Evolutionary History of South American Artiodactyla

Article · May 2016

Guillermo Cassini
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; CONICET; Univer…
84 PUBLICATIONS **1,026** CITATIONS
SEE PROFILE

Nahuel A. Muñoz
Universidad Nacional de La Plata
20 PUBLICATIONS **108** CITATIONS
SEE PROFILE

Evolutionary History of South American Artiodactyla

Guillermo H. CASSINI[1,2,6], Nahuel A. MUÑOZ[3,6] & Mariano L. MERINO[4,5]

[1]División Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Angel Gallardo 470, Ciudad Autónoma de Buenos Aires (C1405DJR), Argentina. gcassini@macn.gov.ar. [2]Departamento de Ciencias Básicas, Universidad Nacional de Luján, Ruta 5 y Av. Constitución, Luján (6700), Buenos Aires, Argentina. [3]División Paleontología Vertebrados, Museo de La Plata, Unidades de Investigación Anexo Museo, FCNyM-UNLP, 60 y 122, La Plata (1900), Argentina. nahuelmunoz@fcnym.unlp.edu.ar. [4]Centro de Bioinvestigaciones, Universidad Nacional Del Noroeste de la Provincia de Buenos Aires, Ruta Provincial 32 km 3.5, Pergamino (2700), Buenos Aires, Argentina. mariano.merino@nexo.unnoba.edu.ar. [5]Comisión de Investigaciones Científicas de la provincia de Buenos Aires (CIC). [6]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

Abstract. South American artiodactyls have a Holartic origin and reached the continent during the Great American Biotic Interchange. Among the 10 extant artiodactyl families, three, Tayassuidae, Camelidae and Cervidae arrived and survived to the present. They participate in the megahervibore climax of spectacularity during the Quaternary, but did not occupy or compete in the megaherbivore niche. They reached their maximum diversity during Lujanian Age, particularly the camelid and cervid families. In the late Quaternary, many of the larger tayassuids, camelids, and cervids (especially those with big antlers) went extinct. In recent times the cervids are the most diverse of South American artiodactyl families, while in Africa bovids are the most diverse. In certain cases there is a remarkable parallelism in ecological niche space and morphology between the continents, for example between African duikers and South American brocket deer. The shared ecomorphological traits seem to be very successful in forested habitats in warm climates.

Keywords: Tayassuidae, Camelidae, Cervidae, Megaherbivor niche, Extinctions, Brocket-Duiker ecomorphotype.

Resumen. Los artiodáctilos de América del sur de origen holártico participaron del intercambio faunístico de mamíferos terrestres entre América del Sur y del Norte. De las 10 familias actuales, han arribado y sobrevivido hasta la actualidad los Tayassuidae, Camelidae y Cervidae, compartiendo el período de mayor esplendor de los megaherbívoros durante el Cuaternario. Sin embargo, los artiodáctilos no ocuparon o compitieron por el nicho de megaherbívoro ni de pastador, incluso luego de su extinción. Durante la edad Lujanenese alcanzaron su máxima diversidad, representada principalmente por camélidos y cérvidos. Los tayasuidos y camélidos de mayor tamaño, y los cérvidos (especialmente los de grandes astas) se extinguieron durante el final del Cuaternario. Actualmente los cérvidos son el grupo de artiodáctilos más diversos de América del Sur como los Bóvidos lo son en África. En ambos continentes se observa un paralelismo notable en la morfología y el nicho ecológico ocupado por duiqueros y corzuelas. Los rasgos ecomorfologícos compartidos parecen ser exitosos en forestas de climas cálidos.

Palabras clave: Tayassuidae, Camelidae, Cervidae, nicho megaherbívoro, Extinciones, ecomorfotipo corzuela-duiquero.

INTRODUCTION

Different mammal lineages converged in having long limbs, and ungual phalanxes covered (or are interpreted to have been covered) with hooves, so they are often referred as hoofed mammals or ungulates despite their phylogenetic relationships. They include the extant terrestrial artiodactyls and perissodactyls, among laurasiatherians, and hyracoids and proboscideans (Paenungulata), among afrotheres, and the extinct South American endemic clades Notoungulata, Litopterna, Astrapotheria, Pyrotheria and Xenungulata. Terrestrial artiodactyls (that is excluding cetaceans; *e.g.*, camels, pigs, hippopotami, giraffes, cattle and deer) occupy diverse habitats and biomes on almost all continents, except Australia and Antarctica. Both morphologically and taxonomically, they constitute the most diverse and rich clade of extant ungulates with 10 families, and at least 89 genera and 242 species; Groves & Grubb (2011) recognized up to 94 genera and 460 species.

Theodor *et al.* (2005) defined artiodactyls on the basis of three characters; paraxonic symmetry of the feet ("even-toed"), a double-trochleated astragalus and six-cusped dp4. They are first known from the earliest Eocene of North America and Eurasia and would show four main evolutionary radiations. The first one, during the early to early middle Eocene, was characterized by small omnivorous forms with bunodont (or bunoselenodont) cheek teeth (Janis, 2000).

The declining levels of CO_2 and higher nitrogen to carbon ratio in plant tissues that occurred during the early Eocene seem to have favored the diversification of artiodactyls. By the late middle Eocene, the three extant suborders Ruminantia, Tylopoda and "Suiformes" (today separated as Suina and Whippomorpha) can be recognized. They were larger than the early Eocene forms and had selenedont check teeth, traits that, particularly in ruminants and tylopods, could be linked to a shift toward some kind of ruminating type of foregut from hindgut fermentation and toward a folivorous from an omnivorous diet (Janis, 2007).

The third radiation included the Neogene expansion of pecoran ruminants (bovids, cervids, giraffids and others). Also, the extant families of modern camels (Camelinae) and peccaries (Tayassuidae) appears by the early to late early Miocene. This radiation is characterized by the acquisition of longer legs (enhanced cursoriality), defenses in the skull of tylopods and ruminants, and high-crowned cheek teeth extending the function tooth life (hypsodonty). This broad ecomorphological type suggests a habit shift from closed to more open habitats (Janis, 2007). During the mid-Miocene climatic optimum artiodactyls and perissodactyls enter Africa by the "*Gomphotherium* land bridge" that connected Africa and Eurasia. This Neogene radiation had its acme at 14 Ma and declined by the late Miocene especially in brachyodont forms (Costeur *et al.*, 2004; Janis *et al.*, 2004).

