (Mayr & Clarke, 2003; Hackett *et al.*, 2008).

Phorusrhacids (Cariamiformes) had their early and near complete history in South America. A member of this group, *Titanis*, participates in the second episode of the exchange between the Americas that took place at about 5.0–4.7 Ma (see Woodburne, 2010, and references cited therein). The latest records in South America are Pliocene–early Pleistocene in age (Tambussi *et al.*, 1999). Recently, Alvarenga *et al.* (2010) described a distal portion of a tarsometatarsus from the late Pleistocene of Uruguay that they assigned to a Phorusrhacidae. At least judging from the published figure, however, the material is very poor, and additional skeletal elements are needed to confirm identification.

Falconidae, which today have a worldwide distribution, seem to have a South American origin. Falcons occur in the late early Miocene Santacrucian localities, but the record is extremely poor when compared with its high modern diversity.

Teratornithidae have a South American origin and did not reach North America until the late Neogene (Campbell & Tonni, 1981). They have a Palaeogene record from Brazil and, after that, during the late Miocene. As phorusrhacids, they move in the Americas in a south–north direction.

Two additional derived taxa, Psittaciformes and Passeriformes, deserve consideration. Psittaciformes (parrots, cockatoos, macaws) represent a very particular group of living birds with a probably Australasian origin (Wright *et al.*, 2008), with a long evolutionary history predating their current panaustral distribution. Approximately 43% of Psittaciformes living species (148 species within the tribe Arini) are in the Neotropics. In Argentina, they are recognized from the late Pliocene and all records are limited to the Pampean Region. All but one (*Nandayus vorohuensis* Tonni & Noriega) are species of the genus *Cyanoliseus* Bonaparte. The burrowing parrot, *Cyanoliseus patagonus*, belongs to the most derived clade of parrots. Tambussi, Acosta Hospitaleche & Horlent (2007) characterize the modern area of distribution as subhumid–dry to semiarid, with rainfall up to 600 mm and, exceptionally, 800 mm, and temperatures not below 8–9 °C. Taking into account the current conditions of the Pampean Region, the *Cyanoliseus* record suggests more arid conditions that at present during the late Pleistocene–Holocene at the southeastern portion of the Pampean Region.

The passerine radiation represents one of the greatest avian success stories of all time. They are strong fliers of small size with exceptionally high metabolic rates. About 58% (5700 species) of the living birds (close to 9700 species) are passerines and they became highly diverse in the Neogene. However, the fossil record of Passeriformes in Argentina is extremely poor. The oldest record corresponds to an undetermined Passeriformes (probably belonging to Tyranni) for the early–middle Miocene (Noriega & Chiappe, 1993) of Pinturas. Fossil Tyranni began to be abundant in Argentina starting in the Pliocene (Tonni & Noriega, 2001). Four species, *Ciclodes major*, *Pseudoseisuropsis nehuen*, *Junco robustus* and an indeterminate species of *Sicalis*, are known from the middle Pleistocene of the Pampean Region. Possibly, the very scarce record of passerines is the result of the sampling mode and does not reflect real absence.

The focus in the present article was on four Neogene associations of birds: one from the late early Miocene, two from the late Miocene and one from the late Pliocene. This choice is not random. First, the Palaeogene record of birds is virtually absent and controversial. Second, the Miocene is a landmark period of transformation in the Patagonian – and South American – physiognomy. This transformation

was the result of several processes: the decrease in marine temperatures, the decrease in humid conditions and the increase in xeric conditions, resulting in the expansion of the steppe across extra-Andean Patagonia and the confinement of the forest to the western areas. The avian fossil record partially reflects these processes but, in several cases, is not especially informative.

However, birds can usefully complement environmental information when they are members of a representative vertebrate assemblage. It is necessary to incorporate a reflection over the context in which we use the term 'association' here. Most of the Neogene material recognized for Patagonia and the Pampas belongs to old collections. The provenance of some of these materials can be doubtful. However, specimens – and taxa – are considered to belong to the same association when they come from the same sedimentary formation, although not necessarily from the same locality (but nearby; e.g. Santacrucian birds). It is very difficult to extrapolate the environmental requirements of the extinguished taxa from the living fauna (that is, actualism). Although substantial advances have recently been made in the recognition of which environmental variables best explain the distribution of some species (tinamids, psittaciforms, cariamids, some anseriforms), substantial information is still absent. Environmental reconstruction from fossil remains will be reliable when those remains correspond to extant species. Major uncertainties arise when the species are not the same.

