14. Reptilian Faunal Succession in the Mesozoic of Patagonia
An Updated Overview

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Introduction

The first synopsis on Mesozoic tetrapods of South America, with a hypothesis of their origin and geographic distribution, was made by Bonaparte (1978, 1979). He successively enlarged this synthesis on the basis of further discoveries that were mainly from the Cretaceous of Argentina (Bonaparte 1986, 1992, 1996). Other, more recent contributions were mostly made by the authors of this book; those references, together with other complementary ones, are included in the previous chapters. The amount of new information published in the last 25 years, particularly information referring to the Mesozoic reptiles of Patagonia, cannot be passed over when systematic studies, phylogenetic analyses, and biogeographic hypotheses are undertaken.

The record of Mesozoic reptiles in Patagonia, with some 121 taxa recognized at the genus or species level (Appendix), comprises data from the Late Triassic (Calvo this volume; Coria and Cambiaso this volume; Salgado and Bonaparte this volume) to the uppermost Maastrichtian (Gasparini this volume), approximately 150 million years (GSA 1999). During this time, the distribution and physiography of seas and land were greatly modified, first by the breakup of Pangaea and then Gondwana, and next by the different geotectonic processes that affected Patagonia and defined the depocenters in which the studied herpetofauna is recorded. A report of these and

			Los Menucos Basin	El Deseado Basin	P. de Agnia Basin	Cañadón Asfalto Basin	San Jorge Basin	Neuquén Basin
Jurassic	Late	Tith						1 2 12 20 29 91 92 97 98
		Kim				42 61		
		Oxf					110 111 112	
	Middle	Clv				40 41 72 82		95 96
		Bth						18
		Baj						89 90 94
		Aal			39			
	Early	Toa						
		Plb						
		Sin						
		Het						
Triassic	Late	Rht						
		Nor	103-107 121	31 38				
		Cm						
	Middle	Lad						
		Ans						
	Early	Ol						
		In						

Figure 14.1. Distribution of Patagonian Triassic and Jurassic reptiles, according to basins and ages (each taxon is indicated with its respective number, as listed in the appendix).

other large geotectonic events that affected the paleorelief of Patagonia is synthesized and illustrated by Spalletti and Franzese (this volume).

Undoubtedly, such events, as well as other minor ones, acted directly on the environment, climate, and biota. The consequences of these processes on the diverse groups of both continental and marine reptiles were different. A new seaway has double consequences in the geographic distribution of the biota: on the one hand, it favors the dispersion of the marine organisms, and on the other hand, it creates a barrier to the continental forms. The case of the Patagonian reptiles of the Jurassic is illustrative in this sense.

The paleontological record is always both incomplete and strongly biased for several reasons, and this is particularly true of the record of Mesozoic Patagonian reptiles. First, not all the Patagonian Mesozoic basins potentially rich in reptiles have been equally surveyed. This is clearly reflected in the number of taxa recorded in these basins; the Neuquén Basin stands out in this regard (Figs. 14.1,

			San Jorge Basin	Austral Basin	Quiriquina Basin	Neuquén Basin	North Patagonian Platform
Cretaceous	Late	Maa	30 36 68	35	11 88	50 55 58 83 87	100 101 102 5 8 10 14 15 16 17 37 54 99
		Cmp				116 117 33 51 53 57 67 69	
		San				7 13 23 24 25 52 71 79 85 86	
		Con				4 9 26 27 28 46 56 76-78 80-81	
		Tur	6 47 49 66			3 34 48 63 64 75	
		Cen	32 43			12 22 45 59 65 74 107 108 112 113 114 117 118 119	
	Early	Alb	84			44	
		Apt	73			60	
		Brm		93		21 62 70 93	
		Hau					
		Vlg					
		Ber				91 97 98 19 20	

Figure 14.2. Distribution of Patagonian Cretaceous reptiles, according to basins and ages. Each taxon is indicated with its respective number, as listed in the appendix.

14.2). In contrast, fieldwork in the Austral Basin has been scarce because of the difficulties of access to the sites and the high costs of exploration, and the result is scarce records compared with those from the Neuquén and San Jorge Basins. Marine reptile remains were mainly found in two areas: at the ingression of the Proto-Pacific over northwest Patagonia (the Neuquén Basin from the end of the Triassic to the Barremian), and at the transgression of the south Atlantic over a large part of this sector (North Patagonian Platform, during the middle Campanian to the Early Paleogene). Between both transgressions, a period of approximately 70 million years passed without marine sediments, and consequently there is no fossil record. In the Chilean Patagonia reptiles, mainly marine forms have been recorded in the Late Cretaceous, suggesting the potential of the findings if systematic fieldwork could be accomplished. Another bias to take into account is the body size of the recorded reptiles. Mid-size to large forms prevail (especially dinosaurs, with almost 50% of the total taxa at generic or specific level; see appendix). This is certainly related to diagenetic processes, but it is also because techniques to obtain microvertebrates are rarely applied.

Even with this bias, Patagonia has an outstanding record of fossil reptiles, and the evolution of Patagonian fauna can be broadly traced during most of the Mesozoic. Here, we aim to organize the information given in previous chapters of this volume in a synthesis ordered by time and by basin (Figs. 14.1, 14.2).

The history of the fauna cannot be separated from the history of the flora, which is most closely related to the paleoenvironmental evolution of the continent and region. For example (and even when there are not enough data to confirm it), some changes of the composition of the fauna of the saurischians along the Cretaceous of Patagonia have been related to certain turnovers in the flora, which in turn would have been produced by climatic and physiographic changes (Coria and Salgado 2005, and references therein).

