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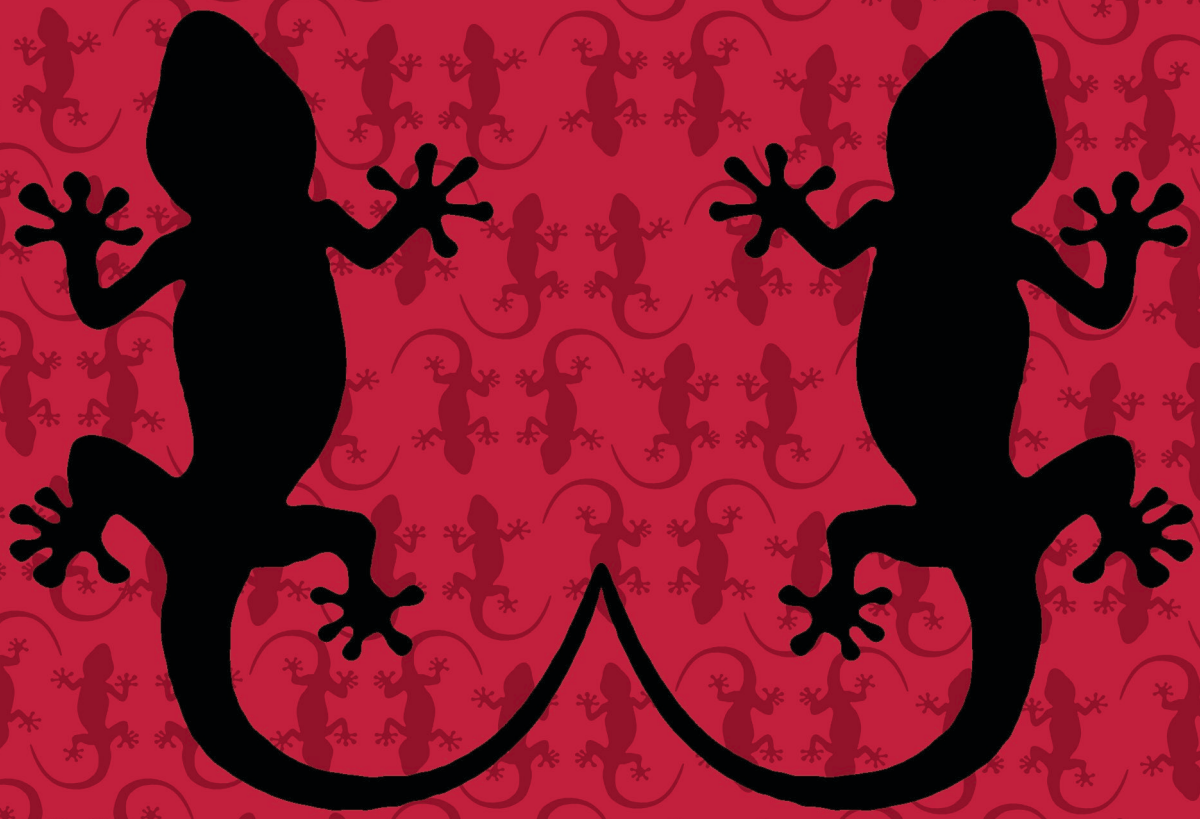

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The Cenozoic lizard record of the Pampean Region

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ABSTRACT
The Pampean Region is a geographic area involving central and eastern Argentina, Uruguay, and southern Brazil. Contrasting with the fauna of squamates that currently inhabits the Pampean Region, the paleontological record is extremely reduced. Teiidae is the best-represented lizard taxon, with its earliest record in the late Miocene. Iguania is present since the early Pliocene onwards, whereas Anguidae is known only in the middle Pleistocene and Phyllodactylidae in the late Pleistocene-early Holocene interval. Other living families present in the region (Gymnophtalmidae, Scincidae) have no fossil representatives. The unique extinct taxon is the teiid *Callopistes bicuspidatus* Chani, 1976. The fossil record includes some taxa presently absent in the paleontological sites; this implies that the Neogene and Quaternary climatic-environmental changes that affected dramatically the avian and mammalian faunas of the Pampean Region, also influenced the biogeographical history of the herpetofauna.