Eduardo Tonni and Kenneth Campbell, in the 1980s, stated that the South American Cenozoic bird fauna was dominated by carnivorous birds, with the giant Phorusrhacidae and Teratornithidae being the most noticeable. We can now add the Falconidae, Accipitridae and Vulturidae (the latter only in the Pampean Region). Other nocturnal raptors (i.e. Strigiformes, owls) have not been recorded during the South American Palaeogene or early Neogene, but they are very abundant from the Palaeogene of the Northern Hemisphere. They argued that this dominance was correlated with a low diversity of large mammals (placental) carnivores. It is very interesting to note that carnivore vertebrate communities in Patagonia were represented predominantly by terrestrial birds and crocodiles (Sebecidae), whereas, in other continents, this role was occupied by the placental carnivores. The high prevalence of carnivorous birds over all other trophic habits continues today, although represented by different taxa (Tambussi, Noriega & Tonni, 1993).

After the connection between both Americas, there was intrusion of potential competitors and invasive species that undoubtedly had an impact on the origi-

nal habitats and biotic structures. Certain groups of birds persisted in their original distribution area, whereas others succumbed or changed their distributions. Rheids that are strictly terrestrial did not extend their distribution to North America, even though the land connection existed; nor did the Tinamids, although they are capable of flight. The Teratornithidae, which would have been excellent flyers and for which a sea barrier would not have been an impediment, have no records in North America until the Pliocene. Other senior groups, such as Anhingidae, Pelecanidae, Ciconiidae, Anatidae, Anhimidae, Presbyornithidae, Rallidae, Falconidae and Accipitridae, established important intercontinental relationships. Other taxa that are now important members of the rich South American avian fauna (e.g. hummingbirds) are unknown in certain periods of geological time. Lineages that were strictly terrestrial, flightless and with giant species persisted for a long time in South America (phorusrhacids, the giant *Brontornis* and rheids). Only the latter survive among the Neogene mammalian predators to date.

Nowadays, the Patagonian avifauna includes approximately 156 terrestrial, 52 aquatic and 11 oceanic breeding species. Bearing in mind the wide extension of Patagonia, exceeding one million square kilometres, it is clear that the Patagonian avifauna is presently impoverished.

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APPENDIX

Fossil birds from selected Patagonian and Pampean localities (see text for current status). Ac, Accipitriformes; An, Anseriformes; Ca, Cariamiformes; Ch, Charadriiformes; Fa, Falconiformes; Pe, Pelecaniformes; Rh, Rheiformes; Sp, Sphenisciformes; Ti, Tinamiformes.

	Taxon	Stratigraphy and age
	Aves Neornithes	Salamanca Formation, early Palaeocene
Rh	Rheiformes	Río Chico Formation, mid-Palaeocene
An	<i>Presbyornis pervetus</i>	Casamayor Formation, mid-Eocene
An	<i>Telmabates antiquus</i>	Casamayor Formation, mid-Eocene
An	Presbyornithidae	Vaca Mahuida Formation, early Eocene
Ac	Accipitridae indet.	Chubut province, lower–mid-Eocene
Ca	Psilopterinae indet.	Sarmiento Formation, late Eocene
Sp	<i>Arthrodytes andrewsi</i>	San Julián Formation, late Eocene–early Oligocene
Sp	<i>Paraptendytes robustus</i>	San Julián Formation, late Eocene–early Oligocene
Sp	<i>Argyrodytes microtarsus</i>	San Julián Formation, late Eocene–early Oligocene
Ca	<i>Physornis fortis</i>	Deseado Formation, late Oligocene
Ca	<i>Andrewsornis abbotti</i>	Deseado Formation, late Oligocene