The fourth artiodactyl radiation occurred during the Plio-Pleistocene and implied the diversification of bovids and the declination of other groups (*e.g.*, giraffids and camelids). Although many extant bovids are browsers and frugivores, by the Pleistocene the craniodental specializations for grazing appear allowing bovids to dominate the late Cenozoic hypsodont grazing niche.

Artiodactyls were part of the exchange of land mammals between South and North American during the Great American Biotic Interchange that occurred with the rising of the Isthmus of Panama bridging South America and North America, especially during the Pliocene. They were represented by only three of the 10 modern families, Tayassuidae, Camelidae and Cervidae, plus a member of the extinct family Palaeomerycidae.

Since the overview paper from Menegaz & Ortiz Jaureguizar (1995), there have been remarkable advances in our knowledge of the migration, distribution and diversity of the South American artiodactyls; three doctoral theses focused on the systematics of species from Argentina (Menegaz, 2000; Gasparini, 2007; Alcaraz, 2010); reports of dromomerycine and peccaries from late Miocene deposits from the Amazon basin; and summarized overviews of these three families (Guerin & Faure, 2009; Merino & Rossi, 2010; Gasparini, 2013; Scherer, 2013). Therefore we need not repeat that work here, instead in this contribution we attempt to explore some events that could have modeled the ways in which evolutionary trends in the tayassuids, camelids and cervids have been constrained.

THE FOSSIL RECORD, EXTINCTIONS AND GEOGRAPHICAL RETRACTION

The oldest fossil record of Artiodactyla in South America is controversial. Recently, Prothero *et al.* (2014) described *Surameryx acrensis*, the only South American Palaeomerycidae, from Brazil, interpreting the age of the presumed source horizon as at least 9.5 Ma (late Miocene).

The first unquestioned artiodactyl record in South America is the tayassuid *Platygonus* (Chapadmalalan age; ca. 3.7 Ma; Woodburne, 2010) from the Pampean region in Argentina (Gasparini, 2013 and references there in). There are other two, although doubtful, oldest records: the two new genera *Sylvochoerus* and *Waldochoerus* (Frailey and Campbell, 2012) from the Miocene of Peru, with questioned systematic and age assignations; and a *Platygonus* (=*Selenogonus*) from the late Pliocene or early Pleistocene of Colombia (Gasparini *et al.*, 2014). Therefore, the Tayassuidae family is recorded from the Pliocene (Chapalmalalan; Cione *et al.*, 2007) to Recent times. They are represented by three genera and comprise medium size ungulates (Table 1). The *Platygonus* and *Catagonus* species have ecomorphological traits that suggest they dwelled in dry and relatively open habitats (*i.e.*, elongation of the rostrum, great development of nasal sinuses and chambers, reduction of the lateral digits in the limbs; Gasparini (2013) and references there in). The existence of these environments during the glacial cycles, could explain their broad distribution in South America (Figure 1 and 2). While *Platygonus* species (the most herbivore and open-habitat adapted genus; see Table 1) became extinct by the early Pleistocene (Ensenadan) in Argentina (Gasparini, 2013; see Solorzano *et al.*, 2015 for Venezuela), *Catagonus wagneri* survive to present times, although restricted to the Gran Chaco. The *Tayassu* species (*T. tajacu* and *T. pecari*; but see Groves & Grubb, 2011) represent a lineage which differentiated in the Southern Hemisphere (middle Pleistocene of Pampean region; Figure 2) and then migrated to North America. Following Gasparini (2013), their recent extensive geographic range and ecological tolerances preclude using them as environmental indicators.

The next artiodactyl family recorded in South America, at about 3.3 Ma (Marplatan age; Woodburne, 2010) of the Pampean region of Argentina is Camelidae, represented by *Lama*. The South American camels (Lamini) arrived in South America during the Pliocene and spans to Recent times (Scherer, 2013). They were represented by five genera, comprising medium to large sized animals (Table 1) and reached their greatest abundance and diversity by late Pleistocene (Lujanian Age; Figure 2B). *Hemiauchenia* was the larger South American camelid (~400 Kg) and was likely a mixed-feeder dwelling in open habitats, mainly in the Pampean region, as well as the smaller *Lama* and *Vicugna* species (Table 1). *Eulamaops* and *Palaeolama* would have been browsers dwelling in open (mixed grass and shrub) and closed habitats respectively (Table 1). After the Lujanian age, the largest and less hypsodont forms *Eulamaops*, *Palaeolama* and *Hemiauchenia* (see Table 1) became extinct. The two smaller species, *L. guanicoe* and *Vicugna vicugna,* with the high-crowned cheek teeth survived with a geographical distribution restricted to dryer and colder regions. Tonni & Politis (1980) and Menegaz *et al.* (1989) hypothesized that the climatic changes that occurred towards the late Holocene (see next section), including an increase in the humidity at continental scale, converted most of the new environments inhospitable to camelids. Cione *et al.* (2009) suggested that the recent distribution of vicugnas, restricted to high plains or Andean altipampas areas could be explained by human pressure. These authors also enumerate many biological reasons (*e.g.*, age at maturity, reproductive rate, population density and reservoirs, etc) by which “the guanaco does not appear to be a species easy to extinguish” (Cione *et al.*, 2009: 137). Alternatively, Cajal *et al.* (2010) claimed that if *L. gracilis* and