KEY WORDS
Iguanidae,
Teiidae,
Anguidae,
Phyllodactylidae,
Cenozoic,
Argentina,
Uruguay,
Brazil.

RÉSUMÉ
Les lézards cénozoïques de la région de la Pampa.
La région de la Pampa est une zone géographique comprenant l'Argentine centrale et orientale, l'Uruguay, et le sud du Brésil. Contrairement à la faune des squamates actuellement vivante dans la Pampa, le registre fossile est très faible. Les Teiidae sont les mieux représentés, les fossiles les plus anciens sont connus à la fin du Miocène. Les Iguania sont présents depuis le début du Pliocène, tandis que les Anguidae sont connus seulement dans le Pléistocène moyen et les Phyllodactylidae dans l'intervalle Pléistocène-début de l'Holocène. Les autres familles actuellement présentes dans la région (Gymnophtalmidae, Scincidae) ne possèdent pas de représentants fossiles. L'unique taxon éteint est le teiid *Callopistes bicuspidatus* Chani, 1976. Le registre des fossiles comprend certains taxons actuellement absents des sites paléontologiques; ceci implique que les changements climatiques et environnementaux du Néogène et du Quaternaire ont considérablement affecté la faune de cette région.

MOTS CLÉS
Iguanidae,
Teiidae,
Anguidae,
Phyllodactylidae,
Cénozoïque,
Argentine,
Uruguay,
Brésil.

INTRODUCTION

The Pampean Region is a geographic area embracing latitudes between 30° and 39°S in central and eastern Argentina, Uruguay, and southern Brazil (Fig. 1A). It borders to the North with the Mesopotamian region and the Chaco plains, to the West with the Sierras Pampeanas and Cuyo, and to the South with the extra-Andean Patagonia, whereas the Río de la Plata and the Atlantic Ocean form its eastern boundary. In Argentina, it includes the provinces of Buenos Aires, Entre Ríos, Santa Fé, Córdoba, La Pampa and San Luis (Fig. 1B). The Pampean Region currently concentrates a lizard fauna coming from various sources, both from the arid west and Patagonia, as well as from Brazilian origin. At the same time, geographic barriers, such as the mountain elevations in the province of Buenos Aires and the vast coastal tract, have promoted particular selection processes that culminated in endemism (Williams 1991).

Pampean fossil lizards have been documented since the 19th and the first part of the 20th century (Ambrosetti 1890; Rovereto 1914; Rusconi 1937; Kraglievich 1947). These records have been summarized and interpreted in classic literature concerning the fossil herpetofauna of South America (Báez & Gasparini 1977, 1979; Estes 1983; Gasparini *et al.* 1986; Albino 1996). These revisions were based on limited and chronologically sporadic records, and the specimens were cited without re-examination of the materials. More recently, paleontological explorations carried out in several sites of the Pampean Region, new methods of extraction of fossil specimens, a better stratigraphical control, and a higher attention to the materials deposited in old scientific collections have provided additional material from diverse locations and ages. 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. The available paleontological data about lizards of the Pampean Region will be summarized in the present contribution in an attempt to evaluate the information that the fossil record can provide concerning the historical evolution of diverse groups of lizards in the region.

MATERIALS AND METHODS

Land mammal ages are a widely used system to establish a time scale for terrestrial faunal record. The biochronological context for the Cenozoic used in this chapter is based on the South American Land Mammal Ages (SALMAs, Pascual *et al.* 1996). The calibration used is showed in Fig. 2. Archaeological sites were not considered in the present summary.

