1 Background for a paleoecological study of the Santa Cruz Formation (late Early Miocene) on the Atlantic Coast of Patagonia

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Abstract

For more than 120 years, the coastal exposures of the Santa Cruz Formation have been fertile ground for recovery of vertebrates from the late Early Miocene (~18 to 16 million years ago, Ma). As long ago as the 1840s, Captain Bartholomew Sulivan collected fossils from this region and sent them to Charles Darwin, who passed them to Richard Owen. Carlos Ameghino undertook several explorations of the region starting in the late 1880s. Carlos' specimens were described by his brother Florentino, who believed that many of the species were more ancient than now understood and represented the ancestors of many Holarctic mammalian orders. Ameghino's novel claims prompted William B. Scott to organize fossil collecting expeditions in the Santa Cruz beds led by John B. Hatcher. The fossils were described in a series of exhaustive monographs with the conclusion that the fauna was much younger than Ameghino thought. Several brief expeditions took place during the twentieth century, led by researchers from different institutions. Since 2003, we have undertaken the collection of over 1600 specimens, including large series of relatively complete skeletons. In this edited volume we have gathered together a group of researchers to study the coastal Santa Cruz Formation and its associated flora and fauna to provide a paleobiological reconstruction of the Santacrucian vertebrate community and to place it in its biotic and physical environment.

Resumen

Por más de 120 años, las exposiciones costeras de la Formación Santa Cruz han sido campo fértil para la recuperación de vertebrados del Mioceno Temprano tardío (~18 to 16 Ma). En la década de 1840, el Capitán Bartholomew Sulivan recolectó fósiles que envío a Charles Darwin, quien se los pasó a Richard Owen. Carlos Ameghino llevó a cabo varias exploraciones de la región, comenzando a fines de la década de 1880. Los especímenes colectados por Carlos fueron descriptos por su hermano Florentino, quien pensaba que muchas de las especies eran más antiguas que lo hoy se entiende y representaban los ancestros de muchos órdenes de mamíferos holárticos. Las novedosas propuestas de Ameghino estimularon a William B. Scott a organizar expediciones lideradas por John B. Hatcher para colectar fósiles en los niveles santacrucenses. Los fósiles fueron descriptos en una serie de monografías exhaustivas, concluyendo que las faunas eran mucho más jóvenes que lo que pensaba Ameghino. Varias expediciones breves lideradas por investigadores de diferentes instituciones tuvieron lugar durante el siglo XX. Desde 2003, hemos recolectado más de 1600 especímenes, incluyendo numerosos esqueletos relativamente completos. En este volumen, hemos reunido un grupo de investigadores para estudiar la Formación Santa Cruz de la costa, su flora y fauna asociada, para realizar una reconstrucción paleobiológica de la comunidad de vertebrados santacrucenses y ubicarla en su contexto biótico y ambiental.

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1.1 Introduction

Exposures on the Atlantic coast of southern continental Patagonia (Figs. 1.1 and 1.2) have been fertile ground for the recovery of fossil vertebrates of the Santa Cruz Formation for more than 120 years. The fossils come from the late Early Miocene, about 18 to 16 Ma, called the Santacrucian Land Mammal Age (Marshall *et al*., 1983, Perkins *et al*., Chapter 2). Through much of the Cenozoic, South American mammals underwent diversification and ecological specialization in isolation from other continents (Simpson, 1980). That isolation was interrupted by two major upheavals, one marked by the arrival of rodents and primates from Africa sometime in the Middle to Late Eocene and the other by the interchange of faunas beginning in the Late Miocene when South America began to establish contact with Central and North America. The Santacrucian marks the peak of known diversification achieved by mammals after the arrival of primates and rodents but before the arrival of North American immigrants (Marshall and Cifelli, 1990).

Between 1887 and 1906, the famous Argentine paleontologist Florentino Ameghino (1853/54 to 1911; Fig. 1.3a) described a plethora of species from a bizarre taxonomic assemblage – very