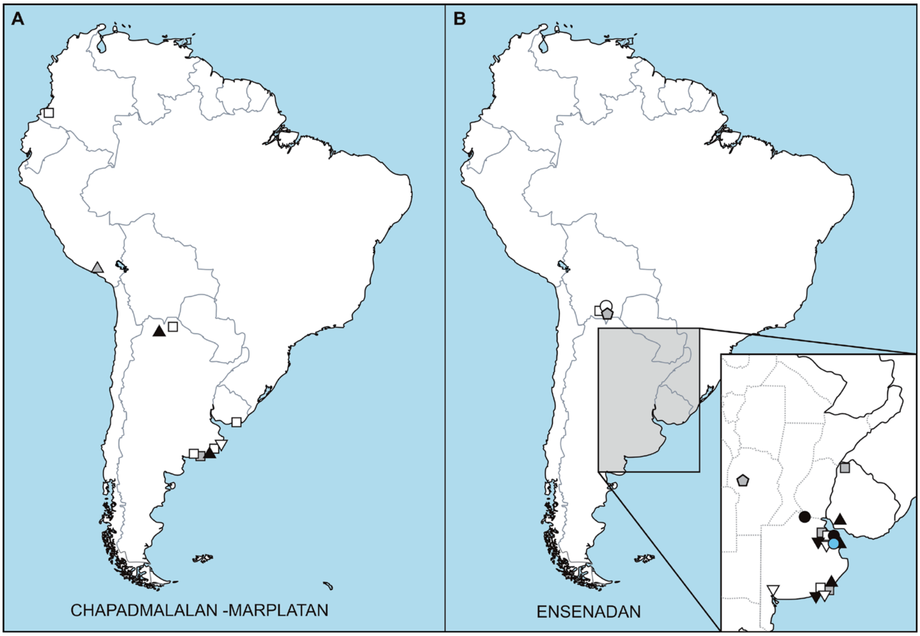

Figure 1. Geographic and temporal distribution of the Tayassuidae, Camelidae and Cervidae on A. Chapalmalalan and Marplatan Ages, and B. Ensenadan Age (after Marshall & Sempere, 1991; Alcaraz, 2010; Gasparini, 2013; Scherer, 2013). Symbols: squares – Tayassuidae (white – *Platygonus* and gray - *Catagonus*); triangles – Camelidae (black – *Hemiauchenia*, gray – *Palaeolama*, inverted black – *Vicugna*, inverted white – *Lama*); Cervidae circles (white – *Charitoceros*; black – *Epieuryceros*; cyan – *Antifer*) and pentagons (gray – *Hippocamelus*).

vicugnas were the same species (Weinstock *et al.*, 2009), then their local extinction at low elevations could be attributed also to anthropic actions (*i.e.*, hunt burden and environmental and ethological changes caused by the presence of humans).

The family Cervidae arrived in South America at approximately 1.8 Ma in the early Pleistocene (Woodburne, 2010) and survive to Recent times. The oldest South American cervids (Ensenadan age) are *Epieuryceros* and *Antifer*, both from the Pampean region (Menegaz & Ortiz Jaureguizar, 1995; Cione *et al.*, 2007). The cervids were represented by 12 genera, medium to large in body size (Table 1). They reached their greatest abundance and diversity by late Pleistocene (Lujanian Age; Figure 2B). Their systematic is complicated because many fossil species are defined based on antlers, and recent phylogenies highlight the paraphyly of *Hippocamelus* and the polyphyly of *Mazama* (Duarte *et al.*, 2008; González *et al.*, 2010; Merino & Rossi, 2010). The present restriction of *Hippocamelus* species to the Andes region (Figure 2B) parallels that of vicugnas (see above). With the exception of *Blastocerus*, all cervids with large antlers (*Agalmaceros, Antifer*, *Charitoceros, Epyeuriceros*, *Morenelaphus* and *Paraceros*) became extinct after the Lujanian age. The decline of these forms lead to the recent deer diversity, dominated by species with "small" antlers and a great diversity of the brockets (*Mazama* spp.).

THE SOUTH AMERICAN MEGAHERBIVORE NICHE

The xenarthrans and five main groups of endemic South American "ungulates" (see above) dominated the herbivorous niche of large herbivores in the Cenozoic faunas

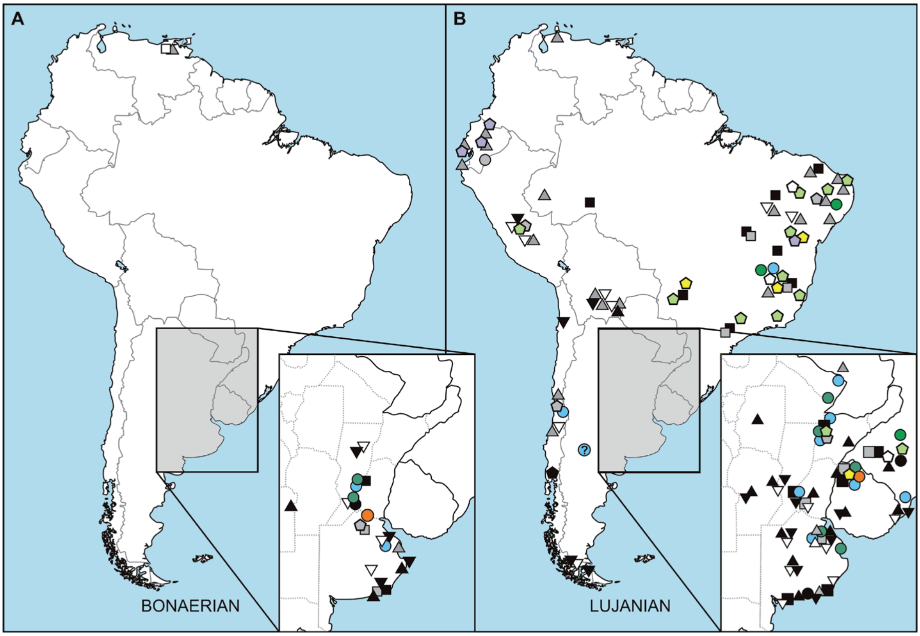

Figure 2. Geographic and temporal distribution of the Tayassuidae, Camelidae and Cervidae on A. Bonaerian Age and B. Lujanian Age (after Marshall et al., 1984; Tomiati & Abbazzi 2002; Ubilla, 2004; Alcaraz, 2010; Gasparini, 2013; Scherer, 2013; Gonzalez et al., 2014; Olivera et al., 2014; Solorzano et al., 2015). Symbols: squares – Tayassuidae (white – *Platygonus*, gray – *Catagonus* and black - *Tayassu*); triangles – Camelidae (white – *Eulamaops*, gray – *Palaeolama*, black – *Hemiauchenia*, inverted white – *Lama* and inverted black – *Vicugna*,); Cervidae circles (white – *Charitoceros*, gray – *Agalmaceros*, black – *Epieuryceros*; cyan – *Antifer*, green *Morenelaphus* and orange - *Paraceros*) and pentagons (white – *Blastocerus*, gray – *Hippocamelus*, black – *Pudu*, yellow – *Ozotoceros*, lilac - *Odocoileus* and green - *Mazama*).

of South America, at least until the late Pliocene. The primates and rodents arrived in South America probably as a result of trans-Atlantic migrations during the late Eocene and early Oligocene (see Pascual, 2006). In addition to the artiodactyls, three herbivore lineages first appeared in South America in the early Pleistocene: gomphotheriids among proboscideans, and equids and tapirids among perissodactyls (Webb, 1991).

