

# An Overview of the South American Fossil Squamates

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## Abstract

The evolution of squamates in South America is the result of the complex geological and paleoclimatic history of this part of the world. The incomplete and episodic fossil record allows us to know only a small part of this evolution. Most Mesozoic squamate remains come from the Patagonian region, but remarkable specimens have also been recovered from Brazil. Both major squamate clades (Iguania and Scleroglossa) are present in the South American Mesozoic. Remains of Mesozoic snakes are common and diverse in Cretaceous deposits, including some of the most primitive terrestrial forms. Paleogene and Neogene squamate remains have been recognized from Argentina, Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. Paleogene lizard record appears to be scarce in comparison to that of the Mesozoic, whereas snakes show an important Paleogene diversity. At least two extant boid snakes appeared during this epoch (*Boa* and *Corallus*). The South American Miocene included some extant genera of Iguania, Teiidae, and Boidae but extinct genera were also present. “Colubrids” appeared at the early Miocene, whereas the first viperid is known from the late Miocene. Most of the Paleogene and early Neogene squamate families and genera have been recognized outside their current range of distribution following favorable climatic conditions for ectothermic vertebrates. During the latest Miocene and Pliocene few extant squamate taxa are found to occur outside their present distribution. The earliest amphisbaenian of South America is known from the Pliocene. Most Pleistocene and Holocene squamate remains are assigned to living genera, and some extant species were recognized. *Anat Rec*, 297:349–368, 2014. © 2014 Wiley Periodicals, Inc.

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Squamata is the most diverse clade of modern reptiles, including more than 9,400 extant species distributed among lizards, amphisbaenians, and snakes (Vitt and Caldwell, 2008; Uetz et al., 2013). The South American fossil record of squamates includes specimens of extant families and genera, as well as extinct forms. Previous studies have summarized and interpreted the fossil record of South American squamates (Báez and Gasparini, 1977, 1979; Gasparini et al., 1986; Albino, 1996a, 2007, 2011a); nevertheless, the earliest reviews were based on scarce, fragmentary, and chronologically discontinuous records supported mostly by fossils studied in the 19th and early 20th centuries. These early studies also lacked strong taxonomic identifications (Báez and Gasparini, 1977, 1979; Gasparini et al., 1986).

Subsequent reviews included new findings, better identifications at low systematic levels, and discussions about the evolution of the squamate fauna (Albino, 1996a,

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2007, 2011a). They were especially focused on the Patagonian fossil record, also providing information on the origin of extant genera of the present South American herpetofauna.

Although fossil squamates have a relatively low diversity compared to living squamates and other clades of reptiles, they provide useful information to reconstruct the evolutionary history of the group. This article is an attempt to concentrate all the present information on South American fossil squamates with the exclusion of strictly aquatic taxa (mosasaurs and their allies), and centered on the biogeographical changes through time.

**MATERIALS AND METHODS**

Fossil materials revised for this work are deposited in the following institutions of Argentina: MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; MLP, Museo de La Plata; MMP, Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”; MPEF, Museo Paleontológico “Egidio Feruglio”; MMH, Museo Municipal de Monte Hermoso; and GHUNLPam, Facultad de Ciencias Exactas y Naturales of the Universidad Nacional de La Pampa.

Comparative osteological specimens used for this revision belong to the following institutions: FML, Fundación Miguel Lillo, Argentina; FMNH, Field Museum of Natural History, USA; MCZ, Museum of Comparative Zoology, USA; MNHN, Museo Nacional de Historia Natural, Chile; MZUSP, Museu da Zoologia, Universidade de São Paulo, Brazil; NMNH, National Museum of Natural History, USA; UMMZ, University of Michigan Museum of Zoology, USA; UNC, Universidad Nacional de Córdoba, Argentina; UNMdP-O, Colección Herpetológica - Sección Osteología, Universidad Nacional de Mar del Plata, Argentina; UNNE, Universidad Nacional del Noreste, Argentina; UNRC, Universidad Nacional de Río Cuarto, Argentina.

For squamate systematic relationships we follow the morphology-based phylogenetic analyses of Gauthier et al. (2012). Paraphyletic taxa are denoted in quotes, whereas metataxa are designated by an asterisk. The biochronological context for the Cenozoic used in this work is based on the South American Land Mammal Ages (SALMAs of Pascual et al., 1996). We follow the calibration given by Gelfo et al. (2009) and Woodburne et al. (2013) for the Patagonian Paleogene, and Vucetich et al. (2007), Cione et al. (2007), and Cione and Báez (2007) for the remaining SALMAs (Fig. 1).

**RESULTS AND DISCUSSION**

**Early South American Squamates**

Crown squamates are known from the Jurassic (Evans, 2003; Longrich et al., 2012a) and their stem is thought to extend deep into the Triassic (Gauthier et al., 2012). Currently, however, Jurassic squamate remains are unknown in South America. Early studies (Huene, 1931; Casamiquela, 1962, 1975; Evans, 2003) had referred different fossils from the Jurassic and Cretaceous of Argentina to Squamata; nonetheless, their identity as squamates has been challenged by others (Estes, 1983; Albino, 2007).

The South American Cretaceous record of squamates is diverse and abundant, and includes both marine and

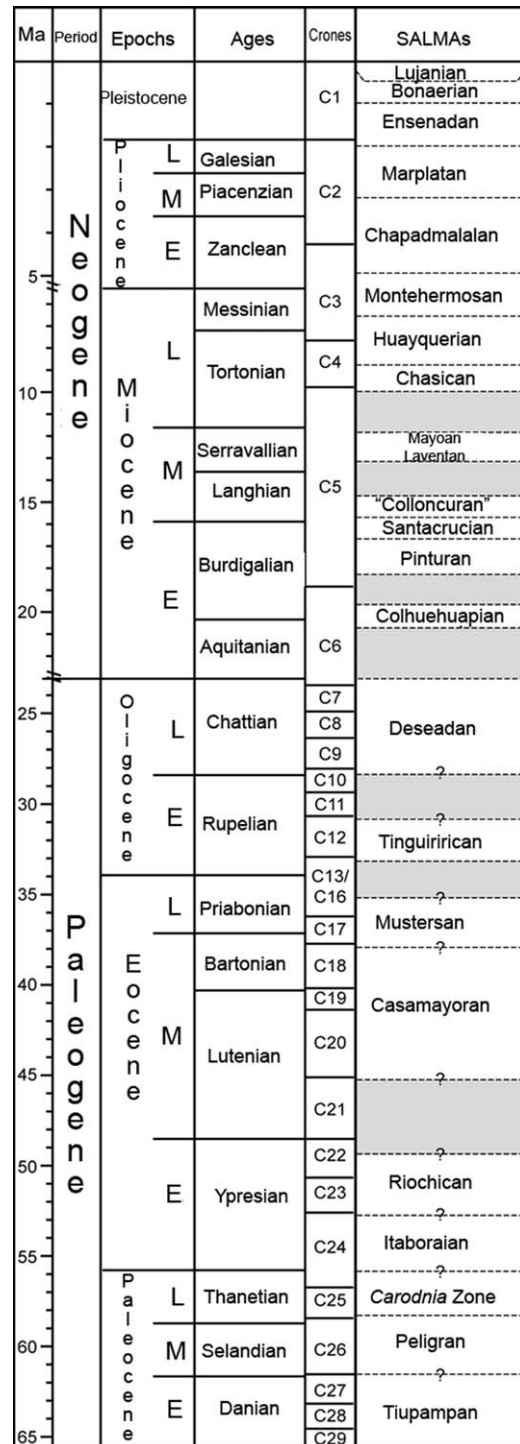


Fig. 1. Paleocene to Recent time scale including time scale for Cenozoic mammalian faunas of South America (SALMA).

continental taxa. The earliest irrefutable lizards recovered in South America are from the late Lower Cretaceous of Brazil (Evans and Yabumoto, 1998; Simões, 2012). This Aptian–Albian lizard fauna from the Araripe Basin is constituted by the very well-preserved *Olindalacerta brasiliensis* (Evans and Yabumoto, 1998) and

*Tijubina ponteii* (Simões, 2012). Evans and Yabumoto (1998) conducted a preliminary phylogenetic analysis to allocate *Olindalacerta* among squamates and, although it forms a sister group to Scleroglossa with *Eichstaettisaurus* (late Jurassic of Germany), it also shows characters shared with the iguanids (i.e., deep pleurodont implantation and long posterodorsal process of the dentary, Evans and Yabumoto, 1998). Likewise, the phylogenetic position of *Tijubina* is very unstable. It was originally classified as a Teiidae (Bonfim-Júnior and Marques, 1997), later excluded from Squamata and referred to Rhynchocephalia (Martill and Frey, 1998), and once more included in Squamata, this time close to the root of the clade (Bonfim-Júnior and Avilla, 2002). More recently, Simões (2012) regarded *Tijubina* as a basal scleroglossan, more derived than *Olindalacerta* and outside Autarchoglossa. To date no definitive phylogenetic analysis of Squamata has included these Aptian–Albian lizards so it is unclear whether or not they are stem Scleroglossa from Gondwana. A further complication is that these fossils are from skeletally immature specimens (Evans and Yabumoto, 1998; Simões, 2012), an issue that is problematic in character coding while building a character matrix for phylogenetic analyses.

The Upper Cretaceous lizard fossil record of South America is composed of isolated fragments from Argentina and Brazil. The earliest of these records is of a frontal from the Cenomanian–Turonian of Patagonia described by Apesteguía et al. (2005). These authors consider that the fused and very constricted frontal (i.e., hour-glass shape) with pronounced ornamentation is of an iguanian (possibly Iguanidae). However, Daza et al. (2012) believe that the character combination listed by Apesteguía et al. (2005) is not exclusive to any lizard group. Independently, and among extant and extinct lizards of Argentina, we only observed the simultaneous presence of these characters in Iguanidae. Thus, we consider valid the tentative assignment given by Apesteguía et al. (2005). Among Iguanidae, Apesteguía et al. (2005) suggested similarities in the dermal sculpturing with the extant tropidurine\* *Liolaemus*. However, the frontal exhibits well-developed supraorbital flanges (Fig. 2 of Apesteguía et al., 2005), that, according to Smith (2009), are present in Polychrotinae\* and Corytophaninae. Also, the dermal sculpturing morphology is similar to that of some Polychrotinae\* (personal observations). These notes suggest possible Polychrotinae\* affinities of this fossil, rather than to Tropidurinae\* (sensu Smith, 2009). The frontal described by Apesteguía et al. (2005) extends the South American presence of Iguania by 30 Ma, to the Cenomanian–Turonian, from the earlier described *Pristiguana* (Maastrichtian, see below).

Also from the Upper Cretaceous, but from sediments of the Turonian–Santonian of Brazil, Nava and Martinelli (2011) recognized a small isolated maxilla which was used to erect the species *Brasiliguana prudentis*. This taxon is considered a member of Iguanidae (sensu Gauthier et al., 2012) based on the presence of a weakly inclined anterior margin of the maxillary nasal process and the pleurodont tooth implantation (Nava and Martinelli, 2011). The maxilla of *Brasiliguana* does not present a strong/large palatine process (Fig. 2 of Nava and Martinelli, 2011), a condition shared with Corytophaninae, Polychrotinae\*, Iguaninae, and Hoplocercinae (Smith, 2009). From the same Brazilian levels as *Brasili-*

*guana*, Candeiro et al. (2009) described an indeterminate non-Serpentes squamate represented by a small and articulated portion of an axial skeleton bearing dorsal vertebrae. Unfortunately no further systematic discussion is possible.

