An overview of the dinosaur fossil record from Chile

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A B S T R A C T
In Chile, the record of dinosaurs in Jurassic and Cretaceous sediments is often restricted to footprints, with few skeletal remains. Tetanuran theropods are known in the Upper Jurassic, and bones of titanosaur sauropods in the Late Cretaceous, including partial skeletons (e.g. \textit{Atacamaititan chilensis} Kellner et al.). Also from the late Cretaceous, an ornithopod vertebra, a pair of theropod teeth and one tarsometatarsus of a gaviiform bird (\textit{Neogaeornis wetzeli} Lambrecht) have been reported. The Cenozoic fossil record comprises abundant and well-preserved marine birds from Eocene and Miocene units, with a specially abundant record of Sphenisciformes and less frequently, Procellariiformes. There is an excellent Miocene - Pliocene record of other birds such as Odontopterygiformes, including the most complete skeleton ever found of a pelagornithid, \textit{Pelagornis chilensis} Mayr and Rubilar-Rogers. Fossil birds are also known from Pliocene and Pleistocene strata. A remarkable collection of birds was discovered in lacustrine sediments of late Pleistocene age associated to human activity. The perspectives in the study of dinosaurs in Chile are promising because plenty of material stored in institutional collections is not described yet. The record of Chilean dinosaurs is relevant for understanding the dynamics and evolution of this group of terrestrial animals in the western edge of Gondwana, while Cenozoic birds from the Region may contribute to the understanding of current biogeography for instance, the effect of the emergence and establishment of the Humboldt Current.

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1. Introduction

Continental vertebrates of the Mesozoic terrestrial fauna of Chile are mainly represented by dinosaurs, with the exception of an aetosaurid from the Triassic of the Antofagasta Region, \textit{Chilensuchus forttae} Casamiquela (Casamiquela, 1980; Desojo, 2003) and another yet undetermined non-dinosaurian Ornithodoria; isolated bones of pterosaurs from the Cretaceous of the Atacama Region (Bell and Suárez, 1989; Martill et al., 2000, 2006); terrestrial crocodiles from the Aysén Region (Lio et al., 2011); and isolated fragments of turtle plates from the Cretaceous of Coquimbo Region (Casamiquela et al., 1969). All other continental vertebrates are represented by dinosaurs.

In the last two decades, knowledge of the record of dinosaurs has received much attention, not only because of the information provided about geological problems, for instance, narrowing the temporal range of continental deposits (e.g. Blanco et al., 2000), but also because of their contribution to the knowledge of the evolution of this clade in this Region of the South American continent, once part of the occidental margin of Gondwana.

Thus, for example, the rich documentation of dinosaur prints in layers of the Jurassic and lower Cretaceous (Moreno et al., 2004; Rubilar-Rogers et al., 2008; among others) allows to appreciate the wide diversity of kind and size of dinosaurs, and the faunistic successions undergone between these periods. Further, the remains of titanosaur fossils found in different points throughout northern Chile can indicate how dinosaurs were affected by geographic restrictions (transgression forming epicontinental seas and expansion of arid zones) from land emerging during the latter part of the mesozoic, and if these phenomena generated isolation such that endemism evolved with regard to other dinosaurs of South America.

During the cenozoic, the dinosaur record is much better represented temporally and in number of discoveries. In the Paleogene and Neogene, avian remains proceed from the rich marine deposits of the Atacama Region (e.g. Bahía Inglesa Formation) and Patagonia.
(Loreto, Río Turbio, and Río Baguales formations). Quaternary records of birds came mainly from lacustrine deposits of the O'Higgins Region (San Vicente de Taguatagua).

The record of cenozoic fossil birds has received great attention, with several contributions dedicated to documenting these materials (Chávez, 2007a,b; Sallaberry et al., 2008, 2010a). So far, implications of these studies include, for example, the effects of the establishment of the Humboldt Cold Marine Current System and the succession of avian faunas throughout the cenozoic in the South Pacific.

The current work presents an overview of the knowledge available about dinosaurs in Chile in recent years, updating previous work that implicitly or explicitly addressed this fauna (e.g. Biese, 1961; Salinas et al., 1991a, 1991b). As a consequence, the present review only considered the materials (Fig. 1) that are available with adequate institutional repository.

1.1. Institutional abbreviations


2. Geological setting

Several records of Mesozoic dinosaurs from Chile are known only by their mention in the literature since the materials were not figured or no hosting institution was properly given in the original publications (e.g. Biese, 1961; Salinas et al., 1991a, 1991b). As a consequence, the present review only considered the materials (Fig. 1) that are available with adequate institutional repository.

2.1. Mesozoic units

Besides the unconfirmed mention (without figures or repository information) of remains referred to Megalosauridae from early Callovian marine beds at Cerritos Bayos, northern Chile (Biese, 1961), the oldest record of dinosaurs in the country is restricted to the upper Jurassic (Salgado et al., 2008). Regrettably, most of the units of interest lack detailed stratigraphic relations, it can be directly correlated with the continental levels of the Quinchamale Formation. As a consequence, the present review only considered the materials (Fig. 1) that are available with adequate institutional repository.

2.1.1. Chacarilla Formation (Galli and Dingman, 1962)

Clastic succession conform by lower marine levels that reach a thickness of 1100 m. They were assigned by Galli and Dingman (1962) to the Oxfordian based on fossil invertebrates. The upper levels are comprised by gray-to-red sandstones that host dinosaur footprints and can be constrained to a minimal Kimmeridgian—lower Cretaceous age based on stratigraphic correlations (Charrir et al., 2007).