The material used in this study is detailed in the Appendix. Systematic and taxonomy of Iguanidae (synonym of Pleurodonta of Frost *et al.* 2001) follows Smith (2009), which is an osteological base study of the systematic relationships of the group. This decision was taken because osteological characters are the only useful for evaluating fossil specimens, and because Smith (2009) relied on a suitable sampling of taxa, which is conservative in taxonomy. Polychrotinae* and Tropidurinae* are considered metataxa and denoted by an asterisk. Recently, three species traditionally considered among the genus *Tupinambis* Daudin, 1802 (*T. duseni* Lönnberg, 1896*, T. merianae* (Duméril & Bibron; 1839) and *T. rufescens* (Günther, 1871)) have been allocated in the genus *Salvator* Duméril & Bibron, 1839 (Harvey *et al.* 2012). Nevertheless, the phylogenetic analysis of Quadros *et al.* (2018) concludes that these three species are nested within *Tupinambis*, forming a clade supported by unambiguous synapomorphies. As the phylogenetic affinities and taxonomic status of this species complex are not completely resolved, and as character states used for the distinction between *Tupinambis* and *Salvator* cannot be used to evaluate the fossil specimens from the Pampean Region, I consider here *Tupinambis* including *Salvator.*

Abbreviations

FML	Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Tucumán province, Argentina;
GHUNLPam	Facultad de Cs. Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, La Pampa province, Argentina;
MACN Pv	Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Argentina;
MCN	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brasil;
MD-FM	Museo Municipal de Ciencias Naturales Carlos Darwin, colección Farola Monte Hermoso, Punta Alta, Buenos Aires province, Argentina;
MMH	Museo Municipal de Monte Hermoso, Buenos Aires province, Argentina;
MMH-FMH	Museo de Monte Hermoso, colección Farola Monte Hermoso, Buenos Aires province, Argentina;
MMP	Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Buenos Aires province, Argentina;
MRJP P	Colección Paleontología, Museo Regional Juan Posse, Buenos Aires province, Argentina;
UNSGH	Universidad Nacional del Sur, Cátedra de Geología Histórica, Bahía Blanca, Buenos Aires province, Argentina.

RESULTS

Since the remains are usually small and have very particular osteological features, the lizards tend to be difficult to recognize in the set of materials recovered from paleontological sites. They are proportionately few in comparison with the remains of mammals, so they can go unnoticed. In addition, the recovered bones are usually disarticulated and broken. Many of the fossil remains may be useless for taxonomic purposes due to the incomplete preservation, or they can be identified only at high taxonomic levels. However, although the fossil record of lizards is even scarce, it permits to recognize extinctions, age of taxa and past distributions. In addition, as many lizards are climatic-sensitive vertebrates, their fossils are useful for performing paleoenvironmental interpretations or contrasting them with those coming from other sources.