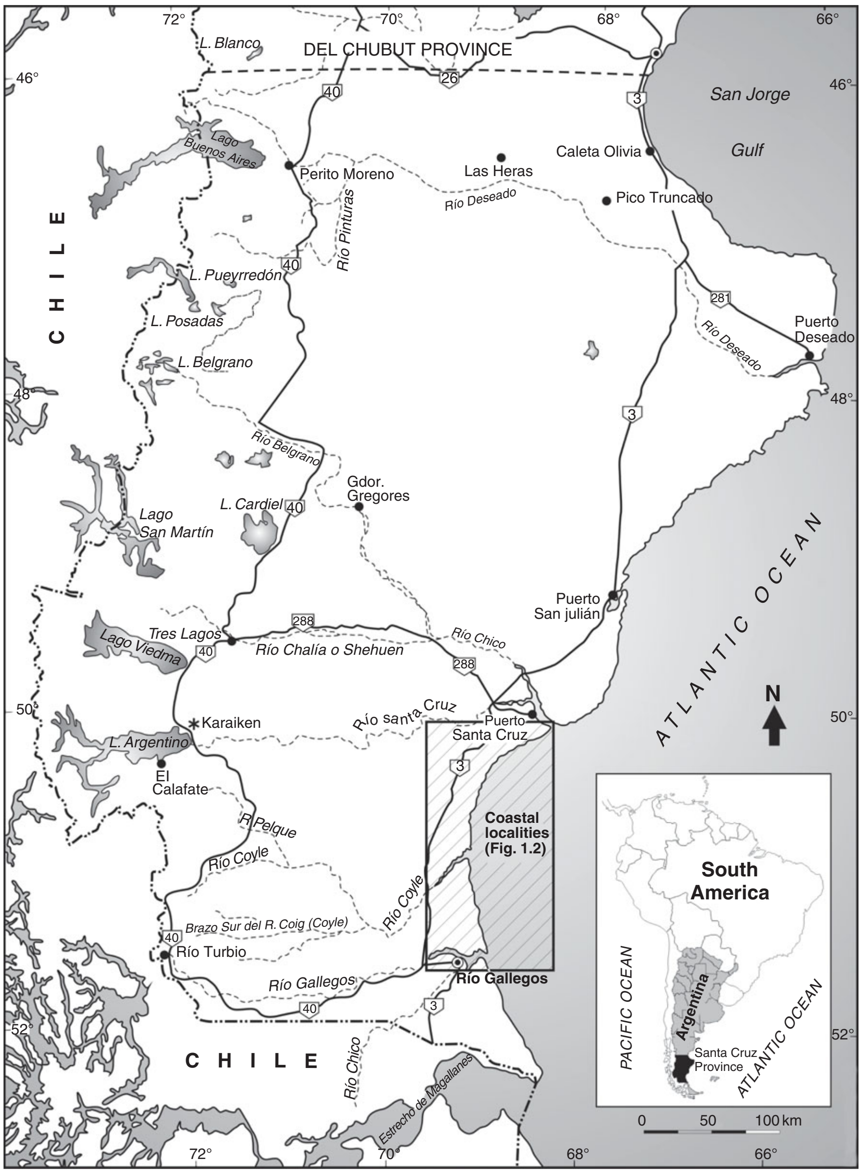

Fig. 1.1. Map of Santa Cruz Province (southern Patagonia, Argentina) and the Santacrucian localities treated in this volume and listed in Appendix 1.1.

different as a consequence of the long isolation of South America from other continents – of large predatory birds, as well as a diverse array of insectivorous, carnivorous, and herbivorous marsupials, glyptodonts, armadillos, sloths, small and large herbivorous hippo-like astrapotheres, rabbit- to cow-sized notoungulates, horse-like and camel-like litopterns, small to medium-sized rodents, and platyrrhine monkeys. Another singular nature of these finds, known even in Ameghino's day, is that the outcrops yield numerous remarkably complete specimens, including skulls with associated skeletons.

Florentino Ameghino believed that many of the species he described were more ancient than we now understand them to be and that he had documented the ancestors of many mammalian orders in South America, including those of artiodactyls, perissodactyls, and even human beings. Hitherto, the fossil record of many mammalian orders had been restricted to northern continents, and it was supposed by most authorities that most or all orders originated there. Ameghino's novel claims prompted W. B. Scott (1858–1947; see Simpson, 1948) from Princeton University, New Jersey, USA, to organize a series of expeditions (see below) to collect fossils in the Santa Cruz beds where the faunas were best known (see Scott's Preface to the Narrative of the *Princeton University Expeditions to Patagonia* by

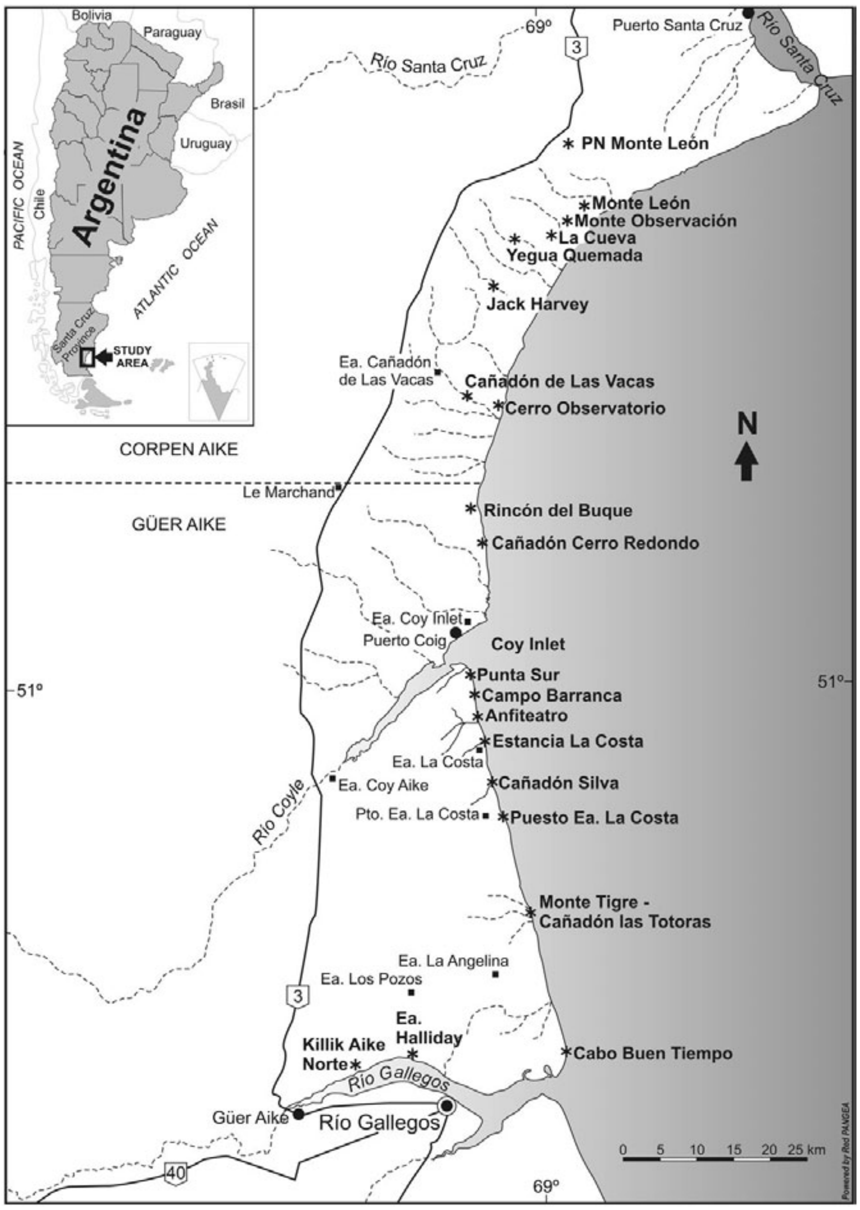

Fig. 1.2. Detailed map of the study area in the coastal Santa Cruz Formation, indicated in Fig. 1.1, and the localities listed in Appendix 1.1. Asterisks indicate localities; filled circles, towns; squares, Estancia (= Ea.).