2.1.2. ‘Quinchamale Formation’ (sensu lato, Maksaev, 1978; Skarmeta and Marinovic, 1981)

Backarc deposits with the lower beds comprising mainly limestones, and shales of Sinemurian to Oxfordian age based on fossil invertebrates (Maksaev, 1978; Vicente, 2006). The upper levels are characterized by evaporites (Vicente, 2006), while its uppermost levels are comprised by quartzites and red, continental shales (Skarmeta and Marinovic, 1981). The Quinchamale Formation is in part equivalent to the Aquino Formation defined by Garcia (1967) as a distinctive belt extended from Sierra Moreno to Huatagondoco locality. This latter unit was dated based on ammonoids at several main localities (e.g. Quebrada Arca and Quebrada Huatagondo, among others, Vicente, 2006), indicating an Oxfordian age for the marine hosting levels that underlies the typical evaporitic beds, assigned to the early Kimmeridgian. In consequence, the age of the continental levels of the Quinchamale Formation is constrained to a maximum mid Kimmeridgian age. In Sierra Moreno, the roof of the unit is conformably overlaid by the volcanic succession Cuesta de Montecristo Volcanites (Charrier et al., 2007), that is partially equivalent to the Arca Formation (Maksaev, 1978) in the Quebrada Arca sector. The presence of dinosaur footprints in Quebrada Arca occurred on multiple layers of sandstones, associated to ripple marks and mud cracks (Rubilar-Rogers and Otero, 2008). Such structures and ichnites are consistent with those described in the upper levels of the Quinchamale Formation, and have not been observed in the volcanic facies of the overlying Cuesta de Montecristo Volcanites (Ladino et al., 1999). This is the reason why the outcrops that host the dinosaur footprints are here assigned to the upper levels of the Quinchamale Formation, and in consequence, constrained to a Kimmeridgian age.

2.1.3. El Toqui Formation (Suárez and De la Cruz, 1994; De la Cruz and Suárez, 2006)

Deposits of a marine transgression over subaerial rocks, conformed mainly by calcareous and volcanoclastic sediments deposited on high-energy shorelines (Charrier et al., 2007). The volcanoclastic levels are characterized by alternating sandstones and sedimentary breccias with some levels of tuffs and ignimbrites, which contains fragmentary bone remains of dinosaurs, as well as fossil trunks and traces. This formation was assigned to the Upper Jurassic (Tithonian) based on stratigraphic correlations and radioisotopic dates (Salgado et al., 2008). It is conformably overlaid by the marine, anoxic sediments of the Katterfeld Formation.

2.1.4. San Salvador Formation (Lira, 1989)

This unit is comprised by paralic and fine-grained continental deposits that overlie through a conformable contact to the Cerritos Bayos Formation (Biese, 1961; Baeza, 1979), and conformably underlie the Cuesta de Montecristo Volcanites. Due to its stratigraphic relations, it can be directly correlated with the continental levels of the Quinchamale Formation exposed in the northern and eastern part of Sierra Moreno, while the beds of the San Salvador Formation represent equivalent levels exposed in the southern part of Sierra Moreno (Charrier et al., 2007). This unit, Moreno et al. (2004) reported the presence of dinosaur footprints, assigned by these authors to the Kimmeridgian—lower Cretaceous. The beds with footprints appear to be consistent in facies and stratigraphic position with the upper levels of the Quinchamale Formation that host dinosaur trackways. In consequence, we propose a tentative Kimmeridgian age for the footprints of the San Salvador Formation (Moreno et al., 2004).

2.1.5. Quebrada Monardes Formation (Muzzio, 1980; Mercado, 1982)

Succession of clastic rocks, mostly reddish in color, exposed in the Precordiller of Copiapó, in the Atacama Region. The basal member is comprised by mid-to-coarse grained sandstones and silstone with cross-bedding (Suárez and Bell, 1986). It was interpreted by these authors (Suárez and Bell, 1986) as a system of braided rivers and eolic dunes with proximity to an inner lake, with several localities hosting dinosaur trackways. It overlies in conformable contact to the marine limestones of the Lautaro Formation assigned to the lower—early middle Jurassic (Segerstrom, 1968), while its roof is uncertain. Due to this, it was
assigned by Suárez and Bell (1986) to the Kimmeridgian—lower Cretaceous, while the basal member hosting dinosaur footprints (Bell and Suárez, 1989) could represent Kimmeridgian beds that are consistent with the age and facies of the backarc units of the second substage (Charrier et al., 2007) with similar ichnologic records.

2.1.6. Tolar Formation (Maksaev, 1978)
This unit is located on the west side of the Domeyko Range, Region de Antofagasta. It is comprised of well-stratified, red succession of breccias, conglomerates and sandstones. Its lower levels unconformably contact with the Early Cretaceous levels of the Arca Formation and probably with the rhyolites of the Peña Morada Formation, while its roof conformably contacts with the volcanic unit Icanche Formation, assigned to the Eocene based on radioisotopic dating (Charrier et al., 2007). The Tolar Formation is assigned to the undifferentiated Late Cretaceous based on stratigraphic correlations. This unit has yielded the type material of Atacamatitan chilensis.

2.1.7. Pajonales Formation (Harrington, 1961)
It comprises continental red sandstones and conglomerates best exposed in the homonymous ravine, on Sierra de Almeyda, Antofagasta Region. It overlies the Pular Formation (Brüggen, 1942) through an angular, erosive discordant contact, and is covered by the same kind of contact with the Guanaqueros Formation (Pino and Fuenzalida, 1988). The dinosaur remains recovered in the

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Fig. 1. Geographic map showing the distribution of localities in Chile that have yielded remains of Mesozoic Dinosauria (marked with a circle): 1) Quebrada Chacarilla. 2) Huatacondo. 3) El Abra. 4) Quebrada Arca. 5) San Salvador. 6) Pajonales. 7) Quebrada Codocedo. 8) Cerro la Isla. 9) Cerro Algarrobo. 10) Picasca. 11) Termas del Flaco. 12) Southern part of Lago General Carrera.
Pajonales Formation have been assigned to Sauropoda indet (Salinas et al., 1991b), and were found in lower levels very close to the discordant contact with the underlying unit. The age of the fossiliferous beds was assigned to the Maastrichtian based on stratigraphic correlation (Salinas et al., 1991b).

