Chapter 6
The Patagonian Fossil Lizards

Adriana María Albino

Abstract The squamates constitute a significant part of the present-day South American herpetofauna, and their fossils provide crucial evidence for understanding the origin and evolution of the main clades. The fossil record of squamates in Patagonia is still scarce but it represents one of the most prolific of all of South America. An updated systematic review of the available information of Patagonian fossil lizards is summarized in this chapter. The oldest lizards of Patagonia are found as far back as the Upper Cretaceous and include materials referred to two of the most diverse extant clades: Iguania and Scincomorpha. Palaeocene and Eocene interestingly do not provide any lizard specimens from this time frame, but the record reappears in the Late Oligocene with iguanians. A significant increase in materials is revealed later in the Neogene. Early Miocene lizards include the first appearance of extant genera (the iguanids *Liolaemus* and *Pristidactylus* and the teiids *Tupinambis* and *Callopistes*). Late Early Miocene deposits provide materials of *Pristidactylus* and *Tupinambis*, whereas an indeterminate tupinambine of the Mid-Miocene is the youngest Neogene record of a lizard in Patagonia. Palaeoclimatic changes affected the distributional patterns of lizards in Patagonia, restricting the distribution of *Pristidactylus* and *Tupinambis*, which, during the Miocene, extended to localities more southern than at present. The uplift of the austral Andean cordillera would have been decisive for the diversification of *Liolaemus* and *Pristidactylus* on both sides the Andes, whereas the trans-Andean teiid *Callopistes* had a widespread distribution in the past, reaching the Pampean Region and Patagonia, in Argentina.

Keywords Iguania · Scincomorpha · Teiidae · Patagonia · Argentina · Cretaceous · Cenozoic

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6.1 Introduction

In spite of the presently high diversity of lizards in Patagonia, the fossil record is still scarce and discontinuous. Patagonian fossil lizards have been documented since the nineteenth century (Ameghino 1893, 1898, 1899). These records, and others made during the last century, have been summarized and interpreted in classic literature concerning the fossil herpetofauna of South America (Báez and Gasparini 1977, 1979; Estes 1983; Estes and Báez 1985; Gasparini et al. 1986; Albino 1996). These early revisions were based on restricted and chronologically sporadic records, and, in many cases, the specimens were only mentioned but the material had not been neither studied nor revised. More recently, new palaeontological explorations carried out in Argentina provided additional material from diverse localities and geological periods. At the same time, the development of a research project focused on the fossil squamates of South America allowed a more rigorous anatomical and taxonomic study of the old and new material. Partial modern reviews concerning Patagonian fossil lizards have been included in Albino (2011) and Albino and Brizuela (2014a, 2015). Although the record is still scarce, it provides valuable information concerning the origin and evolution of modern lizard taxa.

This chapter is an attempt to evaluate the information that the fossil record can provide about the historical evolution of lizards in Patagonia. For this compilation, the geographic and stratigraphic references were revised. In some cases, a discussion about the taxonomic allocation of the remains is provided. Thus, this chapter represents an updated systematic review of the available information for this reptile group in Mesozoic and Cenozoic Patagonia.

Institutional abbreviations are as follows: MACN A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; MACN Pv, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional de Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; MLP, Museo de La Plata, Paleontología de Vertebrados, La Plata, Argentina; MPCA, Museo Provincial "Carlos Ameghino", Cipolletti, Argentina; MPCN, Museo Patagónico de Ciencias Naturales, General Roca, Argentina; MPEF PV, Museo Paleontológico "Egidio Feruglio", Paleontología de Vertebrados, Trelew, Argentina; and MPM PV, Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina.

6.2 The Restrictions of the Fossil Record

The squamates are relatively small animals with gracile skeletons that require an appropriate depositional environment for preservation in good conditions. Fine sediments and low energy produce relatively complete articulate skeletons, but these conditions are not frequent for many continental tetrapod-bearing beds of the Cretaceous and Cenozoic of Patagonia. Thus, squamate remains are usually obtained as a consequence of searching for large reptiles (Mesozoic) or mammals (Cenozoic) that are more numerous than squamates in Patagonian vertebrate deposits. During explorations to obtain fossil squamates, it is frequent to apply a suitable strategy to search for and pick up small bones. Matrix collected in bulk then macerated to produce a concentrate of isolated elements, followed by picking in the lab using a stereoscopic microscope, is the most common way to collect scattered remains of microvertebrates. This technique usually produces large numbers of remains of diverse taxa (fishes, amphibians, reptiles, birds, mammals), which give a more complete picture of the assemblage as a whole, but unfortunately, the recovered bones are disarticulated and, usually, broken. Many of the squamate remains obtained may be useless for taxonomic purposes due to the incomplete preservation, or they can be identified only at high taxonomic levels. Thus, only a small part of the collected sample will be identified. In spite of this, the resulting data are often useful in plotting distributions.