The first researcher to approach the study of the Mesozoic continental tetrapod faunas of Argentina as a whole was Bonaparte (1979, 1986, 1996, and references therein). Later, Novas (1997) and especially Leanza et al. (2004) developed similar faunistic interpretations, the former for South America and the latter for the Cretaceous of the Neuquén Basin. Leanza et al. (2004, 64), in particular, proposed an arrangement of "assemblages," which were based on the tetrapods recorded in a single lithostratigraphic unit and a restricted area within the Neuquén Basin. Leanza et al. aimed to "provide the basis for developing a useful tool for addressing inter-regional correlations" (2004, 82). However, when the whole continental and marine herpetofauna of Patagonia (Argentina and Chile) is analyzed through the Mesozoic, these "assemblages" do not appear clearly.

Given the diversity of the Patagonian record and its temporal and geographic breadth, the main goal of this chapter is to provide an overview of the reptilian Mesozoic faunal succession. The arrangement is temporal, and the selected major faunal intervals indicate the moments with the highest number of recorded taxa. In this synthesis, some discontinuities can be observed in the record of the different groups, which are interpreted in terms of global and regional extinction, turnover, and diversification.

Major Faunal Intervals

Triassic

Unlike the record of Triassic reptiles from northwest Argentina (Bonaparte 1997; Caselli et al. 2001), that of Patagonia is less diverse, which is undoubtedly related to the comparatively scarce fieldwork (Calvo this volume; Coria and Cambiaso this volume; Salgado this volume) and to the relatively smaller Triassic exposures (Bonaparte 1978, 1997). The greatest reptile richness of the Patagonian Triassic is without doubt its paleoichnological diversity (six of the eight taxa at the generic level for the Triassic are ichnites; see appendix). A series of footprints found in rocks of northern Patagonia, in the area of Los Menucos, Río Negro (Vera Formation, Los Menucos Basin, Fig. 14.1; Spalletti and Franzese this vol-

ume, Fig. 2.3B), of the Late Triassic, suggests the presence of theriodonts, anomodonts, and other therapsids with uncertain affinities, in addition to chirotherids and prosauropods (Calvo this volume). The assemblage of ichnological evidence suggests a significant diversity of reptiles in the southwestern end of Pangaea. Likewise, the presence of prosauropods (*Mussaurus patagonicus*) is corroborated by partially complete skeletons both of adults and newborns (Salgado and Bonaparte this volume) found in rocks of the early Late Triassic (Laguna Colorada Formation, Deseado Basin, Fig. 14.1; Spalletti and Franzese this volume, Fig. 2.3B). Heterodontosaurid ornithischian dinosaurs (*Heterodontosaurus* sp.) are also present in the southern tip of Argentina in that same formation (Coria and Cambiaso this volume).

Except for the footprints of coelurosaurs, the clades that the reptilian ichnofauna has been referred to are also present in the Late Triassic of the Argentine northwest and clearly belong to Pangaean groups (Bonaparte 1997). Thus, the heterodontosaurids are also present in the Early Jurassic of South Africa and in the Early Cretaceous of Europe (Báez and Marsicano 2001; Norman et al. 2004; Coria and Cambiaso this volume). Prosauropods also had a worldwide distribution during the Triassic (Galton and Upchurch 2004). In sum, the assemblage of ichnological and bony material evidence suggests that a significant diversity of reptiles with strong Pangaean affinities was present in the southern end of South America.

Early Jurassic

Exploration that sought continental and marine reptiles of the Early Jurassic in Patagonia has been scarce. This has influenced the limited knowledge we currently have of the Patagonian (and South American) herpetofauna of those times, in contrast to those of the Northern Hemisphere, where a spectacular diversification, particularly of diapsids, is observed (see Weishampel et al. 2004).

The single continental reptile of the Lower Jurassic (although it may correspond to the lowest part of the Middle Jurassic) is the basal eusauropod *Amygdalodon patagonicus* (Salgado and Bonaparte this volume), found in Pampa de Agnia, Chubut (Pampa de Agnia Basin, Fig. 14.1; Spalletti and Franzese this volume, Fig. 2.4B). The marine reptiles found in the Neuquén Basin (Spalletti and Franzese this volume, Fig. 2.4B) are limited to vertebrae of a thalattosuchian crocodile of the Lower Jurassic of Mendoza (Gasparini 1981) and some remains of indeterminable ichthyosaurs of Mendoza and Neuquén (Fernández this volume). In contrast, both thalattosuchians and ichthyosaurs of the Early Jurassic of the Northern Hemisphere are numerous and diverse (Bardet 1995; McGowan and Motani 2003).

Middle Jurassic (Aalenian-Callovian)

After the Middle Jurassic, the record of Patagonian reptiles increases significantly, but Pangaean lineages still prevail, at least among dinosaurs (basal eusauropods, basal tetanurans). A single

form of continental reptile is recorded in the Middle Jurassic of the Neuquén Basin from the Aalenian of Mendoza (Spalletti and Franzese this volume, Fig. 2.5A). It is a fragment of a sacrum of a sauropod dinosaur similar to *Amygdalodon,* redeposited in marine sedimentites (Salgado and Gasparini 2004). All the other continental reptiles of the Middle Jurassic are from the scarce exposures of Cañadón Asfalto Basin (Fig. 14.1; Spalletti and Franzese this volume, Fig. 2.5B). In the Callovian of Chubut the basal eusauropod *Volkheimeria* and the Cetiosauridae *Patagosaurus* (Salgado and Bonaparte this volume) have been found. In these levels, the oldest tetanuran theropods of Patagonia were also found: *Condorraptor* (Rauhut 2005), and the putative basal spinosauroid *Piatnitzkysaurus* (Holtz et al. 2004a). The large theropod fauna of the Jurassic of Patagonia, which is mainly composed of basal tetanurans, contrasts markedly with the faunas of large nontetanuran theropods that will characterize the uppermost Cretaceous of Patagonia (the Campanian-Maastrichtian interval). The record of tetanurans is one of the outstanding points of the Middle Jurassic of Patagonia and basically coincides with the first records of the group worldwide, because the single Tetanurae before the Middle Jurassic is *Cryolophosaurus,* from the Lower Jurassic of Antarctica (Holtz et al. 2004b). Although the tetanurans could have been present since the Norian (Arcucci and Coria 2003), they certainly spread globally during the Middle Jurassic.