Many lineages within these Cenozoic faunas showed a tendency to increase maximum body size, with about 40 genera exceeding 100 kg, of which half were strict megaherbivores (*i.e.*, body mass reaching1000 kg ore more; *sensu* Owen-Smith, 1988). Following Vizcaíno *et al.* (2012a) the climax of spectacularity in terms of large body size was reached particularly during the Quaternary (the last 2 My). By this time the megaherbivore niche was dominated by ten genera with high-crowned and ever-growing cheeck teeth (*i.e.*, euhypsodonty, *sensu* Mones, 1982), including nine xenarthrans (glyptodonts and ground sloth's) and one notoungulate (*Toxodon*), plus two genera with relatively high-crowned cheek teeth with finite growth (protohypsodonty, *sensu* Mones, 1982), including one litoptern (*Macrauchenia*) and one proboscidean (*Stegomastodon*; a North American immigrant). By contrast, immigrant artiodactyls clearly dominated the middle to large-sized herbivores; with the exception of *Lama* spp. they all had mostly brachyodont cheeck teeth (Table 1). Following Vizcaíno *et al.* (2012a), the tendency to evolve increased body sizes allowed herbivorous xenarthrans to avoid competition with northern placental lineages, except mastodonts.

Table 1. The artiodactyls' genera represented in South America. Chronology, hypsodonty, body mass and ecological hypotheses.

Genus	**Biocron**	**HI**	**BM (Kg)**	**Habitat**	**Diet**	**Source**
†*Eulamaops*	Lujanian	N/A	150	Open (f)	Browser	(1, 18, 20)
†*Paleolama*	Marplatan - Lujanian	Lowest Lamini	230 (c)	Closed	Browser/Frugivore (NA)	(1, 11,)
†*Hemiauchenia*	Marplatan - Lujanian	∼2.7 (NA)	400	Open	Mixed feeder (NA)	(1, 11, 14, 20)
Lama	Marplatan - Recent	3.46	110	Open	Mixed feeder	(1, 12, 21)
Vicugna	Ensenadan - Recent	4.33	50	Open	Mixed feeder	(1, 12, 21)
†*Platygonus*	Chapadmalalan - Lujanian	> *Tayassu*	30-70	Open (g)	Browser/ mixed-feeder	(2, 3, 13, 15, 20)
Catagonus	Ensenadan - Recent***	1.06	38	Mixed (h)	Omnivore (j)	(3, 12)
Tayassu	Bonaerian - Recent	1.0 - 1.23 (a)	24-32 (a)	Closed (i)	Omnivore	(3, 12, 16, 21)
Blastocerus	Lujanian - Recent	1.49	100/130 (d)	Open	Mixed feeder	(4, 12, 16, 17)
Ozotoceros	Lujanian - Recent	2.12	35/40 (d)	Open	Mixed feeder	(4, 12, 16, 17)
Mazama	Lujanian - Recent	1.3 (b)	8-65 (a)	Closed	Browser/Frugivore	(5, 12, 17)
Pudu	Lujanian - Recent	1.62	5-15 (a)	Closed	Browser	(6, 12, 17)
Hippocamelus	Ensenadan - Recent	1.94 (b)	46-90 (a)	Closed	Browser	(5 ,6 ,12, 17)
†*Antifer*	Ensenadan - Lujanian	N/A	120	N/A	Browser	(6, 14, 20)
†*Epieuryceros*	Ensenadan - Lujanian	N/A	120	N/A	Browser	(6, 14, 20)
†*Morenelaphus*	Bonaerian - Lujanian	N/A	50	N/A	N/A	(6, 18)
†*Paraceros*	Bonaerian - Lujanian	N/A	50	N/A	N/A	(6, 7, 18)
†*Charitoceros*	Ensenadan - Lujanian	N/A	60	N/A	N/A	(8, 9, 19)
†*Agalmaceros*	Lujanian	N/A	120 (e)	N/A	N/A	(10)
Odocoileus	Lujanian - Recent	1.23 -1.59 (a)	20-135	Mixed	Mixed feeder	(10, 12, 17)

Notes: NA: values for North American species for the same genus; N/A: Not available; † (dagger): extinct genera. (a) Lower and higher values for species of the genus; (b) Values for species M. americana and H. bisulcus; (c) Mean of geometric similarity with L. guanicoe and Camelus bactrianus; (d) female/male values; (e) gross comparison with Blastocerus living analogue; (f) Mixed grass and shrub (De Vivo & Carmignotto (2004) Vegetation Type Physiognomy); (g) Arid or semi-arid climates and open or relatively open environments (Gasparini & Ubilla, 2011); (h) Dry forest and shrub (De Vivo & Carmignotto (2004) Vegetation Type Physiognomy); (i) Poor ambient indicator (Gasparini, 2013); (j) Non animal material, but cacti, roots, flowers and fruits (Nowak, 1999). Sources: 1. Scherer (2013); 2. Solorzano et al. (2015); 3. Gasparini (2013); 4. De Oliveira et al. (2014); 5. Alcaraz (2010); 6. Gonzalez et al. (2014); 7. Ubilla (2004); 8. Marshall & Sempere (1991); 9. Marshall et al. (1984); 10. Tomiati & Abbazzi (2002); 11. Semprebon & Rivals (2010); 12. Janis (1988); 13. Rincón et al. (2009); 14. Vizcaíno et al. (2012); 15. Gasparini & Ubilla (2011); 16. Cassini et al. (2012); 17. Duarte & González (2010); 18. Prevosti & Vizcaíno (2006); 19. Smith et al. (2003); 20. Menegaz & Ortiz Jaureguizar (1995); 21. Mendoza & Palmqvist (2008).