6.3 Geographical and Climatic Evolution of Patagonia

Modern-day Patagonia is the result of the interaction of global tectonics, sea level fluctuations and palaeogeographical and palaeoclimatic changes. These events were decisive in the changes that affected distribution patterns of lizards as well as for other taxa (Albino 2011; Albino and Brizuela 2014a, b, 2015). Because of this, a brief summary of the principal events in the geographical and climatic evolution of Patagonia, based on the detailed reconstruction of Iglesias et al. (2011) and Nullo and Combina (2011), is given here.

During the Cretaceous, along with the progressive breakup of Gondwana, the climate was much warmer than today, and temperate climate conditions extended even to the poles. The evolution of Patagonia was in part independent from the evolution of the rest of Gondwana because Patagonia remained connected to Antarctica for a long time facilitating the evolution of a fauna that was endemic of the South America-Antarctica island continent. The transformation process of Patagonia during the Cenozoic included two fundamental events: (1) the opening of the Drake Passage during the Eocene-Oligocene transition, which separated Antarctica from Patagonia and originated cooler conditions, and (2) the increase of the Andean activity during the Miocene, which obstructed the passage of the humid winds and generated a process of desertification (Chap. 3).

Climatically, the Palaeocene and Eocene were quite warm, with tropical conditions extending north and south towards the poles, 10° S beyond their current limit. By contrast, the Oligocene was characterized by cooling and aridity resulted from the development of a semi-permanent ice layer in Antarctica. During the Late Oligocene and the Early Miocene, a time of global warming produced a change to a warmer climate in the Patagonian region. The trend towards global cooling became marked during the Miocene, although with a short episode with increasing of temperatures during the Middle Miocene. After this climatic episode, there was another important cooling event. Late Miocene was characterized by the final demise of megathermal elements in Patagonia. Concomitantly with these changes, biomes moved from tropical forest to steppes, through a sequence comprising subtropical forests, woodland savanna, park savanna and grassland savanna.

6.4 Geochronological Context

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. In Argentina, it is exposed in the Provinces of Neuquén, Mendoza, Río Negro and La Pampa. The estimated ages of each unit that conforms the Neuquén Basin have been mainly obtained from the ages of the superimposed intervals limited by regional unconformities as a result of the tectonosedimentary evolution (Vergani et al. 1995). The Neuquén and Malargüe groups constitute the Upper Cretaceous strata of the Neuquén Basin (Fig. 6.1). They are separated from the previous strata by the Main Miranican unconformity (Leanza et al. 2004). The Neuquén Group was laid down during nearly 20 Ma from the Cenomanian (Candeleros Formation) through to the Campanian (Anacleto Formation) and is separated from the strata of the Malargüe group by the Huantraiquican unconformity (Fig. 6.1). Mesozoic lizards of Patagonia come only from the Candeleros and Anacleto formations.

With respect to the Cenozoic, land mammal ages are a widely used system to establish a time scale for terrestrial faunal record. Each land mammal age is characterized by one or more species of mammals (or a combination of species of

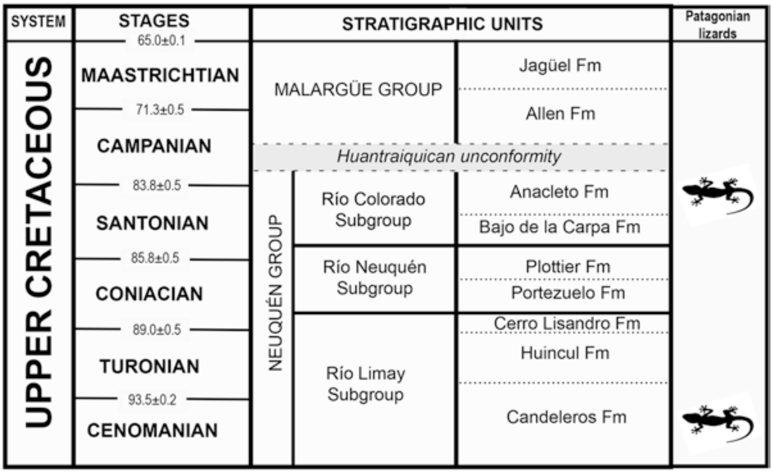


Fig. 6.1 Cretaceous stratigraphy of southern Neuquén Basin. Modified from Leanza et al. (2004)

mammals) that are unique for each period. By examining a large number of faunas of different ages, an entire time scale is erected based on the succession of mammal species. Each unit in the time scale is known as a land mammal age. In South America, most of the land mammal ages have traditionally been based on fossil localities of Patagonia. The biochronological context for the Cenozoic used in this chapter is then based on the South American Land Mammal Ages (SALMA, Pascual et al. 1996). The calibration used follows that given by Gelfo et al. (2009) and Woodburne et al. (2013) for the Patagonian Palaeogene, and Vucetich et al. (2007), Cione et al. (2007) and Cione and Báez (2007) for the remaining SALMAs (Fig. 6.2). Patagonian Cenozoic lizards come from deposits of the Deseadan, Colhuehuapian, Pinturan, Santacrucian and Colloncuran SALMAs.