Hatcher, 1903: vii). The fossils were described in a series of exhaustive monographs (1903–1928) in the *Reports of the Princeton University Expeditions to Patagonia*, edited by Scott between 1903 and 1932 (see Scott, 1903–1905, 1910, 1912, 1928; Sinclair, 1906, 1909; Sinclair and Farr, 1932) with extensive anatomical descriptions and illustrations. The conclusion was that the fauna was much younger than Ameghino had thought, and that most of the similarities that Ameghino identified between the Santa Cruz mammals and their northern counterparts were a consequence of adaptive convergence. In some ways, the size and scope of Scott's edited volumes led later workers to assume that most, if not all, secrets of this fauna had been revealed. In contrast, we see the relative completeness of the taxonomic coverage as an opportunity, not a curse.

George G. Simpson (1902–1984) claimed that the Santacrucian fauna was particularly important for its wealth of nearly complete skeletons of representatives of a phase in South American mammal history in which the communities consisted of a complex mixture of descendants of ancient lineages of the continent (Marsupialia, Xenarthra, Litopterna, Notoungulata, and Astrapotheria) and new forms from other continents (Rodentia and Primates) (Simpson, 1980). Among these mammals, rather peculiar groups such

Fig. 1.3. a, Florentino Ameghino (1853/54 to 1911). b, Francisco P. Moreno (1852–1919). c, Carlos Ameghino (1865–1936). d, John Bell Hatcher (1861–1904).

as xenarthrans (sloths, armadillos, anteaters, and their relatives) and "archaic" ungulates (notoungulates, astrapotheres, litopterns) are abundant and diverse. Also, the best material of Miocene platyrrhine primates comes from this formation. In many cases the "ancient" forms (such as sloths) have quite different morphologies than their surviving relatives, making it difficult to reconstruct their life habits. In the case of platyrrhine primates, although it is much easier to find living analogs, some aspects of their paleobiology are difficult to reconstruct. For example, what were the adaptations that allowed them to survive in a supposedly highly seasonal environment at a latitude of 52° S, about 20° south of the southern limit of the distribution of the extant members of this group?

Despite the quality of the known Santacrucian fossils, paleobiological reconstructions based on functional morphology, biomechanics, or ecomorphology are in short supply and widely scattered in the specialist literature. There were some important contributions in the 1990s, including the first paleobiological approaches on this fauna, such as studies on the masticatory apparatus of armadillos (Vizcaíno, 1994; Vizcaíno and Fariña, 1994, 1997; Vizcaíno and Bargo, 1998), the locomotory apparatus of Miocene sloths (White, 1993, 1997), or the inference of diets of small

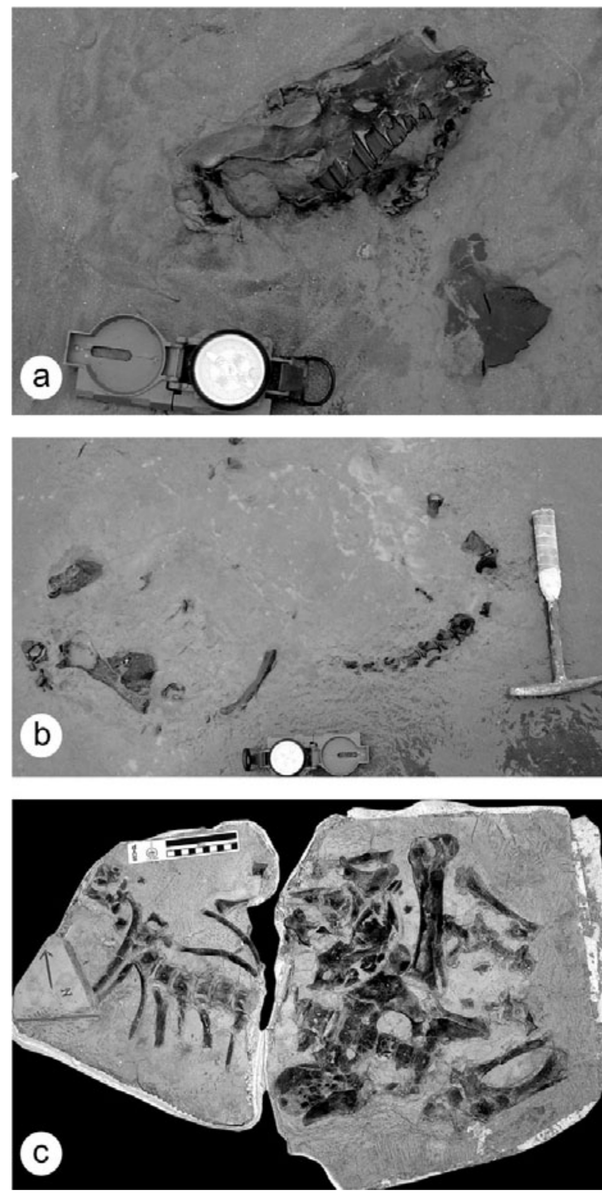

Fig. 1.4. Specimens *in situ* in the field and in the laboratory. a, Skull of the toxodontid *Adinotherium*; b, skeleton of a sloth. c, Specimen (sloth) in preparation at the laboratory of the Museo de La Plata.

marsupials and notoungulates (Dumont *et al.*, 2000; Tauber, 1996). More recently, Townsend and Croft (2008) inferred the diet of Santacrucian notoungulates based on enamel microwear analysis, and Candela and Picasso (2008) performed a morphofunctional analysis of a Miocene porcupine's limbs. Fleagle *et al.* (1997) provided incidental comments on selected taxa of primates.

