

Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages

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Abstract

The Cretaceous terrestrial strata of the Neuquén Basin (northern Patagonia, Argentina) are described together with their tetrapod records. Six local tetrapod assemblages are identified: Amargan (Barremian–Early Aptian), Lohancuran (Late Aptian–Albian), Limayan (Cenomanian–Early Turonian), Neuquenian (Late Turonian–Coniacian), Coloradoan (Santonian–Early Campanian) and Allenian [Late Campanian–Early Maastrichtian (= Alamitense = Alamitian SALMA)]. The last of these includes records from north-eastern Patagonia.

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1. Introduction

The Neuquén Basin is perhaps the best-known sedimentary basin of Patagonia. Its Cretaceous terrestrial beds are some of the most fossiliferous and stratigraphically complete worldwide. It has received special attention since the beginning of the 20th century due to coal and oil prospecting, as well as for providing the first dinosaur remains from South America. This attention has continued increasingly in recent decades because of the abundance of Mesozoic vertebrates.

The basin is well developed in west-central Argentina and eastern Chile between 34° and 41° S. It is exposed in the Argentine territory in the provinces of Neuquén (from which it takes the name), Mendoza, Río Negro, and La Pampa (see Fig. 1). Between 34° and 37° S, it is

restricted to the cordilleran belt as a narrow N–S-elongated strip. Southwards from 37° S it broadens eastwards into an extra-Andean domain where it is known as the Neuquén Embayment (see Digregorio, 1972; Digregorio and Uliana, 1980; Legarreta and Uliana, 1991; Gulisano and Gutiérrez Pleimling, 1995). A narrow belt, however, extends northwards along the axis of the Andean Cordillera up to 31° S (San Juan Province), where it is called the Aconcagua Basin.

The Cretaceous continental beds in this region lie between marine beds of the Agrio and Jagüel formations, forming part of the Mendoza and Malargüe Groups, respectively (see Fig. 2). The lithostratigraphic units of this terrestrial interval are known, from older to younger, as the La Amarga and Lohan Cura formations, the Neuquén Group, and the Allen Formation.

In recent years, the rate of discoveries of tetrapods in these units has improved. Furthermore, geological mapping carried out by the Geological Survey of Argentina between 39°–40° S and 69°–66° 30' W

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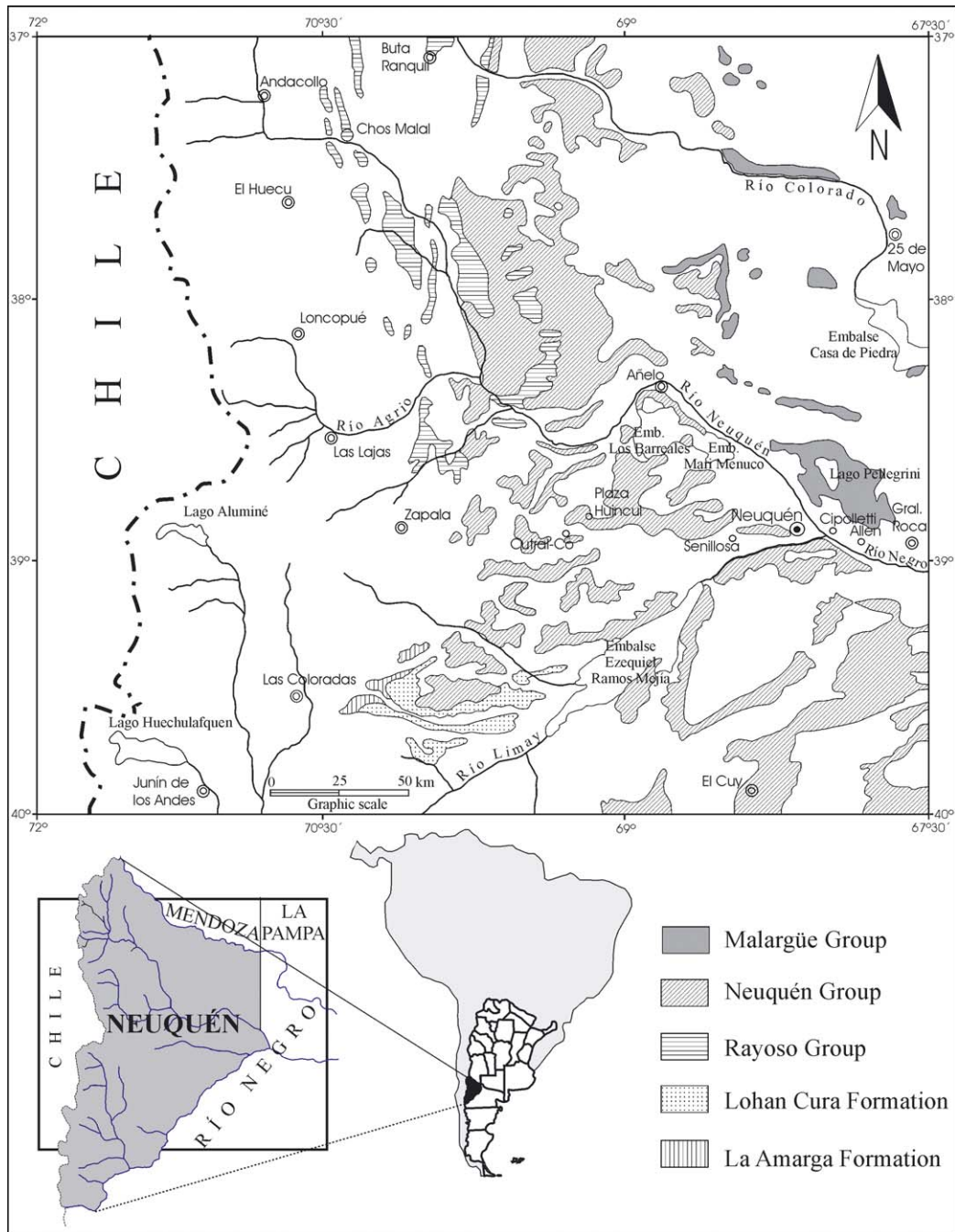


Fig. 1. Distribution of Cretaceous continental strata in west-central Argentina.

(Neuquén and Río Negro provinces) has allowed the clarification of the stratigraphic position and regional distribution of several Cretaceous terrestrial units (Leanza and Hugo, 1997; Hugo and Leanza, 2001a,b). At present, magnetic polarity information is only available for the Anacleto Formation (Dingus et al., 2000). Radioisotopic dating is still lacking for the Neuquén Group, although we are undertaking some studies. The estimated ages of each unit have been mainly obtained from the ages of the superimposed

intervals limited by regional unconformities as a result of the tectosedimentary evolution of the Neuquén Basin (Vergani et al., 1995).

The aim of this paper is to provide a brief description of the terrestrial red-bed units exposed in the southern Neuquén Basin, pointing out their main discontinuities, areal distribution, age, and tetrapod fauna. As a result, a more precise chronostratigraphic framework of the tetrapod-bearing beds is proposed and six local tetrapod assemblages are defined.

SYSTEMS	STAGES (With age boundaries in Ma)	STRATIGRAPHIC UNITS		Ma	TETRAPOD ASSEMBLAGES	
UPPER CRETACEOUS	65.0 ± 0.1	MALARGÜE GROUP (pars)	Jagüel Fm	79		
	MAASTRICHTIAN		Allen Fm			ALLENIAN
	71.3 ± 0.5	CAMPANIAN	<i>Huantraiquican unconformity</i>			
	83.5 ± 0.5	NEUQUEN GROUP	Rio Colorado Subgroup		Anacleto Fm	COLORADOAN
	85.8 ± 0.5		Rio Neuquen Subgroup		Bajo de la Carpa Fm	NEUQUENIAN
	89.0 ± 0.5		Rio Limay Subgroup		Plottier Fm	
	93.5 ± 0.2				Cenomanian	Portezuelo Fm
		TURONIAN			Cerro Lisandro Fm	
	CENOMANIAN		Huincul Fm			
			Candeleros Fm			
LOWER CRETACEOUS	98.9 ± 0.6	<i>Main Miranican unconformity</i>		98		
	ALBIAN	Lohan Cura Fm	Cullín Grande Mbr	117	LOHANCURAN	
	112.2 ± 1.1		Puesto Quiroga Mbr			
	121.0 ± 1.4	APTIAN	<i>Middle Miranican unconformity</i>			
	127.0 ± 1.6	BARREMIAN	La Amarga Fm	Piedra Parada Mbr	128	AMARGAN
				B. de Caichigüe Mbr		
				Puesto Antigüal Mbr		
	HAUTERIVIAN	<i>Initial Miranican unconformity</i>				
		Mendoza Group	Agrio Fm	Transition zone		
	VALANGINIAN		<i>Catanililican unconformity</i>		134	
	BERRIASIAN	Bajada Colorada Fm				
UPPER JURASSIC	141/?/5	Mendoza Group	Picún Leufú Fm	E. Nogueira Gr.	Limay Fm	
	TITHONIAN		Vaca Muerta Fm		Ortiz Fm	
	144.2 ± 2.6		KIMMERIDGIAN	Qda. del Sapo Fm	Pichi P. Leufú Fm	
		<i>Araucanican unconformity</i>		144		
	146					

Fig. 2. Cretaceous stratigraphy of southern Neuquén Basin and the proposed tetrapod assemblages; absolute ages from Remane (2000).

2. Materials and methods

The absolute ages followed in the present paper are those presented at the 31st International Geological

Congress held in Brazil by the IUGS (see Remane, 2000), in agreement with the proposal of the Cretaceous Subcommittee of the International Commission on Stratigraphy (ICS). The Cretaceous terrestrial

stratigraphic chart (see Fig. 2) follows that given by Leanza (1999) and Leanza and Hugo (2001).

The term ‘assemblage’ used in this paper refers to tetrapod taxa discovered in the same lithostratigraphic unit in a restricted area. Therefore, it is worth noting that our assemblages do not refer to palaeocommunities of tetrapods that lived together in a certain terrestrial ecosystem. Moreover, assemblages are not considered ‘vertebrate ages’. Because of possible local variations, this paper is restricted to the relatively well-known southern part of the Neuquén Basin. In order to characterize these assemblages we use information obtained mainly from dinosaurs, crocodyliforms and turtles, because of the still poor record of other taxa such as mammals and frogs.

It is not our aim to make a comprehensive phylogenetic review of any cited clade. However, it is necessary to specify the classificatory schemes taken into consideration for each faunal clade.

Reptilia

Chelonia—Podocnemidoidea (as in Lapparent de Broin, 2000).

Chelonia—Chelidae (as in Gaffney, 1977; Gaffney and Meylan, 1988; Broin and de la Fuente, 1993; Lapparent de Broin and de la Fuente, 2001).

Lepidosauria—Sphenodontia (as in Reynoso, 1998).

Lepidosauria—Squamata (as in Reynoso, 1998).

Lepidosauria—Squamata—Serpentes (as in Rieppel et al., 2002).

Archosauria

Crocodylomorpha—Mesoeucrocodylia—Notosuchia (as in Pol and Norell, in press).

Dinosauria—Ornithischia—Euryopoda—Stegosauria (as in Sereno, 1999).

Dinosauria—Ornithischia—Euryopoda—Ankylosauria (as in Sereno, 1999).

Dinosauria—Ornithischia—Ornithopoda—

Euiguanodontia (as in Coria and Calvo, 2002).

Dinosauria—Saurischia—Sauropoda—

Diplodocoidea (as in Wilson, 2002).

Dinosauria—Saurischia—Sauropoda—Titanosauria (as in Salgado, 2003).

Dinosauria—Saurischia—Theropoda—

Abelisauroidea (as in Coria et al., 2002).

Dinosauria—Saurischia—Theropoda—

Neotetanurae (as in Sereno, 1999).

Synapsida—Mammalia—Cladotheria (as in Portero, 1981).

In order to analyze the faunal assemblages, we use the names in the most accurate way we can. This way, because Madtsoiidae is a widely used name we keep it here but it is expressed as “Madtsoiidae”, the quotes meaning that we are referring to a paraphyletic assemblage of Gondwanan basal alethinophidian snakes (Rieppel et al., 2002), that needs further revision.

Titanosaurs have been treated recently in several publications. Some of these (e.g., Sanz et al., 1999; Curry Rogers and Forster, 2001; Wilson, 2002) avoided the use of the name Titanosauridae because of the nomen dubium status of *Titanosaurus indicus* Lydekker, 1877. However, there are no comparable names in the literature because those recently created are equivalent to diverse titanosaur ingroup clades including a different taxonomic content of titanosaurids. This way, we follow Salgado et al. (1997) and Salgado (2003) in the use of the node-based name Titanosauridae (*Epachthosaurus*, *Saltasaurus*, their most recent common ancestor and all of its descendants), meaning basically, titanosaur with procoelous caudal vertebrae.

We consider that the existence of gigantic or very small dinosaurs in certain strata and not in others is significant for the purposes of this paper. Saltosaurine titanosaur being one order of magnitude less than a basal titanosaurid such as *Argentinosaurus*, we consider the term ‘small’ for a horse-sized sauropod (e.g., *Neuquensaurus*), ‘medium’ for sauropods around 10–15 m in length (e.g., *Andesaurus*) and ‘large’ for sauropods that were around 20 m in length (e.g., *Agustinia*). The term ‘gigantic’ is only used for special cases like *Argentinosaurus*, with a total estimated length surpassing 35 m. In the case of theropods, the term small refers to sizes less than 3 m in length, medium to sizes around 4–8 m in length, and large to sizes more than 9 m in length.