APPENDIX *Continued*

	Taxon	Stratigraphy and age
Ca	<i>Psilopterus affinis</i>	Sarmiento Formation, late Oligocene
?	<i>Pseudolarus guaraniticus</i>	Deseado Formation, late Oligocene
Ca	<i>Ciconiopsis antarctica</i>	Deseado Formation, late Oligocene
An	<i>Loxornis clivus</i>	Deseado Formation, late Oligocene
?	<i>Cruschedula revola</i>	Deseado Formation, late Oligocene
?	<i>Climacarthus incompletus</i>	Deseado Formation, late Oligocene
?	<i>Aminornis excavatus</i>	Deseado Formation, late Oligocene
An	<i>Teleornis impressus</i>	Deseado Formation, late Oligocene
?	<i>Riacama caliginea</i>	Deseado Formation, late Oligocene
Sp	<i>Eretiscus tonni</i>	Gaiman Formation, early Miocene
Sp	<i>Palaeospheniscus bergi</i>	Gaiman Formation, early Miocene
Sp	<i>Palaeospheniscus patagonicus</i>	Gaiman Formation, early Miocene
Sp	<i>Palaeospheniscus biloculata</i>	Gaiman Formation, early Miocene
Sp	<i>Paraptendytes antarctica</i>	Monte León Formation, early Miocene; Puerto Madryn Formation, early late Miocene
Sp	<i>Madrynornis mirandus</i>	Puerto Madryn Formation, early late Miocene
Rh	<i>Opisthodactylus patagonicus</i>	Santa Cruz Formation, late early Miocene
Ti	Tinamidae	Santa Cruz Formation, late early Miocene
?	<i>Anisolornis excavatus</i>	Santa Cruz Formation, late early Miocene
An	<i>Eoneornis australis</i>	Santa Cruz Formation, late early Miocene
An	<i>Eutelornis patagonicus</i>	Santa Cruz Formation, late early Miocene
An	<i>Ankoneta larriestrai</i>	Santa Cruz Formation, late early Miocene
An	<i>Brontornis burmeisteri</i>	Santa Cruz Formation, late early Miocene
Ca	<i>Phorusrhacos longissimus</i>	Santa Cruz Formation, late early Miocene
Ca	<i>Patagornis marshi</i>	Santa Cruz Formation, late early Miocene
Ca	<i>Psilopterus lemoinei</i>	Santa Cruz Formation, late early Miocene
Ca	<i>Psilopterus bachmanni</i>	Santa Cruz Formation, late early Miocene
Ca	<i>Cariama santacruzensis</i>	Santa Cruz Formation, late early Miocene
Fa	<i>Badiostes patagonicus</i>	Santa Cruz Formation, late early Miocene
Fa	<i>Thegornis debilis</i>	Santa Cruz Formation, late early Miocene
Fa	<i>T. musculosus</i>	Santa Cruz Formation, late early Miocene
Pe	<i>Macranhinga</i>	Santa Cruz Formation, late early Miocene
Pe	<i>Liptornis hesternus</i>	Santa Cruz Formation, late early Miocene
Pe	<i>Protibis cnemialis</i>	Santa Cruz Formation, late early Miocene
Rh	<i>Pterocnemia</i>	Cerro Azul Formation, late Miocene
Ti	<i>Nothura</i>	Cerro Azul Formation, late Miocene
Ti	<i>Eudromia sp</i>	Cerro Azul Formation, late Miocene
Ca	<i>Procarriama simplex</i>	Cerro Azul Formation, late Miocene
Ci	<i>Argentavis magnificens</i>	Cerro Azul Formation, late Miocene
Fa	<i>Milvago</i>	Cerro Azul Formation, late Miocene
Pa	Tyraniidae	Cerro Azul Formation, late Miocene
Ci	<i>Leptoptilus patagonicus</i>	Puerto Madryn Formation, early late Miocene
Ac	Accipitridae indet.	Puerto Madryn Formation, early late Miocene
Ca	Psilopterinae indet.	Puerto Madryn Formation, early late Miocene
An	Dendrocygninae	Puerto Madryn Formation, early late Miocene
Rh	<i>Hinasuri nehuensis</i>	Chapadmalal Formation, late Pliocene
Rh	Rheidae indet.	Chapadmalal Formation, late Pliocene
Ti	<i>Nothura parvula</i>	Chapadmalal Formation, late Pliocene
Ti	<i>Eudromia</i>	Chapadmalal Formation, late Pliocene
Ca	<i>Mesembriornis australis</i>	Chapadmalal Formation, late Pliocene
Ca	<i>M. rapax</i>	Chapadmalal Formation, late Pliocene
Ch	<i>Calidris</i>	Chapadmalal Formation, late Pliocene
Ch	<i>Charadrius</i>	Chapadmalal Formation, late Pliocene