In addition to the dinosaurs, the paleoherpetologic list of the Cañadón Asfalto Basin, which has been intensively explored in recent years, includes pterosaurs (Rauhut et al. 2001; Unwin et al. 2004), pancryptodiran turtles (de la Fuente this volume), and sphenodonts (Albino this volume), all of them currently under study.

All the marine reptiles of the Middle Jurassic of Patagonia were found in the Neuquén Basin (Fig. 14.1) and comprise the Aalenian–early Callovian lapse (Spalletti and Franzese this volume, Figs. 2.5A, 2.5B). Those of the Aalenian–early Bajocian lapse are conspicuous members of Gondwana and have particular significance because, except for scarce remains of Europe (Bardet 1995; McGowan and Motani 2003) and Chile (Gasparini et al. 2000), they are completely unknown in other parts of the world. The oldest is an ophthalmosaurian ichthyosaur from the Aalenian of Mendoza, which is also the oldest record of this clade worldwide (Fernández this volume). Likewise, remains of the early Bajocian show the diversity of the marine herpetofauna during that time in the Southern Hemisphere, represented by the rhomaleosaurid pliosaur *Maresaurus coccai* (Gasparini this volume), the Stenopterygiidae ichthyosaur *Stenopterygius cayi* (Fernández 1994, this volume), and the ophthalmosaurian *Mollesaurus periallus* (Fernández this volume). In early Bajocian rocks in Chile, fragmentary remains of ichthyosaurs and plesiosaurs were found, as well as part of a skull referred to the metriorhynchid *Metriohrynchus* sp., which is the oldest record of the genus (Gasparini et al. 2000).

In the late Bathonian, the most complete metriorhynchid of the Middle Jurassic is recorded in the Neuquén Basin, which was referred to *Metriorhynchus* aff. *M. brachyrhynchus* (Pol and Gasparini this volume). Finally, in early Callovian rocks, also of the Neuquén Basin (Spalletti and Franzese this volume, Fig. 2.5B), fragmentary remains of pliosauroid and plesiosauroid plesiosaurs were found (cf. *Muraenosaurus;* cf. *Cryptoclidus*) (Gasparini this volume).

The marine reptiles of the Middle Jurassic of Patagonia (and north-central Chile) belong to the same genera or to closely related forms recorded in the European Tethys (Bardet 1995; O'Keefe 2001; McGowan and Motani 2003), suggesting paleobiogeographic relationships between both areas. In this regard, the Hispanic Corridor was proposed as the most parsimonious way for this interchange, which since the Oxfordian became the Caribbean Corridor that connected the Western Tethys with the Eastern Pacific (Gasparini 1992; Iturralde-Vinent 2003; Gasparini and Iturralde-Vinent 2006).

Late Jurassic (Oxfordian-Tithonian)

The early Late Jurassic of Santa Cruz (San Jorge Basin; Fig. 14.1; Spalletti and Franzese this volume, Fig. 2.6A) yielded an important association of reptile and mammal footprints (Calvo this volume). Some of these footprints, undoubtedly of small theropods (*Wildeichnus navesi, Sarmientichnus scagliai, Delatorrichnus goyenechei*), have been referred to coelurosaurs (Calvo this volume). However, most of those assignments have to be confirmed, because according to current phylogenetic patterns, not all the small theropods belong to this group. If they are indeed coelurosaurs, they would be the oldest ones of Gondwana and would increase the tetanuran diversity of this lapse. Such paleoichnological association, even with putative coelurosaurs, has been described for the Jurassic-Cretaceous of São Paulo State (Bonaparte 1979, Fernándes 2005).

From the Late Jurassic to the pre-Turonian Cretaceous, elements mostly of the late Pangaean lineages are recorded (among sauropod dinosaurs, dicraeosaurids, basal titanosauriforms, and basal diplodocoids), as well as groups that originated and diversified in Gondwana (early Gondwanan lineages, such as the rebbachisaurids, basal titanosaurians, basal allosauroids [carcharodontosaurids], and basal abelisauroids among dinosaurs; and basal mesoeucrocodylians and notosuchians among crocodiles) (Leanza et al. 2004). Although in the Neuquén Basin the continental Jurassic levels are scarce and not well surveyed relative to marine ones, some important remains have been found. For example, in the Tordillo Formation, north of Neuquén, fragments of femur, tibia, and fibula that belong to a lineage of basal eusauropods that would have lasted in Gondwana until the Cretaceous (on the basis of the record of the sauropod *Jobaria* in the Lower Cretaceous of Niger) have been found (García et al. 2003).

In Chubut, Kimmeridgian-Tithonian rocks (Cañadón Asfalto Basin; Spalletti and Franzese this volume, Fig. 2.6A) yielded the neosauropod dinosaurs *Brachytrachelopan mesai* and *Tehuelchesaurus benitezi* (Salgado and Bonaparte this volume). The latter are the single Patagonian representatives of the neosauropod radiation of the Late Jurassic (Wilson and Sereno 1998). The records of *Brachytrachelopan* (Upper Jurassic, Cañadón Asfalto Basin) and *Amargasaurus* (Lower Cretaceous, Neuquén Basin) show the persistence in Patagonia of a late-Pangaean lineage of diplodocoids: the Dicraeosauridae. These sauropods are not recorded in levels after the Barremian, and they probably became extinct before the end of the following interval (Salgado and Bonaparte this volume).