3. The Cretaceous terrestrial beds and their tetrapod records

The oldest red-bed unit in the Cretaceous of the southern Neuquén Basin belongs to the Bajada Colorada Formation, which in turn is unconformably overlain by the marine Agrio Formation through the Catanillican unconformity. The Initial Miranican unconformity is located between the transition zone (gypsum evaporites and clays) of the Agrio Formation and the fluvial conglomerates of the La Amarga Formation. The Lohan Cura Formation overlies the La Amarga Formation through the Middle Miranican unconformity. The Neuquén and Malargüe groups, both forming part of the Rio-grandican cycle of Groeber (1946), constitute the Upper Cretaceous strata of the Neuquén Basin. They are separated from the previous strata by the Main Miranican unconformity.

The Neuquén Group was laid down during nearly 20 myr from the Cenomanian through to the Early Campanian. It is composed of a series of wholly continental red beds consisting of conglomerates, sandstones and claystones corresponding to fluvial, alluvial and playa lake environments. They are generally arranged in recurrent fining-upward sequences. The

Neuquén Group comprises the Candeleros, Huincul and Cerro Lisandro formations (Río Limay Subgroup), Portezuelo and Plottier formations (Río Neuquén Subgroup) and Bajo de la Carpa and Anacleto formations (Río Colorado Subgroup).

Such continental sedimentary conditions together with a large supply of coarse clastics from the west provide evidence of the final isolation of the basin from the Pacific Ocean. The Huantraiquican unconformity separates the Neuquén Group from the Malargüe Group made up of the Allen, Jagüel and Roca formations. The continental units lying between the Agrio and Jagüel formations will be described below.

3.1. La Amarga Formation

Musacchio (1970) established this terrestrial unit. Its type locality is the La Amarga Creek and the nearby northern slope of the China Muerta Hill. It unconformably overlies the transition zone of the marine Agrio Formation and is overlain in the same way by the continental Lohan Cura Formation (Fig. 3). Based on basin analysis, stratigraphical relationships and tectono-sedimentary aspects, this unit may be regarded as Barremian–Early Aptian in age (Leanza and Hugo, 1995, 1997). The total thickness of the La Amarga Formation is approximately 159 m. It is usually divided into three subunits (see Fig. 4), which from base to top are: the Puesto Antigüal, the Bañados de Caichigüe, and the Piedra Parada members (Leanza and Hugo, 1995). The Puesto Antigüal Member (28.9 m) is composed of fluvial channel sands of braided rivers with well-developed palaeosol tops. The Bañados de Caichigüe Member (20.9 m) is composed of white to yellowish lacustrine limestones alternating with black shales and greenish siltstones, from which rich ostracod and palynomorph associations were reported (Musacchio, 1970; Volkheimer, 1978). The Piedra Parada Member (109.4 m) constitutes a thick succession of light brown and reddish, fine- to medium-grained sandstones alternating with pink, reddish and brown–greenish siltstones. The palaeoenvironment corresponds to alluvial systems with well-developed fluvial channels alternating with some swamp lenses and palaeosol tops.

3.1.1. Tetrapod content

From the Puesto Antigüal Member of La Amarga Formation, the ‘spiny’ dicraeosaurid sauropod *Amargasaurus cazaui* (Salgado and Bonaparte, 1991) was found. This is characterized by a remarkable enlargement of the bifid neural spines on its cervical and dorsal vertebrae. Its most closely related species comes from the Late Jurassic of Tanzania (Janansch, 1929; Salgado and Bonaparte, 1991) and Chubut Province (P. Puerta, pers. comm. 2002). Basal diplodocoid and basal titanosauriform teeth also come from the same quarry (pers. obs.).

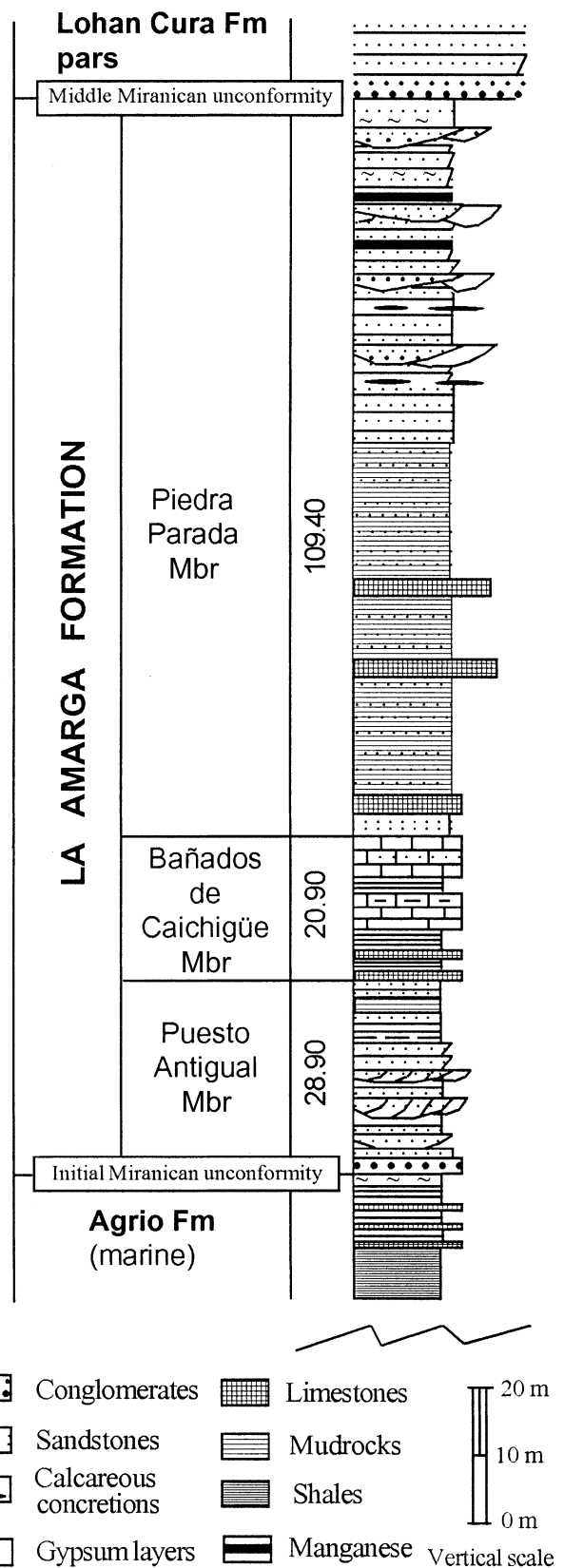


Fig. 3. Stratigraphic column of the La Amarga Formation.

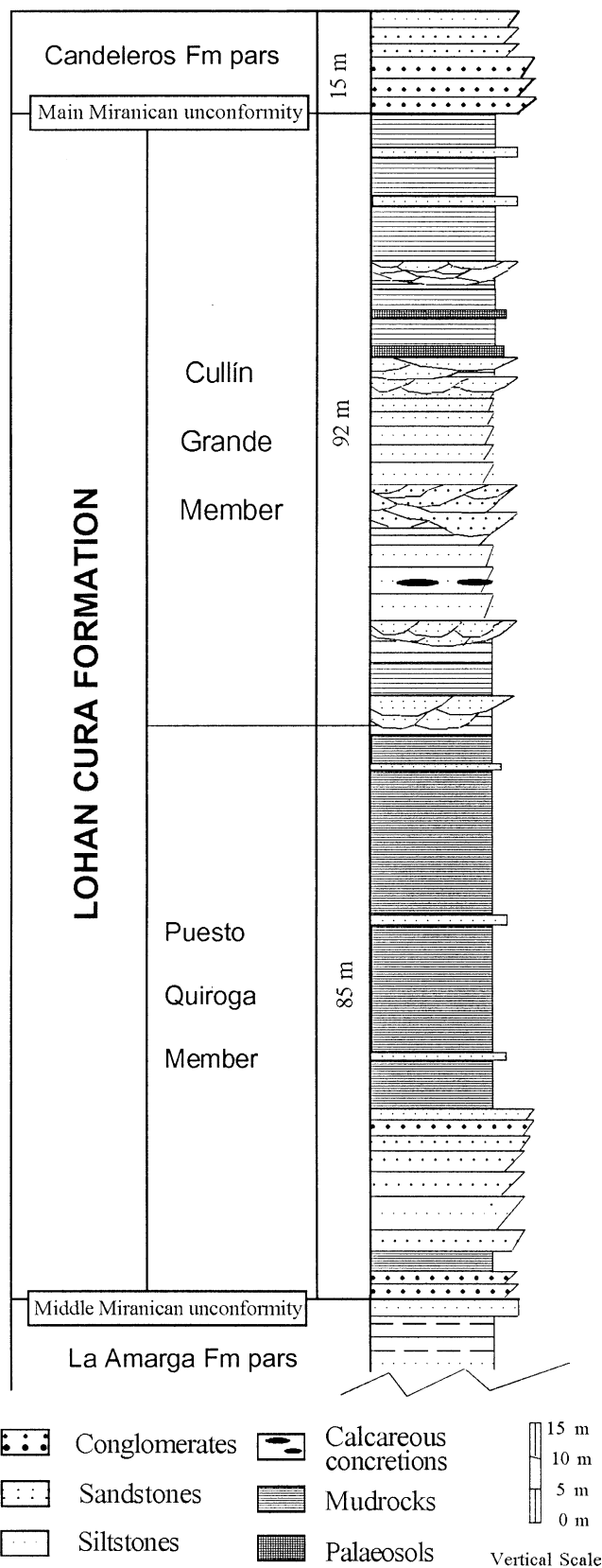


Fig. 4. Stratigraphic column of the Lohan Cura Formation.

The Puesto Antiguo Member has also yielded the abelisauroid theropod *Ligabueino andesi* (Bonaparte, 1996); fragmentary remains of the first known South American stegosaur (Bonaparte, 1996); the trematochampsid crocodyliform *Amargasuchus minor* (Chiappe, 1988) and several specimens of the cladotherian mammal *Vincelestes neuquenianus* (Bonaparte, 1986b; see also Rougier, 1993), the only mammal known for the entire Lower Cretaceous of South America.

3.2. Lohan Cura Formation

This unit was established by Leanza and Hugo (1995) for the continental deposits which unconformably overlie the La Amarga Formation. It is overlain by the Candeleros Formation (Fig. 4). The Lohan Cura Formation is widespread in the southern portion of the Neuquén Basin, extending from national road 40 along the China Muerta Creek up to the vicinity of the Limay River. Apart from the La Amarga Formation, the Lohan Cura Formation overlies the Bajada Colorada and Agrio formations through the Middle Miranican unconformity. Based on tectosedimentary aspects and field relationships, the Lohan Cura Formation can be ascribed to the Late Aptian and Albian and correlated in the central part of the basin with the Rayoso Formation (Leanza, 1999, 2003).

Some years ago this unit was mistaken for the Bajada Colorada Formation, which indeed belongs to the Mendoza Group (see above). Leanza and Hugo (1995) divided the Lohan Cura Formation (177 m) into two subunits (see Fig. 4): the Puesto Quiroga and the Cullín Grande members. The Puesto Quiroga Member (85 m) begins with a well-lithified, brown-reddish, thinning-upwards, polymictic conglomerate 4 m thick, followed by an alternation of 24 m of red and red-brownish conglomeratic sandstones and siltstones. Next 57 m of red–purple and brown–greenish shales and some intercalations of grey–greenish and light green siltstones follows. The Cullín Grande Member (92 m) shows a remarkable development of fluvial channels with high angle cross-stratification with reddish conglomeratic sandstones in alternation with brown–greenish siltstones showing poor stratification. The general trend of the sedimentation pattern is fining- and thinning-upwards and for that reason the brown and light red siltstones and claystones become dominant.

3.2.1. Tetrapod content

In the Cullín Grande Member of the Lohan Cura Formation, in the locality of Cerro Los Leones near Picún Leufú, Leanza and Hugo (1997) discovered a new fossil site of reptile bones and reported this to J. F. Bonaparte. This resulted in the description of the basal titanosaur *Agustinia ligabuei* Bonaparte, 1999 and a new, different titanosaur, the former at least displaying

notable dorsal osteoderms divided into two laminae, each of which is 0.8 m in length (see Leanza, 1999). Rebbachisaurid sauropods were recently collected from the same unit and area (L. Salgado, pers. comm. 2003), but in slightly older strata (J. Bonaparte, pers. comm. 2003). Additionally, from the Rayoso Formation, presumably the Rincón Member (equivalent to the Lohan Cura Formation), comes the rebbachisaurid sauropod *Rayososaurus agrioensis* (Bonaparte, 1996). This taxon extends the record of rebbachisaurids in Patagonia back to the Aptian (Bonaparte, 1996) while the youngest record is Late Cenomanian to Turonian (Salgado, in press) or Campanian according to others (e.g., Jacobs et al., 1993).

Turtle records in the Lohan Cura Formation include two different species of *Prochelidella* (Lapparent de Broin and de la Fuente, 1999, 2001). A short-necked chelid turtle closely related to the genus *Acanthochelys* is also present.