Apart from these Upper Cretaceous records, a poorly preserved dentary from the early Campanian of northern Patagonia (Fig. 2) has been tentatively assigned to the Scincomorpha (sensu Gauthier et al., 2012) by Brizuela and Albino (2011). Not considering the lizards from the Araripe basin of Brazil mentioned above, whose relationships are unclear, this sole dentary is the only evidence of a member of the Scleroglossa in the South American Cretaceous. Within this large clade the Campanian dentary shows affinities with the Scincoidea (sensu Gauthier et al., 2012), and, along with the probable Cordylidae *Konkasaurus* from the Maastrichtian of Madagascar (Krause et al., 2003), suggests that scincoidea-like lizards would have had Gondwanan distribution (Brizuela and Albino, 2011).

The latest Cretaceous lizard comes from the Maastrichtian of Brazil. Estes and Price (1973) erected *Pristiguana brasiliensis* from cranial and appendicular skeletal remains, that they considered of an extinct crown Iguanidae. Though the relationships of *Pristiguana* to other iguanians are unclear, Estes and Price (1973) noticed some similarities with *Enyalioides*, *Hoplocercus* and *Morunasaurus* (e.g., large splenial). They also stated that some characters of the fossil (i.e., tooth morphology, open Meckelian canal, and frontal proportions) are similar to those of Teiidae. Borsuk-Bialynicka and Moody (1984) considered that the arguments for the Iguanidae assignment are not convincing and that *Pristiguana* could be assigned to the Teiidae with equally convincing counter arguments. More recently, Daza et al. (2012) conducted a phylogenetic analysis of Squamata, focused on the Iguania, where they incorporated *Pristiguana*. In this analysis *Pristiguana* forms a clade with *Huehuecuetzpalli* (early Cretaceous of Mexico) sister to Iguania. Therefore, according to Daza et al. (2012), *Pristiguana* is not a member of the crown Iguanidae as argued Estes and Price (1973). Current phylogenetic position of *Pristiguana* is poorly supported, and needs to be reconsidered. The effect of the low number of scored characters (8.8%, Daza et al., 2012) needs to be evaluated critically; it is also possible that direct examination of the specimen could improve our understanding of the phylogenetic position of this fossil species. Nevertheless, without the referring of *Pristiguana* into Iguanidae, the Upper Cretaceous iguanids mentioned above (Apesteguía et al., 2005; Nava and Martinelli, 2011), along with Campanian *Cnephasaurus* and Maastrichtian *Pariguana* from North America (Gao and Fox, 1996; Longrich et al., 2012a), would indicate an important distribution of the Iguanidae in the Americas prior to the end of the Cretaceous.

Overall the South American Mesozoic lizard record is incomplete. During the Lower Cretaceous the lizard fossils are exceptionally well preserved, but restricted to the Araripe fauna of Brazil, with most-likely basal forms of unclear phylogenetic relationships. The situation in the Upper Cretaceous is inverted with poorly preserved fossils that are widely dispersed. The Scleroglossa Mesozoic record is very poor, limited to a tentatively referred single dentary from the early Campanian of Patagonia.



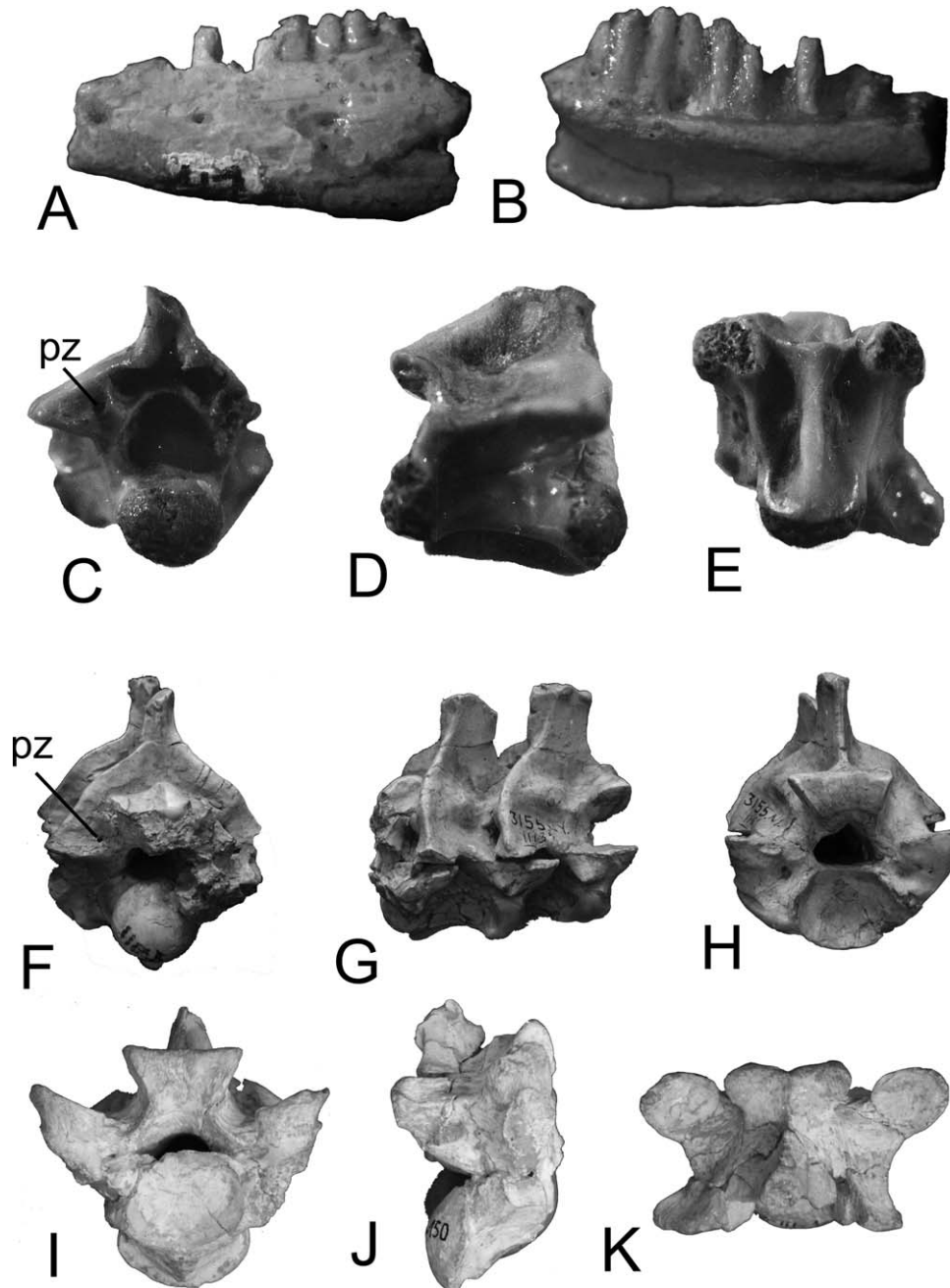


Fig. 2. Some Mesozoic and Paleogene squamate taxa cited in the text. **A–B**, dentary of Scincomorpha in labial (A) and lingual (B) views; **C–E**, trunk vertebra of *Almitophis argentinus* in posterior (C), lateral (D) and ventral (E) views; **F–H**, trunk vertebra of *Madtsoia bai* in posterior (F), lateral (G) and anterior (H) views; **I–K**, trunk vertebra of *Chubutophis grandis* in anterior (I), lateral (J) and dorsal (K) views; pz, parazygantral foramen.

Altogether, present data suggests that the South-American Mesozoic lizards were probably more diverse and abundant than previously thought when the existing known data were restricted to few taxa (e.g., Evans, 2003). Taxa with well-supported systematic assignments (e.g., Nava and Martinelli, 2011; Brizuela and Albino, 2011) correspond to the two main clades, Iguania and Scleroglossa (sensu Gauthier et al., 2012), suggesting

that Mesozoic lizard diversity is not properly illustrated by the existing fossil record and that more taxa will eventually appear.

With respect to Serpentes, remains of this clade are common and diverse in Cretaceous deposits from South America, especially in Patagonia. The record includes some of the most primitive forms of terrestrial snakes, the oldest of which is *Najash rionegrina* from the early

Upper Cretaceous (Cenomanian–Turonian) of Patagonia (Apesteguía and Zaher, 2006). This species was described based on cranial elements and a nearly complete and articulated postcranial skeleton that included a sacrum and almost complete hind limbs (Apesteguía and Zaher, 2006; Zaher et al., 2009). A phylogenetic analysis of these fossil materials indicates *Najash* to be the most basal snake, lying outside the clade consisting of all other snakes (Apesteguía and Zaher, 2006; Zaher et al., 2009). Recently, Palci et al. (2013) modified the diagnosis of this species in the light of relevant considerations that cast doubt on the attribution of type and referred specimens. According to the reevaluation of the fossil material, the subsequent phylogenetic analyses rejected the hypothesis that *N. rionegrina* occupies a position as the most basal snake. Depending on the outgroup, *Najash* is placed (1) in a position basal to all living snakes, but more derived than the fossil forms *Pachyrhachis*, *Eupodophis*, and *Haasiophis*, or (2) as the most basal representative of a clade of fossil snakes that is the sister group of living snakes, or (3) as the most basal representative of a clade of fossil snakes that is located between the Scolecophidia and the Alethinophidia (Palci et al., 2013). *Najash* would have been a snake with body size around two meters long (Zaher et al., 2009). This size is inconsistent with a subterranean lifestyle for this snake suggested by Apesteguía and Zaher (2006). The morphology of the vertebrae of *Najash* allows only for the exclusion of extreme ecological habits, thus, *Najash* would have been a semi-fossorial, semi-aquatic, or surface living form of snake (Albino, 2011a; Palci et al., 2013).

Another snake from the South American Upper Cretaceous is *Dinilyisia patagonica*, originally described by Smith-Woodward (1901) based on a specimen composed by a skull and associated fragments of vertebral column. This species is now the best characterized Cretaceous snake from several fragmentary cranial and postcranial skeletons recovered from various sites in Patagonia, from the Santonian to the early Campanian (Albino, 2007, 2011a). First, Smith-Woodward (1901) noticed *Dinilyisia* has resemblances with aniliids and booids. Then, Romer (1956) classified *Dinilyisia* in its own family, the Dinilysiidae, which is nested within the Booidea. Estes et al. (1970) conducted a detailed study of the skull and considered this snake to be closely related to aniliids and booids but with a greater number of lizard-like characteristics than those present in modern snakes. Rage (1977) estimated that *Dinilyisia* represents the sister group of macrostomatan snakes, whereas Hecht (1982) supported the relationships of *Dinilyisia* with aniliids and booids on the basis of the vertebral morphology. Rieppel (1979) regarded *Dinilyisia* as the sister group of the Alethinophidia. More recently, *Dinilyisia* has been included in several phylogenetic analyses (Caldwell, 1999; Rieppel and Zaher, 2000; Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon, 2002; Scanlon, 2006; Conrad, 2008; Zaher and Scanferla, 2011; Gauthier et al., 2012; Scanferla et al., 2013). All these recent hypotheses show *Dinilyisia* as a relatively basal snake appearing as the sister group of the Alethinophidia or as the sister group to all extant snakes (Scolecophidia + Alethinophidia). *Dinilyisia* was a medium-sized snake of around two meters long, with a relatively large head, and large, dorsally exposed orbits that presumably

exploited semi-aquatic or semi-fossorial environments (Albino and Caldwell, 2003; Albino, 2007).