6.5 Fossil Lizards of Patagonia

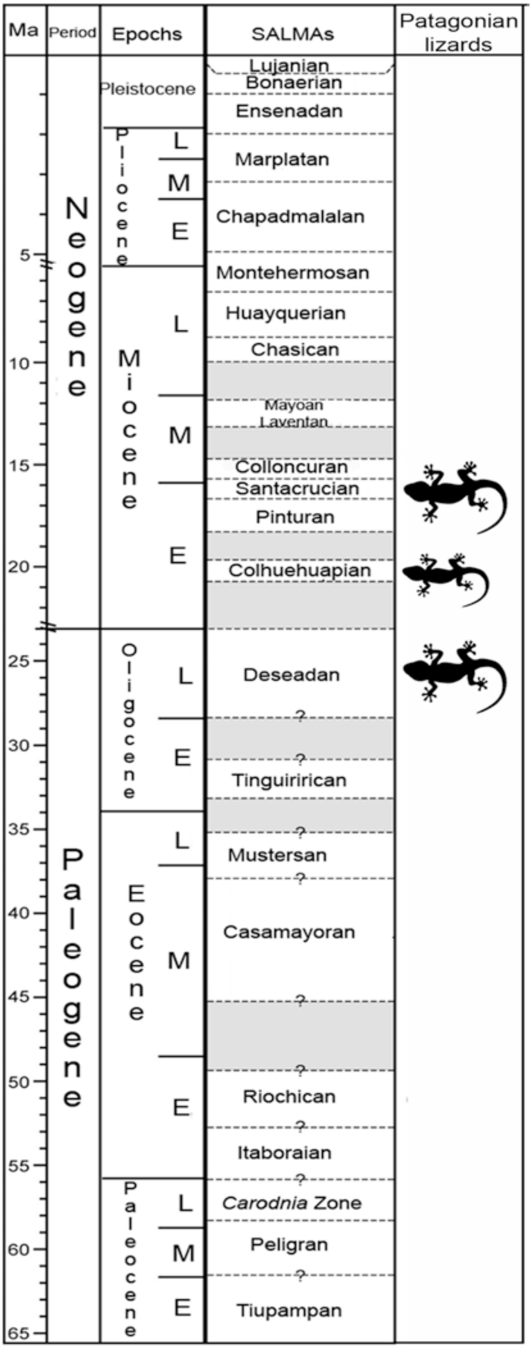
Few lizard species have been described so far for the Mesozoic of Gondwana, producing one of the largest palaeobiogeographical gaps in the knowledge of squamate evolution (Evans 2003). The known lizard diversity in the Mesozoic of South America is extremely restricted; thus, there is an important obstacle in knowing the origin and radiation of these squamates in southern territories.

Lizards first appeared in South America during the Early Cretaceous (Aptian-Albian) but they just became more frequent at the Cenozoic. Currently, only two main clades of lizards are present in the Mesozoic and Cenozoic record of Patagonia; they are Iguania and Scincomorpha. Both taxa emerged in this territory during the Upper Cretaceous.

Iguania Fragmentary remains recovered in Argentina and Brazil support the presence of Iguania in South America since the Mesozoic. The earliest of these records comprises nearly complete fused frontals (MPCA 250) encountered in rocks of the early Late Cretaceous of Patagonia (Apesteguía et al. 2005). The remain was collected in the upper layers of the Candeleros Formation (Cenomanian-Turonian) at the La Buitrera fossil quarry, Cerro Policía, Río Negro Province, northwestern Patagonia [Fig. 6.3 (1)].

The specimen was assigned to an iguanian (possibly Iguanidae) due to a combination of the following features (Apesteguía et al. 2005): (1) the frontals are fused in a sole bone, (2) it is strongly constricted between orbits giving hourglass shape and (3) it bears pronounced ornamentation. Daza et al. (2012) believe that the character combination listed by Apesteguía et al. (2005) is not exclusive to any lizard group whereas Albino and Brizuela (2014a) verify that the simultaneous presence of these characters is only observed in Iguanidae, considering valid the tentative assignation given by Apesteguía et al. (2005). Among Iguanidae, Apesteguía et al. (2005) suggested similarities in the dermal sculpturing with the extant Tropidurinae *Liolaemus*. However, Albino and Brizuela (2014a) noticed that the frontal exhibits well-developed supraorbital flanges, which, according to Smith (2009), are present

Fig. 6.2 Cenozoic time scale for South American Land Mammal Ages (SALMAs)