2.1.8. Hornitos Formation (Segerstrom, 1959)

Breccias and conglomerate levels in coarse sandstone matrix, including lenses of sandstones, calcareous mudstones and limestones, with discrete volcanic levels to the roof. It is assigned to the Campanian–Maastrichtian based on stratigraphic correlations (Sepúlveda and Naranjo, 1982; Charrier et al., 2007). This unit contained titanosaur bone remains (Chong, 1985).

2.1.9. Viñita Formation (Aguirre and Egert, 1965)

It is comprised mainly by andesites and volcano-sedimentary rocks with pyroclastic intercalations. It includes fossiliferous beds with dinosaur bones and continental turtles (Casamiquela et al., 1969), characterized by a reddish matrix with volcanic, well-selected clasts. Its radioisotopic dates in levels of underlying and overlying units allowed constraining the age of the Viñita Formation to the Santonian–Maastrichtian interval (Pineda and Emparrán, 2006).

2.1.10. Bajos del Flaco Formation (Klohn, 1960)

This unit is characterized by basal marine beds with fossil invertebrates (ammonoids) that allow assignation to a Tithonian age. Upper levels are comprised by near-shore, continental beds that include dinosaur trackways (Casamiquela and Fasola, 1968), presenting volcanic levels to the roof. These latter authors assigned an early Cretaceous age to the dinosaur trackways based on their relative stratigraphic position respect to lower Tithonian beds.

2.1.11. Quiriquina Formation (Biró-Bagóczky, 1982)

This unit was formalized by this author, with its type locality on the homonymous island. It is comprised by a basal conglomerate, cross-bedded yellow sandstones with conglomerate lenses, coquinoaceous horizons and green sandstones at the top that include concretionary nodules. It was originally assigned to the Campanian–Maastrichtian and later constrained to the late Maas trichtian based on biostratigraphic correlations (Stinnesbeck, 1996; Salazar et al., 2010).

2.2. Tertiary units

The Paleogene–Neogene units are the most recently studied and produced interesting and abundant avian records (Fig. 2). Like marine Eocene birds of Loreto Formation and the diverse fauna of marine birds of Bahía Inglesa Formation.

2.2.1. Estratos de Algarrobo (Gana et al., 1996)

This succession is conformed by sandstones of variable grain size and hardness, very fossiliferous, with abundant concretionary nodules in different levels. It reaches about 150 m along the coast (95 m of thickness) and overlies the strata of Quebrada Munici puldad through an erosive discordance. The roof of the unit is constrained by a granitic basement through an inferred fault. This unit was assigned to the middle-to-late Eocene based on fossil invertebrates with good chronostratigraphic resolution (Brüggen, 1915; Tavera, 1980).

2.2.2. Río Turbo Formation (Feruglio, 1938; sensu lato.; emend. Hünicken, 1955; sensu Malumián and Caramés, 1997)

This unit, originally defined in Argentina, crops out in part of southernmost Chile. This succession is comprised by sandstones, conglomerates and intercalated coquinoaceous levels. Its age is currently accepted to be middle-to-late Eocene, based on stratigraphic correlations and microfossils (Malumián and Caramés, 1997). This unit has yielded fossils of spheniscid and tentative ardeid birds (Sallaberry et al., 2010b).

2.2.3. Río Baguales Formation (Cecioni, 1956)

Fossiliferous outcrops out in the northern part of Magallanes. Its stratigraphic relationships are not completely clear, nevertheless, it is possible to recognize a thick section of marine sediments that are consistent with the original definition of the Río Baguales Formation (Cecioni, 1956), reason why these are referred to this unit. The age of the beds that host fossil birds is based on the abundant and typical Eocene associated cartilaginous fishes (Sallaberry et al., 2010b).

2.2.4. Loreto Formation (Hoffstetter et al., 1957)

It is comprised mostly by marine sediments that include abundant polyomorphs, wood remains, leaf prints, coal beds, as well as vertebrates, represented by spheniscid penguins and abundant cartilaginous fishes. The age of this unit was recently constrained to the late Eocene (Priabonian) based on vertebrates with good chronostigraphic value, paleobotany and radiometric date (U/Pb Shrimp) (Otero et al., 2012).

2.2.5. La Portada Formation (Ferraris and Di Biase, 1978)

This unit crops out in Mejillones Peninsula, Antofagasta, and is comprised by sandstones, occasional diatomites and fine conglomerates that host a rich vertebrate fauna, including bird remains. The age of this formation was assigned to the Pliocene based on microfossils and fossil invertebrates (Tschihi et al., 1988; DeVries and Vermeij, 1997), as well as radiometric dating (Marquardt et al., 2005; Cortés et al., 2007).