The alternative phylogenetic positions of *Najash* and *Dinilyisia* demonstrate that non-fossorial snakes, with bodies greater than one meter long, likely consumed prey of diverse shapes and sizes, and appear to have developed early in snake phylogeny (pre-macrostromatan) (Albino and Caldwell, 2003; Albino, 2007, 2011a). Thus, they do not provide specific support to the presumption of a subterranean origin of snakes as opposed to the hypothesis of an aquatic origin for this group of squamates, but, together with the record of madtsoiids (see below), indicate that the earliest diversification of terrestrial snakes (i.e., not strictly aquatic nor subterranean) could have occurred in Gondwana (Albino, 2011a).

The record of South American Cretaceous snakes is enhanced with the occurrence of some extinct genera belonging to the Madtsoiidae. These were found in several sites from the Campanian–Maastrichtian of Patagonia (Albino, 1986, 1994, 1996a, 2000, 2007, 2011a; Martinelli and Forasiepi, 2004). The madtsoiids are interpreted as probably a monophyletic group (Scanlon, 1993, 2005; Albino, 1996a) that includes small, medium, and large-sized surface living forms. Recently, Mohabey et al. (2011) considered the presence of a large parazygantral foramen located within a fossa as the unique feature diagnosing Madtsoiidae, and they recognized this character as restricted to the Cretaceous–Paleogene large-bodied taxa *Madtsoia*, the African *Gigantophis*, and, possibly, the Australian *Wonambi* and *Yurlunggur*. However, the smaller Patagonian madtsoiid genera have exactly the same feature on their vertebrae (Albino, 1986, 1994), a large and deep parazygantral foramen adjacent to the zygantrum (Fig. 2). Mohabey et al. (2011) have not detailed arguments to refuse homology; then, this character seems to be a strong apomorphy uniting madtsoiids. Madtsoiids are described to comprise at least 10 genera (LaDuke et al., 2010), five of which have representatives in South American deposits from the Late Campanian–Early Maastrichtian to Eocene (Simpson, 1933; Hoffstetter, 1959; Albino, 1986, 1993, 1994, 1996a, 2000, 2007; Rage, 1998; Martinelli and Forasiepi, 2004). The phylogenetic information that they provide is limited because the remains consist mostly of isolated and fragmented vertebrae, although they are frequent in continental deposits of Cretaceous age. The genera of madtsoiids currently recognized in the Cretaceous of Patagonia include *Alamitophis* (with two species, *A. argentinus* and *A. elongatus*), *Patagoniophis* (*P. parvus*), and *Rionegrophis* (*R. madtsoioides*) (Albino, 1986, 1994). *Alamitophis* and *Patagoniophis* are also recorded from the early Eocene of Australia (Scanlon, 1993, 2005). The early Eocene of Australia also provided a rib fragment referred as cf. *Madtsoia* sp. (Scanlon, 2005), which is a genus of madtsoiid well documented in Paleogene deposits of Patagonia (see below). Thus, the chronological and geographical distribution of these three madtsoiid genera suggests a biogeographical continuity between Australia and southern South America extending across Antarctica between the late Cretaceous and the early Eocene (Scanlon, 1993, 2005; Albino, 2000, 2007). Although phylogenetic position of madtsoiids is debated, the distribution of madtsoiid genera during the Cretaceous and Paleogene in all major Gondwanan landmasses, except Antarctica (LaDuke et al., 2010) suggests

they may have been a product of the earliest Gondwanan diversification of terrestrial snakes as well as for *Najash* and *Dinilysia*.

Another South American Cretaceous snake is the probable “anilioid” *Australophis anilioides* from the Late Campanian–Early Maastrichtian (Gómez et al., 2008). “Anilioidea” is likely a paraphyletic group of basal alethinophidians, prior to the divergence of macrostomatan (sensu Lee and Scanlon, 2002; Gauthier et al., 2012). *Australophis* would be closer in morphology to early Cenozoic *Hoffstetterella* from Brazil and extant South American *Anilius* than to any other snake. This would suggest an early divergent lineage (Gómez et al., 2008). This snake is small, less than one meter in length, likely with fossorial habits similar to the remaining “anilioids.” Its prey was likely restricted to those smaller than its head diameter.

There are two additional Mesozoic squamates from the Campanian–Maastrichtian of South America with uncertain phylogenetic affinities. One of them is a dentary that Gómez (2011) found similar to dentaries of small madtsoiids and to those referred by Zaher et al. (2009) to the basal legged snake *Najash*. However, the dentaries referred to *Najash* by Zaher et al. (2009) have been recently removed from this taxon by Palci et al. (2013). The Campanian–Maastrichtian dentary was found associated with several isolated snake vertebrae of madtsoiids and it likely belongs to one of the already known madtsoiid taxa (Gómez, 2011). The other remains is an isolated vertebra distinct from *Najash*, *Dinilysia* and madtsoiids, and that lacks morphological affinities with any extant group (Albino, 2000). This specimen has been proposed to belong to *Serpentes incertae sedis*, although some plesiomorphic features were also recognized (Albino, 2000, 2007). Scanlon and Hocknull (2008) stated that this vertebra may not represent a snake but it rather resembles a specimen of cf. *Coniasaurus* sp. of Australia, an aquatic dolichosaur related to mosasaurs and snakes. This is probably the right conclusion about this vertebra (Albino, 2011a).

As a whole, the Mesozoic record of squamates suggests that lizards and snakes differ in their diversity and abundance in the Patagonian region through time. This disparity could be attributed, at least in part, to a biased fossil record because lizards are scarce in the Patagonian Cretaceous, but more abundant in other South American sites of the same age. This would demonstrate that they were usual components of the Mesozoic South American herpetofauna. At least two major clades of lizards that survive at the present are also found in the Mesozoic record: Iguania and Scincomorpha, whereas snake findings mostly include extinct and/or relatively basal representatives (*Najash*, *Dinilysia*, madtsoiids, and “anilioids”), most of them without well established relationships with the extant major clades Scolecophidia and Alethinophidia. The updated Mesozoic record demonstrates that South America was richer in both lizards and snakes than previously accepted, and that at least for snakes the southern continents played an important role in the early evolution of the group.

### The Poor Squamate Record of the South American Paleocene

Based on published data, the South American Paleocene lizard record appears to be scarce in comparison to

that of the Mesozoic, whereas snakes show an important Paleogene diversity but mostly concentrated in the Eocene. Nevertheless, unpublished observations provide evidence of a notable diversity of both Paleogene lizards and snakes in South America, including various genera and species of diverse clades. Patagonian deposits contrast with those of lower latitudes in having a relatively lower richness of fossils of lizards. It is not currently known whether the differences between these squamate faunas reflect the lack of lizards in southernmost Paleogene environments or poor sampling of small fossils in Patagonian Paleogene deposits.

Paleocene faunas of Patagonia, such as the well-known Peligran SALMA (Fig. 1), have not provided, thus far, remains of squamates, although lizards and snakes are well represented in other South American regions with Paleocene deposits (de Muizon et al., 1983; Rage, 1991; Head et al., 2009; Scanferla et al., 2013).

The early Paleocene of Tiupampa in Bolivia (Tiupampán SALMA, Fig. 1) has yielded several unnamed lizards and snakes. de Muizon et al. (1983) first noted lizard remains from the early Paleocene of Bolivia which was later listed by Rage (1991). This author described a dentary that has some characters that resemble those of the Teiidae, but since teeth would be deeply pleurodont, the author considered the specimen as of a probable Iguanidae. Several vertebrae were associated to this dentary but they were dismissed by Rage (1991) for systematic purposes. Five other tooth bearing fragments were also recovered from the Tiupampán of Bolivia and considered from different lizard taxa that cannot be allocated within Iguanidae, but without other diagnostic characteristics (Rage, 1991). If confirmed, the systematic placement of the Paleocene dentary to Iguanidae given by Rage (1991), it would be the earliest Iguanidae in the South-American Cenozoic and consistent with the Mesozoic record indicating an ancient presence of Iguanidae on the continent. Apart from the lizards, the Tiupampán fauna of Bolivia has produced snake vertebrae of diverse groups, including an indeterminate “anilioid,” at least two new unnamed genera of small to medium-sized booids, a madtsoiid or boid, and a tropidophiid, all of them indeterminate at lower taxonomic levels (de Muizon et al., 1983; Rage, 1991). This rich snake assemblage demonstrates that booids and tropidophiids were present in South America at least since the early Paleocene. More recently, a new genus and species of snake based on a partial skull was described from these sediments (*Kataria anisodonta*) representing the oldest macrostomatan skull recovered (Scanferla et al., 2013). The fossil mostly includes snout bones of an articulated skull. Its phylogenetic relationships show it would be a derived macrostomatan, basal to the Caenophidia+Tropidophiidae (Scanferla et al., 2013). This finding, together with other evidences, suggests that the origin and early diversification of derived macrostomatans may have taken place in southern continents during the early Cenozoic (Scanferla et al., 2013).

Apart from the records from Bolivia, an exceptionally large-bodied boine snake was described from the middle–late Paleocene of Colombia: *Titanoboa cerrejonensis*, based on articulated and isolated preloacal vertebrae from at least 28 individuals (Head et al., 2009). Vertebrae of *Titanoboa* are the largest recovered to date for any extant or fossil snake. The estimates of body size for



*Titanoboa* greatly exceed those for the largest verifiable body lengths for extant *Python* and *Eunectes* (Head et al., 2009). It would likely have had an anaconda-like ecology (semi-aquatic), with a body length of about 13 m, and a mass of about 1,135 kg, suggesting that this snake may have required a minimum mean annual temperature of 30–34°C to survive (Head et al., 2009). Phylogenetic relationships of *Titanoboa* among Boinae were not tested, although Head et al. (2009) united *Titanoboa* with the extant *Boa constrictor* based on the presence of paracotylar fossae and foramina. Also, the concave anterior border of the zygosphenes in dorsal view of *Titanoboa* vertebrae is a peculiar feature shared with *Boa constrictor* but not other extant boine genera (Albino, 2011b). Both of these characters together with a zygosphenes narrower than the cotyle (wider in *Boa*) only appear in combination in two Boinae from the Eocene of Patagonia: *Chubutophis grandis* from the Casamayoran, and an indeterminate genus from the Mustersan, suggesting closer relationships of Colombian *Titanoboa* with these two Patagonian snakes than to extant *Boa* (Albino, 2012).

Finally, Rage (1981) mentioned the presence of a snake of the genus *Coniophis* from Laguna Umayo, Peru (latest Paleocene–earliest Eocene), but the material has not yet been described.

### The Great Diversity of Eocene Squamates

In clear contrast with the Paleocene, the squamate record in the South American Eocene increases significantly in the diversity of identified taxa. Previous reports concerning South American Eocene squamates include a great diversity of lizards and snakes from São José de Itaboraí in Brazil (Albino, 1990; Rage, 1998, 2001, 2008; Carvalho, 2001), a number of snakes mainly distributed in Patagonian localities of Argentina (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1987, 1993, 1996a, 2011a, 2012; Albino and Carlini, 2008), an association of a lizard and a snake in northwestern Argentina (Donadío, 1985; Albino, 1989), and a marine palaeopheid snake from Ecuador (Hoffstetter, 1958).