The Patagonian marine reptiles of the Late Jurassic were found mainly in Tithonian rocks of the Neuquén Basin (Fig. 14.1; Spalletti and Franzese this volume, Fig. 2.6A), although in some localities of this basin these same genera are recorded in the Berriasian, demonstrating that they cross the J-K boundary (Spalletti et al. 1999; Gasparini 2003; Gasparini and Fernández 2005). Numerically, ophthalmosaurian ichthyosaurs, such as the gigantic *Caypullisaurus bonapartei* and *Ophthalmosaurus* sp., prevailed (Fernández this volume), but other offshore predators were also present. Such is the case of the pliosaurids *Pliosaurus* sp. and *Liopleurodon* sp. (Gasparini this volume) and the metriorhynchids *Geosaurus araucanensis* and *Dakosaurus andiniensis* (Gasparini et al. 2006; Pol and Gasparini this volume). Likewise, the most ancient marine turtles were present in the Proto–Eastern Pacific, such as the eucryptodiran *Neusticemys neuquina* and the panpleurodiran *Notoemys laticentralis* (de la Fuente this volume). Over the Tithonian seas of the Neuquén Basin flew different pterodactyloids, one of them referred to *Herbstosaurus pigmaeus,* and other assigned to a Ctenochasmatoidea (Codorniú and Gasparini this volume; Codorniú et al. 2006).

Many of the genera of Tithonian marine reptiles of Patagonia are also represented in the Northern Hemisphere, mainly in the European Tethys (*Ophthalmosaurus, Pliosaurus, Liopleurodon, Geosaurus, Dakosaurus*), suggesting close biogeographic relationships that were probably favored by the opening of new seaways such as the Caribbean Corridor (Iturralde-Vinent 2003) and the Weddell Sea (Spalletti and Franzese this volume), which connected the south of the Eastern Pacific with the Indian Ocean.

Early Cretaceous–Early Late Cretaceous (Berriasian-Cenomanian)

The oldest reptiles of the Patagonian Cretaceous are marine and were found in the Neuquén Basin. In the Berriasian, the genera *Geosaurus, Dakosaurus* (crocodyliforms), *Liopleurodon* (pliosaurid), and *Caypullisaurus* (ohpthamosaurian ichthyosaur) are recorded, the same as in the Tithonian; consequently, there is no evidence of extinction of pelagic offshore forms in the Jurassic-Cretaceous transition. Later, in coincidence with the shallowing of the Neuquén Basin (Spalletti and Franzese this volume, Fig. 2.6B) in the southern sector, the

only marine reptiles of the Valanginian-Hauterivian are the elasmosaurid plesiosaurs (Lazo and Cichowolski 2003). In the Austral Basin (Spalletti and Franzese this volume, Fig. 2.6B), there are records of Barremian ichthyosaurs in Chile (Fernández and Aguirre-Urreta 2005) and pteranodontoid pterodactyloids in the lower Barremian of western Santa Cruz (Codorniú and Gasparini this volume).

Since the Barremian, when the Proto-Pacific definitively withdrew from the Neuquén Basin (Spalletti and Franzese this volume, Fig. 2.7A), the basin yielded the most complete example of the continental Cretaceous herpetofauna of South America. Only since this moment can the continental faunistic lists of the Neuquén Basin be compared with other Patagonian basins (Austral and San Jorge Basins).

As we said before, Bonaparte was the first to accomplish a systematic study of the tetrapod successions for the Mesozoic of Patagonia (1979, 1986, 1996, and references therein). Recently, Leanza et al. (2004) recognized a series of assemblages for the Cretaceous tetrapods of the Neuquén Basin. Some of the elements these authors report as part of those local faunas or assemblages are recorded also in other basins of Patagonia. Thus, since the Lower Cretaceous, especially since the Aptian, the associations recorded in the Neuquén Basin can be compared with other depocenters of Patagonia on the basis of the presence of common elements.

The main localities that yielded remains of continental reptiles of this interval Berrisasian-Cenomanian are La Amarga (Barremian of Neuquén), Lohan Cura (Aptian-Albian, Neuquén), Ocho Hermanos (Cenomanian, Chubut), Picún Leufú-El Chocón, Plaza Huincul, Cortaderas (Cenomanian of Neuquén), and La Buitrera (Cenomanian, Río Negro).

In the Neuquén Basin, the Berriasian-Cenomanian period includes the Amargan (La Amarga Formation), Lohancuran (Lohan Cura Formation), and Limayan (Río Limay Subgroup) assemblages of Leanza et al. (2004). In the San Jorge Basin, Cretaceous elements of this lapse are recorded in the Matasiete Formation (Martínez et al. 1989) and Cerro Barcino Formation (Apesteguía and Giménez 2001), and in the Lower Member of the Bajo Barreal Formation (Powell et al. 1989; Lamanna et al. 2001; Martínez et al. 2004a,b), where some taxa similar to those of the Limayan assemblage of the Neuquén Basin are recorded (with rebbachisaurid dinosaurs and other basal diplodocoids, titanosauriforms and basal titanosaurs, and carcharodontosaurs).

The end of the Berriasian-Cenomanian period in Patagonia was characterized by a marked faunistic turnover that affected many continental forms. This is relatively well documented for the saurischians of the Neuquén Basin and probably occurred globally for this group (Coria and Salgado 2005). Diplodocoids (rebbachisaurids and other forms of basal diplodocoids) are recorded in all the pre-Turonian Cretaceous, but are absent in the next pe-

riod (Turonian-Santonian). The record of the sauropod *Amargasaurus* in the Barremian of the Neuquén Basin shows the persistence in the Lower Cretaceous of Patagonia, at least until the Barremian, of a lineage that was already present in the Tithonian of the Cañadón Asfalto Basin (*Brachytrachelopan*). In this sense, just as with the marine forms, a continuity between the Late Jurassic and the Early Cretaceous in Patagonia is seen, taking into account different depocenters, although such continuity is not as well documented as in the case of the marine reptiles.

Among dinosaurs, the basal diplodocoids are recorded in the San Jorge Basin (Sciutto and Martínez 1994) and in the Neuquén Basin (Calvo and Salgado 1995; Leanza et al. 2004). This period attested also the appearance and basal diversification of the titanosaurs. Basal forms of this group, such as *Chubutisaurus,* the sauropod of the Matasiete Formation, and *Epachthosaurus* in the San Jorge Basin (del Corro 1975; Martínez et al. 1989, 2004b), *Andesaurus* and the sauropod of the La Antena Quarry (Villa El Chocón) in the Neuquén Basin (Calvo and Bonaparte 1991; Calvo 1999; Simón and Calvo 2002), will survive up to the end of the Berriasian-Cenomanian interval.