3.3. Neuquén Group

Red beds containing dinosaur bones have been known since early 19th century in west-central Argentina. For a long time, they were termed by Keidel (1917) as “Dinosaurier schichten” (= Estratos con Dinosaurios) or “Formación del Neuquén” (Roll, 1941). Stipanovic et al. (1968) were the first authors to use the name Neuquén Group for these strata, which are divided from base to top into Río Limay, Río Neuquén and Río Colorado subgroups (Cazau and Uliana, 1973). The Neuquén Group was deposited in a north-northwest-oriented basin nearly 800 km long and 200–350 km wide, including the southern Mendoza and eastern Neuquén regions. It was laid down between the Cenomanian and Early Campanian, and thus represents a total duration of nearly 24.9 myr. It comprises conglomerates, sandstones, siltstones, claystones and mudrocks (see Fig. 5) predominantly deposited under alluvial processes.

Although several discontinuity-bounded beds are scattered within the Neuquén Group as a result of changes in the relative base level, variable sediment supply and differential accommodation rates (Legarreta and Uliana, 1998), none of them reached the status of the main unconformities already referred to in the Cretaceous strata of the Neuquén Basin (see Fig. 2).

Anomalous behaviour in mass and heat distribution in the Earth’s mantle during the Early Cretaceous led to abnormal activity in the South Atlantic and Pacific mid-oceanic ridges. This led to a maximum spreading rate in the oceanic floors (Larson and Pitman, 1972), favouring the separation of the Gondwanan landmasses. The convergence rate of the plates increased during the Late Cretaceous, making the magmatic arc migrate eastward.

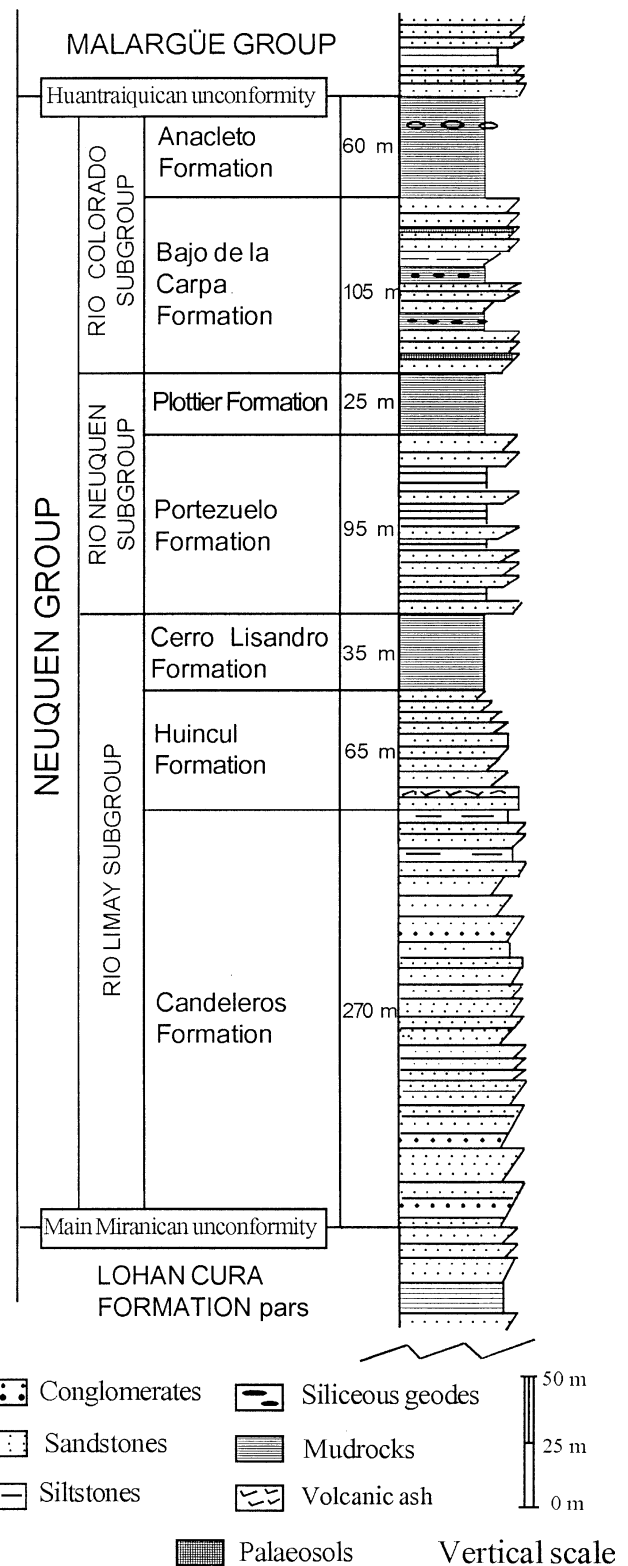


Fig. 5. Generalized stratigraphic column of the Neuquén Group.

This led to a flexural subsidence which allowed the alluvial deposition of the Neuquén Group (Legarreta and Uliana, 1998). Another factor contributing to the accumulation of these beds may have been the uplift of

the west Patagonian orogenic mountain belt. The strong deformation of strata on the eastern flank of the orogene resulted in a thrust and fold belt whose tectonic load was responsible for flexural subsidence. As a result, a foreland basin was developed allowing the accumulation of the Neuquén Group (Ramos, 1988).

3.3.1. Río Limay Subgroup

This stratigraphical unit was established by de Ferrariis (1968) and is composed of the Candeleros, Huincul and Cerro Lisandro formations, with a thickness of at least 350 m. On the basis of basin analysis, its age can be regarded as Cenomanian to Early Turonian. The Río Limay Subgroup is widespread in the southern Neuquén Basin and extends from the national road 40 eastwards to the Santa Lucía de El Cuy region, in northwestern Río Negro Province.

Candeleros Formation

This constitutes the basal unit of the Neuquén Group (Fig. 5) and was established by Keidel (in Wichmann, 1929), its type locality being Candeleros hill situated east of Cerro Lotena in southern Neuquén. It was studied regionally by many geologists including Roll (1939), Herrero Ducloux (1946), Leanza and Hugo (1997) and Hugo and Leanza (2001a) among others. Its maximum thickness is nearly 300 m. It is essentially composed of massive coarse- and medium-grained sandstones and conglomerates, violet, purple, dark red and brownish in colour, deposited in a fluvial environment under braided and meandering regimes, as well as in aeolian conditions (Spalletti and Gazzera, 1989). Sequences are arranged in a thinning- and fining-upward pattern. Palaeosols are frequent in some horizons, whereas dark-brownish siltstones and claystones are present in thin beds, some representing swamp conditions (Cazau and Uliana, 1973; Leanza and Hugo, 1997; Hugo and Leanza, 2001a). The age of the Candeleros Formation may be regarded as Early Cenomanian.

Tetrapod content. This unit has a remarkable faunal record, especially with respect to dinosaurs. Among sauropods, the taxa present include the titanosaur *Andesaurus delgadoi* Calvo and Bonaparte, 1991, and rare primitive titanosaurid sauropods from El Chocón (Calvo, 1999; Simón and Calvo, 2002) and Sierra Chata, 70 km north of Neuquén (Calvo and Salgado, 1998). Rebbachisaurid diplodocoids, such as '*Rayosaurus tessonei*' (Calvo and Salgado, 1995), and a closely related form (Apesteguía et al., 2001; Gallina et al., 2002) are present and are rather abundant. From this unit near the El Chocón area, the giant carcharodontosaurid theropod *Giganotosaurus carolinii* Coria and Salgado, 1995 was discovered as were possible abelisauroid theropods

from a locality 34 km north of Añelo (Calvo et al., 1999) and "La Buitrera" (de Valais and Apesteguía, 2001).

A notable abundance of araripesuchid crocodyli-forms, related to Brazilian and African forms, includes *Araripesuchus patagonicus* Ortega, Gasparini, Buscalioni and Calvo, 2000; and a new form with narrow snouts, frontal nasal openings, and well-developed caniniforms, resembling the head of a fox.

Eilenodontine sphenodontian lepidosaurs (Novas et al. 1999a); "madtsoiid" snakes (Apesteguía et al., 2001), and at least two species of chelid turtles (Lapparent de Broin et al., 1997) assigned to *Procheli-della* Lapparent de Broin and de la Fuente, 2001 were also collected.

Non-reptilian vertebrates were also recorded, including cladotherian mammals (Apesteguía et al., in press), a primitive pipoid frog (Báez and Calvo, 1990) and ceratodontiform fishes (Apesteguía and Agnolin, 2002). Apart from these finds, footprints of different terrestrial reptiles have been reported (Calvo, 1989) in the bedding planes of the Candeleros Formation around Lake Ezequiel Ramos Mexía. The unit is characterized by a diverse footprint record, including titanosauriform sauropods, theropods, pterosaurs and large ornithopods (Calvo, 1991).

Huincul Formation

This unit was established by Keidel (in Wichmann, 1929) and its type locality is situated in the vicinity of Plaza Huincul from which its name is derived. It is widespread in the southern part of the Neuquén Basin in Neuquén Province to the east of national road 40, and in the vicinity of Planicie de Rentería and Santa Lucía de El Cuy regions in the Río Negro Province (Hugo and Leanza, 2001a). It conformably overlies the Candeleros Formation from which it clearly differs by its lighter green-yellowish colours, and it is overlain conformably by the red claystones and siltstones of the Cerro Lisandro Formation (Fig. 5). The thickness of the Huincul Formation varies regionally between 50 and 250 m (see Roll, 1939; Leanza and Hugo, 1997). It is composed of yellowish and greenish fine- to medium-grained (sometimes tuffaceous) sandstones. In the Cerro Policía region, a level of white tuff up to 2.5-m thick is present close to its base. The age of the Huincul Formation is probably Late Cenomanian (Hugo and Leanza, 2001a).

Tetrapod content. The most remarkable reptile from this unit is one of the largest sauropod dinosaurs of them all, the basal titanosaurid *Argentinosaurus huinculensis* Bonaparte and Coria, 1993, as well as a medium-sized titanosaurid (Calvo and Salgado, 1998) and a new gigantic and advanced titanosaurid, recently reported (Simón, 2001). Additional rebbachisaurid sauropod

specimens were also collected (Salgado et al., 1991; Calvo and Salgado, 1998; Calvo, 1999). Theropods from this unit include medium-sized abelisauroids such as *Ilokelesia aguadagrandensis* (Coria and Salgado, 2000) as well as another undetermined abelisauroid found not far from El Chocón (Novas and Bandyopadhyay, 2001; de Valais et al., 2002).

Human-sized basal euiguanodontian ornithopod dinosaurs have been reported from the Río Limay Subgroup (Coria, 1999b) and probably come from the Huincul Formation. At Las Cortaderas, 15 km south of Plaza Huincul, another iguanodontian ornithopod was found not far from an 8-m-long adult carcharodontosaurid theropod and a 5-m-long abelisaurid (Coria and Currie, 1997).

Cerro Lisandro Formation

This is the youngest unit of the Río Limay Subgroup and was first named by Herrero Ducloux (in Fossa Mancini et al., 1938). Its type locality is at Cerro Lisandro, 2.5 km northwest of Senillosa in eastern Neuquén Province. It is easily recognizable by massive red siltstones and claystones, which probably represent swamp environments (Cazau and Uliana, 1973; Leanza and Hugo, 1997; Hugo and Leanza, 2001a). It conformably overlies the yellowish sandstones of the Huincul Formation and is overlain in the same way by the sandy Portezuelo Formation (Fig. 5). Freshwater bivalves have been reported. The thickness of this unit varies between 35 and 75 m. The best exposures are located around the western foothills of the Sierra Barrosa. The age of the Cerro Lisandro Formation can be regarded as Late Cenomanian–Early Turonian (Hugo and Leanza, 2001a).

Tetrapod content. Fossil bones found in this unit belong to crocodylian and pleurodiran turtles. Freshwater bivalves (*Diplodon* spp.) were also found. In levels belonging to the Cerro Lisandro Formation at Sierra del Portezuelo, tiny ornithischian and avialan dinosaurs (Agnolin et al., in press) as well as lepisosteid scales were found. At Cerro Bayo Mesa, 30 km south of Plaza Huincul, the four specimens found of the ornithopod *Anabisetia saldiviai* Coria and Calvo, 2002 were not associated with sauropods (Coria et al., 1996) but with freshwater taxa including fishes, turtles and crocodyliforms. A small abelisauroid theropod has also recently been reported (Paulina Carabajal et al., in press).

3.3.2. *Río Neuquén Subgroup*

The Río Neuquén Subgroup was established by Cazau and Uliana (1973) and constitutes the middle part of the Neuquén Group. It is widely distributed in the southern part of the Neuquén Basin. Excellent

outcrops can be seen in the area around Sierra del Portezuelo and Sierra Barrosa (Neuquén Province) and in the Planicie de Rentería region (Río Negro Province). The subgroup embraces the sandy Portezuelo Formation below and the argillaceous Plottier Formation above. According to new regional geological studies and palaeontological records, the age of this subgroup may be Late Turonian–Coniacian (Leanza and Hugo, 1995, 1997; Hugo and Leanza, 2001a).