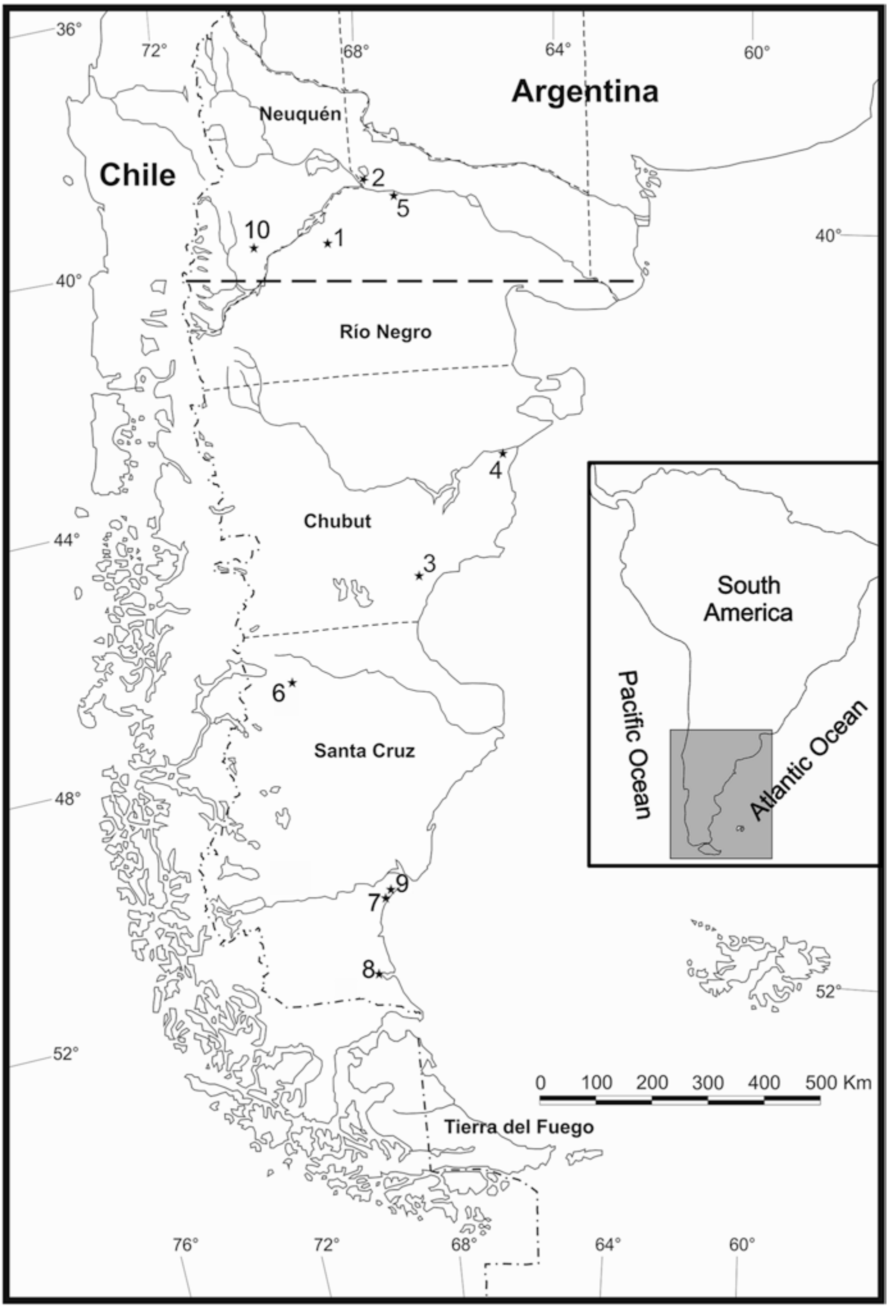


Fig. 6.3 Distribution of Patagonian fossil lizards: (*1*) La Buitrera (Apesteguía et al. 2005); (*2*) Cinco Saltos (Brizuela and Albino 2011); (*3*) Cabeza Blanca (Albino and Brizuela 2014b); (*4*) Gaiman (Albino 2008; Brizuela and Albino 2004); (*5*) Paso Córdova (Quadros et al. 2018); (*6*) Río Pinturas (pers. obs.); (*7*) La Cueva (Ameghino 1899; Albino et al. 2017); (*8*) Killik Aike Norte (Albino et al. 2017); (*9*) Monte León (Ameghino 1893; Brizuela and Albino 2008a; Albino et al. 2017); (*10*) Cañadón del Tordillo (Brizuela and Albino 2008b); the interrupted line shows the southern range limit of extant Tupinambinae

in Polychrotinae and Corytophaninae. These authors also observed that the dermal sculpturing morphology is similar to that of some Polychrotinae. Therefore, the Cretaceous specimen shows a possible Polychrotinae affinities, rather than to Tropidurinae (sensu Smith 2009).

Younger records of other non-acrodontan iguanians in the Upper Cretaceous of South America are represented by two extinct genera and species coming from Brazil: *Brasiliguana prudentis* from the Turonian-Santonian (Nava and Martinelli 2011) and *Pristiguana brasiliensis* from the Maastrichtian (Estes and Price 1973). Hence, the Patagonian specimen together with the species from Brazil supports the idea that, by the phase of the Laurasia-Gondwana division, the Iguania, and possibly the pleurodont Iguanidae clade, constituted already part of the herpetological communities of South America.

Indeterminate non-acrodontan dentaries were mentioned for the Campanian-Maastrichtian of Patagonia (Leanza et al. 2004; Albino 2007; Simões et al. 2017), but they have been recognized as recent remains (Albino 2011).