**The Itaboraian squamate fauna.** Stratigraphic levels bearing Itaboraian fauna (Fig. 1) have not yet been dated by magnetostratigraphic or isotopic methods in either Itaboraí (Brazil, basis for the Itaboraian SALMA) or Las Flores (Patagonia, Argentina) sites. Consequently, the chronology of the Itaboraian SALMA has been indirectly inferred. In the most recent studies the Itaboraian has been regarded as late Paleocene–early Eocene (Olivera and Goin, 2011) or as early Eocene (Gelfo et al., 2009; Woodburne et al., 2013). Here, we follow the opinion of the last authors.

Squamates from the Itaboraian SALMA have been cited many times in different studies regarding fossil squamates, although only the snakes have been properly addressed (Albino, 1990, 1993; Rage, 1998, 2001, 2008). The sediments from the São José de Itaboraí basin in Brazil have produced many squamate remains, but some specimens have also come from Patagonian deposits of Argentina.

The first reports of lizards from the São José de Itaboraí basin in Brazil are those described by Paula Couto (1948, 1958). Later, Estes (1970) reported the

presence of Gekkonidae stating that the material was too fragmentary for a generic assignment. Estes (1970) also noted the presence of at least eight species of iguanids and teiids. The only extensive study on these fossils was the PhD dissertation of Carvalho (2001) who recognized an *Iguania incertae sedis*, a Gekkonidae\*, two Scincomorpha *incertae sedis*, a Teiidae, and two Anguimorpha *incertae sedis*. If these taxonomic assignments are correct, then they represent the earliest record of most of these clades for South America. More formal published descriptions of the Itaboraian lizard remains would substantially improve our understanding of the early evolution of lizards on the continent.

The Itaboraian snake fauna is one of the richest and most diverse fauna of fossil snakes from South America (Albino, 1990, 1993; Rage, 1998, 2001, 2008). All identified snake species are known only from São José de Itaboraí, Brazil (Rage, 2008). The possible exception is *Coniophis precedens* that also occurs in the late Maastrichtian of North America; however, the presence of this species at Itaboraí has not been confirmed (*Coniophis* cf. *C. precedens*; Albino, 1990; Rage, 1998). Until recently, the genus *Coniophis* was based only on plesiomorphic vertebral characters, mainly the lack of a median notch in the posterior border of the neural arch, combined with characters usually present in “anilioid” snakes (small, delicate, and depressed vertebrae, with low neural arch and reduced neural spine, oval cotyle and condyle, Albino, 1990). At present, *Coniophis* is also known from a maxilla, a dentary, and additional vertebrae recovered in Maastrichtian deposits in North America (Longrich et al., 2012b). On the basis of this new material, Longrich et al. (2012b) concluded that *Coniophis* is not an “anilioid” as previously thought, but rather represents the most primitive known snake as showed in their phylogenetic analysis. A revision of all the fossil material previously assigned to *Coniophis* would be necessary to evaluate if this genus is monophyletic and then to recognize its past distribution. Presently, the referral of vertebrae from São José de Itaboraí to *Coniophis* is considered tentative (Albino, 1990; Rage, 1998). The presence of this snake in the North-American Cretaceous and the South-American Paleogene was early interpreted as an evidence of a faunal interchange between North and South America during the latest Cretaceous (Rage, 1981; Estes and Báez, 1985).

Another snake species at São José de Itaboraí is *Hoffstetterella brasiliensis*, which is regarded as an “anilioid” more similar to extant *Anilius* and Cretaceous *Australophis* than to any other member of this group (Rage, 1998; Gómez et al., 2008). *Hoffstetterella* represents the youngest extinct “anilioid” snake of South America since Miocene *Colombophis* was reinterpreted as a probable basal alethinophidian of uncertain affinities (Hsiou et al., 2010).

Madtsoiid snakes are represented at São José de Itaboraí by a single species, *Madtsoia camposi* (Rage, 1998). *Madtsoia* is a genus very common in early Cenozoic deposits of South America with the youngest records in the early–middle Eocene Casamayoran SALMA of Argentina (see below).

The Boidae is the dominant and most diverse family at São José de Itaboraí as observed in almost all terrestrial snake faunas from the Paleogene of the world (Rage, 2008). They include at least two genera of Boinae

and a boid *incertae sedis* (Albino, 1990; Rage, 2001, 2008). Among Boinae, Albino (1990) described an isolated vertebra as an indeterminate genus and species, but later Rage (2001) assigned it to the new extinct Itaboraian species *Waincophis pressulus*. He also added for this fauna another new species of the genus: *W. camera-tus*. The extinct genus *Waincophis* known since the early Eocene Itaboraian (Rage, 2001), was first found in the middle–late Eocene Casamayoran, early Miocene Colhuehuapian, and mid Miocene “Colloncuran” of Patagonia (Fig. 1) (Albino, 1987, 1996b). The systematic relationships of *Waincophis* have been discussed in some papers (Albino, 1987, 1996b; Szyndlar and Schleich, 1993; Rage, 2001). The absence of discrete characters does not support a particular affinity of *Waincophis* with any subfamily of Boidae, although overall morphology appears to be nearest to that of the Boinae.

A well supported genus of Boinae described by Rage (2001) for the Itaboraian is *Corallus priscus*. This species represents the oldest fossil record of this extant Neotropical genus (Rage, 2001). Another boid genus is *Hechtophis* with the species *H. austrinus*, which was tentatively located in the Erycinae by Rage (2001), but considered more recently as a boid *incertae sedis* (Rage, 2008). The assignment of *Hechtophis* to the Erycinae cannot be confirmed because it shows a combination of characters that not only appear to be present in trunk vertebrae of the extant erycine *Lichanura* but also in the extant boine *Epicrates* (Rage, 2008).

Another snake from São José de Itaboraí described by Rage (2008) is *Paraungaliophis pricei* referred to the Ungaliophiinae, a typical Central/South American group whose relationships within the boid complex are discussed. *Paraungaliophis* is a representative of another snake lineage developed early in the Neotropics as well as for the Boinae. Also, the extinct *Itaboraiophis depressus* and *Paulacoutophis perplexus* reported for São José de Itaboraí are referred to the booid assemblage; within them, they are regarded as *incertae sedis* (Rage, 2008). These genera are exclusive of the Brazilian deposits.

Finally, caenophidians are perhaps present at São José de Itaboraí based on a single vertebra tentatively referred to the Russellophiidae (Rage, 2008). Thus far, this family was reported only from the Cretaceous and Paleogene of the Old World, with the earliest representative found in the Cenomanian of Africa (Rage, 2008). Because the referral of the material is tentative no conclusions should be drawn from this record.

Contrasting to the São José de Itaboraí locality in Brazil where a great diversity of squamates was recognized, the Itaboraian SALMA in Patagonia has provided only very fragmentary and isolated vertebrae of indeterminate madtsoiids and boines (Albino, 1993).

***Eocene squamates from Argentina.*** Eocene squamates from Argentina are mainly represented by a number of snake vertebrae distributed in Patagonian localities (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1987, 1993, 1996a, 2011a, 2012; Albino and Carlini, 2008); however, the early Eocene Lumbreira Formation at the northwest of the country is notable for providing associate lizard and snake remains (Donadío, 1985; Albino, 1993). The lizard material recovered from these deposits was first described by Donadío (1985), who erected a new genus and species of Teiidae Tupinambinae, *Lumbrera-*

*saurus scagliai*. Later, Sullivan and Estes (1997) determined that *Lumbrerasaurus* was inadequately diagnosed and considered it *nomen dubium*. *Lumbrerasaurus scagliai* is based on associated fragmentary remains (tooth bearing fragments and vertebrae) that present signs of deformation. Recent re-evaluations of these remains do not find clear diagnostic characters to support a new genus; nonetheless, the affiliation of these fossils with the Tupinambinae is confirmed (Brizuela, 2010). The presence of tupinambine teiids in the early Eocene indicates that the divergence of the two subfamilies (Teiidae and Tupinambinae) had already occurred. This paleontological data is consistent with the molecular data indicating that the most basal Tupinambinae (i.e., *Callopiestes*) would have diverged during the Paleocene (Giugliano et al., 2007). Snake remains from these deposits are being studied at present.

Patagonian Eocene deposits have provided interesting information on snake diversity. The extinct madtsoiid (Madtsoiidae) belonging to the genus *Madtsoia* are present in various deposits corresponding to the Riochican (early Eocene) and Casamayoran (middle–late Eocene) of Patagonia (Fig. 1), mainly represented by vertebrae referable to the species *M. bai* (Fig. 2) (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1993). A second Patagonian genus is the large boine *Chubutophis grandis* (Fig. 2), restricted to the Casamayoran (Albino, 1993). Both extinct genera were very large snakes, probably reaching or perhaps surpassing 10 meters in length (Hoffstetter, 1959; Albino, 1993, 2011a). The palaeoecological role of these large sized snakes was discussed previously (Albino, 1993, 2011a). Aside from these large forms, medium-sized boids have been recorded from the Casamayoran of Patagonia (Albino, 1993, 2011a). At least one specimen of these medium-sized snakes can be referred to as *Boa*, thus constituting the oldest record of this extant genus (Albino, 1993, 2011a; Albino and Carlini, 2008). As stated above, the Casamayoran has also provided the small boid *Waincophis australis* from the Patagonian region (Albino, 1987).

Recently, an isolated snake vertebra was described from the middle–late Eocene Mustersan SALMA (Fig. 1) of Patagonia (Albino, 2012). The strong similarities between this specimen and other South American Paleogene boines (the Paleocene *Titanoboa* and the Eocene *Chubutophis*) indicate close relationships among these snakes. Also, they are closer to the extant *Boa constrictor* than to any other extant boine genus (Albino, 2012). This, together with the recognition of the extant *Boa* and *Corallus* in the Eocene (Albino, 1993, 2011a; Rage, 2001; Albino and Carlini, 2008), and the records of indeterminate boines in Paleocene and Eocene rocks of Brazil, Bolivia, and Argentina (see above), suggests that the earliest diversification of Neotropical boines would have taken place at least as early as in the beginning of the Paleogene (Albino and Carlini, 2008; Albino, 2011a, 2012).

The Patagonian Paleogene record of snakes also demonstrates that large and medium-sized snakes were not only much more widely distributed during the Paleogene than at present, but also included some of the largest snakes ever known, suggesting paleotemperatures significantly higher than today at least until the Mustersan SALMA (Fig. 1) (Albino, 1993, 2011a, 2012). Fossil Patagonian Paleogene mammals suggest the existence of



tropical and subtropical forests (Ortiz Jaureguizar and Cladera, 2006), supporting the inferences based on the presence of these snakes (Albino, 1993, 2011a, 2012).