Portezuelo Formation

This unit was established by Keidel (in Wichmann, 1929) and its type locality is situated in the Sierra del Portezuelo region just where the railroad crosses this range. It conformably overlies the Cerro Lisandro Formation and at its top grades into the more argillaceous Plottier Formation (Fig. 5). The Portezuelo Formation displays excellent exposures around Lake Los Barreales. It is composed of yellowish and red-brownish, medium-grained sandstones and siltstones of a fluvial regime, alternating with light red claystones in a fining- and thinning-upwards sequence. A frequent feature of this unit is the presence of palaeosol tops, which indicates stable conditions through relatively long periods of time. According to Roll (1939) and Leanza and Hugo (1997), the thickness of the Portezuelo Formation varies between 95–130 m. The age of the Portezuelo Formation is Late Turonian–Early Coniacian (Hugo and Leanza, 2001a).

Tetrapod content. The palaeontological record of this unit was substantially increased in the last decade, as reported by Novas (1997a,b). One of the most remarkable theropod dinosaurs is the alvarezsaurid *Patagonykus puertai* Novas, 1996, closely related to *Alvarezsaurus calvoi* (Bajo de la Carpa Formation, Santonian of Patagonia) and *Mononykus olecranus* (Maastrichtian of Mongolia). *Unenlagia comahuensis* Novas and Puerta, 1997, a maniraptoran theropod very close to the basalmost birds, and the large coelurosaur *Megaraptor namunhuaiquii* Novas, 1997b, with sharp manual dromaeosaurid-like ungual phalanges on its hands, were also collected from this unit (see also Calvo et al., 2002). Other tetrapods of this association include another big coelurosaur (Coria et al., 2001) and a troodontid theropod (Novas et al., 1999b). Sauropods of the Portezuelo Formation include both procoelian- and amphiplatyan-tailed large titanosaurs (Salgado and Calvo, 1993; Calvo et al., 2001a,b; Calvo, 2002). Ornithopods still constitute an unknown component of the Portezuelo Formation fauna although small specimens (Porfiri and Calvo, 2002), human-sized individuals (Calvo and Porfiri, in press), and 7-m-long forms (Coria, 1999b) were reported from the Río Neuquén Subgroup, probably the Portezuelo Formation.

Crocodyliforms are rather scarce in the taxonomic list for this unit, but at least a basal mesoeucrocodylian was collected (D. Pol, pers. comm. 1998). The turtles are more diversified here than in older strata. They are represented by the chelid *Prochelidella portezuelae* de la Fuente, 2003 and the podocnemidoid *Portezueloemys patagonica* de la Fuente, 2003. These records represent the first discovery of taxa belonging to the two main groups of pleurodiran turtles (Chelidae and Pelomedusoides) in the Patagonian Upper Cretaceous. This discovery confirms the coexistence of North-Gondwanan (pelomedusoids) with South-Gondwanian (chelids) elements during the Late Turonian–Early Coniacian (de la Fuente, 2003) in north-western Patagonia.

Plottier Formation

This unit was defined by Herrero Ducloux (in Fossa Mancini et al., 1938). The type locality is north of Plottier, in the vicinity of Neuquén City airport. It conformably overlies the Portezuelo Formation with which it interfingers, and is overlain by the Bajo de la Carpa Formation (Fig. 5). The Plottier Formation is hard to distinguish in the field, the only difference from the Portezuelo Formation being the higher proportion of argillaceous content. It is composed of light red massive claystones with thin layers of pink siltstones. Its maximum thickness is nearly 25 m. Its age is regarded as Late Coniacian (Hugo and Leanza, 2001a).

Tetrapod content. Few tetrapod fossils have been recorded from this unit. Coria et al. (2001) reported the presence of some fossils from the top of the Portezuelo Formation at Sierra Barrosa. However, these discoveries were recently reassigned to the Plottier Formation (Coria and Currie, 2002). Among them are a large basal coelurosaur which adds support to the idea that a large and previously unknown basal coelurosaur radiation took place in South America by Turonian–Coniacian times (Apesteguía, 2002). A fragmentary mammal jaw and titanosaurid bones were also mentioned. Bonaparte and Gasparini (1980) recorded cf. *Antarctosaurus giganteus* from the Plottier Formation at Aguada del Caño, near Neuquén City.

3.3.3. *Río Colorado Subgroup*

The Río Colorado Subgroup was established by Cazau and Uliana (1973) and constitutes the upper third of the Neuquén Group. It is widely distributed in the southern Neuquén Basin. Excellent outcrops may be seen in the area between Neuquén City and Sierra del Portezuelo (Neuquén Province) and in the region around Planicie de Rentería (Río Negro Province). It is divided into the sandy Bajo de la Carpa Formation below and the argillaceous Anacleto Formation above. According to new regional geological studies and

palaeontological records, the age of this subgroup is considered to be Santonian–Early Campanian (Leanza, 1999; Hugo and Leanza, 2001a,b).

Bajo de la Carpa Formation

This unit, defined by Herrero Ducloux (in Fossa Mancini et al., 1938) is, together with the Candeleros Formation, one of the most homogeneous and characteristic units of the Neuquén Group. It crops out from the Sierra del Portezuelo area in south-central Neuquén to the Bajo de Santa Rosa region in the northern part of Río Negro Province (Hugo and Leanza, 2001b). It conformably overlies the Plottier Formation and is overlain in the same way by the Anacleto Formation (Fig. 5). This is the only unit of the Neuquén Group which overlies to the east the Upper Permian–Middle Triassic (or earliest Jurassic?) plutonic–volcanic basement of the North Patagonian Massif. It is composed of coarse-grained, light violet and pink sandstones of fluvial origin. Rain drops, chemical nodules, palaeosols and siliceous geodes are very abundant throughout the unit. Reddish siltstones and claystones form thin beds between the hard sandstone layers. The Bajo de la Carpa Formation may reach 105 m in thickness. According to Bonaparte (1991), the age of this unit is Santonian (see also Hugo and Leanza, 2001a).

Tetrapod content. The reptile record of this unit comprises the chicken-sized alvarezsaurid theropod *Alvarezsaurus calvoi* Bonaparte, 1991; the abelisauroid *Velocisaurus unicus* Bonaparte, 1991; the enanthiornithine bird *Neuquenornis volans* Bonaparte, 1991 and *Patagopteryx deferrariisi* Alvarenga and Bonaparte, 1992. Sauropod bones are not rare but only recently, diagnostic material was found, assigned to cf. *Lap-latasaurus* (Apesteguía and Gallina, in press).

The crocodyliform record is significant, although *Notosuchus terrestris* Woodward, 1896, whose canini-forms, tall maxilla, and fore-nasal openings give it a dog-like aspect, is by far the dominant species. There are other closely related terrestrial crocodyliforms, such as *Comahuesuchus brachybuccalis* Bonaparte, 1991, with a flat and wide snout that resembles a large toad, and also terrestrial hunters, such as the peirosaurids (Price, 1955; Bonaparte, 1991; Gasparini et al., 1991). Around Lake Los Barreales, crocodyliform remains referred to as peirosaurids such as *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández, 1991 and *Peirosaurus tommini* Price, 1955 are recorded (see Gasparini et al., 1992; Danderfer and Vera, 1992). It is uncertain whether *Cynodontosuchus rothi* Woodward, 1896, came from this unit. The Bajo de la Carpa Formation has also yielded beautifully preserved skeletons of the primitive snake *Dinilysia patagonica* Woodward, 1901. The turtles are represented by *Lomalatachelys neuquina* Lapparent de

Broin and de la Fuente, 2001, a chelid turtle closely related to *Chelus* and a podocnemidoid pleurodiran (see de la Fuente, 1993). Some nests containing small eggs ascribed to a basal avian (probably *Neuquenornis*; see Schweitzer et al., 2002) have also been recorded.

Anacleto Formation

The Anacleto Formation is the highest unit of the Neuquén Group. This formation was defined by Herrero Ducloux (in Fossa Mancini et al., 1938). Its type locality is in the Aguada de Anacleto area, located 40 km west of Neuquén City. It conformably overlies the Bajo de la Carpa Formation and is unconformably overlain by the Allen Formation, which forms part of the Malargüe Group (Fig. 5). It displays a very uniform lithology. It is composed of purple and dark red claystones with sporadic, small siliceous light blue geodes. The thickness of the Anacleto Formation varies between 60 and 90 m and its age is considered to be Early Campanian (Leanza, 1999; Dingus et al., 2000; Hugo and Leanza, 2001a,b).

Tetrapod content. From the “Huayquería occidental”, immediately to the west of Paso Córdoba (Río Negro Province), in strata belonging to the Anacleto Formation according to the field observations of Hugo and Leanza (2001a), Wichmann (1916) reported the finding of a gracile titanosaurid dinosaur later studied by von Huene (1929) who named it *Antarctosaurus wichmannianus*. Near the Cinco Saltos locality, the rather abundant saltosaurine titanosaurid *Neuquensaurus australis* (Lydekker, 1893) was recorded from beds belonging to this unit. This new generic name was given by Powell (1986, 1992) to Lydekker’s *Titanosaurus australis* because of the abundant differences between this taxon and the Indian species *Titanosaurus indicus*. Besides this, the gracile aspect of the titanosaurid *Laplataosaurus araukanikus* (von Huene, 1929) resembles Indian sauropods. Another titanosaurid closely related to the saltosaurines is *Pellegrinisaurus powelli* Salgado, 1996. A new titanosaurid was recently reported from Auca Mahuida, as well as possible embryos preserved inside its eggs (Chiappe and Coria, 2000; Chiappe and Dingus, 2001). In the Rincón de Los Sauces area, especially at Loma del Lindero (Neuquén), Cañadón Río Seco (Neuquén) and Arroyo Seco (Mendoza), very complete titanosaurids were collected (Calvo et al., 1997; González Riga, 1998, 1999b; González Riga and Calvo, 2001). At the last locality, a large, gracile titanosaurid coexisted with small, robust species. Bonaparte (1998b) listed the theropod *Abelisaurus comahuensis* Bonaparte and Novas, 1985, as coming from the Allen Formation at the Cinco Saltos locality, but this species is now considered to come from the Anacleto Formation (Heredia and Salgado, 1999). Additionally,

the new abelisaurid theropod *Aucasaurus garridoi* was reported from Auca Mahuevo (Coria and Chiappe, 2000; Chiappe and Dingus, 2001; Coria et al., 2002). A new theropod dinosaur was recorded from Loma del Lindero, Rincón de los Sauces (Calvo and González Riga, 1998) and bird icnites from Sierra Barrosa (Coria et al., 2001).

The ornithischian record includes the basal ornithopod *Gasparinisaura cincosaltensis* Coria and Salgado, 1996 (see also Salgado et al., 1997). Recently, Albino (2002) described a fragmentary lower jaw that might belong to a teiid lizard, while Goin et al. (1986) recorded a mammalian jaw.

3.4. Malargüe Group

The Malargüe Group or “Malalhueyan” of Groeber (1946) forms the upper section of the Riograndican cycle. It overlies the Neuquén Group through the Huantraiquican unconformity. From base to top it is composed of mostly fluvial and lacustrine beds (Allen Formation), followed by an Atlantic flooding episode (“Káwas Sea”; Casamiquela, 1978) represented by both clastic (Jagüel Formation) and carbonate (Roca Formation) sediments. The group ranges in age from Late Campanian to Danian. It is worth noting that the Cretaceous/Tertiary boundary in the Neuquén Basin occurs in marine sediments (i.e., the Jagüel Formation).

Allen Formation

This unit is equivalent to the “Senoniano Lacustre” (Wichmann, 1924) of northern Patagonia, but its first mention as a stratigraphic unit was by Fossa Mancini et al. (1938). Its type locality is on the left bank of the Negro River close to Paso Córdoba (see Roll, 1939). However, Uliana and Dellapé (1981) have proposed a neostatotype section at El Caracol, in the eastern part of Bajo de Añelo. For many years, the Allen Formation was regarded as the youngest unit of the Neuquén Group. Based on field evidence, Uliana (1974) and Andreis et al. (1974) later considered it as the basal unit of the Malargüe Group, lying just below the marine beds of the Middle–Upper Maastrichtian Jagüel Formation (Fig. 6). The formation is an extremely important unit as it displays a varied spectrum of continental sedimentary facies of mostly fluvial and lacustrine environments. It is widely distributed in the eastern region of Neuquén Province and in the northern part of Río Negro Province.