One question that arises is why artiodactyls did not surpassed the one ton (see Table 1)? Or, in other words, why they did not succeed in the struggle for the megaherbivore niche? Certainly, with some exceptions (*e.g.*, river hippos and giraffes in Africa), extant artiodactyls never reach the size of a megaherbivore (Janis, 2007). The functional ruminant strategy in tylopods and pecorans of repeated mastication and moderately long gut retention times, in order to improve the cellulose digestion, might be limiting the amount of food they can ingest (Clauss *et al.*, 2009). This fact agrees with Clauss *et al.* (2003) previous hypothesis of an abdominal space limitation for accommodating a rumenoreticulum of a given size, which predicts that no grazing ruminants (or tylopods) will be larger than the largest extant Bovinae (*i.e.*, ~ 1000 kg) and that no browsing ruminants (or tylopods) will be larger than the largest extant giraffids (*i.e.*, ~1200 kg) (see also Steuer *et al.*, 2014). Apparently South America was not the exception; artiodactyls never compete for the megaherbivore niche.

It is well known that with the exception of the African continent and, very high latitudes and islands, megamammals vanished about 10000 years ago (Martin & Steadman, 1999). In South America, also most large mammals (46 species) present during the late Lujanian became extinct (Cione *et al.*, 2009). Following Koch & Barnosky (2006) all mammalian species larger than 320 kg, with 79% of those between 100 and 500 kg and ~35% of those ranging from 10 to 100 kg became extinct. Climatic catastrophes, gradual climate change, and overkill by human hunters were the most recognized explanations for this late Quaternary extinction (LQE) (Tonni *et al.*, 2003; Koch & Barnosky, 2006; Cione *et al.*, 2009; Vizcaíno *et al.*, 2012a and references therein).

Despite the explanations of the extinctions, after the LQE the megaherbivore niche remains vacant, and immigrant artiodactyls dominate the medium to large size herbivorous niche instead. In addition, no South American artiodactyls became a grazer specialist (*i.e.*, diet composed of >90% monocots and no seasonal or geographic variability) neither develop high-crowned cheek teeth (Table 1; with exceptions of *Lama* and *Vicugna*), contrary to the bovid radiation in Africa (see Janis 2007).

THE BROCKET-DUIKER ECOMORPHOTYPE: ANALOGIES BETWEEN SOUTH AMERICA AND AFRICA

The evolutionary history of artiodactyls in South America is relatively recent; they became the most diverse middle to large herbivores (*i.e.*, 10 to 100 Kg and 100 to 1000 kg respectively) in the continent today. Paradoxically, the same late Pleistocene and Holocene global events could have simultaneously affected the faunas and disrupted the pattern of shared analogous similarities between South America and Africa (*e.g.*, post-Miocene open-formation faunas included medium to large grazers and browsers, all preyed upon by specialized carnivores), extirpating the savanna from large mammals in the former and leading to their diversification in the latter (De Vivo & Carmignotto, 2004). These authors summarized ecological, behavioral and biogeographical patterns that involve past and recent mammal faunas on both continents and compared them with continental-level reconstruction of the changes in vegetational physiognomy. They conclude that present-day faunistic differences (megaherbivore niche vacancy and absence of grazer specialists in South America) would arise because open habitats remained far more extensive in Africa than in South America during the more humid phases of the Holocene. Whereas in Africa, bovids are the most diverse group of artiodactyls, in South America the cervids are. Following Gagnon & Chew (2000) dietary classifications of the 78 extant bovid species (excluding caprines), about 34 % are grazers, a category absent in cervids and other South American artiodactyls (Merino & Rossi, 2010). An interesting point is that the

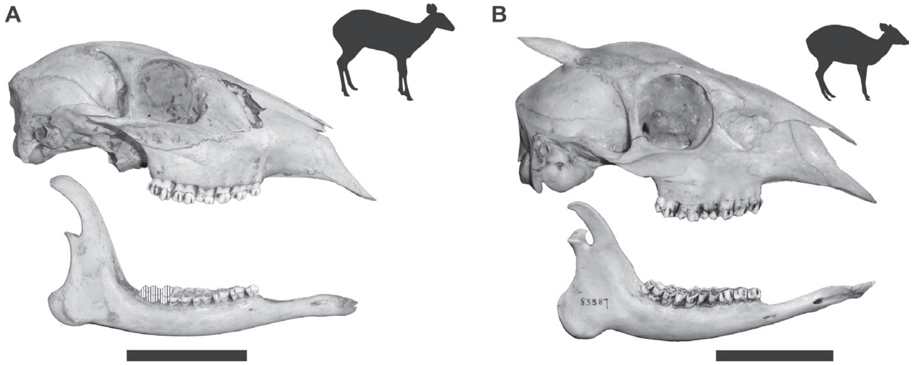

Figure 3. Brocket-Duiker morphotypes (Skull and silhouettes) of South American cervids and African bovids A. Amazonian brown brocket deer *Mazama nemorivaga* MZUSP 33476 and B. Red duiker *Cephalophus natalensis* AMNH 83387. Scale bar 50 mm.

diversity of African frugivores (∼24%; comprised exclusively by *Cephalophus* spp. "duikers") surpasses the browsers and mixed-feeders (∼21% for each). Although less diverse, the South American cervids are represented by 17 species, of which ∼60% (brockets; ∼70% including pudues) share the duiker ecomorphological traits (*i.e.*, rounded back, long hind legs, low withers, large facial glands and small horns/antlers for general body shape (Geist, 1971; Merino & Rossi, 2010), short and wide skull in the region of the orbits/zygomatic arch, proportionally large braincase and short rostrum (Merino *et al.*, 2005); Figure 3). Following Duarte & González (2010), the diets of five species of South American cervids is inadequately known (mainly those of the Paramos in Northwest South America), but the remaining 12 could be assigned to one of the diet categories from Gagnon & Chew (2000) (Table 2). Surprisingly, as in African bovids, the diversity of frugivores surpasses the browsers (∼42% vs. ∼33%) and mixed feeders (∼25%). Pudues seem to be mainly browsers, feeding also on fruits, but not predominantly. A special case is that of *M. gouazoubira*, which in some areas of their broad distribution have seasonal fruit preferences, but it is more like a browser living on bushy grasslands or along forest borders. There is a remarkable parallelism between duikers and brockets in their ecological niche (diet and habitat preferences) and morphology (general body shape and skeleton). Geist (1971) postulated that these ecomorphological traits appear to be very successful for small ruminants (and rodents) in warm climates (see also Rocha-Barbosa *et al.*, 2015, and references therein). The events that may have been involved in their success could be climatic and anthropological. De Vivo & Carmignotto (2004) claim that on both continents the Holocene Climatic Optimum resulted in the spread of closed forest environments over previously open landscapes, establishing the evergreen and semi-evergreen rain forest areas in which these forms dwell today. As Cione *et al.* (2009) pointed out, the mammals that avoided extinction are inhabitants of areas of relatively difficult access for humans, such as forests and cerrados; mountainous areas and wetlands. These areas are inhabited by extant members of the three artiodactyl families, and undoubtedly the closed areas benefit the expansion of frugivores particularly the brockets.