### The Oligocene: A Transitional Period

The fossil record of squamates is not homogeneous throughout the Paleogene. Currently, a large temporal gap exists between the Mustersan (middle–late Eocene) and the Colhuehuapian (early Miocene) of Patagonia (Fig. 1), where no squamates have been documented, except for some undescribed snake remains (Simpson, 1933; Simpson et al., 1962; Albino, 1996a). This gap is starting to be filled with findings from the Deseadan SALMA (late Oligocene) of Patagonia (Fig. 1). An unidentified tooth bearing fragment and two vertebrae are presently being studied by the authors. The tooth bearing fragment is poorly preserved, conserving only the base of pleurodont teeth, whereas one of the vertebrae is relatively well preserved, and shows a morphology different from snake vertebrae and all other lizard vertebrae recovered so far from the Cenozoic of Argentina. Another postcranial remain is represented by a snake vertebral centrum.

### The Distribution and Diversity of Squamates in the Miocene

Both lizards and snakes are well represented in Neogene deposits of South America. The lizard record includes the earliest representatives of extant genera of Iguania and Teiidae. Relative to the Cretaceous and Paleogene, snakes have a moderately diverse Neogene record, with the presence of boids, the more advanced “colubrids” and viperids, and a nonidentified taxon, whereas lizard record was substantially increased during the last years with fossils from diverse sites and ages, especially in Argentina.

**Patagonian miocene squamates.** Squamates are well represented in sediments from the early Miocene Colhuehuapian to the mid Miocene “Colloncuran” of Patagonia (Fig. 1). The fossil-bearing beds of the Colhuehuapian in Patagonia have provided one of the most relevant associations of South American Miocene squamates, mainly including the extant iguanians *Pristidactylus* and *Liolaemus* (Fig. 3), the modern teiid *Tupinambis*, the extinct boids *Waincophis* and *Gaimanophis*, and indeterminate “colubrids” (Albino, 1996b,c, 2008; Brizuela and Albino, 2004). Also in Patagonia, the Pinturan (early Miocene) and the Santacrucian (late early Miocene) SALMAs (Fig. 1) have provided remains of “colubrid” snakes (Albino, 1996c; Fernicola and Albino, 2012), but only the Santacrucian contributed with lizards, especially with the teiid *Tupinambis* (Fig. 3) (Ameghino, 1889, 1893; Brizuela and Albino, 2008a; Fernicola and Albino, 2012). Iguanians have also been recognized in various Santacrucian sites (Albino, 1996a). Ameghino (1889) described three species of the extinct iguanian genus *Erichosaurus* from southernmost Argentina, but currently this genus is considered invalid and the remains are provisionally considered as an indeterminate Iguanidae (Fernicola and Albino, 2012).

Deposits from the “Colloncuran” (mid Miocene) contributed remains of a teiid tupinambine (*Tupinambis* sp.

or *Crocodylurus* sp., Brizuela and Albino, 2008b), and of the snakes *Waincophis* and an indeterminate Boinae (Albino, 1996b,c). Although the best preserved specimen attributed to *Waincophis* is nearly identical to the Eocene Casamayoran holotype *W. australis* (distinguished by its smaller size), it should be considered *Waincophis* sp. The small size of the Miocene snakes contrasts with those of most Paleogene Patagonian snakes (see above). Considering that snakes of colder regions are almost all small-sized (Parker and Grandison, 1977), the presence of smaller snakes in the Patagonian Neogene with respect to those from earlier periods might be related with decreased temperatures. This would suggest a possible climatic deterioration in the region. This interpretation is consistent with known changes in mean global annual temperatures reported for this epoch (Zachos et al., 2001). Although decreases in temperatures may have prevented the development of large snakes in the Patagonian region during the Miocene, the climatic conditions were yet temperate enough to permit the presence of tupinambine teiids and small boid snakes. Tupinambine teiids reached approximately the 50° S and 70° W during the Santacrucian and “Colloncuran” respectively (Brizuela and Albino, 2008a,b), whereas boid snakes were found close to the 44° S during the Colhuehuapian and around 40° S and 70° W during the “Colloncuran” (Albino, 1996b). Also, “colubrid” distribution extended as far as the 50° S during the Santacrucian (Albino, 1996c). At present, tupinambine distributional limit is at the 40° S (Brizuela, 2010), whereas boid distribution is limited at the 34° S (Waller, pers.comm.). “Colubrids” are present in southern environments of Patagonia (Cei, 1986) but not at the highest latitudes reached during the Miocene. Thus, the distributional range of the squamates in Patagonia during the beginning of mid Miocene is in concordance with the timing of the Miocene Climatic Optimum event (17–15 Ma, Böhme, 2003).

Among the Patagonian Miocene squamates, both iguanians *Pristidactylus* and *Liolaemus* are established in the present ecosystems of Patagonia showing an important diversification at both sides of the Andean Cordillera. Contrarily *Tupinambis* and boids are now restricted to the northernmost part of the Patagonia region in the case of *Tupinambis* or absolutely absent from this region in the case of boids (Albino, 2011a). “Colubrids” presently inhabit the Patagonia region but some Miocene records come from sites south of its present distribution (Albino, 1996c). The progressive decrease in temperatures through the middle–late Miocene and later (Ortiz-Jaureguizar and Cladera, 2006) would have caused the restriction in the distribution of tupinambine teiids and boids to environments with more temperate climates (Albino, 2008, 2011a). The present southernmost population of *T. rufescens* in northern Patagonia (Cei and Scolaro, 1982) is likely a relic of the more widespread teiid distribution (Albino, 2011a). Also “colubrids” would have been affected by these climatic modifications disappearing from southernmost Patagonia. 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

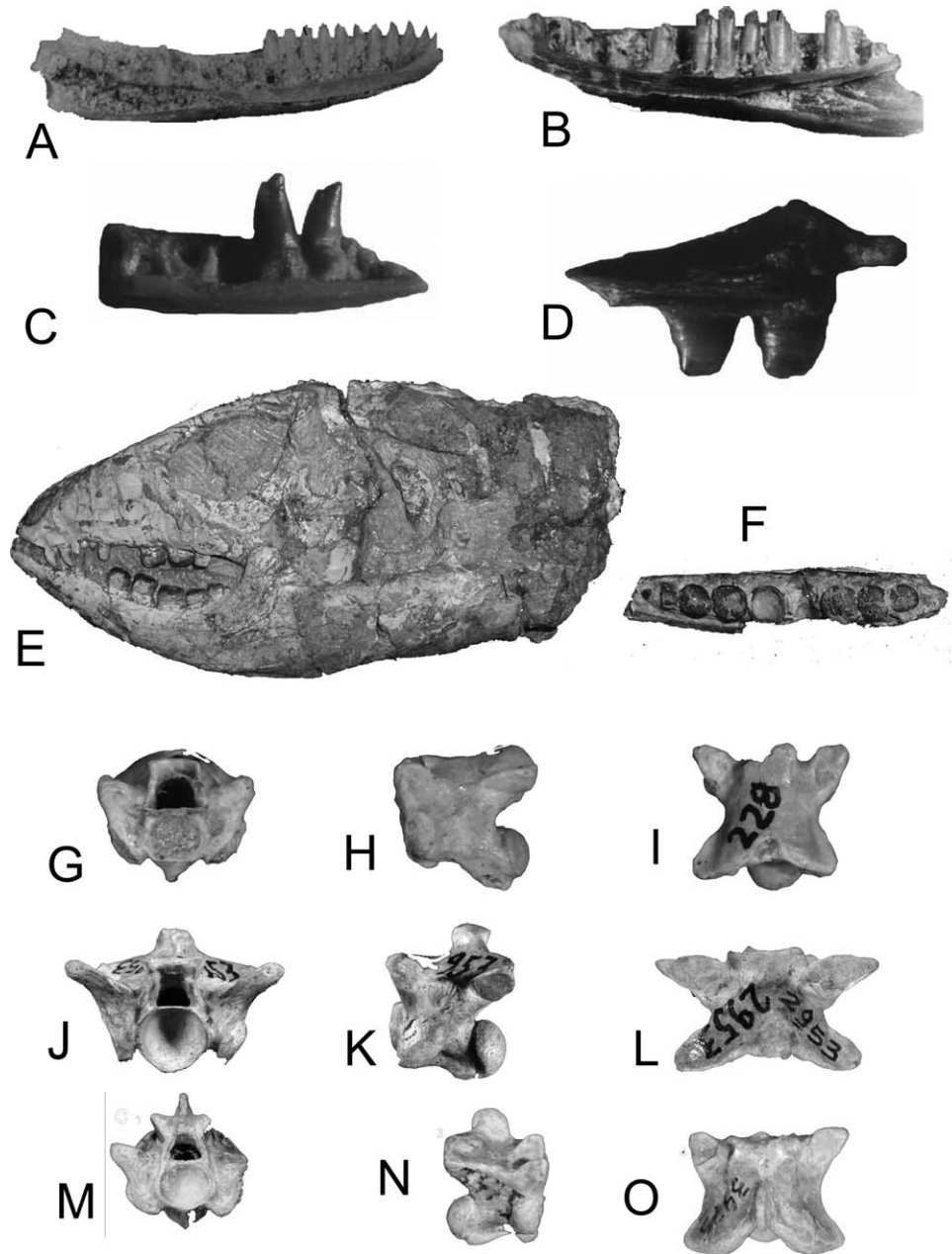


Fig. 3. Some Miocene squamate taxa cited in the text. **A**, *Liolaemus* sp. (left dentary in lingual view), **B**, *Pristidactylus* sp. (right dentary in lingual view), **C–D**, *Tupinambis* sp. (C, fragmentary right dentary in lingual view; D, fragmentary right maxilla in labial view); **E–F**, *Paradracaena colombiana* (E, skull in left lateral view; F, teeth in occlusal

view); **G–I**, trunk vertebra of *Colombophis portai* in anterior (G), lateral (H) and dorsal (I) views; **J–L**, trunk vertebra of *Colombophis spinosus* in anterior (J), lateral (K) and dorsal (L) views; **M–O**, Trunk vertebra of *Eunectes* sp. in anterior (M), lateral (N) and dorsal (O) views.

(Pascual et al., 1996). In Patagonia, the climate became cooler and dryer with more marked seasonality (Ortiz-Jaureguizar and Cladera, 2006; Barreda et al., 2007). These changes would have affected the distribution of *Tupinambis* fixing its current distributional limits north to the parallel 40° S (Albino et al., 2006; Albino, 2011a). The more varied environmental subdivision that would have taken place as a consequence of these climatic changes would have favored vicariance events in south-

ernmost populations of the iguanians *Liolaemus* and *Pristidactylus* (Albino, 2008, 2011a).

**Non-Patagonian miocene squamates.** Apart from Patagonia, Miocene deposits from Colombia, Venezuela, Peru, Brazil, and central Argentina have provided interesting remains of both lizards and snakes.

The mid Miocene Laventan fauna of Colombia (Fig. 1) has provided, among others, indeterminate iguanians,

the extinct teiid *Paradracaena colombiana* (Fig. 3), the extant genus *Tupinambis* (*Tupinambis* sp.), the first scolecophidian snake for South America, the basal alethinophibian snake *Colombophis portai* (Fig. 3), the extant boid *Eunectes*, and indeterminate “colubrids” (Estes, 1961; Hoffstetter and Rage, 1977; Estes, 1983; Hecht and LaDuke, 1997; Sullivan and Estes, 1997). Other mid Miocene South American localities have also provided remains of squamates: the teiid *Paradracaena* was recognized in Peruvian Amazonia deposits (Pujos et al., 2009), and a number of snake vertebrae have come from the middle Miocene of Venezuela (Head et al., 2006). Among the latter, a single vertebra was referred to *Colombophis* cf. *C. portai*, and other specimens were described as Boinae indeterminate (Head et al., 2006) but then re-evaluated as cf. *Eunectes* (Hsiou and Albino, 2009).