Later to the Upper Cretaceous, an Early Palaeocene dentary from the Tiupampan SALMA of Bolivia (Rage 1991) could be the earliest Iguanidae in the South American Cenozoic. A well-preserved mandible and a fragment of a maxilla reported for the Early Eocene (Itaboraian SALMA) of Brazil (Carvalho 2001) are consistent with the Mesozoic and Early Palaeocene record, supporting an ancient presence of Iguanidae in South America, but the material is not sufficiently well preserved to provide evidence of relationships with any current iguanid subfamily.

During a long time, the fossil record of Iguania in South America had an occurrence large gap between the Early Eocene and Early Miocene (Albino 2011; Albino and Brizuela 2014a). Recently, fossils found in levels attributed to the Late Oligocene of the Sarmiento Formation (Deseadan SALMA) at the locality of Cabeza Blanca, in Chubut Province [Fig. 6.3 (3)], partially fill this interval (Albino and Brizuela 2014b). The squamates recovered in this Patagonian site include two remains which belong to lizards: a tooth-bearing fragment appertaining to a maxilla or dentary (MPEF PV 1460) and an isolated presacral vertebra (MPEF PV 1463). The first was assigned to an indeterminate Iguanidae, whereas the latter probably belongs to an Iguaninae (Albino and Brizuela 2014b). Until the moment, no other Palaeogene iguanian was reported for South America.

For the Neogene, the Early Miocene fossil-bearing beds of the Sarmiento Formation at Gaiman [Fig. 6.3 (4)], in Chubut Province (Colhuehuapian SALMA), have provided one of the most relevant associations of South American fossil lizards where both iguanians and scincomorphs are present (Brizuela and Albino 2004; Albino 2008). Iguania are well represented by many fragmentary remains deposited in MPEF PV and MLP, most of them indeterminate at low taxonomic levels. Among the best-preserved specimens, dentaries and maxillae assigned to extant iguanian genera (*Pristidactylus* and *Liolaemus*) were recognized for first time (Albino 2008). The calibration of the Colhuehuapian SALMA was recently dated around 20–21 Ma (Dunn et al. 2013); this means that the mentioned genera are old components of the Patagonian lizard communities since they are presently diverse in this territory.

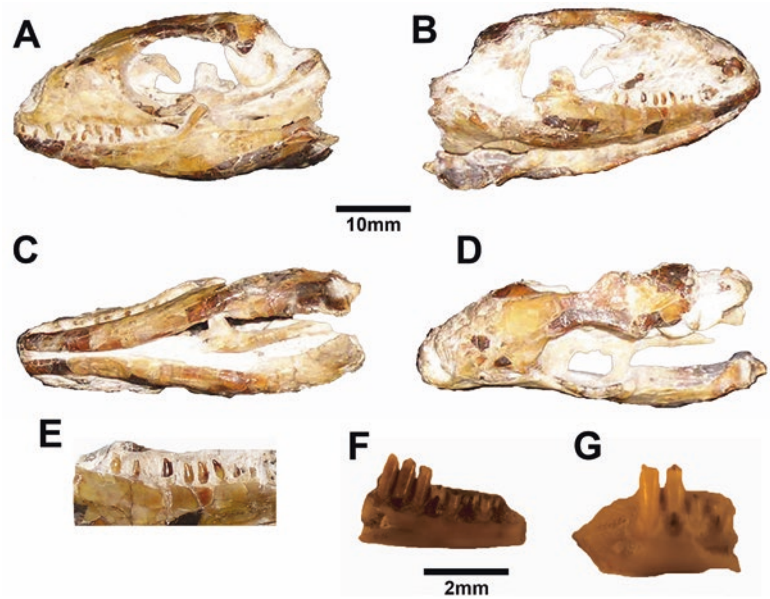


Fig. 6.4 (**a**–**e**) *Callopistes* from the early Miocene of Chichinales, skull in left (**a**), right (**b**), ventral (**c**) and dorsal (**d**) views; teeth of the right dentary (**e**); (**f**–**g**) fragmentary toothed remains of probable Iguania from the early Miocene of Río Pinturas

The Pinturan SALMA (Early Miocene) in Ea. Los Toldos, Río Pinturas, Santa Cruz Province [Fig. 6.3 (6)], provided highly fragmentary and undescribed remains (MACN-SC 316 and 317) of probable Iguania (Fig. 6.4, personal observation).