The formation is composed mainly of a red or yellowish lower psammitic member, a middle lacustrine section with grey–greenish shales and an upper part with gypsum, limestones and stromatolitic limestones (see Andreis et al., 1974). In the Paso Córdoba region it is up to 50 m thick. Hugo and Leanza (2001a) proposed a correlation of the basal member with the Angostura

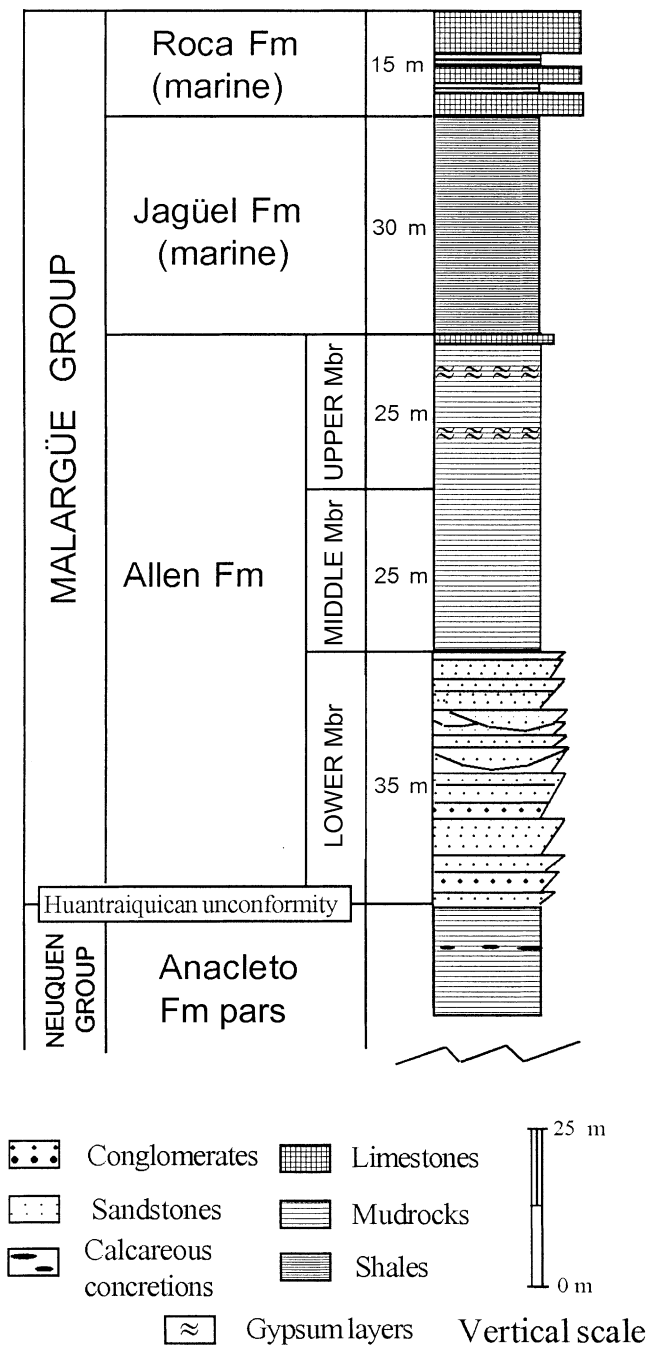


Fig. 6. Generalized stratigraphic column of the Malargüe Group.

Colorada Formation (Volkheimer, 1973) and of the middle and upper members with the Los Alamos Formation (Franchi and Sepúlveda in Bonaparte et al., 1984) of north-eastern Patagonia. Less accurate correlations with the Allen Formation could be suggested for the Loncoche, Paso del Sapo, and the base of La Colonia formations, exposed in Mendoza and Chubut provinces. The age of the Allen Formation may be Late Campanian, and it is conceivable that it may also represent the Early Maastrichtian (see Hugo and Leanza, 2001a,b), taking into account that the earliest foraminiferal records in the

overlying Jagüel Formation are of Mid Maastrichtian age (Nañez and Concheyro, 1996).

Tetrapod content. The reptile record of the Allen Formation and correlative units includes rather abundant saltasaurine titanosaurs such as *Rocasaurus muniozi* (Salgado and Calvo, 1999; Salgado and Azpilicueta, 2000), and the derived eutitanosaurian *Aeolosaurus* (Salgado and Coria, 1993; Powell, 1986). Ornithischians are an important component in this fauna, as evidenced by the findings at Salitral Moreno (Powell, 1987; Salgado and Coria, 1996). Hadrosaurid ornithomimids (i.e., *Kritosaurus australis* Bonaparte et al., 1984) are common in the Los Alamos Formation at Los Alamos, the Angostura Colorado Formation at Laguna Carri-Laufen and the Allen Formation at Salitral Moreno (Río Negro Province). They are also present in the Allen Formation of the Islas Malvinas (La Pampa Province), the La Colonia Formation at Bajada del Diablo (Chubut Province), and the Loncoche Formation at Buta Ranquil (northern Neuquén Province). An indeterminate lambeosaurinae was also collected at Salitral Moreno (Powell, 1987). Theropod dinosaurs include the highly derived abelisaurid *Carnotaurus sastrei* in the La Colonia Formation (Chubut Province), and the abelisaurid *Quilmesaurus curriei* (Coria, 2001) and a new maniraptoran theropod (Novas et al., in press), both from the Allen Formation. Although ornithomimid birds have been recovered from Salitral Moreno and Los Alamos, only those from the former locality could be assigned with certainty to the Carinatae (*Lime-navis patagonica* Clarke and Chiappe, 2001). Enantiornithes, so common in the Bajo de la Carpa (Neuquén and Río Negro) and Lecho formations (Salta) have not definitely been recovered from the Allen Formation.

Diverse crocodyliforms include basal mesoeucrocodylians and neosuchians. The turtle record shows the presence of abundant chelids and meiolaniids (see Broin and de la Fuente, 1993; Lapparent de Broin and de la Fuente, 2001; de la Fuente et al., 2001). The former is represented by new unnamed South American short and long-necked species (see Broin and de la Fuente, 1993). Among the long-necked chelids is *Yaminuechelys gasparinii* de la Fuente et al. 2001, related to the extant South American *Hydromedusa*.

Bonaparte and Novas (1985) and Bonaparte (1998a) recorded the theropod *Abelisaurus comahuensis* from the Allen Formation at Lake Pellegrini (Río Negro Province). However, this specimen is now considered to come from the Anacleto Formation (Heredia and Salgado, 1999).

4. The tetrapod assemblages

In the framework of the tectosedimentary evolution of the area studied, six tetrapod assemblages can be recognized (see Fig. 7 and Table 1). These are

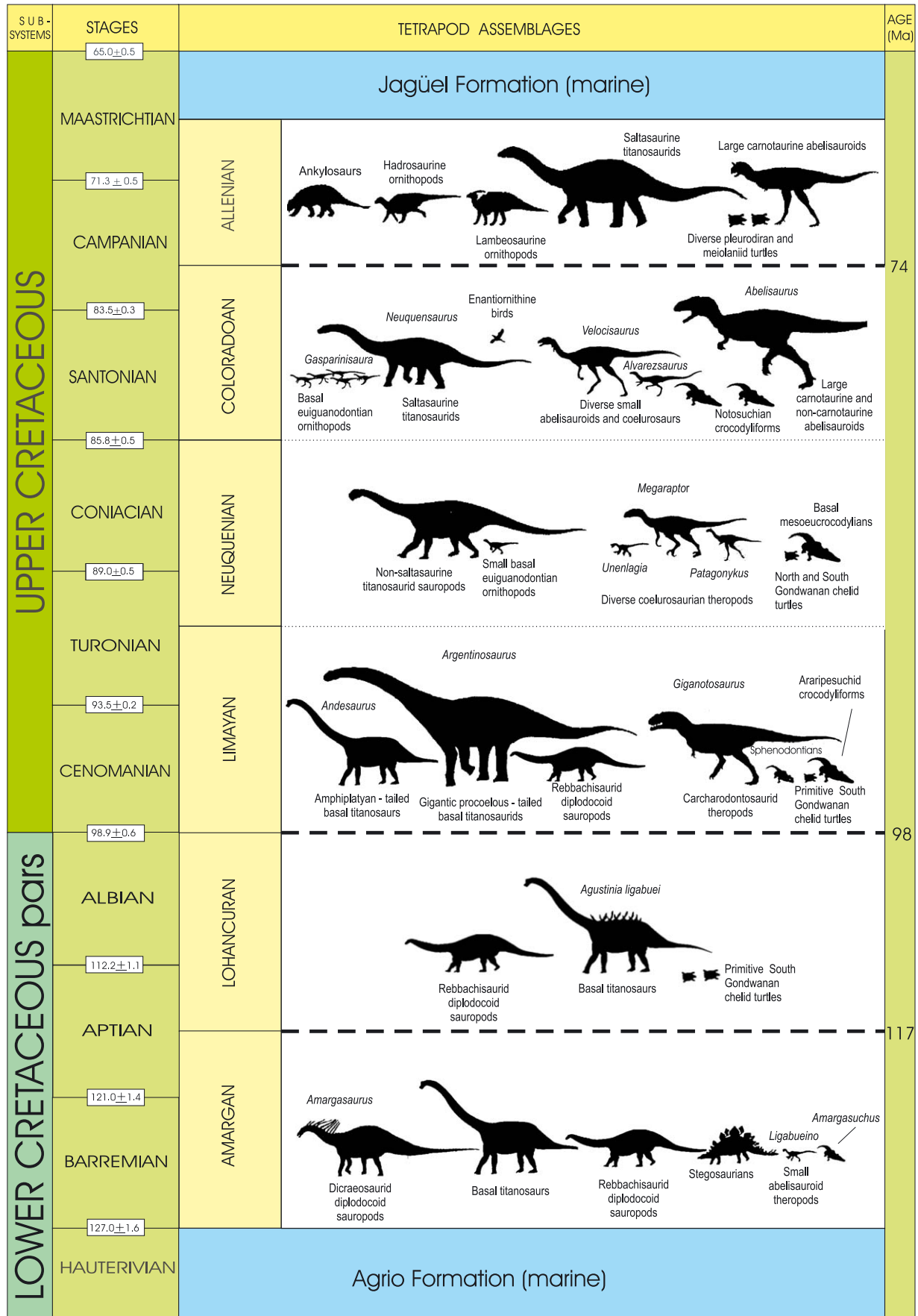


Fig. 7. Proposed tetrapod assemblages for the Cretaceous of the Neuquén Basin, Argentina. The tetrapod shadows have been taken or modified from Rich (1996), Novas (1996), Wilson and Sereno (1998) and Sereno (1999).

Table 1

Tetrapod assemblages of the Cretaceous of the Neuquén Basin

Tetrapod assemblages	Composition
<p>Amargan</p> <p>Age: Barremian–Early Aptian</p> <p>Definition: ‘Spiny’ dicraeosaurid neosauropods; rebbachisaurid diplodocoids; basal titanosauriforms; basal abelisauroid theropods; <i>Kentrosaurus</i>-like stegosaurian ornithischians.</p> <p>Main stratigraphic units: La Amarga Formation</p>	<p>Sauropoda—Dicraeosauridae—<i>Amargasaurus cazau</i> Salgado and Bonaparte, 1991.</p> <p>Sauropoda—Rebbachisauridae indet. (SA, pers. obs.).</p> <p>Sauropoda—Titanosauriformes—basal form (SA, pers. obs.).</p> <p>Theropoda—Abelisauroidea—<i>Ligabueino andesi</i> Bonaparte, 1996.</p> <p>Ornithischia—Stegosauridae indet. (Bonaparte, 1996).</p> <p>Crocodyliformes—Trematochampsidae—<i>Amargasuchus minor</i> Chiappe, 1988.</p> <p>Mammalia—Cladotheria—<i>Vincelestes neuquenianus</i> Bonaparte, 1986b.</p>
<p>Lohancuran</p> <p>Age: Late Aptian–Albian</p> <p>Definition: Large, gracile non-titanosaurid titanosaurs with broad tooth crowns, amphiplatyan entire series of caudal vertebrae and elongate osteoderms; rebbachisaurid diplodocoids (shared with Limayan); large carcharodontosaurid theropods at San Jorge Basin and isolated teeth in Neuquén Basin (shared with Limayan); small primitive chelid turtles related to <i>Acanthochelys</i> (shared with Limayan).</p> <p>Main stratigraphic units: Lohan Cura and Rayoso formations</p>	<p>Sauropoda—Titanosauria—<i>Agustinia ligabuei</i> Bonaparte, 1999.</p> <p>Sauropoda—Rebbachisauridae—<i>Rayososaurus agrioensis</i> Bonaparte, 1996; Rayoso Formation, Neuquén.</p> <p>Chelonia—Chelidae—<i>Prochelidella</i> spp.</p>
<p>Limayan</p> <p>Age: Cenomanian–Early Turonian</p> <p>Definition: Medium-sized, gracile non-titanosaurid titanosaurs with broad tooth crowns, and a large number of amphiplatyan caudal vertebrae; large to gigantic titanosaurids with procoelous caudal vertebrae, broad tooth crowns and true hyposphenes or parallelized structures on dorsal vertebrae; rebbachisaurid diplodocoid sauropods (shared with Lohancuran); abundant and large carcharodontosaurid theropods (probably shared with Lohancuran); small to medium-sized abelisauroid theropods (shared with Neuquenian); abundant medium-sized euiguanodontian ornithopods (AFNP); araripesuchid mesoeucrocodylians and rare neosuchians; large eilenodontine sphenodontians; medium-sized limbed “Madtsoiid” snakes; small South-Gondwanan chelid turtles related to <i>Acanthochelys</i> (shared with Lohancuran and Neuquenian).</p> <p>Main stratigraphic units: Candeleros, Huincul, Cerro Lisandro formations</p>	<p>Sauropoda—Titanosauria—<i>Andesaurus delgadoi</i> Calvo and Bonaparte, 1991.</p> <p>Sauropoda—Titanosauridae—<i>Argentinosaurus huinculensis</i> Bonaparte and Coria, 1993.</p> <p>Sauropoda—primitive Titanosauridae from El Chocón fauna (Calvo, 1999; Simón, 2001; Simón and Calvo, 2002).</p> <p>Sauropoda—Titanosauridae indet. from Sierra Chata (Calvo and Salgado, 1998).</p> <p>Sauropoda—Diplodocoidea—<i>Rebbachisauridae</i>—<i>Rayososaurus tessonei</i> (Calvo and Salgado, 1995) and allied (Calvo and Salgado, 1998) as well as La Buitrera rebbachisaurid (Gallina et al., 2002).</p> <p>Theropoda—Carcharodontosauridae—<i>Giganotosaurus carolinii</i> Coria and Salgado, 1995.</p> <p>Theropoda—8-m-long indet. Carcharodontosauridae from Las Cortaderas (Coria and Currie, 1997).</p> <p>Theropoda—Abelisauroidea—<i>Ilokelesia aguadagrandensis</i> Coria and Salgado, 2000.</p> <p>Theropoda—5-m-long Abelisauroidea indet. from El Chocón area (Novas and Bandyopadhyay, 2001; de Valais et al., 2002); 34 km north of Añelo (Calvo et al., 1999); a 5-m-long specimen from Las Cortaderas (Coria and Currie, 1997) and a small one from Cerro Bayo Mesa (Paulina Carabajal et al., in press).</p> <p>Theropoda—Coelurosauria indet.—(Apesteuguía et al., unpublished).</p> <p>Ornithischia—Euiguanodontia—<i>Anabisetia saldiviai</i> (Coria, 1999a; Coria and Calvo, 2002).</p> <p>Ornithischia—Euiguanodontia—cf. <i>Gasparinisaura</i> sp. (Coria, 1999a).</p> <p>Ornithischia—Euiguanodontia indet., from Cerro Bayo Mesa (Coria et al., 1996) and Las Cortaderas (Coria and Currie, 1997).</p> <p>Crocodyliformes—Mesoeucrocodylia—<i>Araripesuchus patagonicus</i> Ortega, Gasparini, Buscalioni and Calvo, 2000.</p> <p>Crocodyliformes—Mesoeucrocodylia—<i>Araripesuchus</i> sp. (Apesteuguía et al., 2001; Pol et al., 2001; Carignano et al., 2002).</p> <p>Crocodyliformes—Neosuchia indet. (Carignano et al., 2002).</p> <p>Crocodyliformes indet. (Coria et al., 1996).</p> <p>Lepidosauria—Sphenodontia—Eilenodontinae indet. (Novas et al., 1999a; Apesteuguía et al., 2001).</p> <p>“Madtsoiidae” indet. (Apesteuguía et al., 2002).</p> <p>Chelonia—Chelidae—<i>Prochelidella</i> spp. (Lapparent de Broin et al., 1997; Lapparent de Broin and de la Fuente, 1999, 2001).</p>