Apart from Colombia, Peru and Venezuela, one of the most relevant South American Miocene vertebrate assemblages is known from the late Miocene southwestern Brazilian Amazonia (Amazonas and Acre States), where an interesting diversity of squamates is recognized (Hsiou and Albino, 2009; Hsiou et al., 2009, 2010). This fauna includes cf. *Paradracaena* sp., *Colombophis* (with the new species *C. spinosus*, Fig. 3), *Eunectes* sp., aff. *Epicrates* sp., *Waincophis* sp., and indeterminate “colubrids” (Hsiou and Albino, 2009; Hsiou et al., 2009, 2010). This squamate association suggests some ecological similarities among the mid and late Miocene faunas of northern South America, supported by the presence of the teiid lizard *Paradracaena*, the basal alethinophidian *Colombophis*, and the boid snake *Eunectes* (Hsiou and Albino, 2009; Hsiou et al., 2009, 2010). The predominance of tropical faunal elements and associated environments with aquatic habitats (rivers, swamps, and shallow lakes) developed in tropical rainforests matches the presumed lifestyle of lizards and snakes recorded from these regions (Hsiou and Albino, 2010).

Among these squamates, *Paradracaena* is considered the sister taxon of *Dracaena* (Sullivan and Estes, 1997) and from the morphology of the dentary, especially the modification of the posterior teeth into massive, flattened mushroom-shaped teeth, it is probable that *Paradracaena* resembled the modern teiid *Dracaena* in its malacophagous dietary habits. It could thus be assumed that *Paradracaena* lived in an environment similar to the habitat of *Dracaena*, specifically river and swampy areas and dense vegetation (Pujos et al. 2009).

*Colombophis* was a medium to large-size genus of snake, with measures similar to those of the extant species *Boa constrictor*, in spite of which, it was considered to belong to the “Anilioidea” (Hoffstetter and Rage 1977; Sullivan and Estes, 1997; Head et al., 2006). Nevertheless, the allocation of this genus into the “Anilioidea” has not been resolved conclusively and, it should probably be considered a basal alethinophidian of uncertain affinities (Hsiou et al., 2010). The distribution of *Colombophis* extends from the north to the southeast of South America during the Miocene, surviving until the late Miocene (Hsiou et al., 2010). The vertebral morphology of *Colombophis*, especially that of *C. spinosus*, is partly compatible with the lifestyle proposed for *Dinilysia patagonica*. This is due to the combination of factors that include medium–large size, depressed neural arch, and high neural spine. According to Albino and Caldwell

(2003), these characters indicate a semi-fossorial or semiaquatic lifestyle.

Among the northern South American Miocene snakes, the extant boids *Eunectes* and probably *Epicrates* have been recognized. The extinct species *Eunectes stirtoni* was described based on an incomplete basisphenoid and a right prootic that, as reported by Hoffstetter and Rage (1977), are distinct in morphology from those of extant *Eunectes murinus*. Unfortunately, the present location of this material is unknown (Rage, personal communications) preventing a systematic revision. While the validity of *Eunectes stirtoni* is questioned (Hecht and LaDuke, 1997), snake vertebrae from mid and late Miocene of Venezuela and late Miocene of Brazil are now clearly referred to *Eunectes* sp. (Hsiou and Albino, 2009, 2010), which is a genus with semi-aquatic lifestyle. All these records indicate a Miocene geographical distribution of the genus in northern South America following tropical conditions and associated environments. This also supports the origin of *Eunectes* in or before the Miocene (Hsiou and Albino, 2009). The identification of aff. *Epicrates* in late Miocene deposits of Brazil represents the oldest record of this mainly arboreal genus and suggests its origin as early as the Miocene (Hsiou and Albino, 2010). The unique extinct boid snake found in the late Miocene of Brazil is *Waincophis* sp. which implies the survival of this genus, known as early as the Eocene (Albino, 1987) until the late Miocene (Hsiou and Albino, 2010). Indetermined “Colubridae” enriched the record of Miocene snakes in northern South America (Hoffstetter and Rage, 1977; Hsiou and Albino, 2010).

The posterior disappearance of the lizards *Paradracaena* and *Tupinambis* from northern South America would have been related with an increase in aridity of their habitat. The increase in the aridity of the upper Magdalena River valley, in Colombia, would have been a consequence of the uplift of the Eastern and Central Cordilleras. In Peru, the increase in aridity would have followed the reduction of the Pebas Lake/Pebas Sea, a large long-lived lake-wetland system that occupied northwestern Amazonia (Albino et al., 2006; Pujos et al., 2009).

Apart of these squamate records in northern South America, outcroppings in various sites of central Argentina have provided an abundant and taxonomically diverse squamate assemblage for the upper Miocene of South America. Mostly, the mammalian fauna recovered in these sediments are assigned to the late Miocene Huayquerian SALMA (Fig. 1) (Verzi et al., 1995, 1999; Montalvo et al., 1996, 1998; Verzi, 1999). However, in one locality (Caleufú) some taxa suggest a younger age, probably at the end of the late Miocene, close to but somewhat older than the Montehermosan SALMA (Fig. 1) (Verzi et al., 2003). The squamates provided by these outcroppings include the teiid *Tupinambis* and diverse snakes (“colubrids” and viperids) (Albino et al., 2006; Albino and Montalvo, 2006). The viperid constitutes the oldest record of the family in South America. Wüster et al. (2002) suggested that the ancestor of *Bothrops* was the first viperid to colonize South America, probably during the early–middle Miocene (between 23 and 10Mya). Thus, the terrestrial connection between Central and South America presumably occurred during the mid–late Miocene (12.9–11.8Mya) (Iturralde-Vinent and MacPhee, 1999). It was possible to consider a hypothesis that viperids first



entered South America prior to the closure of the Isthmus of Panama and this is supported by the fossil record in the late Miocene (Albino and Montalvo, 2006). More recently, Kirby et al. (2008) demonstrated that southern Central America existed as a peninsula connected to northern Central America and North America as early as 19 Ma suggesting that the entrance of viperids could have occurred earlier, but at date there are not records of viperids to support this later hypothesis.

### Miocene–Pliocene Squamates of South America

Data on squamates from the upper Miocene–Pliocene of South America have significantly increased in recent years especially through the revision of old material from various deposits of Argentina.

**Northeastern, northwestern and central Argentina.** In central Argentina, Kraglievich and Reig (1954) reported the presence of a maxilla of *Tupinambis* coming from the Huayquerian–Montehermosan (late Miocene–early Pliocene). Donadío (1983, 1984) reported this specimen as *T. merianae*, although he did not describe the material or justify the taxonomic allocation, and then inferred paleoclimatic conditions different from the present ones based on the current absence of this species in the locality. A formal description of this specimen and discussion of its characters was recently published by Brizuela and Albino (2012a) who rejected the conclusions of Donadío (1983, 1984) and assigned the maxilla to *Tupinambis* sp. In the same paper, Brizuela and Albino (2012a) discussed the validity of the extinct lizard genus *Propodinema* from the “Mesopotamian” (Miocene–Pliocene) of northeastern Argentina (*P. oligocena* and *P. paranaensis*). This genus was first described by Ambrosetti (1890) based on two hemimandibles. The remains are lost at present; nevertheless, the detailed description made by Ambrosetti (1890) allowed Brizuela and Albino (2012a) to consider them as synonyms of *Tupinambis* sp.

Recently, the first iguanid specimens from the Pliocene of South America have been recovered. Included in these fossils, is *Uquiasaurus heptanodonta* described by Daza et al. (2012). Phylogenetic analysis of this taxon by Daza et al. (2012) indicates it is basal to extant Tropidurinae\* (i.e., Liolaemini, Tropidurini, *Liocephalus*). Among these lizards, *Uquiasaurus* is more morphologically similar to Liolaemini, particularly the extant *Liolaemus*, from which *Uquiasaurus* differs in having a higher premaxillary tooth count (Daza et al., 2012). Another specimen co-occurring with *Uquiasaurus* has been assigned to *Liolaemus* (Daza et al., 2012).

**The Atlantic coast of the Pampean region.** Outcroppings along the southeastern coast of the Buenos Aires province in Argentina have provided diverse squamate remains from the Montehermosan, Chapadmalalan and Marplatan ages (Fig. 1). Some of them include teiid lizards (*Callopiestes* and *Tupinambis*), a boid, “colubrid” and viperid snakes, and the earliest amphisbaenian of South America (Rovereto, 1914; Chani, 1976; Albino, 1989, 1992; Albino and Quintana, 1992; Albino and Montalvo, 2006; Albino and Carlini, 2008; Albino et al., 2009; Brizuela and Albino, 2008c, 2012b; Brizuela, 2010).

Within teiids, a partial skull of a tupinambine from the late Miocene–early Pliocene Montehermosan SALMA

was first described by Chani (1976) as the extinct species *Callopiestes bicuspidatus* (Fig. 4). Revision of this fossil (Brizuela and Albino, 2008c; Brizuela, 2010) has strongly supported assignment to *Callopiestes* and the validity of the extinct species based on the use of characters different from those considered diagnostic by Chani (1976). The biogeographical significance of this record has long been recognized (Báez and Gasparini, 1977) since recent distribution of *Callopiestes* is restricted to Chile to Ecuador west of the Andes (Kause, 1985). The accompanying vertebrate fauna at the fossil locality indicates warm and humid conditions (Pascual and Odreman Rivas, 1971; Gasparini et al., 1986; Albino, 1992) (contra Chani, 1976). These conditions differ significantly from those currently exploited by the extant xerophytic species *Callopiestes maculatus* and *C. flavipunctatus* living west to the Andes. This suggests that *C. bicuspidatus* had different climatic requirements than the extant species of the genus. The late Miocene–early Pliocene presence of *Callopiestes* in the Atlantic coast of South America, the probable early Oligocene diversification of the genus, and its likely origin through vicariance (following the Andes uplift) (Guiliano et al., 2007) are all indicative of a large and unknown history of *Callopiestes* east to the Andes. This ancient eastern radiation could explain the presumed dissimilar climatological requirements of the extant and extinct species.

Lizard remains from the Montehermosan and lower Chapadmalalan ages were assigned to *Tupinambis* sp. (Albino et al., 2009). Specimens from the Montehermosan sensu lato (Montehermosan + Chapadmalalan) were first described as four extinct species of *Tupinambis* (*Tupinambis preteguixin*, *T. prerufescens*, *T. brevisrostris*, and *T. multidentatus*) by Rovereto (1914), but then, revised and reinterpreted as *Tupinambis* sp. (Fig. 4) (Brizuela, 2010). Brizuela and Albino (2012b) documented the presence of *Tupinambis* sp. in Upper Chapadmalalan and Marplatan units. The extinct species *T. onyxodon* (Fig. 4) described by Kraglievich (1947) is considered invalid and previous citations of *T. merianae* (Reig, 1958; Báez and Gasparini, 1977; Donadío, 1983; Gasparini et al., 1986; Albino, 1996a) have been reevaluated as *Tupinambis* sp. (Brizuela and Albino, 2012b).