In summary, it seems to be a convergent evolution to a brocket-duiker morphotype in two artiodactyl families in Africa and South America (bovids and cervids respectively). While in Africa it leads to the diversification of one clade, the Cephalophinae, in South America occurs at least twice; within the gray brocket clade and within the red brocket clade of Duarte *et al.* (2008).

Table 2. Extant South American cervids assigned following Gagnon and Chew (2000) diet categories scheme.

Browser–grazer intermediates (30–70% of dicots and monocots, >20% fruits)	**Browsers** (>70% dicots)	**Frugivores** (>70% fruits, little or no monocots)	**no data**
B. dichotomus	*H. bisulcus*	*M. americana*	*M. nana*
O. bezoarticus	*H. antisensis*	*M. temama*	*P. mephistopheles*
O. virginianus	*M. gouazoubira*	*M. bororo*	*M. rufina*
	P. puda	*M. nemorivaga*	*M. bricenii*
		M. pandora	*M. chunyi*

FINAL REMAKS

Four artiodactyl families arrived to South America during the Great American Biotic Interchange, of which three survive into the Recent (Tayassuidae, Camelidae and Cervidae)

Artiodactyls reach their maximum diversity in the Lujanian age (late Pleistocene – early Holocene) with the largest part of the diversity to be seen in the camelids and cervids.

Although artiodactyls where contemporaneous with the South American megafauna, they did not compete within megaherbivore niches, perhaps due to physiological restrictions, nor did they become a grazer specialist.

Some genera, such as *Vicugna* and *Hippocamelus,* were abundant in the Pampean region during the Lujanian but now have a more limited distribution restricted to the Andean regions.

With the exception of *Blastocerus* all South American cervids that had large antlers became extinct after the Lujanian.

The climatic event of the Holocene Climatic Optimum reshaped the Recent vegetation structure in both Africa and South America, and could partially explain the enhanced and parallel diversity of small- to medium-sized frugivorous African bovids and South American cervids in closed forest habitats.

ACKNOWLEDGMENTS

We thank the editors of this volume and the Comisión Organizadora of the 30th Jornadas Argentinas de Paleontología de Vertebrados for inviting us to participate; to Jonathan Perry, Richard F. Kay, Sergio F. Vizcaíno and Pablo Teta, for their valuable suggestions that greatly enhanced this manuscript. This is a contribution to the projects UNLu 650/14 (GHC) and PICT 2013-0143 (ANPCyT), and UNLP N750 to Dr. S.F.Vizcaíno. GHC dedicate this essay to the memory of Lucas E. Santana (1975-2015) "*Trenes y camiones, están quietos estancados…*"

REFERENCES

Alcaraz, M. A. 2010. *Sistemática de los cérvidos (Mammalia, Artiodactyla) del Pleistoceno de las áreas extraandinas de Argentina*. Tesis doctoral. Universidad Nacional de La Plata. La Plata. 317.

Cajal, J., Tonni, E. P., Tartarini, V. 2010. The extinction of some South American camelids: the case of Lama (Vicugna) gracilis. *Mastozoología Neotropical*. **17**: 129-134.

Cassini, G. H., Vizcaíno, S. F., Bargo, M. S. 2012. Body Mass estimation in Early Miocene native South American Ungulates: a predictive equation based on 3D landmarks. *Journal of Zoology*. **2287**: 53-64.

Cione, A., Tonni, E., Bargo, S., Bond, M., Candela, A., Carlini, A., Deschamps, C., Dozo, M., Esteban, G., Goin, F., Montalvo, C., Nasif, N., Noriega, J., Ortiz Jaureguizar, E., Pascual, R., Prado, J., Reguero, M., Scillato-Yané, G., Soibelzon, L., Verzi, D., Vieytes, E., Vizcaíno, S., Vucetich, M. 2007. Mamíferos continentales del Mioceno tardío a la actualidad en la Argentina: cincuenta años de estudios. *Ameghiniana, Publicación Especial*. **11**: 257-278.

Cione, A. L., Tonni, E. P., Soibelzon, L. 2009. Did humans cause the Late Pleistocene-Early Holocene mammalian extinctions in South America in a context of shrinking open areas? En: Haynes, G. (eds), *American megafaunal extinctions at the end of the Pleistocene*, 125-144. Springer. New York.

Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G., Streich, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*. **136**: 14-27.

Clauss, M., Nunn, C., Fritz, J., Hummel, J. 2009. Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*. **154**: 376-382.

Costeur, L., Legendre, S., Escarguel, G. 2004. European large mammals palaeobiogeography and biodiversity during the Neogene. Palaeogeographic and climatic impacts. *Revue de Paléobiologie*. **9**: 99-109.

De Oliveira, P. V., Ribeiro, A. M., Ximenes, C. L., Sales Viana, M. S., Holanda, E. C. 2014. Tayassuidae, Cervidae e Tapiridae da gruta do Urso fóssil, Holoceno, parque nacional de Ubajara, Ceará, Brasil. *Revista Brasileira de Paleontologia*. **17**: 417-434.

De Vivo, M. & Carmignotto, A. P. 2004. Holocene vegetation change and the mammal faunas of South America and Africa. *Journal of Biogeography*. **31**: 943-957.