Despite continued fieldwork for more than a century, the coastal Santa Cruz Formation, especially south of Río Coyle (also called Coy or Coig Inlet), continues to yield a rich assortment of skulls and articulated skeletons (Fig. 1.4),

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probably in greater abundance than anywhere else in South America. Because the collected material is often in an excellent state of preservation, the fossils of the Santa Cruz Formation are the best record for interpreting the biological diversity of mammals in the southern part of South America (Patagonia) prior to the Great American Biotic Interchange (GABI), with an approach similar to that already used in another important region with vertebrate fossils at La Venta (Middle Miocene), Colombia, in northern South America (Kay *et al*., 1997). The spectacular completeness of the fossil remains we recovered from Santacrucian localities of the Atlantic coast allows a detailed examination of the ecological dimensions of pre-interchange mammalian communities. Knowledge of mammalian community structure at this time provides reciprocal illumination on the nature and impact of faunal immigration that occurred later.

In the work described in this edited volume, we bring together a group of researchers to study the ~18–16 Ma coastal Santa Cruz Formation of Patagonia and its flora and fauna. We have the luxury that the systematics of the mammalian taxa is generally agreed upon. Thus, the focus is paleoecological rather than taxonomic. Our main purpose is to reconstruct the paleobiology of the Santacrucian vertebrate community and to place it in its biotic and physical environment.

Some work has been undertaken in the past to reconstruct aspects of the composite paleoecology of the Santa Cruz Formation based on the composition of its mammalian remains. In a landmark paper, Pascual and Ortiz-Jaureguizar (1990) examined faunal change among South American Cenozoic mammals based on the percentages of herbivorous species with different tooth crown heights. For chronologic units they used South American Land Mammal Ages. They included the Oligocene–Miocene Deseadan, Colhuehuapian, and Santacrucian mammal faunas collectively as the "Patagonian Faunistic Cycle," and recognized two subcycles within it – Deseadan and Pansantacrucian. The latter encompasses the Colhuehuapian and the Santacrucian Land Mammal Ages (Fig. 1.5). From low-crowned and rooted to high-crowned, rootless and ever-growing cheek teeth, they recognized four categories: brachydont, mesodont, protohypsodont, and euhypsodont. According to their analysis, by the beginning of the Patagonian Faunistic Cycle (Late Oligocene) many families of mammals had evolved protohypsodont and euhypsodont cheek teeth, a phenomenon they attribute to the increase in the number of grazing species coevolving with the spread of grasslands at mid-Patagonian latitudes. Further changes noted between the Deseadan and Pansantacrucian subcycles included a decrease in brachydont genera from 15% to 6%, and an increase in mesodont taxa from 31% to 48%; protohypsodont forms decline slightly from 31% to 23% and euhypsodont taxa remain

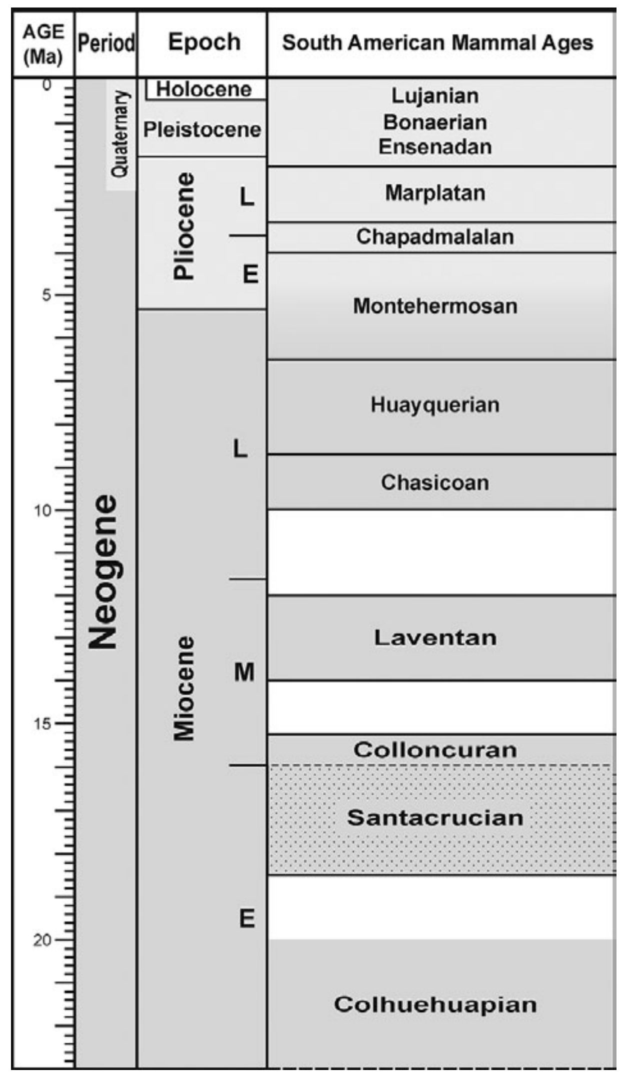

Fig. 1.5. Chronologic chart of the Neogene including the South American Land Mammal Ages (SALMA).

at 23%. These changes are attributed to a shifting balance of grassland and woodland habitats provided by a "park savanna" in Santacrucian times. Such analyses, while broadly useful, lack the kind of stratigraphic and chronologic precision so valuable for an understanding of ecological conditions at a single place and within a narrow range of time. The Santa Cruz Formation offers a unique window for reconstructing the structure of a South American mammalian paleocommunity with precise stratigraphic and geographic control. To date, just one analysis of Santacrucian faunas has been published within this more narrowly restricted scope. Croft (2001) used cenogram analysis (originally, a plot of vertebrate body sizes within a community, a method developed by Valverde, 1964) to interpret paleoenvironmental conditions for some of the best-known South American fossil mammal assemblages from the

Eocene to the Pleistocene. These were then compared to more traditional interpretations (based on herbivore craniodental and postcranial adaptations) to evaluate congruence between the different methods of paleoenvironmental reconstruction. Croft's paleoenvironmental interpretations based on cenogram analyses of Santacrucian faunal levels differ from that of Pascual and Ortiz-Jaureguizar based on herbivore hypsodonty. Croft interpreted the Santacrucian mammalian fauna as indicating a wetter and more wooded environment than Pascual and Ortiz-Jaureguizar had supposed. Croft suggested that the lack of congruence might result from a relatively depauperate mammalian predator diversity distinctive of South American faunas during much of the Cenozoic (e.g. prior to the Great American Biotic Interchange).