Within the theropod dinosaurs, the first Abelisauria, a group that probably originated in Gondwana (Coria this volume), are recorded. In the Neuquén Basin, remains of abelisaurs are recorded in the La Amarga Formation (the noasaurid *Ligabueino andesi,* Bonaparte 1996), the Candeleros Formation (*Ekrixinatosaurus,* Calvo et al. 2004), and the Huincul Formation (the neoceratosaur *Ilokelesia,* Coria and Salgado 1998). In Chubut, in turn, in levels of the Bajo Barreal Formation, the abelisaur *Xenotarsosaurus bonapartei* is recorded together with other remains of indeterminate species (Martínez et al. 1986, 2004a,b; Lamanna et al. 2002).

Another Gondwanan group of large theropods, the carcharodontosaurids, is recorded, in the San Jorge Basin, *Tyrannotitan* (Aptian) (Novas et al. 2005b), and in the Neuquén Basin, *Giganotosaurus* (early Cenomanian) (Coria and Salgado 1995) and *Mapusaurus* (Coria and Currie 2006). All the carcharodontosaurids of the Neuquén Basin belong to the clade of the giganotosaurines. These are not likely to have spread over Africa, even when a connection was possible (Sereno et al. 2004). The giganotosaurs, as well as the remaining carcharodontosaurids, apparently became extinct by the end of this interval. Although carcharodontosaurid-type teeth are recorded in the next interval (Veralli and Calvo 2004), it is not certain whether they actually belong to carcharodontosaurids (Coria this volume).

Other groups of continental reptiles were present in Patagonia in this lapse, besides the dinosaurs. The oldest ones are the basal crocodyliform *Amargasuchus* and the pterodactyloids of the Barremian in the Neuquén Basin. It is not until the end of the period (Cenomanian) that the first notosuchians (*Araripesuchus*) (Pol and Gasparini this volume), chelid turtles (*Prochelidella*) (de la Fuente this volume), iguanids (Apesteguía et al. 2005), and the sphen-

odontid *Kaikaifilusaurus* (Apesteguía and Novas 2003; Simón and Kellner 2003) are recorded.

Turonian-Santonian

This interval is represented in the Neuquén Basin in the associations of the Neuquenian and part of the Coloradan (only the forms recorded in the Bajo de la Carpa Formation) of Leanza et al. (2004). In the remaining Patagonian basins, it is not yet clear which formations represent this interval–probably the Barreal Formation in some sectors (J. Rodríguez personal communication 2005). But the knowledge of the herpetofauna of this interval comes almost exclusively from the Neuquén Basin (Fig. 14.2). In the Austral Basin, south of Schuén River (Santa Cruz Province) at Mata Amarilla locality, and south of Lago Viedma, at Cerro de los Hornos, a rich fossil reptile fauna has been recorded that is probably Coniacian or Santonian in age, and that is currently under study (Goin et al. 2002; Novas et al. 2002).

Several localities of this period, especially the Turonian-Coniacian of the Neuquén Basin (Portezuelo Formation), have been intensively studied in recent years, the most outstanding of which are Sierra del Portezuelo (Novas and Puerta 1997; Novas 1998; Novas and Pol 2005) and the Futalognko Site at Lago Los Barreales (Calvo et al. 2002). Some of the most spectacular findings of dinosaurs and other reptiles of recent years were found here. The last stages of this interval are undoubtedly represented by the Bajo de la Carpa Formation, Neuquén Province. Remains of this unit have been known since the first discoveries of Santiago Roth by the end of the nineteenth century (Salgado this volume).

During the interval Turonian-Santonian, South America became progressively isolated from other continents. Accordingly, the forms recorded in Patagonia belong to Late Gondwanan lineages, groups that have evolved and diversified after the breakup of Gondwana (Bonaparte 1996; Novas 1997; Leanza et al. 2004).

Concerning dinosaurs, the derived titanosaurs (or titanosauroids sensu Salgado 2003) diversified after the extinction of the basal titanosaurs (andesauroids, epachthosaurines, and like forms) and the diplodocoids. The latter occurred by the end of the Cenomanian; in the Neuquén Basin, the time frame is represented by the top of the Huincul Formation, and in the San Jorge Basin by the base of the Upper Member of the Bajo Barreal Formation. In other continents (clearly North America), and unlike what is observed in Patagonia, the decline of sauropods by the end of the Early Cretaceous resulted in the diversification of ornithischians (Bakker 1978; Coria and Salgado 2005).

Bonaparte (1979) was the first to see that in Patagonia, sauropods with amphiplatyan caudal vertebrae (recorded in the Lower Cretaceous) are replaced (in the Upper Cretaceous) by others with procoelous caudals (or titanosauroids sensu Salgado 2003). Bonaparte attributed the flourishing of Titanosauridae (sensu Powell 2003) to the extinction of those "pre-Senonian sauropods" of am-

phiplatyan caudals. Powell et al. (1989), in turn, recorded an assemblage of elements of both associations (sauropods with amphiplatyan caudals on the one hand, and procoelous on the other) in a single lithostratigraphic unit (the Bajo Barreal Formation in the San Jorge Basin), although they were certainly found in different levels. Today, we know that those sauropods with procoelous caudals—"pre-Senonians," as named by Bonaparte (1979, 234), or "non-titanosaurid" according to Powell et al. (1989, 170)—in fact belong to two different lineages of basal diplodocoid and basal titanosaur sauropods, respectively (Lamanna et al. 2001; Salgado and Coria 2005).