2.2.6. The Bahía Inglesa Formation (Rojo, 1985)

Located on the coast of Atacama Region (Rojo, 1985). It comprises phosphatic sandstones and conglomerates that overlie the Oligocene–early Miocene Gravas de Angostura unit and is discordantly covered by the Pleistocene unit of Estratos de Caldera (Marquardt et al., 2000). Also the unit is in lateral contact with fluvial deposits of the Gravas de Copiapó. Most of the fossil vertebrates come from the phosphatic “bonebed” (sensu Walsh and Naish, 2002), including an unusual abundance and diversity of pinnipeds (Walsh and Naish, 2002), cetaceans (Gustein et al., 2009) and cartilaginous fishes (Long, 1993; Suárez et al., 2004). The age of this formation is constrained to the middle Miocene–early Pliocene based on radioisotopic dates on K/Ar (Marquardt et al., 2000), and middle Miocene–late Pliocene on Sr (Achurra et al., 2009) that are consistent with the chronostatigraphic distribution of several fossil vertebrates hosted in the unit (Suárez and Marquardt, 2003). In the Bahía Inglesa Formation at least 4 localities are distinct, in order of antiquity, “Las Arenas”, “Mina Fosforita”, “El Morro”, and “Los Negros”, and “Las Arenas”, with bird remains mentioned in this work from the four units mentioned before.

2.2.7. Coquimbo Formation (Moscoso et al., 1982)

Marine terraces conformed by sandstones and conglomerates, in part phosphatic, with abundant fossil invertebrates and vertebrates (the latter including birds), exposed on the coast of north-central Chile. The age of this unit was originally assigned to the Pliocene and later constrained to the middle Miocene–early Pliocene based on fossil invertebrates (Cowiech and Frassinetti, 1990). Additional radioisotopic dates on Sr indicate 14.6 Ma for beds near the base and 2 Ma for their uppermost levels (Le Roux et al., 2005).
2.2.8. Horcón Formation (Thomas, 1958)

It is comprised almost entirely by sandstones and less frequent fine conglomerates, exposed in the coast of central Chile. Its age was assigned to the Pliocene based on fossil invertebrates (Tavera, 1960).

2.2.9. Curamallín Formation (González and Vergara, 1962)

Unit that crops out in the cordilleran part of south-central Chile. Lacustrine beds conformed by fine limolites, claystones and fine sandstones, assigned to the middle–late Miocene (Niemeyer and Muñoz, 1983). This unit has yielded bird remains in beds with radioisotopic date (K–Ar), indicating 17.5 ± 0.6 and 13.0 ± 1.6 Ma (Suárez and Emparan, 1995).

2.3. Pleistocene units

The following units are not ordered stratigraphically in formally described formations, so the term “locality” is used to refer to the deposits (Fig. 2).

2.3.1. Taguatagua

Systematic excavations were carried out since 1967. An absolute dating of 11,380 ± 320 years was obtained with Carbon14 from the level with human artifacts (Montané, 1968). Fossils of birds were found along with remains of gomphoteran crocodylomorphs, horses and human tools of archaeological interest. Although the
larger fauna has been previously recognized (e.g. Casamiquela, 1970; Casamiquela, 1976), besides minor mention in previous work, the smaller fauna has been studied only recently, comprising micromammals, amphibians (Jiménez-Huidobro et al., 2009) and birds.

2.3.2. Mocha Island

Located in the Lebu province, Biobío Region, the first paleontological and geological studies of this island were carried out by Tavera and Veyl (1958) who recognized Miocene levels and assigned them to the Ranquil Formation (García, 1968) from the nearby peninsula of Arauco, while an underlying unit was assigned to Navidad Formation. Toward the south of the island Pliocene levels were also recognized. Later studies of the invertebrate fauna were carried out by Nielsen and Frassinetti (2007) who describe that, with minor differences, the fauna of the island resembles Navidad and Ranquil formations. Finger et al. (2007) consider that Ranquil and Navidad formations are equivalent in age, sedimentology, fauna and history of deposition. The Pleistocene levels are the only in which remains of birds have been reported. These are recognized as sandstones that are found in a terrace of marine abrasion, these levels also contain much fractured remains of invertebrate shells.

2.3.3. Lower Pilauco

This paleoindian site is found inward to the “los Notros” neighborhood in the city of Osorno. Absolute dating delivers an age of 14,649 ± 382 years. Casually discovered in 1986, since 2007 systematic excavations have been carried out at this site. Initially, remains of mastodons were recovered and more recently, other large and small-sized mammals (horses, chingues, rodents) as well as insects, coprolites and plant remains (González-Guarda et al., 2008; Montero et al., 2008).

3. Jurassic

The oldest bone remains of dinosaurs in Chile correspond to materials of two theropods (Theropoda and Tetanurae indet) from the Toqui Formation (late Jurassic, Tithonian) in the Aysén Region (south Chile). These materials correspond to an appendicular skeleton composed of a right ilium (SNGM-1889), proximal end of left tibia (SNGM-1885), partial left pes, astragalus and calcaneum, distal tarsal IV, metatarsal II–IV and articulated phalanges (SNGM-1888) and distal end of right tibia (SNGM-1901) assigned to Theropoda; and dorsal vertebrae (SNGM-1894, 1898, 1900, 1903) and a partial left manus (SNGM-1887) referred to Tetanurae (Salgado et al., 2008).

Interesting assemblages of sauropod and theropod ichnites are known from the Tithonian of central Chile (Moreno and Pino, 2002; Moreno and Benton, 2005; Rubilar-Rogers, 2006) found in a coastal layer belonging to the Bafios del Flaco Formation (late Jurassic, Tithonian). Other prints have been interpreted as belonging to ornithopods including an ichnospecies Camptosaurusichnus fasolae (Casamiquela and Fasola, 1968), however, given the preservation it is difficult to evaluate this proposal and these prints have been alternatively referred as Ornithopoda indet (Rubilar-Rogers, 2003). In nearby layers, the presence of dinosaur bones has been mentioned (Salinas et al., 1991b), however, the destiny of this material is unknown and thus this information cannot be confirmed.