The task of the present work is to reconstruct the mammalian community structure and paleoclimate during the Santacrucian. This subject is of particular importance because the Santacrucian assemblage represents the world's most southern continental fauna and flora from the time interval known as the Mid-Miocene Climatic Optimum (MMCO). In the Early Miocene between 17 and 15 Ma, warm surface water transported southward by the Brazil Current extended subtropical conditions southward from Amazonia (Barron *et al*., 1985; Hodell and Kennett, 1985). Much of the Andean uplift had not yet occurred (Blisniuk *et al*., 2005; Ramos and Ghiglione, 2008), so Andean rain-shadow effects had not yet been established. This poleward spread of warmer and wetter climates coincides with the appearance of mammalian taxa adapted to a humid and warm climate, such as primates, low-crowned erethizontid rodents, and anteaters (among other faunal elements) (Fleagle *et al*., 1997; Kay *et al*., 2008; Kay, 2010). The spread of cooler and more arid conditions, a consequence of global cooling, onset of glaciations, and Andean uplift, began in the Middle Miocene and led to the regional extirpation of many of these faunal elements after about 15.5 Ma (Kay *et al*., 1998; Tejedor, 2006). Deposits of the Early Miocene Santa Cruz Formation (*sensu lato*) fall within the MMCO interval of warm climate. Nevertheless, the climatic conditions must have been unusual and without modern equivalents, given that seasonality in energy availability at ~50° S latitude must have had an effect upon biotic productivity, as it does today (Kaufman, 1995). A point of emphasis that we asked the contributors to consider is the importance of climatic conditions for the presence of their groups, so as to refine our understanding of mid-Miocene continental climate at southern latitudes.

1.2 Historical background

The nineteenth century saw a rapid rise in the exploration of South America. The industrial revolution fueled the expansionist, colonialist, and imperialist spirit that had characterized European nations for almost four centuries. Owing to the growing ambition to expand cultural horizons that fostered the prevailing ideals of progress and growth of reason on the one hand and strong demand for raw materials and new consumers on the other, the most powerful states sought new territories to take advantage of their resources and populations. Many exploratory expeditions had their attached naturalists who performed the dual role of collecting information, allowing an expansion of knowledge, while also identifying new natural products for exploitation, thus encouraging commercial growth. The fossils that promised to tell the fascinating remote history of life on Earth were among the many interests that spurred the imagination of naturalists who, after a long journey by sea, reached American shores. Marshall (1976) gave an account of the history of the explorations, early collectors, and major paleontological expeditions to Santa Cruz. In the following compilation that contextualizes the historical background for our research we have avoided duplicating his effort.

Fossil collecting in Santa Cruz began in January 1845, when Captain Bartholomew Sulivan (1810–1890), in command of the HMS *Philomel* and a former shipmate of Charles Darwin (1809–1882) aboard the HMS *Beagle*, discovered fossils on the cliffs of the estuary of the Río Gallegos (Brinkman, 2003). While some of his crew collected fresh water in preparation for a voyage to the Falkland Islands (which had been taken by the British in January 1833, some six months before Darwin collected his first fossils from nearby Bahía Blanca), Sulivan, who was interested in the spectacular bluffs that flank the estuary on its northern bank, landed about 12 miles upriver. Drawing on the training he received from Darwin, Sulivan collected several specimens from fallen blocks and produced a profile detailing his geological observations. He sent his collection to Darwin, who passed the fossils on to Richard Owen (1804–1982) of the Hunterian Museum of the Royal College of Surgeons of London. The great anatomist described what proved to be the first Miocene vertebrates from South America based on these fossils. Among the specimens were those that Owen described as types of the ungulate-like *Nesodon imbricatus* and *Nesodon sulivani*, the latter after its collector. Years later, Florentino Ameghino would regard it as synonymous with the former, thus denying Sulivan his well-deserved tribute (Brinkman, 2003). During the same year Sulivan, as commander of the HMS *Philomel*, participated in the battle of Vuelta de Obligado on the Río Paraná that pitted the small Argentine army against the Anglo-French forces that had blockaded the port of Buenos Aires. Sulivan captured the flag of the Argentine battery, but returned it 38 years later, honoring the courage and bravery of the Argentine soldiers (Vizcaíno, 2008). In subsequent years Sulivan encouraged Darwin to intercede with the British Admiralty to mount a new expedition to collect in the Río Gallegos area. Sulivan himself probably returned to Río Gallegos between 1848 and 1851, and made new collections when he traveled on his own initiative to the Falkland Islands. Sulivan's and Darwin's persistence eventually payed off: in March 1863, the Admiralty sent Sulivan to collect fossils on the banks of the Río Gallegos with his son James Y. F. Sulivan (1838/9–1901) and the naturalist Robert Oliver Cunningham (1841–1918). The specimens were sent to Thomas Henry Huxley (1825–1895). The great naturalist handed them over to Owen's successor as curator of the Royal College of Surgeons, William Henry Flower (1831–1899), who described another ungulate-like mammal, *Homalodotherium cunninghami*.