Duarte, J. M. B., González, S., Maldonado, J. E. 2008. The surprising evolutionary history of South American deer. *Molecular Phylogenetics and Evolution*. **49**: 17-22.

Duarte, J. M. B. & González, S. 2010. *Neotropical Cervidology. Biology and medicine of Latin American deer*. FUNEP & IUCN. Jaboticabal, Brasil & Gland, Switzerland. 393 pp.

Frailey, C.D. & Campbell, Jr. K.E. 2012. Two new genera of peccaries (Mammalia, Artiodactyla, Tayassuidae) from Upper Miocene deposits of the Amazon Basin. *Journal of Paleontology*. **86**: 852-877.

Gagnon, M. & Chew, A. E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy*. **81**: 490-511.

Gasparini, G. M. 2007. *Sistemática, biogeografía, ecología y bioestratigrafía de los Tayassuidae (Mammalia, Artiodactyla) fósiles y actuales de América del Sur, con especial énfasis en las especies fósiles de la provincia de Buenos Aires*. Tesis doctoral. Universidad Nacional de La Plata. La Plata. 504.

Gasparini, G. M. & Ubilla, M. 2011. *Platygonus* sp. (Mammalia, Tayassuidae) in Uruguay (Raigón? Fm.; Pliocene-early Pleistocene), comments about its distribution and palaeonvironmental significance in South America. *Journal of Natural History*. **45**: 2855-2870.

Gasparini, G. M. 2013. Records and stratigraphical ranges of South American Tayassuidae (Mammalia, Artiodactyla). *Journal of Mammalian Evolution*. **20**: 57-68.

Gasparini, G. M., Rodriguez, S. G., Soibelzon, L. H., Beilinson, E., Soibelzon, E., Missagia, R. V. 2014. Tayassu pecari (Link, 1795)(Mammalia, Cetartiodactyla): comments on its South American fossil record, taxonomy and paleobiogeography. *Historical Biology*. **26**: 785-800.

Geist, V. 1971. The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World Deer and the genus Bison. *Quaternary Research*. **1**: 283-315.

Gonzalez, E., Rafael labarca, R., Chavez-Hoffmeister, M., Pino, M. 2014. First fossil record of the smallest deer cf. *Pudu* Molina, 1782 (Artiodactyla, Cervidae), in the Late Pleistocene of South America. *Journal of Vertebrate Paleontology*. **34**: 483-488.

González, S., Duarte, J. M. B., Maldonado, J. E. 2010. Molecular phylogenetics and evolution. En: Duarte, J. M. B. & González, S. (eds), *Neotropical Cervidology. Biology and medicine of Latin American deer*, 12-17. FUNEP & IUCN. Jaboticabal, Brasil & Gland, Switzerland.

Groves, C. & Grubb, P. 2011. *Ungulate Taxonomy*. The Johns Hopkins University Press. Baltimore. 309.

Guerin, C. & Faure, M. 2009. The Cervidae (Mammalia, Artiodactyla) of the Upper Pleistocene/ Lower Holocene deposits of the Serra da Capivara National Park Region (Piaui, Brazil). *Geobios*. **42**: 169-195.

Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in Ungulate Mammals, and the correlation of these factors with dietary preference. En: Russell, D. E., Santoro, J. P., Sigoneau-Russell, D. (eds), *Teeth Revisited: Proceedings of the VII International Symposium on Dental Morphology*, 367-387. Mém. Mus. natn. Hist. nat. Paris.

Janis, C. M. 2000. Patterns in the evolution of herbivory in large terrestrial mammals: the Paleogene of North America. En: D, S. H. (eds), *Evolution of herbivory in terrestrial vertebrates*, 168 - 222. Cambridge University Press. Cambridge.

Janis, C. M., Damuth, J., Theodor, J. M. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **207**: 371-398.

Janis, C. M. 2007. Artiodactyl paleoecology and evolutionary trends. En: Prothero, D. R. & Foss, S. E. (eds), *The evolution of artiodactyls*, 292-302. John Hopkins University Press. Baltimore.

Koch, P. L. & Barnosky, A. D. 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution, and Systematics*. 215-250.

Marshall, L. & Sempere, T. 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review. En: Suaréz-Soruco, R. (eds), *Fósiles y Facies de Bolivia Vol. I - Vertebrados*, 631-652. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos.

Marshall, L. G., Berta, A., Hoffstetter, R., Pascual, R., Reig, O. A., Bombin, M., Mones, A. 1984. Mammals and Stratigraphy: geochronology of the continental mammal•bearing Quaternary of South America. *Palaeovertebrata, Montpellier, Mémoire extraordinaire*. **14**: 1-76.

Martin, P. S. & Steadman, D. W. 1999. Prehistoric extinctions on islands and continents. En: MacPhee, R. D. E. (eds), *Extinctions in near time: causes, contexts and consequences*, 17–56. Kluwer/Plenum. New York.

Mendoza, M. & Palmqvist, P. 2008. Hypsodonty in ungulates: An adaptation for grass consumption or for foraging in open habitat? *Journal of Zoology*. **274**: 134-142.

Menegaz, A., Goin, F., E, O. J. 1989. Análisis Morfológico y Morfométrico multivariado de los representantes fósiles y vivientes del género Lama (Artiodactyla Camelidae). Sus implicancias sistemáticas. Biogeográficas. Ecológicas y Biocronológicas. *Ameghiniana*. **26**: 153-172.

Menegaz, A. & Ortiz Jaureguizar, E. 1995. Los artiodáctilos. En: Alberdi, M., Leone, G., Tonni, E. (eds), *Evolución biológica y climática de la región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental*, 311-337. Monografías Museo Nacional de Ciencias Naturales. Madrid.

Menegaz, A. 2000. *Los Camélidos y Cérvidos del Cuaternario del sector Bonaerense de la región pampeana: La Plata, Argentina, Universidad Nacional de La Plata Facultad de Ciencias Naturales y Museo*. Tesis doctoral. Universidad Nacional de La Plata. La Plata. 206.

Merino, M. L., Milne, N., Vizcaíno, S. F. 2005. A cranial morphometric study of deer (Mammalia, Cervidae) from Argentina using three-dimensional landmarks. *Acta Theriologica*. **50**: 91-108.