An assemblage of theropod prints was reported by Moreno et al. (2004) at the locality of San Salvador in the Antofagasta Region consisting of sauropod and theropod prints. The sauropod prints are narrow-gauged, a condition of sauropods with narrow hips (e.g. Diplodocimorpha). Three kinds of theropod prints are mentioned. Such association of narrow-hipped sauropods with theropods is characteristic of the Jurassic period, which is in concordance with the age proposed by Moreno et al. (2004) for the red sedimentites from the “Estación” member of the San Salvador Formation as belonging to the Kimmeridgian.

At least four trackways of narrow-hipped sauropods (aff. Brontopodus) and an isolated theropod print were reported from Quebrada Arca (Quinchamal Formation) in the Antofagasta Region (Rubilar-Rogers and Otero, 2008). These trackways were attributed to this ichnogenus for its wide-gauge trackway, step angle greater than 100°, and the absence of claw marks in the manus. The theropod is distinguished by the separation of the digits with acuminate distal ends. Several hundreds of prints were also identified from photographs taken by amateurs, in different crops of this sedimentary sequence, data that still requires systematic recopilation. These sedimentary sequences extend for several kilometers and it is possible that several dinosaur types remain yet to be found.

Biese (1961) mentions the presence of remains of a Megalosauridae in sandstones from the Tithonian of the Cerritos Bayos Formation. This finding could not be confirmed since the ultimate destiny of this material is unknown.

4. Cretaceous

In situ Cretaceous prints are documented from the Codocedo ravine, the Tambería ravine, Los Pantanos, cerros bravos and cerro La Isla (Bell and Suárez, 1989). These tridactyl prints may correspond to theropods.

Fragmentary dinosaur bones were collected from cerro La Isla. A caudal vertebra was mentioned by Bell and Suárez (1989) (identified by A.C. Milner) as belonging to an “Ignauodonid”. This would be the only reference to skeletal remains of ornithischians in Chile, however, this material is not available and its destiny is unknown, thus it is impossible to confirm this specimen’s taxonomic assignation. Also from cerro La Isla, a sauropod ulna or fibula is mentioned but as in the previous case the destiny of this important material is unknown.

In the upper Jurassic–lower Cretaceous range, great assemblages of dinosaur prints are known from the Chacarilla Formation in northern Chile.

At “site III” of the Chacarilla ravine and unusual assemblage of theropod dinosaurs is described (80% of ichnites referred to this group, the remaining 20% belonging to ornithopods) where at least two pedal morphotypes can be distinguished (Rubilar-Rogers et al., 2008).

These generally large predators which indicate these carnivores were established during the lower Cretaceous in the occidental margin of Gondwana. In other outcrops of the same ravine there are narrow and wide-gauged prints of trackways of sauropods (related to the ichnogenera Parabrontopodus and Brontopodus) as well as some trackways possibly belonging to Thyreophora. Toward the base of the Chacarilla Formation, ornithopod prints were reported that are consistent with a Cretaceous age for this formation (Blanco et al., 2000; Rubilar-Rogers et al., 2000). The prints of the Chacarilla Formation were made in a meandriform river paleoenvironment.

Tridactyl prints were reported in Huatacondo ravine by Salinas et al. (1991b), who suggested these could belong to theropods and ornithopods.

The first new species of non-avian dinosaur ever discovered in Chile A. chilensis Kellner et al. (2011) was found in the Tolar Formation. This titanosaur comprises a right femur, a proximal end of a humerus, two dorsal vertebrae, two posterior caudal vertebrae, dorsal ribs and a plate-shaped bone referred as part of a sternal plate (Kellner et al., 2011, Fig. 3). It is worth noting that the remains of A. chilensis reveal a gracile titanosaur with femur proportions different to those of titanosauruses of similar body size.

In order to establish the phylogenetic position of A. chilensis, a preliminary cladistic analysis using parsimony was performed for
this review. The data matrix used here corresponds to the one proposed by Wilson (2002), which was specifically designed to test sauropod phylogeny at the genus level. It was possible to score only nineteen characters for *A. chilensis*, out of a total of 324 characters in Wilson’s matrix (presented in Appendix). The analysis of the matrix was performed using PAUP* software version 4.0 (Swofford, 2003) with ACCTRAN as character-state optimization and unordered multistate characters. In this analysis *A. chilensis* is included as a Lithostrotia (Fig. 4), a clade that includes the most recent common ancestor of *Saltasaurus* and *Malawisaurus* and all its descendants (Upchurch et al., 2004). A heuristic search produced 21 most parsimonious trees (MPTs) with a length of 434 steps (CI = 0.6; RI = 0.8). In the strict consensus tree *A. chilensis* appears inside Lithostrotia group more closely related to *Saltasaurus* than to *Malawisaurus*, in a node that includes a politomy with Saltasauroidea, *Nemegtosaurus*, *Rapetosaurus* and *Titanosaurus Colberti*. In a posterior phylogenetic analysis Curry-Rogers (2005) proposed a more inclusive definition for Saltasauroidea, which includes genera such as *Malawisaurus*, *Rapetosaurus*, *Nemegtosaurus* and *Titanosaurus* considered non saltasauroids by Wilson (2002). However, the database of Curry-Rogers (2005) is of little help, because in the matrix there are a lot of uninformative characters, resulting in wide polytomies and low support values for titanosaur ingroups. Additionally a revision of all titanosaur taxa is beyond the purpose of the present work. A broader data set (not available at the moment) with more characters may change the hypothesis of relationships of this specimen specially in reference to Saltasauroidea. Up to the moment another specimen referred to the Lithostrotia clade is reported for the Cretaceous of the Atacama Region (SNGM-1; Rubilar-Rogers et al., in prep.), however, the scarce materials of *A. chilensis* and the geographic distance of these records (approximately more than 700 km) makes it difficult to comment on the relationship between these specimens.