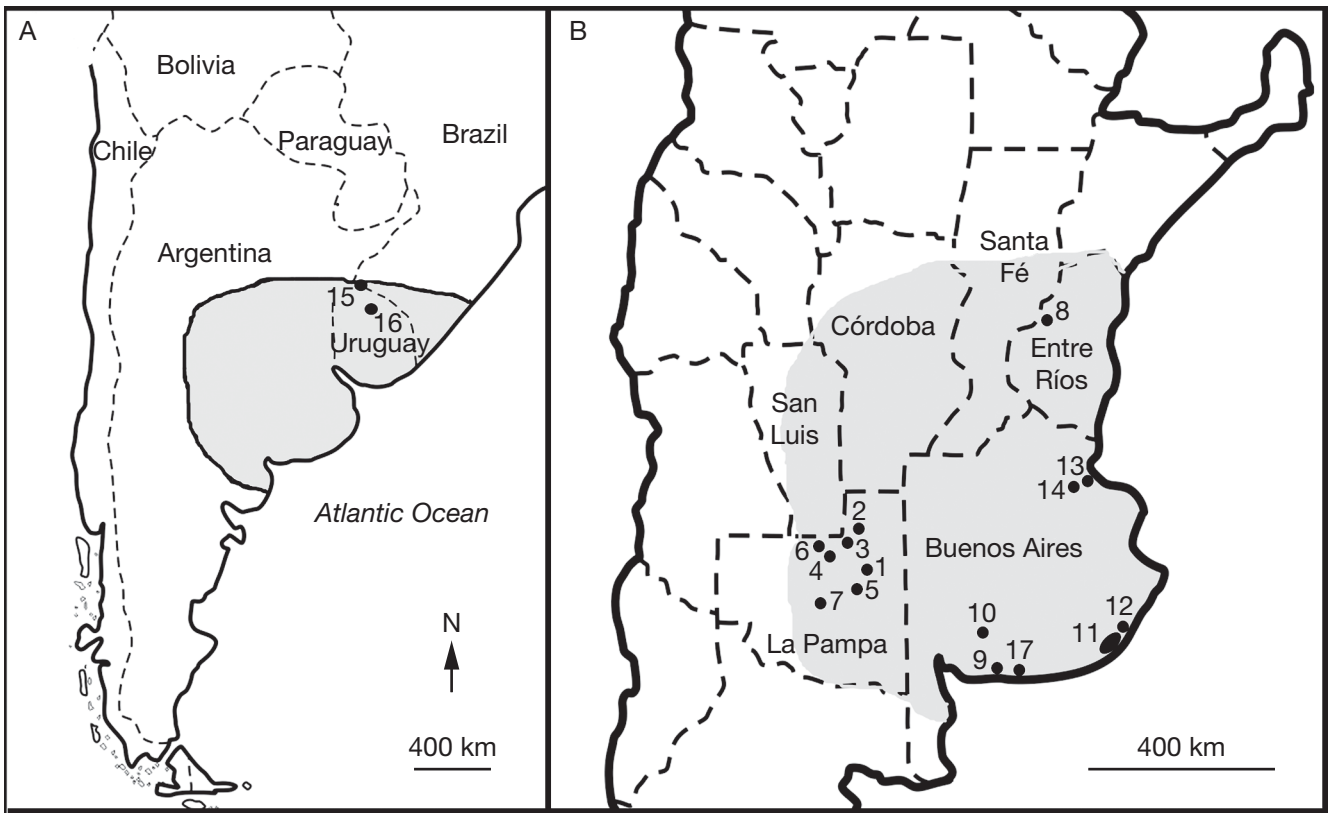

FIG. 1. — Paleontological localities with fossils of Cenozoic lizards from the Pampean region. Bajo Giuliani (**1**); Caleufú (**2**); Estancia Ré (**3**); Loventué (**4**); Quehué (**5**); Telén (**6**); Cerro La Bota (**7**); Paraná (**8**); Farola Monte Hermoso (**9**); Dique Paso Piedras (**10**); coastal cliffs between Mar del Plata-Miramar (**11**); Constitución (**12**); Villa Lugano (**13**); Mariano Acosta (**14**); Uruguaiana (**15**); Uruguay (**16**); Camping Americano (**17**).

The fossil record of lizards in the Pampean Region represents the most prolific for the interval Late Miocene-Holocene of entire South America. The earliest records are from the Huayquerian SALMA (late Miocene) of La Pampa and Entre Ríos provinces, Argentina (Fig. 1B). In La Pampa province, the material coming from levels of the Cerro Azul Formation in the localities Bajo Giuliani, Caleufú, Estancia Ré, Loventué, Quehué and Telén (Fig. 1B[1-6]) have provided remains assigned to the teiid *Tupinambis* (Fig. 3A, B) (Albino *et al.* 2006; Albino *et al.* 2013). In Cerro La Bota locality (Fig. 1B[7]), an indeterminate teiid probably related to *Ameiva* Meyer, 1795 or *Kentropyx* Spix, 1825 was recognized (Fig. 3C) (Albino *et al.* 2013). The Mesopotamian vertebrate assemblage from the lower levels of the Ituzaingó Formation which crop out along the cliffs of the Paraná River, near the city of Paraná, in Entre Ríos province (Fig. 1B[8]), includes remains of *Tupinambis* (originally *Propodinema paranaensis* Ambrosetti, 1890 and *P. oligocena*, Ambrosetti, 1890). Estes (1983) considered all the fossils studied by Ambrosetti (1890) as *Tupinambis paranaensis* (including *P. paranaensis* and *P. oligocena*), although suggesting it was a senior synonym of *T. preteguixin* Rovereto, 1914 from the Monte Hermoso Formation (see below). Although the material is currently lost, descriptions made by Ambrosetti (1890) allow rejecting the validity of the species *T. paranaensis*, this record being considered as *Tupinambis* sp. (Brizuela & Albino 2012a).