Iguanians have also been recognized in various Santacrucian sites (Albino 1996, 2011). In 1899, Florentino Ameghino erected the extinct iguanid genus *Erichosaurus* based on tooth-bearing remains recovered from sediments of the Santa Cruz Formation (Santacrucian SALMA) in the locality La Cueva, southeastern Santa Cruz Province [Fig. 6.3 (7)]. The age of the Santa Cruz Formation is currently estimated in about 18 to 16 Ma, corresponding to the late Early Miocene (Perkins et al. 2012). Ameghino (1899) described three species of *Erichosaurus* from this formation (*E. diminutus*, *E. bombimaxilla* and *E. debilis*), which Estes (1983) considered nomina dubia. A preliminary revision of the remains was made newly by Fernicola and Albino (2012), invalidating *Erichosaurus* and its species. The holotype of *Erichosaurus debilis* is represented by a right dentary articulated to the surangular (MACN A 5807), whereas that of *Erichosaurus diminutus* is a right maxilla (MACN A 2272). The specimens were at last redescribed by Albino et al. (2017), concluding that *E. debilis* and *E. diminutus* are indeterminate species of the extant polichrotine *Pristidactylus*. With respect to the holotype of *E. bombimaxilla*, it includes three fragments of toothed bones (MACN A 2283a, b and c) presumably corresponding to a right dentary of a single individual. It has been identified as an indeterminate iguanid (Albino et al. 2017). In addition, a new partial left hemimandible, including splenial and dentary (MPM PV 4337), was collected not long ago in Santacrucian levels of the locality Killik Aike Norte, the southernmost locality where Cenozoic lizards were found [Fig. 6.3 (8)]. It also corresponds to an indeterminate species of the genus *Pristidactylus* (Albino et al. 2017), but this species would be clearly different from that represented by the specimen MACN A 5807. Dimensions of the maxilla MACN A 2272 are not equivalent to those of neither MACN A 5807 nor MPM PV 4337, although this could be because it corresponds to a younger individual of one of these species (Albino et al. 2017).

Other reports of Iguania in Patagonia come from Quaternary archaeological sites of Mendoza (*Leiosaurus*) and Santa Cruz Provinces (*Liolaemus*) (Mengoni Goñalons and Silveira 1976; Van Devender 1977; Albino and Franco 2011; Albino 2017).

Scincomorpha Cretaceous lizard remains from Brazil and Argentina provide evidence about the presence of Scincomorpha in South America since the Mesozoic. The oldest scincomorph lizard is the recently described *Calanguban alamoi* from the Early Cretaceous of northeastern Brazil (Simões et al. 2014), which, together with *Tijubina pontei* (Bonfim-Júnior and Marques 1997) and *Olindalacerta brasiliensis* (Evans and Yabumoto 1998) from the same Crato Formation, represent the oldest squamates known to date in South America.

With respect to Patagonia, Brizuela and Albino (2011) have tentatively assigned a poorly preserved dentary from the Upper Cretaceous of northern Patagonia to the Scincomorpha. The material, badly preserved, comes from deposits of the Anacleto Formation at Cinco Saltos, Río Negro Province [Fig. 6.3 (2)]. This dentary reinforces the evidence given by *Calanguban* about the presence of Scleroglossa in the South American Cretaceous. Within the Scincomorpha, the Patagonian dentary shows affinities with the Scincoidea suggesting that Scincoidea-like lizards would have had Gondwanan distribution (Brizuela and Albino 2011).

Cenozoic South American scincomorphs also constitute part of the diverse, but undescribed, Itaboraian lizard fauna of Brazil (Carvalho 2001). They demonstrate that the principal clades of lizards probably were diversified in South America at least since the Early Eocene (Albino 2011). Early Eocene deposits of the Lumbrera Formation in northwestern Argentina (Salta Province) provided remains of an extinct teiid lizard (Tupinambinae, *Lumbrerasaurus scagliai*) corroborating the presence of scincomorphs in the Palaeogene (Brizuela and Albino 2016). In spite of this early record, scincomorphs are completely absent from the Palaeogene of Patagonia.

In contrast with the Palaeogene, Neogene deposits of Patagonia are relatively fertile in scincomorph remains, including extant genera of teiids. Early Miocene deposits of Gaiman [Chubut Province, Fig. 6.3 (4)] and Chinchinales [Río Negro Province, Fig. 6.3 (5)], provided relevant Colhuehuapian lizard remains that include the genera *Tupinambis* and *Callopistes*, respectively (Fig. 6.4) (Brizuela and Albino 2004; Quadros et al. 2018). These records support the minimum age of origin of both genera in ~20–21 Ma. Brizuela and Albino (2004) first described remains attributed to *Tupinambis* based on fragmentary dentaries and maxillae deposited in the MACN Pv, whereas the articulated skull assigned to *Callopistes* is placed in the MPCN.

In 1893, Florentino Ameghino named two reptilian taxa for three small, fragmentary jaws from the Miocene of southeastern Argentina ("*Diasemosaurus occidentalis*" and "*Dibolosodon typicus*"), but he never described the specimens in detail or figured them. The remains had been discovered in Monte León locality [Fig. 6.3 (9)], in deposits currently considered belonging to the Santacrucian SALMA (late Early Miocene). Brizuela and Albino (2008a) redescribed these specimens and identified them as fossil dentaries (MACN A 621 and MACN A 5806-a) and a maxilla (MACN A 5806-b) of an indeterminate species of the extant teiid *Tupinambis*. They constitute the southernmost records of teiids.

Deposits from the Colloncuran (Mid-Miocene) at Cañadòn del Tordillo, near Piedra del Águila [Neuquén Province, Fig. 6.3 (10)], also contributed with remains of a teiid Tupinambine (*Tupinambis* sp. or *Crocodilurus* sp., Brizuela and Albino 2008b). Excluding the iguanian specimens coming from archaeological sites, the Colloncuran remains constitute the youngest fossil record of lizards in Patagonia.