An interesting fact is that in comparison with other titanosours of the same size, *A. chilensis* has slender proportions. Under this assumption we plotted measurements in different sections of the femur of saltasauroids such as *Titanosaurus falloti*, *Titanosaurus robustus*, *Saltasaurus loricatus*, *Opisthocoelicaudia skarzinsky*, *Rapetosaurus krausei*, *Alamosaurus sanjuanensis*, *Magyarosaurus dacus*, *Neuquensaurus australis* and the specimens referred to the

Fig. 3. Bones of *Atacamatitan chilensis*, so far the only new species of dinosaur discovered in Chile. A–H, dorsal vertebrae in A–B, E–F, anterior view and C–D, G–H lateral view; I–L, rib; M–N, humerus; and O–P, right femur. nc: neural channel, pl: pleurocoel, lb: lateral bulge. Scale bar equals 10 cm. Illustrations: Jocelyn Navarro.
last species MCS-5/28 and MCS-5/25 indicated as *Neuquensaurus* C and *Neuquensaurus* D (Fig. 5). In the case of *A. chilensis* the measurement of the distal condyles is only estimated, due to diagenetic distortion. In the graph it is possible to see the gracile limbs of the Chilean specimen.

The evolution of these differences may relate to geographic isolation or special environmental conditions during the Cretaceous in northern Chile, restricted to a slender continental border surrounded by epicontinental seas that were only connected to the mainland by its southern portion, a predominant condition during the Cretaceous in the north and central Chile. The evolution of these slender-limbed titanosaurs could relate to this restricted area, which could be compared with the island rule of ecological theory (e.g. Foster, 1964). This hypothesis requires a comparison with more taxa and a deeper study of geological conditions during the Upper Cretaceous in the Atacama Desert, including the dynamics of deserts in northern Chile. Slender limbs may reflect a general evolutionary trend of a lineage including the Chilean specimens. To discuss this possibility, a complete phylogenetic analysis, including some taxa suspected of dwarfism (e.g. *Magyarosaurus*) is necessary (Rubilar-Rogers, 2008).

Elements of another sauropod specimen referred to Titanosauriformes (Rubilar-Rogers, 2005) have been recovered from the same Tolar Formation which indicates the potential for further discovery of more specimens. Large-sized bones (SGO.PV. 322) were found in the Pajonales Formation (Upper Cretaceous). P. Taquet (in Salinas et al., 1991b) identified these remains as titanosaurian sauropods. Since only the diaphysis of these bones is preserved, it is impossible to identify them at a less inclusive level than Sauropoda (Rubilar-Rogers, 2003).

Several fossil remains of titanosaurian sauropods have been reported for the Viñita Formation, including the incomplete proximal portion of a right humerus, part of a left scapulo-coracoid, rib fragments, ischium fragment, the proximal portion of a metapodial bone, and an incomplete centrum of a caudal vertebra. Based on these materials Casamiquela et al. (1969) distinguish at least two kind of titanosaurs. The proximal portion of the humerus was compared and referred to the genus *Antarctosaurus* (cf. *Antarctosaurus wichmannianus*), while the scapulo-coracoid was reconsidered to be an undetermined titanosaur. Rubilar-Rogers (2003) pointed out that the affinities of the humerus fragment to *A. wichmannianus*, cannot be discussed since this element is not used in the diagnosis of this taxon (Powell, 1986). More recently, additional material has been found and described for this same site. This includes the anterior half of a large dorsal vertebra, which preserves the base of the spine and part of the neural arch (SGO.PV. 959, Vargas et al., 2000). Additionally two teeth assigned to titanosaurs were reported (Salinas and Marshall, 1991; see also Rubilar-Rogers, 2003). The distal ends are preserved which...
An interesting specimen of titanosaur was found in the Hornitos Formation comprising several axial and appendicular elements. This material is currently under study (Rubilar-Rogers et al., in prep.). Previously Chong (1985) reported a fragment of a left humerus and rib segments from the same geological unit that was identified and assigned to the Titanosauridae by Bonaparte (in Chong, 1985).

The only material of Mesozoic birds known from Chile proceeds from the Quiquiquina Formation, an isolated metatarsal referred to a species of diving bird Neogaeornis wetzeli Lambrecht (1929). Another similar element was mentioned by Oliver-Schneider (1940) found in San Vicente bay, however, it was not illustrated nor adequately described.

Salinas et al. (1991a) reported remains of a large bone from the strata of Quebrada Blanca that was attributed to a dinosaur, possibly a sauropod.

Salinas et al. (1991a) mentioned the presence of dinosaur bones and “large bones” in cerro Negro and cerro Mesa, both localities belonging to the Las Chicas Formation. However, the destiny of these materials is unknown. Thus, these may even belong to marine reptiles since they are found in predominantly marine levels.

5. Paleogene

The fossil record of Dinosauria in Chile after the K/T event is restricted to the living order Neornithes of modern birds. The fossil record of birds in Chile has been revised in several publications (Chávez, 2007a; Sallaberry et al., 2008, 2010a) but the increasing work on the group and different localities have made every review rapidly obsolete.

The fossil record of birds in the Paleogene is represented by levels strictly of middle to late Eocene age from central Chile (Fm. Algar-robo) and best represented in southernmost Chile (with three localities) (Sallaberry et al., 2010b; Yury-Yáñez et al., in press), contrary to the previous assumption that Paleogene marine vertebrate-bearing strata were absent in the Chilean record (Clarke et al., 2003; Chávez, 2007a).