Examples of titanosauroid dinosaurs of this interval are *Mendozasaurus, Rinconsaurus*, and "*Antarctosaurus*" *giganteus*. Salgado and Bonaparte (this volume) recognize in addition the persistence of a lineage of titanosaurs with amphiplatyan caudals.

Within the theropod dinosaurs, the basal abelisauroids seem to have lasted during the Turonian-Santonian interval as the single members of the large continental predators of the Lower Cretaceous, facing the extinction of carcharodontosaurs of the previous interval. Although a few remains of this age are known (the abelisauroid *Bayosaurus pubica*, for example; Coria this volume), the abelisaurs are abundant in the following interval (Campanian-Maastrichtian). Abelisaurs from the Turonian-Santonian lapse probably shared the role of large predators with the large tetanuran theropods: coelurosaurs and the middle-sized dromaeosaurid-related forms (*Unenlagia* and *Neuquenraptor*). Small alvarezsaurid theropods present in this period are likely to have lasted until the following interval (Coria et al. personal communication).

During the Turonian-Santonian lapse of Patagonia, other group of reptiles were diversified in addition to the dinosaurians. Such is the case of the chelid turtles (*Prochelydella, Lomalatachelys*) and Podocnemidoidae (*Portezueloemys*) (de la Fuente this volume), notosuchians (*Notosuchus, Comahuesuchus, Pehuenchesuchus, Cynodontosuchus*), and peirosaurids (*Lomasuchus, Peirosaurus*) (Pol and Gasparini this volume) and the first ophidians (*Dinilysia*) (Albino this volume). The oldest birds of Patagonia are also recorded, with two lineages already well differentiated: the flying enantiornithines (*Neuquenornis*) and the flightless basal ornithuromorphs (*Patagopteryx*).

There is no record of marine herpetofauna during the Turonian-Santonian lapse in Patagonia.

Campanian-Maastrichtian

In the Neuquén Basin, this span of time encompasses the Anacleto Formation (part of the continental tetrapod assemblage included in the Coloradan) and the Allen Formation (Allenian assemblages) (Leanza et al. 2004), besides the marine Jagüel Formation. In the San Jorge Basin, the continental levels of the Campanian-Maastrichtian were deposited in the upper part of the Bajo Barreal Formation and the Laguna Palacios Formation. In the Austral

Basin, the deposits of this time belong to the continental Pari Aike Formation (Novas et al. 2004, 2005a). Outside the area of these basins, the taxa of this interval are those recorded in the Allen and Jagüel Formations (central and south Río Negro Province), Los Alamitos Formation (southeast of this province), and Angostura Colorada and Coli-Toro Formations (south-southwest of the province).

According to Leanza et al. (2004), during this period, in the Neuquén Basin, the taxa of continental tetrapods recorded in the lower Campanian (Anacleto Formation) would form a single assemblage (Coloradan) with the taxa recorded in the underlying Bajo de la Carpa Formation, Santonian in age. However, in this chapter, we gather all the Campanian-Maastrichtian continental reptiles in a single interval, because they basically belong to the same taxa, as well as forms that would have entered from North America since the Middle Campanian.

The events characterizing this interval are, in the case of sauropod dinosaurs, the appearance of the Saltasaurini (only in the Neuquén Basin) and the expansion and diversification of the Aeolosaurini (Neuquén and San Jorge Basins, Salgado and Coria 1993; Casal et al. 2002; Powell 2003). These latter are also recorded in the Campanian-Maastrichtian of Brazil (Kellner and Azevedo 1999), suggesting an expansion of their area of distribution during the Campanian. Among the theropods, both in Northern and Central Patagonia, the abelisaurs seem to definitively dominate as large predators (the megaraptors disappear from the record), with the Abelisaurinae and Carnotaurinae recorded first. According to the record, only the tetanuran *Quilmesaurus* (Allen Formation in the Neuquén Basin) would have coexisted with large abelisaurs during this period. But in Laurasia, the large tetanurae do not disappear but rather multiply, as do the ornithischians in the case of herbivorous forms.

Other dinosaur groups appear in the Patagonian record as the hadrosaurs and ankilosaurs (Coria and Cambiaso this volume). The former undoubtedly come from the Northern Hemisphere, probably North America, through an array of islands emerged in the present Caribbean Sea. In this regard, Iturralde-Vinent and McPhee (1999) and Iturralde-Vinent (2003) point out that this connection occurred between the middle Campanian and the early Maastrichtian, approximately 5 Ma, enough time to permit an important faunistic interchange. Hadrosaurs are recorded in the San Jorge Basin (with *Secernosaurus*) and in the North Platform (with *Kritosaurus* and an indeterminate genus of Lambeosaurinae) (Coria and Cambiaso this volume). There are no records in the Austral Basin to date, although the remains of this group of ornithopods found in Antarctica clearly indicate that by the end of the Cretaceous, these forms already inhabited Patagonia at least north of the Antarctic Peninsula. No certain records of ceratopsids have been reported so far for Patagonia; however, they were important in the faunas of the Late Cretaceous of North America (Coria

and Cambiaso this volume, where a discussion on the status of the alleged ceratopsian *Notoceratops bonarelli* is presented). Another group recorded in the Campanian-Maastrichtian of Patagonia is that of the dromeosaurid theropods (Novas et al. 2003), which were very abundant in the Cretaceous of North America. However, they are also recorded in levels that correspond to the previous interval (Novas and Pol 2005). Concerning the Patagonian and Antarctic ankylosaurs, it is not certain that they have Laurasian lineages (Salgado and Gasparini 2006). In sum, the importance of the incoming North American reptiles, beyond the abundant record of several different species of hadrosaurs, is still uncertain.

As stated above, the forms recorded in the early Campanian—at least those for the Neuquén Basin—before the settlement of the connection with North America (found in the Anacleto Formation) seem to be the same (even at the genus level, as the case of the sauropod *Neuquensaurus* [Salgado unpublished data]) as the following continental formations (Allen Formation of the Neuquén Basin) because a turnover or extinction caused by the entering of northern forms was not seen.