Merino, M. L. & Rossi, R. V. 2010. Origin, systematics and morphological radiation. En: Duarte, J. M. B. & González, S. (eds), *Neotropical Cervidology. Biology and medicine of Latin American deer*, 2-11. FUNEP & IUCN. Jaboticabal, Brasil & Gland, Switzerland.

Mones, A. 1982. An equivocal nomenclature: What means hypsodonty? *Paläontologische Zeitschrift*. **56**: 107-111.

Nowak, R. M. 1999. *Walker's Mammals of the World*. Johns Hopkins University Press. Baltimore, Maryland. 2015.

Owen-Smith, N. 1988. *Megaherbivores. The influence of very large body size on Ecology*. Cambridge University Press. Cambridge. 369.

Pascual, R. 2006. Evolution and geography: The biogeographic history of South American land mammals. *Annals of the Missouri Botanical Garden*. **93**: 209-230.

Prevosti, F. J. & Vizcaíno, S. F. 2006. Paleoecology of the large carnivore guild from the late Pleistocene of Argentina. *Acta Palaeontologica Polonica*. **5**: 407–422.

Prothero, D. R., Campbell, K. E., Beatty, B. L., Frailey, C. D. 2014. New late Miocene dromomerycine artiodactyl from the Amazon Basin: implications for interchange dynamics.

Journal of Paleontology. **88**: 434-443.

Rincón, A. D., Parra, G. E., Prevosti, F. J., Alberdi, M. T., Bell, C. J. 2009. A preliminary assessment of the mammalian fauna from the Pliocene-Pleistocene el Breal de Orocual locality, Monagas state, Venezuela. *Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin*. **65**: 593-620.

Rocha-Barbosa, O., Fiuza de Castro Loguercio, M., Cassinos, A., Silva Climaco das Chagas, K., Abreu dos Santos, J. 2015. Ecomorphological and locomotor diversity in caviomorph rodents with emphasis on cavioids. *Sarem Series A: Mastozoological Research*. **1**: 139-166.

Scherer, C. S. 2013. The Camelidae (Mammalia, Artiodactyla) from the quaternary of South America: cladistic and biogeographic hypotheses. *Journal of Mammalian Evolution*. **20**: 45-56.

Semprebon, G. M. & Rivals, F. 2010. Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **295**: 131–145.

Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H., Haskell, J. P. 2003. Body mass of late Quaternary mammals. *Ecology*. **84**: 3403-3403.

Solorzano, A., Rincon, A. D., McDonald, H. G. 2015. A new mammal assemblage from the Late Pleistocene el Breal de Orocual, northeast of Venezuela. En: Harris, J. M. (eds), *La Brea and beyond: The paleontology of asphalt-preserved biotas*, 125-150. Science Series 42. Natural History Museum of Los Angeles County.

Steuer, P., Südekum, K. H., Tütken, T., Müller, D. W., Kaandorp, J., Bucher, M., Clauss, M., Hummel, J. 2014. Does body mass convey a digestive advantage for large herbivores? *Functional Ecology*. **28**: 1127-1134.

Theodor, J., Rose, K., Erfurt, J. 2005. Artiodactyla. En: Rose, K. D. & Archibald, J. D. (eds), *The rise of placental mammals: origins and relationships of the major extant clades*, 215-233. Johns Hopkins University Press. Baltimore.

Tomiati, C. & Abbazzi, L. 2002. Deer fauna from Pleistocene and Holocene localities of Ecuador (South America). *Geobios*. **35**: 631–645.

Tonni, E. P. & Politis, G. 1980. La distribución del guanaco (Mammalia, Camelidae) en la provincia de Buenos Aires durante el Pleistoceno tardío y Holoceno. Los factores climáticos como causas de su retracción. *Ameghiniana*. **17**: 53-66.

Tonni, E. P., Cione, A. L., Soibelzon, L. H. 2003. The Broken Zig-Zag: Late Cenozoic large mammal and tortoise extintion in South America. *Revista del Museo Argentino de Ciencias Naturales*. **5**: 1-19.

Ubilla, M. 2004. Mammalian biostratigraphy of Pleistocene fluvial deposits in northern Uruguay, South America. *Proceedings of the Geologists' Association*. **115**: 347-357.

Vizcaíno, S. F., Cassini, G. H., Toledo, N., Bargo, M. S. 2012a. On the evolution of large size in mammalian herbivores of Cenozoic. En: Patterson, B. D. & Costa, L. P. (eds), *Bones, clones, and biomes: the history and geography of Recent Neotropical mammals*, 76-101. University of Chicago Press. Chicago.

Vizcaíno, S. F., Cassini, G. H., Toledo, N., Bargo, M. S. 2012b. On the evolution of large size in mammalian herbivores of Cenozoic faunas of southern South America. En: Patterson , B. D. & Costa, L. P. (eds), *Bones, clones and biomes: an 80-million year history of Recent Neotropical mammals*, 76 - 101. University of Chicago Press. Chicago, USA.

Webb, S. D. 1991. Ecogeography and the great American interchange. *Paleobiology*. **17**: 266-280.

Weinstock, J., Shapiro, B., Prieto, A., Marín, J. C., González, B. A., Gilbert, M. T. P., Willerslev, E. 2009. The Late Pleistocene distribution of vicuñas (Vicugna vicugna) and the "extinction" of the gracile llama ("Lama gracilis"): New molecular data. *Quaternary Science Reviews*. **28**: 1369-1373.

Woodburne, M. O. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution*. **17**: 245-264.

Esta publicación constituye la Sexta Edición de las Contribuciones Científicas del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". El presente volumen, titulado "Historia Evolutiva y Paleobiogeográfica de los Vertebrados de América del Sur" incluye una selección de artículos originales realizados por especialistas reconocidos en cada una de las temáticas tratadas. En cada contribución se lleva adelante un panorama sintético sobre la evolución de un grupo en particular de vertebrados sudamericanos, con especial énfasis en el registro fósil de Argentina.

Este volumen, compuesto por 37 artículos, será de gran utilidad para los investigadores especializados, y se constituirá, sin lugar a dudas, en una cita obligada para los interesados en la historia evolutiva de los vertebrados fósiles de Sudamérica.