Neuquenian

Age: Late Turonian–Coniacian

Definition: Large and robust titanosaurid sauropods with mostly procoelous caudal vertebrae (some rare amphiplatyan), with mostly slender but also broad tooth crowns and devoid of hyposphenes on dorsal vertebrae; alvarezsaurid theropods (shared with Coloradoan); large basal coelurosaurian theropods; small South-Gondwanan pleurodiran chelids (shared with Lohancuran and Limayan); North-Gondwanan podocnemidoid pleurodirans (AFNP).

Main stratigraphic units: Portezuelo, Plottier formations

Coloradoan

Age: Santonian–Early Campanian

Definition: Small, robust and armoured saltasaurine titanosaurid sauropods (AFNP); large, gracile non-saltasaurine eutitanosaurs; large carnosaurine abelisauroid theropods (AFNP); alvarezsaurid theropods (shared with Neuquenian); velocisaurid abelisauroids; enantiornithine birds (AFNP); small-sized basal euiguanodontian ornithopods; notosuchian crocodyliforms; chelidae turtles closely related to *Chelus*; podocnemidoid turtles (shared with Neuquenian and Allenian); dinilysidae snakes; ?teiid lizards.

Main stratigraphic units: Bajo de la Carpa, Anacleto formations

Chelonia—Chelidae indet. from Cerro Bayo Mesa (Coria et al., 1996).

Mammalia—Cladotheria closely related to Dryolestoidea (Apesteguía et al., 2002, in press).

Anura—Pipoidea indet. Báez and Calvo, 1990.

Anura—? “Leptodactylidae” indet. (SA pers. obs.).

Sauropoda—Titanosauria—amphiplatyan-tailed specimens (Salgado and Calvo, 1993).

Sauropoda—gigantic indeterminate titanosaurid—(Calvo et al., 2001a,b).

Sauropoda—Titanosauridae—*Antarctosaurus giganteus* von Huene, 1929.

Sauropoda—Titanosauridae—*Mendozasaurus neguyelap* González Riga, 2003.

Theropoda—Coelurosauria—*Megaraptor namunhuaiquii* Novas, 1997b; (Calvo et al., 2002).

Theropoda—Large basal coelurosaur (Coria et al., 2001; Coria and Currie, 2002).

Theropoda—Maniraptora—? Dromaeosauridae—*Unenlagia comahuensis* Novas and Puerta, 1997.

Theropoda—Maniraptora—? Dromaeosauridae (Poblete and Calvo, in press).

Theropoda—Troodontidae indet. (Novas et al., 1999b).

Theropoda—Carcharodontosauridae (Veralli and Calvo, in press).

Theropoda—Alvarezsauridae—*Patagonykus puertai* Novas, 1996.

Ornithopoda—Small, medium-sized and up to 7-m long (Coria, 1999a; Porfiri and Calvo, 2002; Calvo and Porfiri, in press).

Mesoeucrocodylia indet. (D. Pol, pers. comm. 2003).

Chelonia—Chelidae—*Prochelidella portezuelae* de la Fuente, 2003.

Chelonia—Podocnemidoidea—*Portezueloemys patagonica* de la Fuente, 2003.

Mammalia indet. from Plottier Formation at Sierra Barrosa (Coria et al., 2001).

Sauropoda—Titanosauridae—*Antarctosaurus wichmannianus* von Huene, 1929.

Sauropoda—Titanosauridae—*Laplatasaurus araukanikus* (von Huene, 1929) Powell, 1986.

Sauropoda—titanosaurid from Auca Mahuevo, Anacleto Formation (Chiappe and Dingus, 2001).

Sauropoda—titanosaurids from Loma del Lindero, Rincón de los Sauces (Calvo et al., 1997; González Riga, 1998).

Sauropoda—titanosaurids from Cañadón Río Seco, Neuquén (González Riga and Calvo, 2001).

Sauropoda—large gracile titanosaurid from Arroyo Seco, Mendoza (González Riga, 1998, 1999a).

Sauropoda—small robust titanosaurid from Arroyo Seco, Mendoza (González Riga, 1998, 1999a).

Sauropoda—Eutitanosauria—*Pellegrinisaurus powelli* Salgado, 1996.

Sauropoda—Titanosauridae—Saltasaurinae *Neuquensaurus australis* (Lydekker, 1893) Powell, 1992.

Theropoda—Abelosauridae—*Abelisaurus comahuensis* Bonaparte and Novas, 1985.

Theropoda—Abelosauridae—Carnosaurinae—*Aucasaurus garridoi* Coria et al., 2002 (see also Coria and Chiappe, 2000; Chiappe and Dingus, 2001).

Theropoda—Abelisauroidea indet. (Calvo and González Riga, 1998).

Theropoda—Abelisauroidea—Velocisauridae—*Velocisaurus unicus* Bonaparte, 1991.

Theropoda—Alvarezsauridae—*Alvarezsaurus calvoi* Bonaparte, 1991.

Theropoda—Avialae—*Patagopteryx deferrariisi* Alvarenga and Bonaparte, 1992.

Theropoda—Avialae—Enantiornithes—*Neuquenornis volans* Bonaparte, 1991.

Theropoda—Avialae—ichnites from Sierra Barrosa (Coria et al., 2001).

Ornithopoda—*Gasparinisaura cincosaltensis* Coria and Salgado, 1996.

Crocodyliformes—Notosuchia—*Notosuchus terrestris* Woodward, 1896.

Crocodyliformes—Notosuchia—*Comahuesuchus brachybuccalis* Bonaparte, 1991.

Crocodyliformes—Baurusuchidae—*Cynodontosuchus rothi* Woodward, 1896.

Crocodyliformes—Peirosauridae—*Lomasuchus palpebrosus* Gasparini et al., 1991.

Crocodyliformes—Peirosauridae—*Peirosaurus tominni* Price, 1955.

Squamata—Teiidae? (Albino, 2002).

(continued on next page)

Table 1 (continued)

Tetrapod assemblages	Composition
<p>Allenian (= Alamitense = Alamitian SALMA)^a Age: Late Campanian–Early Maastrichtian Definition: Armoured small saltasaurine titanosaurs (shared with Coloradoan); large and advanced non-saltasaurine eutitanosaurs (SA, pers. obs. at Salitral Moreno); highly derived and large carnosaurine abelisauroid theropods (shared with Coloradoan); ornithure (AFNP) and non-ornithure ornithothoracine birds; hadrosaurid and ankylosaurian ornithischians (AFNP); high crocodyliform diversity including both mesoeucrocodylians and neosuchians; ‘Madtsoiidae’ snakes; non-eilenodontine sphenodontians (pers. obs. at Los Alamos); teiid and indeterminate iguanian lizards (pers. obs. at Los Alamos); highest Cretaceous diversity of chelid turtles; meiolaniid turtles (AFNP); dryolestoids, symmetrodonts, gondwanatheres, australosphenid and probably triconodont mammals. Main stratigraphic units: Allen, Angostura Colorado, Loncoche, Los Alamos and La Colonia formations (although the last two are not in the Neuquén Basin)</p>	<p>Alethinophidia—Dinilysidae—<i>Dinilysia patagonica</i> Woodward, 1901. Chelonia—Chelidae—<i>Lomalatachelys neuquina</i> Lapparent de Broin and de la Fuente, 2001. Chelonia—Podocnemidoidea—?Podocnemididae indet (de la Fuente, 1993; Broin and de la Fuente, 1993). Mammalia indet.—Goin et al., 1986.</p> <p>Sauropoda—Titanosauridae—<i>Aeolosaurus</i> sp. (Powell, 1986; Salgado and Coria, 1993) and related species → Angostura Colorado Formation. Sauropoda—Titanosauridae—<i>Aeolosaurus</i>-like species → Loncoche Formation (González Riga, 1999a). Sauropoda—Titanosauridae—<i>Rocasaurus muniozi</i> (Salgado and Azpilicueta, 2000). Theropoda—Abelisauridae?—<i>Quilmesaurus curriei</i> Coria, 2001. Theropoda—Abelisauridae—<i>Carnotaurus sastrei</i> Bonaparte, 1985 → La Colonia Formation. Theropoda—Avialae—Ornithothoraces indet. (Chiappe, 1992). Theropoda—Avialae—Carinatae—<i>Limenavis patagonica</i> Clarke and Chiappe, 2001. Ornithopoda—Hadrosauridae—<i>Kritosaurus australis</i> Bonaparte et al., 1984, and Hadrosaurinae indet. → Los Alamos Formation, Angostura Colorado Formation, Loncoche Formation, La Colonia Formation. Ornithopoda—Hadrosauridae—Lambeosaurinae indet. (Powell, 1987). Ankylosauria—Nodosauridae indet. (Salgado and Coria, 1996). Chelonia—Chelidae—short-necked chelids closely related to <i>Phrynos</i>, long-necked chelids related to <i>Chelus</i> and the group composed by <i>Chelodina</i> + <i>Hydromedusa</i> (Broin and de la Fuente, 1993). Chelonia—Chelidae—<i>Palaeophrynos patagonicus</i> Lapparent de Broin and de la Fuente, 2001. Chelonia—Chelidae—long-necked chelid related to <i>Hydromedusa</i> and <i>Yaminuechelys gasparinii</i> de la Fuente et al., 2001. Chelonia—Meiolaniidae—cf. <i>Niolamia</i> sp. (Broin, 1987; Broin and de la Fuente, 1993). Serpentes—‘Madtsoiidae’—<i>Alamitophis argentinus</i> Albino, 1986 → Los Alamos Formation. Serpentes—‘Madtsoiidae’—<i>Patagonophis parvus</i> Albino, 1986 → Los Alamos Formation. Serpentes—‘Madtsoiidae’—<i>Rionegrophis madtsoioides</i> Albino, 1986 → Los Alamos Formation. Serpentes—‘Madtsoiidae’ indet. → Loncoche Formation (González Riga, 1999b). Mammalia—Triconodonta—<i>Austrotriconodon mckennai</i> Bonaparte, 1986b. Mammalia—Triconodonta—<i>Austrotriconodon sepulveda</i> Bonaparte, 1992. Mammalia—Gondwanatheria—<i>Ferugliotherium windhausenii</i> Bonaparte, 1986b. Mammalia—Gondwanatheria—<i>Gondwanatherium patagonicum</i> Bonaparte, 1986b. Mammalia—Symmetrodonta—<i>Bondesius ferox</i> Bonaparte, 1990. Mammalia—Dryolestoidea—<i>Groebertherium stipanicicia</i> Bonaparte, 1986b. Mammalia—Dryolestoidea—<i>Groebertherium novasi</i> Bonaparte, 1986b. Mammalia—Dryolestoidea—<i>Leonardus cuspidatus</i> Bonaparte, 1990. Mammalia—Dryolestoidea—<i>Mesungulatum houssayi</i> Bonaparte and Soria, 1985. Mammalia—Dryolestoidea—<i>Reigitherium bunodonta</i> Bonaparte, 1990. Mammalia—Dryolestoidea—<i>Casamiquelia rionegrina</i> Bonaparte, 1990. Mammalia—Dryolestoidea—<i>Rougietherium tricuspis</i> Bonaparte, 2002. Mammalia—Dryolestoidea—<i>Alamitherium bishopi</i> Bonaparte, 2002. Anura—Pipidae indet. (Báez, 1987) → Los Alamos Formation. Anura—‘Leptodactylidae’ indet. → Los Alamos (Báez, 1987) and Loncoche Formation (González Riga, 1999b).</p>

^a The synonymy with previously proposed ‘tetrapod ages’ is only partial.