Among snakes, the Montehermosan sensu lato have provided remains of boids, “colubrids,” and viperids (aff. *Bothrops*) (Albino, 1989, 1992; Albino and Montalvo, 2006). The boid specimen first referred as? *Boa* by Albino (1992) is now considered an indeterminate Boinae and suggests that, by the Pliocene, the boines still inhabited regions where they are not found today, surpassing the current limit of 34° S (Albino and Carlini, 2008). Only “colubrids” come from the Chapadmalalan and Marplatan of Argentina (Fig. 1) (Albino and Quintana, 1992).

Another squamate clade, Amphisbaenia, first appears in South America during the Pliocene (Fig. 4). The material is from the Upper Chapadmalalan of southeastern Buenos Aires province, in Argentina (Brizuela and Albino, 2012b). The fossils consist in many post-cranial elements referred to *Amphisbaena* sp. (Brizuela and Albino, 2012b).

### Latest Paleontological Records

South American Pleistocene and Holocene deposits containing squamate specimens are distributed in many

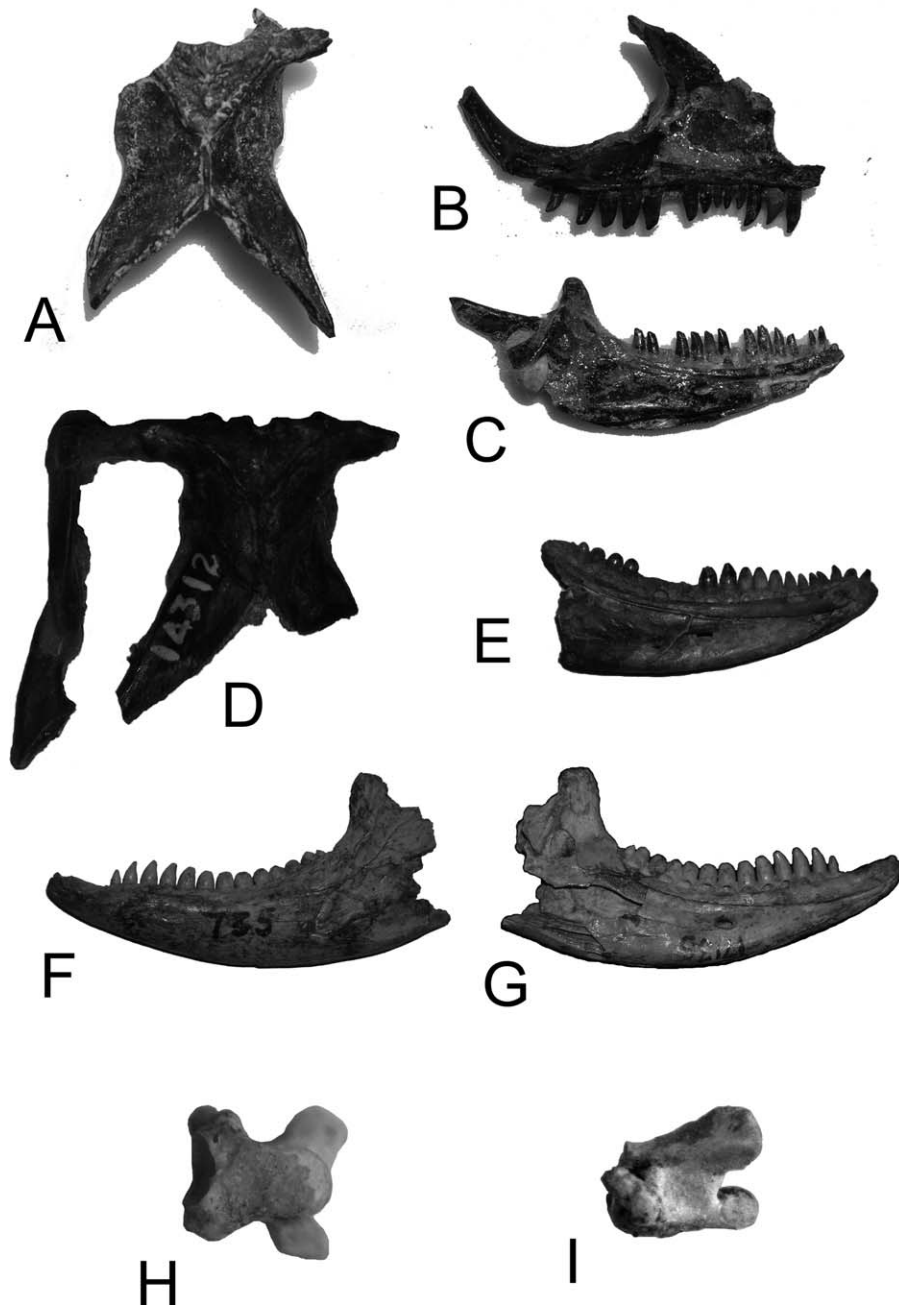


Fig. 4. Some Miocene-Pliocene squamate taxa cited in the text. **A–C**; *Callopiastes bicuspidatus*, A, parietal in dorsal view, B, articulated left lacrimal, maxilla, prefrontal, jugal and palatine in lingual view, C, articulated left angular, articular, dentary and surangular in lingual view; **D–G**, *Tupinambis* sp., D, articulated parietal, postorbital and

squamosal in dorsal view, E, left dentary and splenial in lingual view, F and G, left dentary with partially conserved coronoid, angular and surangular in labial (F) and lingual (G) views; **H–J**, vertebra of Amphisbaenidae indet. In ventral (H) and lateral (I) views.

countries, but fossils from Argentina are notable in quantity and diversity.

Extant genera of Teiidae and Iguanidae are the main components of the Pleistocene lizard fauna of South America, but Gekkonidae and Anguinae are also recorded. In general, the locality records are consistent with the recent ranges of the respective taxa. As in the beginning of the Neogene, *Tupinambis* was extensively

distributed during the Pleistocene in Argentina, Bolivia, Brazil, and Uruguay (Rusconi, 1937; Hoffstetter, 1963, 1968; Estes, 1983; Ubilla and Perea, 1999; Hsiou 2007). But, unlike the Miocene record of the genus, many of these specimens have not been described, and in some cases the material could not be found (e.g., Rusconi, 1937). Hsiou (2007) described the extinct species *Tupinambis uruguianensis* from Brazil, though its validity

has been recently questioned (Scanferla et al., 2009; Brizuela, 2010). The Teiinae “*Ameiva*” and *Dicrodon* have also been mentioned for the Pleistocene of Brazil and Ecuador (Hoffstetter, 1970; Estes, 1983), but the remains have still not been described. The mention of *Dicrodon* is interesting since it is a basal Teiinae thought to have originated during the Eocene–Oligocene by vicariance (Guiliano et al., 2007). Teiinae and Tupinambinae remains have also been described from Argentina and several Brazilian Pleistocene–Holocene sites and they were mostly determined at levels of genera and species. Camolez and Zaher (2010) described many specimens from Brazil that they assigned to *Tupinambis*, “*Ameiva*” *ameiva*, and “*Cnemidophorus*” *ocellifer*. Albino (2005) described “*Cnemidophorus*” sp. from Argentina, an occurrence outside the current range of the genus. The Holocene Teiidae record is similar to that of the Pleistocene, with many references but few descriptions and all within their recent distributional limits. There are mentions of Tupinambinae (*Tupinambis* sp., *Tupinambis teguixin*) and Teiinae (“*Ameiva*” sp., “*Cnemidophorus*” *ocellifer*, *Teius oculatus*) in Brazil (de Queiroz, 2004; Camolez and Zaher, 2010; Hsiou et al., 2012), whereas all Holocene references from Argentina are of *Tupinambis* sp. (de la Fuente, 1999; Brizuela, 2010). Thus, it is possible to note that Teiidae have become more diverse since the end of the Miocene, with many extant genera of both subfamilies.

Regarding Iguanidae, they were also found within their recent geographical limits, but unlike Teiidae, most cited fossils have been described. Hoffstetter (1970) mentioned *Iguana* sp. in the Pleistocene of Ecuador. Late Pleistocene of southern South America has provided Iguanidae from Chile (*Liolaemus* cf. *lineomaculatus*) and Argentina (*Leiosaurus bellii*, *Liolaemus* sp.) (Van Dender, 1977; Núñez et al., 2005; Agnolin and Jofré, 2011). Moreover, Camolez and Zaher (2010) described iguanids of the subfamilies Polychrotinae\* (cf. *Enyalius*, *Polychrus* sp.) and Tropidurinae\* (*Tropidurus* sp.) from several Holocene sites of Brazil, whereas Albino (2005) described a very rich and diverse association of lizards among which at least two species of *Liolaemus* were identified (*L. darwini* and *L. multimaculatus*).

Some lizard families have a very poor fossil record, this is the case of Anguinae and Gekkonidae, both part of the extant South-American lizard fauna. The only described South American Anguinae (*Diploglossus* cf. *D. fasciatus*) is from the Holocene of Brazil (Camolez and Zaher, 2010). Gekkonidae (*Homonota*) are thus far only known from the late Pleistocene (Agnolin and Jofré, 2011) and late Pleistocene–Holocene (Albino, 2005) of Argentina. *Homonota* is a semiarid adapted gecko that is part of two fossil squamate associations that draw attention because of their diversity and, because both fossil associations are at lower latitudes than comparable Recent associations. Both associations are from central Argentina. The oldest, from the late Pleistocene, is composed by *Homonota*, *Anops kingii* and *Liolaemus*. The other association is from the late Pleistocene–Holocene, and it includes Teiidae (“*Cnemidophorus*” sp.), Tropidurinae\* Iguanidae (*Liolaemus darwini*, *Liolaemus multimaculatus*, *Liolaemus* sp.) and Gekkonidae (*Homonota* sp.). In both cases the ensembles are indicative of more arid and cooler environments during the latest Pleistocene of central Argentina.

Regarding Amphisbaenia, a short portion of an articulated column of an amphisbaenid, originally considered as a lizard (Rusconi, 1937), was recovered from the mid Pleistocene of Argentina. Later examination of the fossil determined it corresponds to an extinct species of Amphisbaenidae (*Amphisbaena marelli*, Torres and Montero, 1998), although the validity of this species has recently been questioned (Scanferla et al., 2009). The late Pleistocene record of Amphisbaenia in South America is geographically dispersed. From Brazil, Gans and Montero (1998) described two extinct species of Amphisbaenidae on the basis of cranial remains: *Amphisbaena braestrupi* and *Amphisbaena laurenti*. Along with these taxa, Gans and Montero (1998) also described an Amphisbaenia *incertae sedis*, represented by cranial and postcranial elements. However, part of these remains could be of *Amphisbaena laurenti* (Gans and Montero, 1998). Cranial remains of Amphisbaenidae have also been recovered in the late Pleistocene of Argentina and assigned to *Anops kingii* and *Amphisbaena heterozonata* (Scanferla et al., 2006; Agnolin and Jofré, 2011). Likewise, Hoffstetter (1968) mentioned two vertebrae from the late Pleistocene of Bolivia. One of them is incomplete but the other is similar to those of *Leposternon*, although Hoffstetter (1968) did not provide the characters supporting this assertion. Last, Camolez and Zaher (2010) described an Amphisbaenidae indet. and *Leposternon* sp. from the Holocene of Brazil. At present, and regarding *Leposternon* as an Amphisbaenidae (contra Kearny, 2003), only this family is represented in the South-American Neogene.