In 1877, Francisco P. Moreno (1852–1919; Fig. 1.3b) explored Patagonia and collected the first fossil mammals from the Early Miocene Santa Cruz beds along the valley of the Río Santa Cruz; these specimens were described by Florentino Ameghino (Ameghino, 1887, 1889). Until the later nineteenth century, Patagonia was mostly inaccessible owing to poor transportation systems and conflicts with native peoples. The naval transport line, founded in 1880, allowed the establishment of settlements and villages, and was the sole supplier of basic necessities in the region, transporting goods, medicine, fuel, passengers, and news. Taking advantage of this new mode of travel, Florentino's brother, Carlos Ameghino (1865–1936; Fig. 1.3c), then Travelling Naturalist of the Museo de La Plata, first came to Santa Cruz in 1887. Moreno, Director of the Museo de La Plata, had sent Carlos to follow up on his earlier discoveries (1877) along the banks of Río Santa Cruz. Rusconi (1965: 58) noted that on this first trip Carlos collected more than 2000 specimens of Tertiary mammals belonging to more than 120 species, of which only a dozen had been previously known. That same year, Florentino (Ameghino, 1887), then Vice-Director of the Museo de La Plata, published on the fossils collected by Carlos. This journey initiated a remarkable series of geological and paleontological expeditions which lasted for 15 years. Extensive accounts of Carlos' trips are available in Rusconi (1965) and Vizcaíno (2011). In the succeeding decades Carlos discovered many other fossil-bearing localities spread over a wide belt extending from the Gulf of San Jorge to Tierra del Fuego, between the Atlantic coast and the Andes.

By 1890 the Ameghino brothers had become estranged from the Museo de La Plata because of differences with Moreno. On an independently financed trip between June 1, 1890 and July 20, 1891, Carlos, while returning from Puerto Gallegos to the Cordillera, explored the north bank of the Río Gallegos and several areas near its mouth. This second part of the expedition was not accidental, as the brothers knew of Sulivan's finds and had long awaited the opportunity to study the area and collect more fossils. In truth, Carlos was not particularly impressed by Sulivan's collecting area, despite Carlos' surprising discovery (for those latitudes) of the first Tertiary fossil remains of monkeys. His visit, however, resulted in the discovery of the Atlantic coast localities, which have yielded the abundant and well-preserved Early Miocene continental fossil vertebrates that were crucial to understanding the vertebrate lineages that evolved in South America during its long geographic isolation. These discoveries have inspired and influenced many paleontologists. In a letter to Florentino dated March 10, 1891 (Torcelli, 1935, Vol. 21), Carlos wrote:

> The banks of the Río Gallegos, contrary to my expectations, have not provided much, mainly because of the difficulties experienced in exploring the usually inaccessible cliffs, and I remain amazed by the discovery, many years ago now, of remains of *Homalodontotherium* [sic] and *Nesodontes*, animals very rare in these formations. However, by dint of perseverance, I have been able to recover small pieces with some regularity… (Torcelli, 1935, Vol. 21, page 12, lines 7–14)
>
> But the most interesting object collected here is a small lower jaw with teeth of an animal that I at first could not refer to any of the known animals, and that kept me puzzled until my last trip, at which point I was able to learn, not without surprise, its true significance: it is nothing less than the first known fossil remains of monkeys of the Republic… (page 12, lines 27–32)
>
> But if Gallegos has not satisfied all my hopes, I have discovered a site on the sea coast, between Coyle and Gallegos, which, by its wealth and layout, I have no hesitation to declare the most important examined so far in Patagonia, and where I collected truly superb pieces, as you will soon know. (page 13, lines 12–16)
>
> This site is located on the sea beach, facing the Indian Camp site Corrigenkaik, somewhat closer to the mouth of Coyle. The great feature of this remarkable site is that it is below the level of the sea, in an arrangement quite equal to that of Monte Hermoso, and therefore only recognizable at low tide. (page 13, lines 17–22)

Based on the letters to Florentino Ameghino (Torcelli, 1935; Vizcaíno, 2011), Carlos worked at Corriguen Aike between 1891 and 1893 on at least three and possibly four occasions.

In 1889, Florentino was replaced as the paleontologist of the Museo de La Plata by the French geologist Alcides Mercerat. For a time, Mercerat competed, though not very successfully, with Carlos at collecting fossils in Santa Cruz. Mercerat was appointed Secretary of the Museum in 1891, but left in 1892 over his own disagreements with Moreno. During the last part of his tenure, the Travelling Naturalist was Carlos V. Burmeister who, in 1891, collected Santacrucian fossils from a locality known as Monte Observación (see below). In a brief account, Burmeister (1891) noted that his collection had already been housed in the Museo de

La Plata and would be described in a later publication. In 1892, he collected fossils from a wide region between the Atlantic coast and the Cordillera and the Ríos Santa Cruz and Chalía (Burmeister, 1892; Riccardi, 2008).

The fossils collected in the Santa Cruz beds by Moreno (in 1877) and other Museo de La Plata staff (between 1887 and 1892) were published by Mercerat (1890, 1891a–f), Moreno and Mercerat (1891a, b), and F. Ameghino (1887, 1889). Many of these specimens were reviewed by Lydekker (1893, 1894). The stratigraphic context of these finds was established in detail by Mercerat (1897), who between 1892 and 1895, as researcher at the Museo Nacional de Buenos Aires, produced 10 regional profiles south of the Río Santa Cruz (Mercerat, 1896, 1897). These contributions established the proper relationship between the Santacrucian Land Mammal Age and the marine Patagonian Stage, as they are currently understood.