→ arrows mean that data are from units outside the Neuquén Basin sensu stricto. AFNP (all following, not previously) means that the taxon first appears in this faunal assemblage and is present in all of the following assemblages.

considered here to be tetrapod remains discovered in the same lithostratigraphic unit within a restricted area (see also Section 5).

4.1. Amargan tetrapod assemblage

The Amargan tetrapod assemblage is commonly found in rock units constrained between the transition zone of the marine Agrio Formation below and the Lohan Cura Formation above. The age of the tetrapod-bearing units is probably Barremian–Early Aptian.

4.1.1. Characterization

This assemblage is characterized by the co-occurrence of Late Pangaeian members. This implies elements of clades distributed along Pangaea during the Jurassic (e.g., basal neosauropods, basal neotetanurans, basal neoceratosaurs, eurypodans and basal iguanodontians). However, most of the taxa present are not recorded outside Gondwana in coeval deposits, suggesting some degree of incipient Gondwanan endemism. These latter include non-diplodocid diplodocoids such as dicraeosaurids (Salgado and Bonaparte, 1991) and rebbachisaurids (SA, pers. obs.); basal diplodocoids, basal titanosauriforms (teeth, pers. obs.); basal abelisauroid theropods and *Kentrosaurus*-related stegosaurs. Most of the Amargan fauna has been used to suggest certain similarities with the Late Jurassic African fauna (Bonaparte, 1986a; Salgado and Bonaparte, 1991). Although trematochampsid crocodyliforms and well-preserved cladotherian mammals were also found, the lack of taxonomic accuracy for the former or comparable records for the latter make it difficult to use them for characterizing this assemblage.

The presence in Central Patagonian basins of latest Jurassic and Early Cretaceous basal titanosauriforms (Rauhut et al., 2001; Apesteguía and Giménez, 2001) and dicraeosaurids (P. Puerta, pers. comm. 2003), makes it highly probable that both groups constituted part of the Late Pangaeian fauna, represented here by the Amargan assemblage. Following poor and conflicting data from other Gondwanan regions for the Early Cretaceous, other possible members of Gondwanan assemblages of the same age but yet to be recorded could be basal ornithomimosaurids, oviraptorosaurs, basal neoceratopsians (according to Albian records of Australia; Rich, 1996), and basal tyrannoraptorans (according to Aptian records of Brazil).

4.2. Lohancuran tetrapod assemblage

The Lohancuran tetrapod assemblage is commonly found in rock units constrained between the Middle Miranican unconformity below and the Main Miranican

unconformity above. The age of the tetrapod-bearing units can be regarded as Late Aptian–Albian.

4.2.1. Characterization

This assemblage is characterized by the co-occurrence of typical Early Gondwanan lineages. Among sauropods, this involves basal titanosaurs and rebbachisaurids. Among the former, the large non-titanosaurid basal titanosaur sauropods exhibit amphiplatyan caudal vertebrae, gracile, elongate forearms and sometimes spine-like dermal armour. The other sauropod components are basal diplodocoids such as rebbachisaurids.

Theropod dinosaurs are still unreported from this assemblage, but the presence of carcharodontosaurids and basal titanosaurians of the same age in Central Patagonia suggests that such theropods could be present. An isolated tooth shows a morphology that resembles carcharodontosaurids (SA, pers. obs.).

Crocodyliforms have not been found in the Neuquén Basin, but basal mesoeucrocodylians are present in Aptian rocks from Central Patagonia (D. Pol, pers. comm. 2003). The Lohancuran turtles are small and smooth-shelled pleurodirans (about 25 cm in length), the oldest unarguable members of Chelidae (see Lapparent de Broin and de la Fuente, 2001), closely related to the extant South American genus *Acanthochelys*.

Although the findings are scarce, the different types of dinosaurs recorded in the Neuquén Basin possess spiny projections on their backs. In the case of *Amargasaurus* (Amargan assemblage), they are expansions of bifid neural spines; in *Agustinia* they are long osteoderms, and in *Rayososaurus*, as in all rebbachisaurids, they are remarkably tall neural spines, about seven times the centrum height. The possession of these non-homologous features, especially noteworthy in sauropods, but also in Early to ‘mid’ Cretaceous African theropods and ornithopods (e.g., *Spinosaurus*, *Ouranosaurus*), suggests non-phylogenetic causes such as special devices to cope with environmental conditions. These taxa form part of the Lower Cretaceous ‘Spiny Fauna’ (Apesteguía, 2002). Furthermore, although widespread in the Jurassic of Pangaea, the only ornithischian found was a stegosaur, a group characterized by the development of bony projections on their backs.

4.3. Limayan tetrapod assemblage

The Limayan tetrapod assemblage is commonly found in rock units constrained between the Main Miranican unconformity at its base and the Portezuelo Formation above, the main units involved being the Candeleros, Huincul and Cerro Lisandro formations. The age of these rocks is probably Cenomanian–Early Turonian. The tetrapod assemblage is partially equivalent to the ‘Albian–Cenomanian association’ of Bonaparte (1998b).

4.3.1. Characterization

The assemblage is characterized by the co-occurrence of Early Gondwanan lineages. Among sauropods, the abundance of basal diplodocoids (i.e., rebbachisaurids) is characteristic. These constitute the last indubitable record of a diplodocoid sauropod (Calvo and Salgado, 1995, 1998; Salgado et al., 1991; Calvo, 1999; Apesteguía et al., 2001; Gallina et al., 2002). Their extinction or diminution in younger strata was related to the mid Cretaceous global extinction of sauropod dinosaurs (Gallina et al., 2002; Salgado, in press; Salgado et al., in press). Only a lower jaw related to the Coloradoan assemblage was proposed to be part of this group (Jacobs et al., 1993) but recent titanosaurid findings (SA, in prep.) demonstrate that purported diplodocoid features are also present in titanosaurids.

Titanosaurs also form part of this assemblage. Medium-sized non-titanosaurid titanosaurian sauropods are relatively common (Calvo and Bonaparte, 1991; Bonaparte and Coria, 1993; Calvo, 1999; Simón, 2001). The first gigantic titanosaurids also occur (Salgado et al., 1991; Calvo and Salgado, 1998; Calvo, 1999; Simón, 2001; Simón and Calvo, 2002) and show procoelous caudal vertebrae and several primitive features such as amphiplatyan tail vertebrae, hyposphene–hypantrum vertebral articulations and broad tooth crowns.

Abundant, gigantic and medium-sized basal neotetanuran theropods such as carcharodontosaurids (Coria and Salgado, 1995; Coria and Currie, 1997) also form part of this assemblage, as well as medium-sized neoceratosaurs such as abelisauroids (Coria and Currie, 1997; Calvo et al., 1999; Coria and Salgado, 2000; Novas and Bandyopadhyay, 2001; de Valais and Apesteguía, 2001; Coria, 2001; de Valais et al., 2002; Paulina Carabajal et al., in press). Small non-avian maniraptoran theropods are also present (Apesteguía et al., 2001), but until their phylogenetic position can be clarified they are not useful to characterize the assemblage. Medium-sized basal euiguanodontian ornithomorphs (Coria et al., 1996; Coria and Currie, 1997; Coria, 1999b) can also be included as part of the Limayan assemblage.

Araripesuchid basal mesoeucrocodylians are also recorded (Ortega et al., 2000), as well as some scarce and quite large unnamed putative neosuchians (Carignano et al., 2002). Among lepidosaurians is the first record from anywhere in the world of a Late Cretaceous sphenodontian lepidosaur, belonging to the large eilenodontines. Furthermore, it represents a unique Gondwanan eilenodontine sphenodontian. A new basal alethinophidian (or “madtsoiid”) snake is remarkably abundant at some levels (Novas et al., 1999a; Apesteguía et al., 2001). Small, freshwater chelid turtles closely related to *Acanthochelys* are present, but are not especially diverse (Lapparent de Broin et al., 1997;

Lapparent de Broin and de la Fuente, 1999, 2001); they also occur in the Lohancuran assemblage. Dryolestoid-derived mammals (Apesteguía et al., in press) and pipoid anurans (Báez and Calvo, 1990) are also recorded.

4.4. Neuquenian tetrapod assemblage

The Neuquenian tetrapod assemblage is commonly found in rock units belonging to the Neuquén Subgroup (Portezuelo and Plottier formations). The Santa Lucía de El Cuy Formation (Hugo and Leanza, 2001a) is also equivalent to this interval. The age of these rocks is Late Turonian–Coniacian. The assemblage is partially equivalent to the ‘Turonian–Coniacian association’ of Bonaparte (1998b). It is also necessary to clarify here that the ‘Neuqueniense’ Vertebrate Age of Bonaparte (1991), also includes the whole fauna of the Bajo de la Carpía Formation, here included in the Coloradoan tetrapod assemblage.

4.4.1. Characterization

The Neuquenian assemblage is characterized by the establishment of a distinctive South American Late Cretaceous fauna (Apesteguía, 2002), although it is theoretically possible that similar faunas could have been living in Africa by that time. The Neuquenian tetrapod assemblage includes the co-occurrence of typical North-Gondwanan lineages, such as podocnemidoid turtles and, perhaps, large non-Neoceratosaurian theropods (especially coelurosaurs). The latter are abundant when compared to abelisauroids, a ratio that abruptly changes in the overlying Coloradoan assemblage. Although the absence of taxa cannot characterize an assemblage, the absence of diplodocoids in the Neuquenian assemblage, related by some authors to the Laurasian extinction of sauropods, is at least as significant as the abundance of non-saltosaurine eutitanosaurs. The latter includes medium-sized and sometimes gigantic eutitanosaur (with procoelous mid-caudal vertebrae) and a few andesauroid (amphiplatyan mid-caudals) sauropods, including gracile and robust taxa (Bonaparte and Gasparini, 1980; Salgado and Calvo, 1993; Calvo et al., 2001a,b; Calvo, 2002). Narrow tooth-crowned taxa are more abundant than broad tooth-crowned taxa (Calvo and Grill, in press).

Theropods include non-avian maniraptorans (Novas and Puerta, 1997), such as possible dromaeosaurids, troodontids, alvarezsaurids (Novas, 1996; Chiappe and Coria, 2003) and large basal coelurosaurs that seem to constitute an endemic radiation (Novas, 1997b; Coria et al., 2001; Coria and Currie, 2002; Calvo et al., 2002). Carcharodontosaurid theropods were still present (Veralli and Calvo, in press; SA, pers. obs.) but not abundant. A few possible neornithe remains were also recorded (Agnolin et al., in press).

Although an increasing quantity of small (Porfiri and Calvo, 2002; SA, pers. obs.), medium-sized (Calvo and Porfiri, in press) and up to 7-m-long basal iguanodontian ornithopods (Coria, 1999b) are also present, the phylogenetic resolution is still too poor to permit an assemblage characterization. The same can be said for some still poorly known mesoeucrocodylians (D. Pol, pers. comm. 1998).

The turtles include at least two groups: short-necked chelids (related to extant *Acanthochelys*) and podocnemidoids (Lapparent de Broin and de la Fuente, 2001; de la Fuente, 2002, 2003), confirming the presence of North-Gondwanan pelomedusoids together with South-Gondwanan chelids. The mammalian history remains poorly known, the discovery of a mammal jaw being the only record for this unit (Coria et al., 2001).

4.5. Coloradoan tetrapod assemblage

(= Greater Gondwanan Endemic Dinosaur Domain, Apesteguía, 2002)

The Coloradoan tetrapod assemblage is typically found within the Río Colorado Subgroup (Bajo de la Carpa and Anacleto formations). The age of these rocks can be regarded as Santonian–Early Campanian. It is necessary to clarify that the ‘Neuqueniense’ Vertebrate Age of Bonaparte (1991) includes, among other remains, the whole fauna of the Bajo de la Carpa Formation, here considered as Coloradoan.

4.5.1. Characterization

The Coloradoan assemblage is characterized by the highest known diversity of Gondwanan titanosaurid sauropods and abelisauroid theropods. The abundant titanosaurids include the first appearance in Patagonia of small, robust and armoured saltasaurines (Lydekker, 1893; Powell, 1992), as well as large and gracile basal eutitanosaurs (von Huene, 1929; Powell, 1986; Salgado, 1996; Calvo et al., 1997, 1999; González Riga, 1998, 1999a; Chiappe and Dingus, 2001; González Riga and Calvo, 2001). Putative saltasaurines were also reported from the Cenomanian Itapecurú Formation in Brazil (Medeiros, 2002). If this is correct, Patagonian saltasaurines could constitute a second migratory wave completing the faunal mixture with northern Gondwanan forms already detected for the Neuqueniense assemblage. However, the recent report of hadrosaurids from the Itapecurú Formation (Avilla et al., 2003) might indicate possible taxonomic misidentification, or stratigraphic uncertainty in the provenance horizon.