With respect to snakes, most Pleistocene remains could be assigned to living taxa. The record includes Boidae, “Colubridae,” Viperidae and Elapidae. In Argentina, boids are represented by *Boa constrictor* from the Lujanian age (Late Pleistocene, Fig. 1) (Albino and Carlini, 2008). The specimens described in this article represent the first snake record for the Lujanian and provide the minimum age for this species of boid snake. These fossils are outside of the range of the modern distribution of the species, because *Boa constrictor* is not found today in the Mesopotamian region of Argentina (Entre Ríos, Corrientes and Misiones provinces). This species occupies environments of the semiarid “Chaco” biome in provinces west to the Paraná river (Catamarca, Córdoba, Chaco, Formosa, Jujuy, La Rioja, Mendoza, Salta, San Juan, San Luis, Santa Fé, Santiago del Estero, and Tucumán). The paleoclimatic interpretation based on mammals indicates that, at least during a large part of the Pleistocene, the Mesopotamian region would have had a more humid and warmer climate, with a marked influence of Brazilian fauna that would have continued even during the last interglacial period (Carlini et al., 2004). The break between the Mesopotamian and the Brazilian fauna subsequent to the Late Pleistocene, which occurred as a result of the changes in the main rivers that delimit this region (Paraná and Uruguay), would have established the insularity conditions of Mesopotamia, leading to the extinction of some Brazilian elements. The disappearance of *B. constrictor* from this area may be attributed to this isolation (Albino and Carlini, 2008).

“Colubrids” are well represented in the Miocene and Pliocene of South America through indeterminate forms (see above), but fossils of extant genera are just described



for the Pleistocene. Several extant “colubrid” genera have been recorded from the Lower–Middle Pleistocene of Argentina, including the pseudoboines *Clelia* sp. and *Boiruna* cf. *B. maculata* (Scanferla, 2006), and the xenodontines *Lystrophis* and *Philodryas* (Scanferla, Cenizo and de los Reyes, 2005; Scanferla, Agnolin and Boglino, 2009). *Clelia* (*C. rustica*) and *Philodryas* (*P. patagoniensis*) have also been documented from the Upper Pleistocene–Holocene (Albino, 1999, 2001). Among them, records of *Clelia*, *Philodryas* and *Lystrophis* are from regions where they are distributed today (Albino, 1999, 2001; Scanferla et al., 2005). The record of *Boiruna* in the Buenos Aires province is outside the current geographical range of the species of the genus, indicating warmer environmental conditions at the end of the Ensenadan age (Fig. 1) than today (Scanferla et al., 2009).

Within viperids, records from Argentina increase during the Pleistocene–Holocene (Albino, 1995, 1999; Albino et al., 2002; Scanferla and Nenda, 2005). They include the presence of the extant genus *Bothrops* with the species *B. alternatus* in the Upper Pleistocene–Holocene (Albino, 1999, 2001). A possible earlier record of the genus comes from the Lower–Middle Pleistocene in northeastern Buenos Aires province (Scanferla and Nenda, 2005). This last fossil indicates that during more humid periods, *Bothrops* lived in areas where they do not currently inhabit, probably because these areas are now too arid and urbanized (Scanferla and Nenda, 2005; Albino and Montalvo, 2006).

Snake fauna from the Late Pleistocene to Recent found in Brazil has been recently studied by Camolez and Zaher (2010). It includes the four genera of boids that occur presently in this country: *Boa* (*B. constrictor*), *Corallus* (cf. *C. hortulanus*), *Epicrates* (*E. cenchria*), and *Eunectes* (*E. murinus* and *Eunectes* sp.). “Colubrids” are represented by *Mastigodryas* cf. *M. bifossatus*, *Chironius* sp., *Pseustes* cf. *sulphureus*, *Tantilla* sp., *Helicops* gr. *leopardinus*, and cf. *Philodryas*. Some vertebrae were referred by these authors to the viperids *Bothrops* sp. and *Crotalus durissus*. Finally, cranial and vertebral remains were identified as the species *Micrurus corallinus* and *Micrurus* sp., representing the first record of elapids in South America. In addition to the Brazilian record, the late Pleistocene of southwestern Brazilian Amazonia has yielded a vertebra of an indeterminate viperid (Hsiou and Albino, 2010).

Apart from the diverse Pleistocene squamate fauna of Argentina and Brazil, Porta (1965) observed the presence of the “colubrid” *Synophis* aff. *S. bicolor* in the Late Pleistocene of Colombia, whereas indeterminate viperids come from the Upper Pleistocene of Venezuela (Head et al., 2006). The reports of boid and viperid remains in the upper Pleistocene of Bolivia (Hoffstetter, 1968) cannot be confirmed, because the material has not been described or illustrated.

This summarized record of snakes suggests that some elements of the South American snake fauna have been well established since the Pleistocene.

## CONCLUSIONS

The diversity of extinct squamates is poor in South America compared with other parts of the world. Partially, this might be explained by geographic causes (e.g., some taxa were unable to enter South America before

the Miocene), but also because the insufficient fieldwork to look specifically for squamates. Also, most of the richest paleontological sites in South America are from the Cretaceous and Paleogene of Patagonia, but Neogene sediments are scarce in this territory and not very prolific in others. Although the present diversity of squamates is much higher in the north of South America than in the south, paleontologically productive sediments are concentrated in southern South America. In addition, the studies on fossil squamates are concentrated in Argentina and Brazil, whereas other countries did not produce work teams in this topic. Furthermore, the South-American paleoclimatic evolution, including strong modifications of environments at high latitudes, suggest that many clades of squamates have disappeared or could never occupied vast regions of South America.

Generalized conclusions about the evolution of the squamates in South America is difficult taking into consideration the incomplete and episodic fossil squamate record and the complex geological and paleoclimatic history of South America. However, some aspects may be detailed.

1. The Mesozoic squamate record is mainly from the Patagonian region. During the Cretaceous, concurrent with the progressive breakup of Gondwana, there was a global climatic warming. Thus, the Cretaceous climate was one of the warmest climates ever, much warmer and more humid than today (Nullo and Combina, 2011). These conditions would have provided favorable scenarios for early squamate diversification. In South America, two major extant clades of lizards (Iguania and Scleroglossa) would have been already present together and included with a rich ensemble of primitive terrestrial snakes mostly integrated by extinct forms. These basal snakes suggest that the earliest diversification of terrestrial snakes (i.e., not strictly aquatic nor subterranean) would have occurred in Gondwana.
2. Although Patagonia was situated in the Warm Temperate Biome during the Late Cretaceous and Paleogene, southern Patagonia was in close proximity to the Antarctic Peninsula, thus a link with East Australasia via West Antarctica was maintained (Iglesias et al., 2011). This connection would have permitted some continuity between Patagonian and Australian madtsoiid snake fauna.
3. At the beginning of the Paleogene, the global paleoclimatic distributions were about the same as those of the latest Cretaceous. The Paleocene and Eocene climates were quite warm, reaching a thermal maximum at the end of the Paleocene. Tropical conditions extended north and south towards the poles, about 10° beyond their current limit (Nullo and Combina, 2011). Giant snakes developed in northern South America during the Paleocene following the high temperatures that facilitate the evolution of large body sizes. Also, a well diversified Patagonian Eocene snake fauna thrived, including some of the largest known snakes. Tupinambine teiids and boid snakes, as well as derived macrostomatan, first emerge during the Paleocene, and at least two extant boid genera would have appeared during this epoch (*Boa* and *Corallus*).

4. Contrasting with the early Paleogene, the Oligocene was characterized by cooling and aridity. This environmental change occurred because of the transition from a Warm House to a Cold House that occurred in the Oligocene. This was followed during the late Oligocene and the early Miocene by a period of global Warming (Nullo and Combina, 2011; Iglesias et al., 2011). These changes would have affected the Patagonian squamate fauna, but the Oligocene squamate record remains too incomplete to draw conclusions. Nevertheless, it appears that large snakes disappeared from the Patagonian region corroborating a global decrease in temperature following the Paleogene.
5. The South American Miocene was characterized by a diverse and thriving squamate fauna in northern South America and Patagonia. It included some extant genera (the iguanian *Liolaemus* and *Pristidactylus*, the teiid *Tupinambis*, the boids *Eunectes*, *Corallus* and *Epicrates*). Extinct genera were also present (the teiid *Paradracaena*, the snake *Colombophis*, the boids *Waincophis* and *Gaimanophis*). “Colubrids” appeared at the early Miocene, whereas the first viperids are known from the late Miocene, both of them entering South America prior to the complete closure of the Isthmus of Panama.
6. The early and mid Miocene Patagonian squamate record is consistent with a climate cooler than those present during the Paleogene. The predominance of vertebrate elements in mid and late Miocene in northern South America indicates that the environments were characterized by open areas with forestation along rivers, swamps, and shallow lakes in a seasonal dry-humid tropical climate. This would explain the development of a squamate fauna composed by extant taxa exploiting such environments (*Tupinambis*, *Eunectes*, *Corallus*, *Epicrates*) as well as extinct forms with comparable ecological preferences (*Paradracaena*).
7. During the Miocene, greater rates in the Andean uplift combined with the fall in global temperatures contributed to the development of extreme aridity, and climates with stronger seasonality. This occurred particularly in eastern areas, and further differentiated the Andean and the Extra-Andean regions (Iglesias et al., 2011). There are no records of squamates from Patagonia after the Miocene but it is possible to compare with the present squamate fauna of this region to recognize that these climatic and environmental changes differentially affected the groups of squamates. Whereas tupinambine teiids, boid snakes, and “colubrids” brought their distribution northwards, the iguanians underwent vicariance events resulting in a greater diversification on both sides of the Andean Cordillera. In northern South America, the uplift of the Eastern and Central Cordilleras in Colombia increased in the aridity of the upper Magdalena River valley coincident with the extinction of squamate taxa (*Paradracaena*, *Colombophis*). The reduction of the Pebas Lake/Pebas Sea system is also coinciding with the disappearance of some squamate taxa.
8. During the latest Miocene and Pliocene some squamate elements are still outside their present range (the tupinambine *Callopiastes*, boid snakes). The earliest amphisbaenian of South America is from Pliocene deposits.
9. Most Pleistocene and Holocene squamate remains can be assigned to living genera: *Liolaemus*, *Leiosaurus*, *Tropidurus*, *Enyalius*, *Polychrus*, *Homonota*, “*Cnemidophorus*,” “*Ameiva*,” *Tupinambis*, *Amphisbaena*, *Anops*, *Boa*, *Corallus*, *Epicrates*, *Eunectes*, *Boiruna*, *Lystrophis*, *Philodryas*, *Clelia*, *Mastigodryas*, *Chironius*, *Pseustes*, *Tantilla*, *Helicops*, *Synophis*, *Bothrops*, *Crotalus*, and *Micrurus*. Some extant species have also been recognized. Punctuated climatic and environmental changes during Late Pleistocene resulted in changes in the distributional patterns of the mentioned genera (*Boa*, *Boiruna*, *Bothrops*; probably *Homonota* and “*Cnemidophorus*”). Thus, the general present squamate fauna would be already established, but changes in the distribution of the taxa would have still taken place.

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