6.6 Origin and Evolution of the Lizard Fauna of Patagonia Based on the Fossil Record

In 1983, Richard Estes proposed a hypothesis about the early evolution of lizards in which the separation of Laurasia and Gondwana during the Jurassic produced northern populations of scleroglossans and southern ones of iguanians. As a result of the breakup of Gondwana, South America and Antarctica formed an independent island continent that was isolated to the north and east by oceans. According to Presch (1974), Estes (1983) and Estes and Báez (1985), a short terrestrial connection between North America and northern South America occurred during the Upper Cretaceous, permitting migration of vertebrates in both senses; thus, iguanians would have migrated to the North whereas scleroglossans (teiioids) to the South. Recent discoveries suggest that the earliest radiation of Iguania, and then the separation of Iguania and Scleroglossa, could have taken place at least at the end of the Triassic, before the fragmentation of the Pangaean supercontinent (Evans 2003). Based on the fossil record detailed here, it is possible to support the idea that the Iguania inhabited South America and, in particular, Patagonia, as early as by the phase of the Laurasia-Gondwana division. The Early Cretaceous South American lizard *Calanguban* suggests that scincomorphs were already present in this continent during the Aptian/Albian. In addition, the discovery of an acrodontan lizard (*Gueragama sulamericana*) in the Turonian-Campanian of Brazil provides evidence that a group of lizards, which is entirely absent in South America today, occurred in this continent back in the Cretaceous (Simões et al. 2017). This whole scenario suggests that the pattern of distribution of daughter lineages on Laurasia and Gondwana was probably far more complex than imagined. Thus, future discoveries of South

American fossil lizards could provide better evidence in relation to the early diversification of squamates.

As already mentioned, during the Cretaceous there was a global climatic condition much warmer than today, geographically uniform and extended to the poles (Nullo and Combina 2011). Favoured by the temperate climate conditions, relatively large-bodied snakes were frequent components of the Patagonian Cretaceous herpetofauna (Albino and Brizuela 2014a), whereas both iguanians and scincomorphs lizards, found in the same deposits that some of these snakes, were of small size. Presumably, other reptiles, as sphenodonts and dinosaurs, which were numerous and represented by a huge diversity of forms (Leanza et al. 2004), occupied the niches appropriate for large-bodied lizards. This would explain the absence of large lizards in the Patagonian Cretaceous.

For the Late Palaeogene, the presence of an Iguaninae at a latitude of 45° S in the late Oligocene of Patagonia (Albino and Brizuela 2014b) is unexpected because these lizards are presently absent from the Argentine territory. Extant Iguaninae are mainly distributed from United States through Central America and the Caribbean, reaching Brazil and Paraguay in South America; hence, the iguanine recovered in the Patagonian Palaeogene greatly exceeds the present range of distribution of the group. This could be explained considering that a global warming event occurred during the Late Oligocene (Nullo and Combina 2011) potentially extending the climatological conditions necessary to support thermal requirements of the iguanines and thus allowing their presence as south as Patagonia. Iguanines are known from the Late Eocene of North America at equivalent mid-latitudes (46° N) supporting a greater distribution in the Palaeogene in comparison to the present day (Albino and Brizuela 2014b).

With respect to the Neogene, Colhuehuapian lizards of Patagonia include earliest records of extant genera of Iguanidae (*Liolaemus*, *Pristidactylus*) and Teiidae (*Tupinambis*, *Callopistes*). At least two of these genera (*Pristidactylus* and *Tupinambis*) were also recorded for the Santacrucian. At present, iguanids inhabit as south as the Tierra del Fuego Island (Cei 1986). The material from the Santacrucian represents the southernmost fossil records of lizards in South America and indicates that iguanids distributed in southern Patagonia as back as the late Early Miocene (Albino et al. 2017).

According to data regarding present distribution of *Liolaemus* and *Pristidactylus* in Patagonia (Breitman et al. 2014; Minoli et al. 2015), the Miocene record of *Liolaemus* at the locality of Gaiman, in Chubut Province, does not contrast with its current range of distribution, whereas the fossil record of *Pristidactylus* is rather southern that at the present time. In Argentina, six species of *Pristidactylus* are distributed in disjunct areas over a 29° to 45° S latitudinal range (Minoli and Avila 2011). The Early Miocene distribution of the genus in Gaiman locality does not coincide with the reported present distribution of the genus in this department, although it has been recognized at such latitudes (43° S) and up to the northernmost limit of the Santa Cruz Province (46° S) (Minoli and Avila 2011; Avila et al. 2018). The late Early Miocene record of the genus in southern Santa Cruz Province (beyond the 50° S) implies a more widespread range of dispersion to the south (Albino et al. 2017).