Different lineages of abelisauroid theropods such as abelisaurines (Bonaparte and Novas, 1985), carnosaurines (Coria and Chiappe, 2000; Chiappe and Dingus, 2001), velocisaurids (Bonaparte, 1991) and indeterminate medium-sized taxa are present (Calvo and González Riga, 1998), showing perhaps the largest known

abelisauroid diversity. Additionally, maniraptoran theropods include derived alvarezsaurids (Bonaparte, 1991) and enantiornithine birds (Alvarenga and Bonaparte, 1992; Bonaparte, 1991; Coria et al., 2001), but no large forms. The rise of saltasaurines (previously restricted to north-eastern Brazil), the probable loss of large endemic coelurosaurs and the diversification of abelisauroid theropods could be related events (Apesteguía, 2002). Small, closely related basal iguanodontian ornithopods are not rare (Coria and Salgado, 1996; Salgado et al., 1997).

Crocodyliforms are remarkable, not only in their diversity but also in their quantity (Woodward, 1896; Price, 1955; Bonaparte, 1991; Gasparini et al., 1991). They include a good sample (representing more than 60% of reported tetrapods from the assemblage) of mammal-toothed notosuchian crocodyliforms (basal mesoeucrocodylians). Dinilysid snakes (Woodward, 1901) represent a local radiation of basal alethinophidians that is also accompanied by an endemic radiation of teiid lizards (Albino, 2002). Podocnemidoid pleurodiran turtles and chelids closely related to *Chelus* (Broin and de la Fuente, 1993; de la Fuente, 1993; Lapparent de Broin and de la Fuente, 2001), also form part of this rich assemblage. Although the single mammal recorded from this unit was thought to represent a metatherian, its affinities remain uncertain (Goin et al., 1986; Marshall and de Muizon, 1988) and thus is not significant in characterizing the assemblage.

4.6. Allenian tetrapod assemblage

(= Alamitense Bonaparte, 1991 = Alamitian SALMA Flynn and Swisher, 1995)

The Allenian tetrapod assemblage occurs in strata constrained between the Huantraiquican unconformity at its base and the marine Jagüel Formation above. The age of these units is Late Campanian–Early Maastrichtian. The Allenian tetrapod assemblage is partially equivalent to the Alamitense of Bonaparte (1986b), the ‘Campanian–Maastrichtian association’ of Bonaparte (1998b) and to the Alamitian SALMA of Flynn and Swisher (1995). The main stratigraphic unit of the Neuquén Basin yielding this tetrapod assemblage is the Allen Formation. However, the equivalent units in north-eastern Patagonia (the Angostura Colorado and Los Alamitos formations) represent similar environments, age and faunas, so their taxa are also included to give a more accurate picture of the Allenian assemblage. Together, these formations contain a variety of extraordinary fossils. New findings in Southern Mendoza and La Pampa provinces, both at the northern limits of the Neuquén Basin, also help to understand some faunal clues from the Allen Formation and equivalent units. Contrary to the view of Powell (1986), the tetrapod taxa found around Cinco Saltos and the Lago Pellegrini area

belong to the Anacleto Formation and not to the Allen Formation (see Heredia and Salgado, 1999). On the other hand, although *Carnotaurus sastrei* was originally regarded as from the Aptian–Albian Cerro Barcino Formation in Chubut Province, Ardolino and Franchi (1996) noted that it came from the La Colonia Formation.

4.6.1. Characterization

The Allenian assemblage is characterized by the co-occurrence of highly derived members of typical Gondwanan lineages and probable immigrants from the Northern Hemisphere. Among the former, there are small, armoured saltasaurine titanosaurs (Salgado and Azpilicueta, 2000), closely related large and advanced eutitanosaurs (Powell, 1986 and SA, pers. obs. at Salitral Moreno and Bajo Santa Rosa) and large, highly derived *Carnotaurus*-like abelisaurid theropods (after the record from the La Colonia Formation, continuous at that time with the easternmost Neuquén Basin; Bonaparte, 1985; Bonaparte et al., 1990), as well as some other lesser indeterminate abelisauroids. Onithure and non-ornithure ornithothoracean birds are also found together.

Among the immigrants, there are hadrosaurine and lambeosaurine allochthonous hadrosaurid ornithopods (Bonaparte et al., 1984; Powell, 1987; González Riga, 1999a; González Riga and Casadío, 2000) and ankylosaurian ornithischians (Salgado and Coria, 1996). It may become possible to add other Laurasian taxa, but only after a careful taxonomic revision of the abundant but fragmentary bones already collected, and/or the discovery of better preserved specimens. Furthermore, several supposedly Laurasian taxa have a possible Gondwanan counterpart, making it difficult to determine the allochthonous condition of some taxa (e.g., Tyrannoraptora, Ceratopsia, Ornithomimosauria, Dromaeosauridae, Ankylosauridae; see Rich, 1996; Novas et al., in press).

Non-dinosaurs include fragmentary materials of a diverse array of crocodyliforms, a high diversity of “madtsoiid” snakes (Albino, 1986), lizards (teiids and indeterminate iguanians?), and non-eilenodontine sphenodontians. Turtles comprise the most diverse chelid assemblage of the whole Cretaceous. The latter includes different groups of South American short and long-necked (related to *Hydromedusa*) chelids, and the first appearance of meiolaniids (Broin, 1987; Broin and de la Fuente, 1993; Lapparent de Broin and de la Fuente, 1999, 2001; de la Fuente et al., 2001). A remarkable record of mammals has also been reported, especially including dryolestoids, but also symmetrodonts, gondwanatheres, and perhaps triconodonts and australosphenids (Bonaparte and Soria, 1985; Bonaparte, 1986b, 1990, 1992), as well as pipoid and ‘leptodactylid’ frogs,

both from the Los Alamitos (Báez, 1987) and the Loncoche (González Riga, 1999b) formations.

5. Discussion and significance of the tetrapod assemblages

Knowledge of Neuquén Basin tetrapods has accumulated during the last century and particularly in the last 20 years. It has allowed us to associate them with different stratigraphical units displaying some common faunistic patterns that we term tetrapod assemblages.

Evolution is not static but also is not homogeneous. The different components of a biota have distinct evolutionary patterns and rhythms that restrict its stratigraphic utility. As knowledge of rock units and the record of their fossil contents is increased, faunal assemblages become better known, allowing recognition of successional patterns. The discovery of an enantiornithine bird in red beds is not evidence enough to assign it to the Bajo de la Carpa Formation, but when it is found in association with the crocodyliform *Notosuchus*, the snake *Dinilysia* and small alvarezsaurid theropods, the risk of making a wrong assumption is relatively low. However, the use of vertebrate, tetrapod or reptile ages should be avoided because of their informal biochronological meaning and the very limited record and low reliability that tetrapods provide for comparing rock units. Accordingly, tetrapod assemblages are considered here as tetrapod remains discovered in the same lithostratigraphic unit within a restricted area.

From the palaeontological aspect, it is worth noting that Ameghino (1903) recognized a number of faunistic sequences in the Cenozoic of Argentina based on the “evolutive grade” of their components. In the past 35 years, his ideas have been adapted by other authors and have given rise to well-known “Mammal Ages” (Pascual et al., 1965) or, more recently, to the South American Land Mammal Ages (SALMA) of Flynn and Swisher (1995).

Bonaparte (1986b, 1987, 1990, 1991, 1992) began to use ‘Vertebrate Ages’ for the Cretaceous of South America, pointing out that what actually defines them is in fact their whole vertebrate content, especially the reptiles (Bonaparte, 1992). In this way, he criticized the ‘Alamitian’ (‘Alamitense’) biochron of Ortíz Jaureguizar and Pascual (1989) because it was based only on mammals; the same was said of the ‘Amargan’ (‘Amarguense’) biochron. Accordingly, Bonaparte (1991) created the following two ‘Vertebrate Ages’ (VA) for the Cretaceous of South America, as follows:

Alamitian V. A. (= Edad Vertebrado Alamitense Bonaparte, 1986b): includes the tetrapod fauna from the Middle section of the Los Alamitos Formation (Río Negro Province), the upper section of the

Loncoche Formation (Mendoza Province) and the Allen Formation (Río Negro and Neuquén provinces) (see Bonaparte, 1986b, 1987, 1990, 1992). Neuquenian V. A. (= Edad Vertebrado Neuqueniense Bonaparte, 1991): includes the tetrapod fauna from the Bajo de la Carpa Formation (Bonaparte, 1991).

More recently, Bonaparte (1998b) has concluded that there are three main successive faunistic assemblages of land tetrapods in the Cretaceous of South America:

Albian–Cenomanian Assemblage, whose faunal content in the present scheme is restricted to the Neuquén Basin, and partially belongs to our Limayan tetrapod assemblage. Turonian–Coniacian Assemblage (= Neuquenian V. A. Bonaparte, 1991), whose faunal content in the present scheme is restricted to the Neuquén Basin, and partially belongs to our Neuquenian tetrapod assemblage. Campanian–Maastrichtian Assemblage (= Alamitian V. A. Bonaparte, 1991), whose faunal content in the present scheme is restricted to the Neuquén Basin, and belongs to our Allenian tetrapod assemblage.

Similarly, Novas (1997c) noted four ‘Major Intervals’ of the Cretaceous of South America: Hauterivian (La Amarga), Aptian–Albian, Cenomanian–Santonian (all Neuquén Group), and Maastrichtian.

Apesteuguía (2002) recently characterized a series of three main evolutionary stages and domains for tetrapod faunas, based on dinosaurian faunas.

First (Earliest Cretaceous–Early Aptian): with derived relics of widespread global Jurassic faunas, mainly basal neosauropods, basal neotetanuran theropods, basal neoceratosaurs (inferred from Late Jurassic faunal lists from Central Patagonia; Rauhut and Puerta, 2001; Rauhut et al., 2001; Rauhut, 2002) and stegosaurian ornithischians.

Second (= Gondwanan) (Late Aptian–Early Campanian): constituted faunas in which the isolation from Laurasia originated endemisms at generic and sometimes family level. It is divided into three domains: (1) Early Gondwanan (Late Aptian–Mid Cenomanian), mainly represented by carcharodontosaurid theropods, basal titanosaur and diplodocoid sauropods; (2) South American (Late Cenomanian–Coniacian), mainly represented by endemic coelurosaurs, titanosaurid sauropods and basal euiguanodontian ornithopods. At this level, the record shows the loss of dominance of basal titanosaurs, diplodocoid sauropods and carcharodontosaurid theropods, together with the diversification of titanosaurids and large endemic coelurosaurs; (3) Greater Gondwanan (Santonian–Early Campanian), mainly represented by abelisauroid theropods and saltasaurine titanosaurs. The rise of saltasaurines (previously restricted to northern Brazil) is evident, as is the probable loss of large endemic coelurosaurs and the diversification of abelisauroid theropods.

Third (Late Campanian–Early Maastrichtian): the establishment of land connections between Gondwana and Laurasia produced mixed faunas in several regions, as evidenced by the contact of North America with South America; and the abundant Gondwanan fauna in the Maastrichtian of Europe and Asia.

The late survival of plesiomorphic clades (e.g., temnospondyls from the Cretaceous of Australia; ceratodontiform dipnoans from the Upper Cretaceous of South America); and the theoretical appearance because of the presence of its sister group and the early appearance in the fossil record of highly derived groups must be taken into account in order to discuss fossil faunal associations and their characterization.

Because of their weaker dispersal barriers, marine faunas are spread more easily and widely than terrestrial faunas. As a result, it is possible to consider a single index fossil as an age indicator. However, because terrestrial environments can be conditioned by the isolation of a particular area, provinciality can arise more easily, allowing the survival of ‘archaic’ elements in isolated refugia. Furthermore, the random nature of the fossil record, and the strong biases produced by terrestrial palaeoenvironmental conditions, in contrast with marine environments, means that the assignation of a certain rock with its faunal content to some particular age, should not be based on a single index fossil. To prevent further possibilities of error, several taxa should be considered simultaneously. In this way, the error is substantially reduced.

Changes of tetrapod assemblages in an area represent major events that transformed the biotic composition (e.g., environmental changes, volcanism, transgressive events, evolution). Some of these are indicated in the geological record by regional unconformities.

6. Conclusions

Present knowledge of terrestrial fossil biotas in the Neuquén Basin is still poor, restricting the possibility of building a reliable database. However, some peculiarities of the tetrapod faunas seem to be evident enough to allow us to formulate a brief characterization of the Cretaceous continental strata of the southern part of the basin and their dominant tetrapod assemblages. The term assemblage refers to tetrapod taxa coming from the same lithostratigraphic unit within a certain region.

As a result, six tetrapod assemblages are recognized here: Amargan (Barremian–Early Aptian); Lohancuran (Late Aptian–Albian); Limayan (Cenomanian–Early Turonian); Neuquenian (Late Turonian–Coniacian); Coloradoan (Santonian–Early Campanian) and Allenian [Late Campanian–Early Maastrichtian (= Alamitense = Alamitian SALMA)]. As discussed in this paper, tetrapod assemblages cannot be used in order

to determine the age of a certain stratigraphic unit. However, by defining them locally and within a concise stratigraphical framework, such assemblages could provide the basis for developing a useful tool for addressing inter-regional correlations.

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