Lizard remains corresponding to the Montehermosan SALMA (early Pliocene, Tomassini *et al.* 2013) have been recovered from levels of the Monte Hermoso Formation exposed in the cliffs of Farola Monte Hermoso, 17 km of Pehuén-Có, Buenos Aires province, Argentina (Fig. 1B[9]). They include the teiids *Tupinambis* sp. (Rovereto 1914; Albino *et al.* 2009) and *Callopistes bicuspidatus* Chani, 1976 (Chani 1976; Brizuela & Albino 2017). Rovereto (1914) described four extinct species of *Tupinambis* from this site: *T. brevirostris* (Fig. 3D), *T. multidentatus* (Fig. 3E), *T. prerufescens* and *T. preteguixin* (Fig. 3F), but Estes (1983) considered *T. preteguixin* as the only valid species and the other ones as junior synonyms of it. Later, Brizuela (2010) questioned the validity of this species and considered it as *Tupinambis* sp. The extinct teiid *Callopistes bicuspidatus* (Fig. 3G-I) was originally described by Chani (1976) and later re-described by Brizuela & Albino (2017). The characters used in the original description made by Chani (1976) were not useful for the systematic assignation. Brizuela & Albino (2017) confirmed the generic allocation of these remains into *Callopistes* Gravenhorst, 1838, as well as the validity of the extinct species *C. bicuspidatus*, but based on characters different from those used in the original description. In addition to the teiid specimens, an isolated dentary of an indeterminate Iguanidae came from the Montehermosan of Dique Paso Piedras, southwestern Buenos Aires province (Deschamps 2005; Fig. 1B[10]).

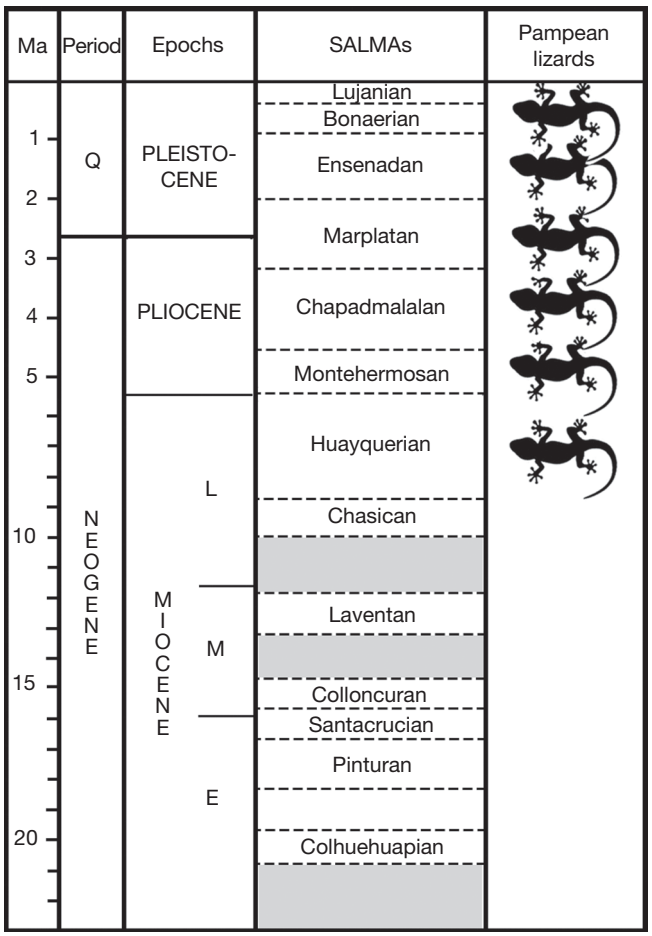

FIG. 2. — Time scale for Cenozoic mammalian faunas of South America (SALMAs).