In letters to Florentino dated October 1892, Carlos mentioned that he had met Mercerat on the ship to Santa Cruz and that he seemed to be a competent geologist. Carlos also pointed out that he was planning to do further work at Monte Observación (see below) and Corriguen Aike to prevent Mercerat finding several specimens that he had left marked in the field during a previous effort. In a letter written at Monte Observación and dated February 1893, Carlos reported that Mercerat was wasting time in Santa Cruz. In a letter in June 1893, Florentino confirmed that Mercerat was back in La Plata; and several months later he asked Carlos about a farm that Mercerat had purchased on the Río Coyle (a farm of 7500 hectares – rather small for Patagonia – named "Pechorok-Aike"; Lenzi, 1980: 355). In March 1894, Carlos confirmed that Mercerat and his family were living at this property, but in May 1895, he reported that Mercerat had gone broke, had been in jail in Río Gallegos for swindling, and had vanished from Santa Cruz. Mercerat's fossil collection was being held by a creditor from Coyle, who was planning to sell it. We do not know what became of this collection.

As mentioned above, Florentino's timely publication of the Santa Cruz collections and, particularly, some of his novel scientific conclusions prompted William B. Scott to mount an expedition to collect fossils in the Santa Cruz beds. This was led by the so-called "King of Collectors," John B. Hatcher (1861–1904; Fig. 1.3d), then Curator of the Department of Vertebrate Paleontology at Princeton University. Three expeditions were launched between 1896 and 1899. The first one extended from March 1896 until July 1897; the second from November 1897 to November 1898; and the third from December 1898 to September 1899. About Corriguen Aike, Hatcher wrote:

> It was in the sandstones of this shelving beach, near Corriguen Aike, that we discovered the rich deposit of fossil bones mentioned above. At this point, as at most places throughout this beach, erosion has taken place along the bedding planes, so that over considerable areas the surface of the beach represents essentially the same geological horizon. At this particular locality the dark green sandstones in which the bones were imbedded bore evidence of having been deposited over the flood plain of some stream or shallow lake. On walking about over the surface at low tide, there could be seen the skulls and skeletons of those prehistoric beasts protruding from the rock in varying degrees of preservation. At one point the skull and skeleton of *Nesodon* would appear, at another might be seen the limbs or perhaps the teeth of the giant *Astrapotherium* just protruding from the rock, while a little farther on a skull and jaws of the little *Icochilus* grinned curiously, as though delighted with the prospect of being thus awakened from its long and uneventful sleep. On one hand, the muzzle of a skull of one of the larger carnivorous marsupials looked forth, with jaws fully extended and glistening teeth, the characteristic snarl of the living animal still clearly indicated, while at frequent intervals the carapace of a *Glyptodon* raised its highly sculptured shell, like a rounded dome set with miniature rosettes, just above the surface of the sandstones. Throughout eighteen years spent almost constantly in collecting fossil vertebrates, during which time I have visited most of the more important localities of the western hemisphere, I have never seen anything to approach this locality near Corriguen Aike in the wealth of genera, species and individuals. (Hatcher, 1903: page 72, lines 17–22; page 73, lines 1–19)

Princeton University's final expedition started as a collaborative effort with the American Museum of Natural History, New York, represented by paleontologist Barnum Brown (1873–1963). However, by April 1899, Hatcher left Patagonia for fieldwork in Corrientes Province (northeast of Argentina) and Paraguay. Apparently, the first part of the expedition to the west was not a complete success and Hatcher was not interested in continuing to explore the coastal localities where he had conducted so much of his previous work; Brown remained working in the east of Santa Cruz Province until January 1900 (Dingus and Norell, 2010).

Towards the end of the nineteenth century, the famous French paleontologist Albert Gaudry (1827–1908) asked André Tornouër, a young French immigrant to Argentina, to collect fossils from Patagonia for the Muséum national d'Histoire naturelle, Paris. In a letter dated June 1900, Florentino confirmed that Tornouër had made some collections from the Santa Cruz beds.

The frenzy over Santacrucian fossils had apparently subsided by the beginning of the twentieth century. In a letter dated October 1901, Florentino announced that Hatcher had returned home and was not planning to return to Patagonia, that the expedition from the museum in New York had also returned with many Santacrucian fossils, and that the Museo de La Plata had no one working in Patagonia: "*Parece que al fin se han cansado*" (It seems that they finally got tired).

Brief expeditions were led by Handel T. Martin (University of Kansas) just after the turn of the last century (1903–1904), and by Elmer Riggs (1869–1963; Field Museum of Natural History, Chicago) in the 1920s (Marshall, 1975, 1976). Martin arrived in Buenos Aires in late 1903, and traveled from Bahía Blanca to Río Gallegos in January 1904 on the steamer *Chubut* (see Martin, 1904, for a brief narrative of the expedition). His party collected fossils at Killik Aike Norte Estancia (then Felton's Estancia, about 15 km west of Río Gallegos), from the bluffs along the Río Gallegos and in the coastal flats from Cabo Buen Tiempo (Cape Fairweather) and to about 48 km farther north (thus as far as Corriguen Aike). All the specimens collected were shipped to Lawrence, Kansas. Some are still in the Paleontology Section, University of Kansas, and a smaller portion is in the Natural History Museum, London (and elsewhere).

Riggs led one expedition to Patagonia (see Riggs, 1926, 1928 for short reports) from November 1922 to May 1923. As Hatcher and Martin had done, he collected at Felton's Estancia, La Angelina Estancia, and Corriguen Aike, but also 10 miles north of Coy Inlet (= Wreck Flat or Smith's Rock Flat). His efforts produced 282 specimens, cataloged in the Field Museum, belonging to 32 mammal species (according to field determinations) and a few birds. Among these are 177 skulls, as well as a few reasonably complete skeletons (Riggs, 1928).

Most paleontological expeditions to Argentine Patagonia during the past three decades have concentrated on a few easily accessible sites, mostly on the Atlantic coast, while other localities have been neglected. In the early 1980s Rosendo Pascual (who for almost four decades acted as head of the División Paleontología Vertebrados of the Museo de La Plata) led brief forays to several Santacrucian localities. Later in the 1980s and 1990s, Miguel Soria (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"), John Fleagle (State University of New York, USA), and others made extensive collections north of Río Coyle, at Cerro Observatorio (see below for a clarification of the name of the site), among other places, where fossils are numerous but less complete than those from Corriguen Aike. Collectively, the work of these expeditions helped clarify several aspects of the systematics of these mammals and placed the geochronology of the Santa Cruz Formation on a firm footing.