From the middle Campanian to the Maastrichtian-Paleogene, a South Atlantic transgression related to the subsidence of wide areas of the austral portion of South America partially covered Patagonia, forming a large archipelago with lagoons, open embayments, and marine environments. This ingression of the Atlantic covered several continental depocenters such as the Neuquén, San Jorge, and Austral Basins (Spalletti and Franzese this volume, Fig. 2.8B), but their deposits surpassed the limits of the previous basins. (In Fig. 14.2, when taxa of this interval have been recorded in sedimentite outcroppings in the mentioned basins, they are included in the column of the corresponding basin, but when the record is from a locality outside these limits, it is included in the column of North Patagonian Platform.)

Most of the reptiles of the Campanian-Maastrichtian transgression were found in the first three Mesozoic basins—Neuquén, San Jorge, and Austral—and were the continental forms (although littoral) that prevailed in both amount and taxonomic diversity (Fig. 14.2). Likewise, it is noteworthy that all these continental forms, as well as other formerly associated marine ones, belong to the Campanian and Campanian–early Maastrichtian (Bonaparte 1987; González Riga 1999; Gasparini et al. 2001; Martinelli and Forasiepi 2004), whereas those found in uppermost Maastrichtian rocks are, to date, exclusively marine reptiles (Gasparini et al. 2003). Accordingly, in the Quiriquina Basin, in south-central Chile, and also in the late Maastrichtian (Stinnesbeck 1986), plesiosaurs, mosasaurs, and marine turtles and birds have been found.

The cheloniofauna of the lowlands of Trapalcó and Santa Rosa is similar to the fauna described for the Los Alamitos and La Colonia Formations, and to other lithostratigraphic units of the Upper Cretaceous of Patagonia that are exposed in areas outside of previous continental basins (de la Fuente this volume).

With regard to the marine reptiles of the Campanian and Cam-

panian–early Maastrichtian, only plesiosaurs and mosasaurs have been found in the Argentinean Patagonia, along with marine turtle remains found above the K-P boundary in the Province of La Pampa (de la Fuente and Casadío 2000). Generally, disarticulated remains are most common, in accordance with coastal or mixed environments, and policotylids (*Sulcusuchus erraini*) and elasmosaurids have been found (Gasparini this volume).

The reptiles of the uppermost Maastrichtian that have been preserved in strictly marine environments are generally more complete, and they belong to elasmosaurids (*Aristonectes parvidens*, *Mauisarus* sp., *Tuarangisaurus? cabazai*) (Gasparini this volume) and mosasaurs of at least three different species: *Plioplatecarpus* sp., *Mosasaurus* cf. *M. hoffmani,* and an indeterminate species of Mosasaurinae (Gasparini et al. 2005b; M. Fernández personal communication 2005). In Chilean Patagonia, also in late Maastrichtian sedimentites, the following taxa have been recorded: the elasmosaurids *Aristonectes* sp., cf. *Mauisaurus;* mosasaurs; eucryptodiran pancheloniid turtles (de la Fuente this volume); and modern birds of the Family Gaviidae, or loons (Chiappe this volume). The distribution of elasmosaurids suggests that these pelagic reptiles moved both along the southwest of the Proto-Pacific and the south of the South Atlantic, reaching the north of the Antarctic Peninsula through the Weddell Sea (Gasparini et al. 2003).

Conclusions

Evidence yielded by the analysis of the systematic chapters of this volume (chapters 3–12) suggests a rough correspondence among some geodynamic macroevents that affected the distribution of seas and lands during the Mesozoic, particularly in Patagonia (Spalletti and Franzese this volume), with the succession of their herpetofauna. Likewise, local extinction seems to be coincident with the evolution of each basin, as well as some faunistic turnovers–particularly the one occurred during the Middle-Late Cretaceous in the Neuquén Basin, where currently the largest number of Mesozoic Patagonian taxa is recorded.

1. Pangaea predominated during the Triassic and most part of the Jurassic. Accordingly, the Late Triassic herpetofauna of Patagonia is composed of clades of Pangaean distribution (see Holtz et al. 2004b, figs. 27.6, 27.7). This is the case of the theriodonts, anomodonts, chirotherids (based on their ichnological record), prosauropods, and heterontosaurid ornithischians (bony record). This assemblage demonstrated a high diversity by the end of the Triassic in the southwestern end of Pangaea. Interestingly, in Patagonia and the rest of South America, none of these groups crosses the Triassic-Jurassic boundary as they do in other continents (Galton and Upchurch 2004; Norman et al. 2004; Marsicano et al. 2005). However, as already discussed, it has to be recognized that little has been explored in the Lower Jurassic of South America; hence, at first sight, this can appear biased.

2. According to recent paleogeographic reconstruction (Blakey 2001), the definitive break of Pangaea into two supercontinents, Laurasia and Gondwana, occurred in the Late Jurassic. However, some events anticipated that separation, such as the Hispanic Corridor that intermittently connected the Central Atlantic with the Eastern Pacific up to its definitive opening in the Oxfordian (Iturralde-Vinent 2003). In accordance with the distribution of macro- and microinvertebrates (Damborenea 2000), the Hispanic Corridor played a main role in the interchange between the western Tethys and the Eastern Pacific. Precisely, the marine herpetofauna of the Middle Jurassic of the Neuquén Basin (and north-central of Chile) has strong affinities with that recorded in the Lower-Middle Jurassic of Europe, sharing genera (*Stenopterygius*, *Metriorhynchus*) and like forms (*Maresaurus*, cf. *Muraenosaurus*, cf. *Cryptoclidus*).

3. In continental Patagonia, some Pangaean elements (basal eusauropods, basal tetanurans, pancryptodiran turtles) persisted during the Early and Middle Jurassic. One of the outstanding points of the Middle Jurassic of Patagonia is the tetanuran dinosaurs, whose record approximately matches with the first records of the clade worldwide (Holtz et al. 2004b).