Paleogene fossil birds are almost entirely restricted to the order Sphenisciformes (penguins), marine diving birds exclusively from the Southern Hemisphere, which lost their ability to fly. Because of their heavy bones, and their high colonial concentrations, is one of the best represented marine vertebrates during the Cenozoic (de la Cruz, 2007). Also the record of aquatic birds attributed to Ardeidae and a record of a supposed marine bird is considered in the currently understudied Chilean Paleogene (Sallaberry et al., 2010b; Yury-Yáñez et al., in press).

Paleogene fossil penguins are recognized from three localities in Magallanes Region, southernmost Chile, described in Sallaberry et al. (2010b): Río de Las Minas (Loreto Formation Hoffstetter et al., 1957), Sierra Dorotea (Río Turbio Formation Feruglio, 1938; sensu lato; emend. Hünicken, 1955; sensu Malumíán and Caramés, 1997), and Sierra Baguales (Río Baguales Formation, Cecioni, 1956).

In these formations, fossil penguins are represented by two fragments: an ungual phalanx, and a tarsometatarsus in Río de las Minas. Even though the tarsometatarsus is very diagnostic in penguin taxonomy, the poor preservation of this fossil does not allow a more accurate designation. However, the high level of fusion of the metatarsals is considered a common feature of Paleogene penguins, not shared by the crown group Spheniscidae (Göhlich, 2007) that comprises the extant species and dates back to the middle Miocene. The ungual phalanx also is considered similar to one described from the late Eocene of Seymour Island, Antarctica (fig. 19i–j; Jadwiszczak, 2006a). Sierra Baguales represents the poorest record of fossil penguins: two heavily eroded fragments of humeri which are recognized by the flattened cross section that is characteristic of penguins.

![Figure 5. Charts showing femur width in different specimens of titanosaurs (n = 1 for each species, except Neuquensaurus C and D). A, ratio between the width at midshaft and total length in natural logarithmic scale. B, width of femur across the shaft: 1) width of condyles, 2) width at the distal quarter, 3) width at the midshaft, 4) width at proximal quarter, 5) width at the lateral bulge level, 6) width at femoral head level. Note that the Chilean species (A. chilensis) show low values of width/length ratio (below) and greater relative length than width values (above).](image-url)
In contrast, Sierra Dorotea yields the largest amount of fossil penguins with seven remains, including one that can be assigned at genus level as *Palaeeudyptes*. This genus represents one of the most widespread fossil penguins from the Paleogene being registered in Australia, New Zealand, and Antarctica (besides Chile). Jadwiszczak (2011) proposed it to be congeneric with the endemic penguin fossils from southern Peru, such as, *Injayacu* or *Icadyptes* (Clarke et al., 2007; 2010). More recently it has been proposed that both genera of giant penguins, *Anthropornis* and *Palaeeudyptes* from the Eocene of Antarctica should be considered monospecific (Jadwiszczak and Mörs, 2011) and not two separate species.

Highly abundant in the marine La Meseta Formation from Seymour Island are the fossils of penguins. Assignations of bones different to the tarsometatarsus, the most diagnostic element of Eocene penguins (Myrcha et al., 2002) were based on dubious criteria, such as, size (Jadwiszczak, 2006b) highly criticized (Tambussi et al., 2006). The finding of articulated skeletons of *Palaeeudyptes gunnari* allows correlating bones for which taxonomical criteria were problematic such as the humerus (Acosta-Hospitaleche and Reguero, 2010). In the light of the new data it is being reassigned to *Palaeospheniscus* from the Coquimbo Formation (Acosta-Hospitaleche et al., 2006a). This extinct genus is considered in the present of the species *S. humboldti* described from the late Miocene of Chile (Soto-Acuña et al., 2008). Records from Bahía Inglesa Formation assigned to Argentinean genera (such as *Paraptenodytes* or *Palaeospheniscus*) were reassigned to extinct taxa, particularly cranial remains. The taxonomical problem of Miocene Chilean penguins have been discussed elsewhere, and here we will only be considering recent assignments accepted in previous reviews, in which all cranial and appendicular remains (with the exceptions listed above) are restricted to extant genera of the crown group (Chávez, 2007a; b; Acosta-Hospitaleche and Canto, 2005; Acosta-Hospitaleche and Canto, 2007; Acosta-Hospitaleche et al., 2006a; 2008).

Palaeeudyptes from southern Peru, such as, *Injayacu* and *Icadyptes* *Anthropornis* are both recovered from different levels of the Bahía Inglesa Formation. *P. calderensis* was recovered from late Miocene levels of phosphatic deposits and comprises a species in the size range of the extant members of the genera. *P. grandis* is a large sized extinct species that was recovered from Pliocene levels of the Bahía Inglesa Formation near the size of the extant king penguin (*Aptenodytes forsteri*). From the late Miocene levels of Bahía Inglesa Formation there are records belonging to the extant genus *Spheniscus* and characterized by their big size. *Spheniscus urbanis* and *Spheniscus magellanicus* are represented by several neurocranial, an isolated rostrum and appendicular bones (Soto-Acuña et al., 2008; Chávez, 2007c, 2006). Only *S. urbanis* is known from associated skeletons from the levels of “El Morro” locality from the Bahía Inglesa Formation (Yury-Yáñez et al., 2009) and is also represented (by cranial remains) in the Chañaral de Aceituno locality from the Coquimbo Formation (Chávez, 2005). Besides Spheniscidae, seven other families of Neornithes are known from the Chilean Neogene fossil record: Diomedeidae, Procellariidae, Phalacrocoracidae, Sulidae, Anhingidae, Falconidae and Pelagornithidae. The order Procellariformes is the second best represented in Bahía Inglesa Formation (after penguins) and comprises two families. Diomedeidae (mollymawks or albatrosses) is known from associated skeletons from the levels of “El Morro” locality from the Bahía Inglesa Formation (Yury-Yáñez et al., 2009) and is also represented (by cranial remains) in the Chañaral de Aceituno locality from the Coquimbo Formation (Chávez, 2005). The diversity of sulids (also exclusively from Bahía Inglesa Formation) comprises big sized forms with affinities to known
species in Pisco Formation (Peru), and two other size classes, all recognized as belonging to the genus Sula. Three forms of Sulididae are known (Walsh and Hume, 2001; Chávez and Stucchi, 2006; Soto-Acuña et al., 2009) Sula cf. variegata, Sula magnu and Sula cf. sulita. S. magna should be considered the best represented based in cranial remains. Other family, Phalacrocoracidae, is based on appendicular bones that were described by Walsh and Hume (2001).