Tupinambine teiids, and especially the genus *Tupinambis*, also have a past distribution extended beyond the current limit that is at the 40° S (Fig. 6.3). They reached the 43° S during the Colhuehuapian (Brizuela and Albino 2004), whereas they approximately reached the 50° S and 70° W during the Santacrucian and Colloncuran, respectively (Brizuela and Albino 2008a, b). Therefore, the distributional range of both *Pristidactylus* and the tupinambines during the Early Miocene could be explained taking into account the warm conditions developed at this time as far as southern Patagonia, from the incipient eastern slopes of the Andes to the Atlantic coast. These conditions would have extended at least until the Mid-Miocene. The progressive decrease in temperatures through the Middle–Late Miocene and later (Nullo and Combina 2011) would have caused the restriction in the distribution of *Pristidactylus* and tupinambine teiids to environments with more temperate climates (Albino 2008, 2011; Brizuela and Albino 2004, 2008b; Albino and Brizuela 2014a, 2015). The present southernmost population of *Tupinambis rufescens* in northern Patagonia (Cei and Scolaro 1982) is likely a relic of its broader distribution. The distribution and diversity of *Pristidactylus* at both sides of the Andes (Minoli and Avila 2011) probably were determined by the elevation of the Andean cordillera during the Miocene, producing subsequent vicariance events, as it was the case for the genus *Liolaemus* (Albino 2008).

The cooling after the Miocene Climatic Optimum event in southern South America was accompanied with the retreat of an important marine transgression ("Mar Paranaense") and the uplift of the Andes (Quechua phase) which gave way to the "Edad de las Planicies Australes" during the Late Miocene–Early Pliocene (Pascual et al. 1996). In Patagonia, the climate became cooler and the vegetation was similar to the present, with the steppe expanding across extra-Andean Patagonia, and the forest restricted to the westernmost areas where rainfall was still abundant (Nullo and Combina 2011). Unfortunately, fossil records of Patagonian lizards after the Colloncuran are so far absent.

With respect to the tupinambine teiid *Callopistes*, the current presence of the two extant species *Callopistes flavipunctatus* and *C. maculatus* is restricted to a trans-Andean distribution, throughout Chile, Peru and Southern Ecuador. The unique described fossil remains of the genus came from the Montehermosan SALMA (Late Miocene–Early Pliocene) in southeastern Buenos Aires Province, on the Atlantic coast of Argentina. This record corresponds to the extinct species *Callopistes bicuspidatus* (Chani 1976; Brizuela and Albino 2017). Recently, a new fossil record of the genus was reported for the Colhuehuapian of Patagonia (Quadros et al. 2018) confirming that *Callopistes* had a much broader distribution in the past, reaching cis-Andean areas of the Pampean Region and Patagonia. Molecular data indicate that *Callopistes* would have diverged from all other Tupinambinae during the Palaeocene (Giugliano et al. 2007). The uplift of the mountain system during the Miocene could have caused the divergence of the species at both sides of the Andes (Brizuela and Albino 2017). The present distribution and diversity of the genus is therefore relictual.

6.7 Conclusions

The fossil record of squamates in Patagonia is still scarce but it represents one of the most prolific of entire South America. Observation of the current fossil record reveals that some taxa comprising the present Patagonian herpetofauna have a considerable antiquity in this region. The presence of lizards in Patagonia extends back as far as the Late Mesozoic.

The Patagonian Mesozoic record of lizards gives a noticeable contrast to the pattern of conservation of snakes, which produced exquisitely preserved skeletons that provide relevant phylogenetic information about the origin and basal evolution of the clade (Albino and Brizuela 2014a, 2015). The deposits where snakes have been recovered but lizards have not are also rich in medium- to large-bodied vertebrate taxa as crocodiles, dinosaurs and birds (Leanza et al. 2004). Taking into account that lizards are usually recovered in Mesozoic deposits of other territories, especially of Laurasia (Evans 2003), the scarcity of lizard remains in the Patagonian Mesozoic could be consequence of a combination of two factors: the small size of the specimens that inhabited Patagonia and the unusual presence of lizards in the vertebrate communities of this region. Nevertheless, the presence of both iguanians and scincomorphs in the Patagonian Cretaceous, together with the Brazilian Mesozoic record, reveal that South America would have played an important, and still unknown, role in the early diversification of squamates.

Two fundamental gaps currently exist in the lizard fossil record of Patagonia: one is from the Late Cretaceous (Anacleto Formation) to the Late Oligocene (at least 50 million years), and the other is from the Mid-Miocene to the Holocene (Figs. 6.1 and 6.2). The Mesozoic is poorly sampled by comparison with the Cenozoic. Therefore, the record is not complete enough to give a reliable picture of the evolution of lizards in Patagonia. The Miocene interval has produced most of the taxonomically informative fossil remains, including present-day taxa as the genera *Liolaemus*, *Pristidactylus*, *Tupinambis* and *Callopistes*.

Palaeoclimatic and palaeoenvironmental changes affected the distributional patterns of lizards in Patagonia. The trend towards global cooling from the Mesozoic to the Late Miocene, and the changes of biomes from tropical forests to steppes, would have affected the Patagonian lizard fauna restricting to the north the distribution of *Pristidactylus* and *Tupinambis* that reached the southernmost localities during the Early Miocene. Palaeogeographical changes, especially the uplift of the Andes, would have conditioned the occurrence of vicariance events with subsequent diversification at both sides of the Andes in *Liolaemus* and *Pristidactylus*, whereas unknown event(s) caused the disappearance of *Callopistes* east of the Andes, which signify a decreasing of its diversity.

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