Few further systematic efforts to collect here were made before the work of Adán A. Tauber (Universidad Nacional de Córdoba, Argentina). Tauber surveyed the geology of the Santa Cruz Formation south of Coy Inlet, reidentified the most productive fossil sites and levels, and made important collections (about 250 specimens, mostly housed at the Museo de Paleontología, Universidad Nacional de Córdoba, Argentina) (Tauber, 1994, 1997). In the past few years, Marcelo Tejedor (Centro Nacional Patagónico, Argentina) and Laureano González (Universidad Nacional de la Patagonia "San Juan Bosco," Argentina), among others, have conducted expeditions in the western part of Patagonia near the Andes.

Since 2003, we have undertaken the collection of over 1600 specimens, including large series of relatively complete skeletons. All belong to the Museo Regional Provincial Padre M. J. Molina of Río Gallegos (Santa Cruz Province, Argentina). On average, a team of eight people (Fig. 1.6) collected fossils for 15 to 25 days over nine field seasons from several localities situated along an approximately 50-km stretch of the Atlantic coast south of the Río Coyle (Figs. 1.1 and 1.2, and see below for location and description of localities). Virtually all identifiable specimens were collected without bias to size and taxonomic interest. While half of the crew worked recovering medium to large, articulated skeletons, the other half prospected and collected smaller specimens (Fig. 1.7).

1.3 Present environment

While more than 80% of South America lies in the tropical zone (within about 23° of the equator), the southernmost part of the continent reaches about 55° S, not far from the polar circle (~66° S). The uneven distribution of land along this latitudinal gradient and the high elevations of the Andes to the west (which act as a barrier to humid winds from the Pacific Ocean) decisively influence the varied continental landscapes. East of the Andes, tropical and subtropical forests dominate in the north, exceeding all other biomes in the diversity of their flora and fauna. Southward, this dominant biome largely gives way to tropical deciduous forests, woodlands and temperate grasslands, and these in turn are replaced south of the Río Colorado by the steppes of Patagonia that extend to the southernmost tip of continental South America. A geographic unit of just more than one million square kilometers, Patagonia borders the Andes on the west and includes the Tierra del Fuego archipelago at its southern extent. Extra-Andean Patagonia is now cold and arid, and it has been characterized as one of the windiest regions in the world: strong, dry, and westerly winds are among its characteristic climatic features, emphasizing the semi-arid or arid nature of the region. Yearly rainfall is highest in the Patagonian Andes, exceeding 2000 mm. In the central part of Patagonia, annual precipitation ranges from 125 mm in the central-east to 500 mm in the west, concentrated in the coldest months of the year (April to September). The average annual temperature is ~12 °C and annual rainfall is ~300 mm. The decrease in rainfall from west to east influences a gradient of vegetation types: forest, grassy steppe, grassy-shrublands, and steppe (Leon *et al.*, 1998). The flora is dominated by shrubs and herbs (steppe) with morphological and physiological features associated with environmental stress (Barreda and

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Fig. 1.6. Field teams who worked during the summer seasons between 2003 and 2011. a, **2003**: from left to right, (back row) Jonathan Perry, Carlos Luna, Sergio Vizcaíno, Juan Moly, Adán Tauber, (front row) Susana Bargo, Mariella Bruno, Sonia Cardozo, Mary Palacios. b, **2004**: (back row) Jorge Battini, C. Luna, J. Perry, Nick Milne, S. Vizcaíno, Richard Kay, S. Bargo, A. Tauber, (front row) Andy, Teddy and Alex Battini. c, **2005**: Leonel Acosta, Juan Fernicola, Anne Weill, S. Vizcaíno, R. Kay, Francisco Prevosti; (in front) S. Bargo. d, **2006**: F. Prevosti, S. Vizcaíno, Michael Malinzak, S. Bargo, R. Kay, J. Fernicola; (front) L. Acosta. e, **2007**: (back row) F. Prevosti, Lucas Pomi, S. Vizcaíno, S. Bargo; (front row) L. Acosta, Néstor Toledo, J. Perry, J. Fernicola. f, **2008**: (back row) Guillermo Cassini, N. Toledo, J. Fernicola; (middle row) S. Vizcaíno, S. Bargo, R. Kay; (front row) Gerry De Iuliis, L. Acosta. g, **2009**: R. Kay, S. Bargo, L. Acosta, J. Perry, S. Vizcaíno. h, **2010**: J. Perry, N. Toledo, Nahuel Muñoz, L. Acosta, J. Fernicola, R. Kay, S. Bargo, S. Vizcaíno. i, **2011**: S. Vizcaíno, N. Muñoz, J. Perry, L. Acosta, S. Bargo, J. Fernicola, Verónica Krapovickas, Laura Cruz, Siobhan Cooke.

Palazzesi, 2007). Only in western Patagonia, close to the Andes, is rainfall sufficient to allow the development of forests with a dense understory of tree ferns, vines, and shrubs.

The aridification of Patagonia is a fairly recent geological occurrence that resulted from the interplay of regional paleogeographic and tectonic events, and global paleoclimatic changes. The isolation of Antarctica from Australia and South America caused a general trend towards cooler conditions and led to the development of major ice sheets in Antarctica. Uplift of the Patagonian Andes produced an important (and still present) orographic rain shadow to the east of this mountain belt during Miocene times, causing a progressive increase in aridity (Blisniuk *et al*., 2005). All of these changes led to the expansion of a cooler and drier climate throughout the Patagonian landscape. For further information on the vegetational history of Patagonia during the Cenozoic see Barreda and Palazzesi (2007).