With the Neogene marine avian fauna, the Pelagornithidae is the most outstanding bird family, typically known from Paleogene and Neogene levels from every continent. Until now, in Chile, it is only recognized from the late Miocene of Bahía Inglesa Formation based on several isolated remains and the complete articulated skeleton of Pelagornis chilensis, which Mayr and Rubilar-Rogers (2010) considered as the bird with the largest well established wingspan, within both living and extinct birds (Fig. 6). This specimen is also important due to its exquisite preservation, allowing cranial—postcranial correlations which were impossible until this finding. Based on Mayr and Rubilar-Rogers (2010), it is highly probable that all Bahía Inglesa Formation material (several isolated bones) belong to the genus Pelagornis, coinciding with earlier identifications (Chávez et al., 2007).

Undescribed fossil birds from the Pliocene of the Horcón Formation have been mentioned (Carrillo-Bricheño et al., 2011) as Charadriiformes, Sphenisciformes and Phalacrocoracidae, but at least one fossil of Spheniscus from this unit is recognized at the genus level (Yury-Yáñez et al., 2010b).

Two records of Neogene birds are ascribed to the non-marine birds, the Falconidae Milvago sp. from La Portada Formation (Emslie and Guerra Correa, 2003) and M. chilensis described as flightless and big sized snake bird (Anhingidae; Alvarenga, 1995).

7. Quaternary
A large number of unpublished materials (hundreds of isolated specimens) have been recovered from the Pleistocene of San Vicente de Taguatagua, mainly from plaster jackets of vertebrate remains recovered by Lautaro Núñez and Rodolfo Casamiúquila in the 1980’s. These comprise well-preserved and diagnostic remains that will allow determining temporal variation in the taxa composition of the zone from the Pleistocene to present.

Bird remains have also been found at the Pleistocene locality of Pilauco Bajo, in the city of Osorno which have been informally mentioned and are currently under study (Montero et al., 2008). The collection of the department of Geology of the University of Chile houses undetermined fragments from the Pleistocene of Mocha Island of penguins of similar size to the modern genus Spheniscus that were collected by Tavera and Veyl in 1958, but remain unstudied.

8. Conclusions and perspectives
No dinosaur remains have been recorded from the Triassic period in Chile. However, this trend may be more related to the lack of systematic field work rather than the absence of such remains. The Triassic outcrops of the strata of El Bordo, in the Antofagasta Region, are auspicious since they consist of a sequence of lacustrine deposits where two forms of non-dinosaurian archosaurs have been found. Projected prospection of such outcrops should be a priority because of the great importance that these levels represent for understanding the evolutionary history of dinosaurs.

For now, Jurassic dinosaurs are scarcely represented. The discovery of theropod skeletons in the Aysen Region and the deposits of dinosaur footprints from the Antofagasta Region are promising. Doubtless, more material of theropod dinosaurs can be recovered from the strata of “El Toqui” and possibly new prints will be documented in quebrada Arca.

Cretaceous deposits have delivered a very abundant record of dinosaur prints that allow us to know about the fauna of the time despite the absence of skeletal remains. Some formations of this period overlie Jurassic deposits, such that it becomes possible to understand changes in faunal composition across these periods. Additionally, the titanosaurs represent the best-documented non-avian dinosaurs in Chile. Doubtless, new forms of these dinosaurs will continue to be discovered in sites like La Higuera ravine in the Atacama Region, where new and more complete specimens are likely to be collected.

As mentioned above, teeth possibly belonging to a dromaeosaurid are the only cranial remains of non-avian currently known from Chile. If this identification is correct, this evidence would be the first record of this kind of dinosaur from Chile and one of the few currently known for Gondwana.

The only record of birds from the cretaceous in Chile is two isolated tarsometatarsi from the Quiriquina Formation. This material is important since it is one of the few occurrences of Mesozoic birds known for Gondwana. New field work in this formation is necessary in order to find new evidence of these birds. Until now, there is no information from Chile about other terrestrial taxa that must have co-existed with dinosaurs during the Mesozoic, such as mammals and ophidians. This fact is defined mainly by the lack of systematic search for other components of the Mesozoic biota. Reports of lizards and amphibians must be corroborated since current mentions are unclear and the destiny of these materials is unknown.

Continental Mesozoic vertebrates are very important to narrow down possible ages of continental levels (Blanco et al., 2000; Rubilar-Rogers, 2003). Thus they will continue to be a good tool for establishing biochrones of Mesozoic continental levels in Chile.
Among perspectives for research on dinosaurs and other Mesozoic continental vertebrates, an interesting problem is the degree of endemism that may have evolved in relation to the separation produced by epicontinental seas.

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Appendix

List of characters codified for *A. chilensis* based in the matrix from Wilson (2002).

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