4. In agreement with the separation of Gondwana, the continental herpetofauna of Patagonia is represented from the end of the Jurassic up to the Cenomanian by some late-Pangaean lineages, together with other mainly Gondwanan lineages. The former are represented among the dinosaurs by dicraeosaurids, basal titanosauriforms, and basal diplodocoids. The Gondwanan lineages of dinosaurs are rebbachisaurids, basal titanosaurians, basal allosauroids (carcharodontosaurids), and basal abelisauroids; and among other groups, chelids and mesoeucrocodylians. The oldest coelurosaurian dinosaurs would be represented by a series of footprints in the Late Jurassic of Patagonia and south Brazil (Fernandes 2005), although this assignment has to be restudied. Unresolved phylogenetic relationships of the sphenodontids of Patagonia preclude determining whether they were related to Pangaean or Gondwanan groups.

5. Concerning the marine herpetofauna of the Late Jurassic–Early Cretaceous, its composition seems to be more closely related to the regional evolution of the Neuquén Basin (Spalletti and Franzese this volume). During the Tithonian-Berriasian, almost all the reptiles were offshore pelagic forms (*Caypullisaurus*, *Dakosaurus*, *Pliosaurus*, *Liopleurodon*, *Neusticemys*). However, when the south of the basin shallowed, the Proto-Pacific began to withdraw to the northwest of Patagonia (toward the Valangian-Hauterivian), only elasmosaurids are recorded. Since the Barremian, there are no records of marine reptiles in Patagonia, except in the southwest of the Austral Basin facing the Pacific (*Platypterygius*).

6. No extinction is observed by the end of the Jurassic. On the contrary, most pelagic reptiles (*Dakosaurus*, *Geosaurus*, *Liopleurodon*, *Caypullisaurus*) cross the Jurassic-Cretaceous boundary.

Likewise, but in the continental environment, the sauropod *Amargasaurus* (Barremian of the Neuquén Basin) indicates the persistence in the Lower Cretaceous of a lineage already present in the Tithonian of the Cañadón Asfalto Basin (*Brachytrachelopan*).

7. Their isolation continued with the separation of South America from South Africa in the Aptian-Albian (Blakey 2001), and in the Turonian-Santonian lapse, the continental reptiles still belonged to late Gondwanan lineages (Bonaparte 1996; Novas 1997; Leanza et al. 2004). This is the case for the derived titanosaurs (titanosauroids sensu Salgado 2003), and possibly for abelisaurs. The record of titanosauroids begins in Patagonia in levels deposited immediately after the opening of the South Atlantic (Calvo and Salgado 1998). Although titanosauroids are also recorded in the Upper Cretaceous of continental Africa (Smith et al. 2001), the evolutionary history of the group in this continent is still mostly unknown. The record of abelisaurs in the Cenomanian of Niger suggests that the South America–Africa connection could have been working at least up to that point (Sereno et al. 2004). Chelid turtles and podocnemidoids (*Portezueloemys*), the basal *Dinilysia,* the madtsoiids, the diverse class Notosuchia (*Araripesuchus, Notosuchus, Comahuesuchus, Cynodontosuchus*), and basal neosuchians (*Lomasuchus, Peirosaurus*) are also outstanding Gondwanan elements of Patagonia during this interval.

8. During the Campanian-Maastrichtian, several large geodynamic events affected the faunistic composition of Patagonia. On the one hand, the connection between the Americas (Iturralde-Vinent 2003) should have favored the faunistic interchange, although it is currently impossible to determine how they could have affected it. In the Patagonian continental herpetofauna, there are some northern elements, such as the hadrosaurs and probably the ankylosaurs, although in the latter, unsolved phylogenetic relationships prevent us from recognizing the extent of their relationships to those of North America (Salgado and Gasparini 2006).

Other important events affected Patagonia regionally. A major ingression of the South Atlantic (North Patagonian Platform and Austral Basin) turned Patagonia into a wide archipelago. Because of this, frequent associations of mixed marine and continental fauna are recorded, essentially in late Campanian–early Maastrichtian levels.

9. During the Campanian-Maastrichtian lapse, the Saltasaurini sauropod dinosaurs (recorded exclusively in the Neuquén Basin) appeared, and the Aeolosaurini (recorded in the Neuquén and San Jorge Basins, and in the Bauru Basin in Brazil) diversified. Among theropods, the abelisaurs dominate as large predators. The large megaraptors, characteristic of the Turonian-Coniacian interval, disappeared from the record.

10. In marine areas of the interval Campanian–early Maastrichtian, elasmosaurid and polycotylid (*Sulcusuchus*) plesiosaurs are recorded. The South Atlantic ingression over Patagonia accelerated during the Late Cretaceous–Danian (Spalletti and Franzese this

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volume), and the fossil-bearing levels belong to the last stages of the Mesozoic, including the record of several species of mosasaurs (*Plioplatecarpus* sp., *Mosasaurus* cf. *M. hoffmani,* Mosasaurinae indet.) and clasmosaurid plesiosaurs (*Aristonectes, Tuarangisaurus? cabazai,* cf. *Mauisaurus* sp.). In the area of Quiriquina, Chile, in late Maastrichtian rocks, marine herpetofauna is recorded, such as mosasaurs, plesiosaurs (*Aristonectes,* cf. *Mauisarus*), pancheloniid turtles, and gaviid birds. The record of marine reptiles continues in the Paleocene as the osteopygine of La Pampa.

11. Although the history of Patagonian marine reptiles is documented–although preliminary up to the end of the Mesozoic—there is no record of the last stages of the successions in continental forms. Their record is truncated after the middle Maastrichtian, a lapse of approximately 4 Ma—long enough to hide the reasons for the end. The K-P boundary marks the great extinction, and this is also seen in Patagonia (Gasparini et al. 2003). From the great taxonomic diversity of the Mesozoic, only the chelids, meiolanids, madtsoine boids, and sebecosuchians survived in the Paleogene.

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