The genus *Tupinambis* was moreover recorded in levels containing a fauna corresponding to the lower Chapadmalalan SALMA (early-late Pliocene) of the site Farola Monte Hermoso (Albino *et al.* 2009). This genus has been similarly found in upper Chapadmalalan levels (late Pliocene) of the coastal cliffs of Chapadmalal, between Mar del Plata and Miramar, Buenos Aires province (Fig. 1B[11]; Brizuela & Albino 2012b). Bolet & Evans (2011) also described *Tupinambis* specimens from the Chapadmalalan, which would have been found on the cliffs of the site Chapadketral (currently known as La Estafeta), between Mar del Plata and Miramar (Fig. 1B[11]). Another record coming from the upper Chapadmalalan of the coastal cliffs between Mar del Plata and Miramar (Fig. 1B[11]) is an almost complete fossil frontal of an Iguanidae (Polychrotinae*) recovered at the locality of San Eduardo del Mar (Brizuela *et al.* 2011).

Kraglievich (1947) described the extinct species *Tupinambis onyxodon* based on material recovered in levels of the Marplatan (late Pliocene-early Pleistocene) of Barranca Parodi, another locality of the coastal cliffs between Mar del Plata and Miramar (Fig. 1B[11]). However, this species is currently considered invalid and the material was assigned to *Tupinambis* sp. (Fig. 3J) (Brizuela & Albino 2012b).

The Ensenadan (early-middle Pleistocene) and Bonaerian SALMAs (middle Pleistocene) are well represented in the coastal cliffs of Constitución, north of Mar del Plata city, Buenos Aires province (Fig. 1B[12]). The Ensenadan provided remains of an indeterminate Iguanidae, whereas the first fossil of an Anguidae of Argentina, corresponding to the living genus *Ophiodes*, comes from the Bonaerian of this locality (Brizuela *et al.* 2015).

Remains attributable to *Tupinambis* sp. have been found in Lujanian deposits (late Pleistocene) of Villa Lugano, a neighborhood of Buenos Aires city, Buenos Aires province (Fig. 1B[13]; Rusconi 1937), but the material is now lost. Remains assigned to the iguanid *Liolaemus* sp. and the gecko *Homonota* sp. were found in Bonaerian or Lujanian deposits on the banks of the Reconquista river, in the locality Mariano Acosta, around 42 km west Buenos Aires city (Fig. 1B[14]; Agnolin & Jofré 2011).

Bolet & Evans (2011) described other Pleistocene material of *Tupinambis* from the province of Buenos Aires, but exact levels and locality are unknown. The mention of *Liolaemus* sp. in Bonaerian levels of an unknown locality of the Buenos Aires province (Scanferla *et al.* 2009) is not supported by any description.

Late Pleistocene deposits of the Touro Passo Formation at Touro Passo Creek, Uruguaiana, Rio Grande do Sul State, Brazil (Fig. 1B[15]), and Sopas Formation in northern Uruguay (Fig. 1B[16]) have provided specimens of *Tupinambis* (Ubilla & Perea 1999; Hsiou 2007). The former was recognized as the extinct species *T. uruguaianensis* Hsiou, 2007, although recent phylogenetic studies suggest that it should be allocated to the genus *Dracaena* Daudin, 1801 (Quadros *et al.* 2018). The record from Uruguay was mentioned as *Tupinambis* cf. *T. teguixin* (Ubilla & Perea 1999) but it is considered as *Tupinambis* sp. by Brizuela (2010).

Lizard remains were also described from the late Quaternary (late Pleistocene-early Holocene) of the Camping Americano locality, situated about 5 km south-southwest of Monte Hermoso, Buenos Aires province, Argentina (Fig. 1B[17]). Remains consist of several toothed remains which have been referred to at least two species of iguanids (*Liolaemus multimaculatus* (Duméril & Bibron, 1837) and *L. darwinii* (Bell, 1843)), one of gecko (*Homonota* sp.), and one of teiid (*Cnemidophorus* sp.).

DISCUSSION

The records of lizards in the Pampean Region are continuous through the late Miocene to Holocene. Pampean Cenozoic lizards come from deposits of the Huayquerian, Montehermosan, Chapadmalalan, Marplatan, Ensenadan, Bonaerian and Lujanian SALMAs (Fig. 2). The specimens come from 18 paleontological sites of Argentina (distributed in La Pampa, Buenos Aires and Entre Ríos provinces), one locality of Uruguay, and one of Brazil. The lizard bearing sediments of Buenos Aires province concentrate the most of the records (Fig. 1) and show the greatest diversity. The Teii-

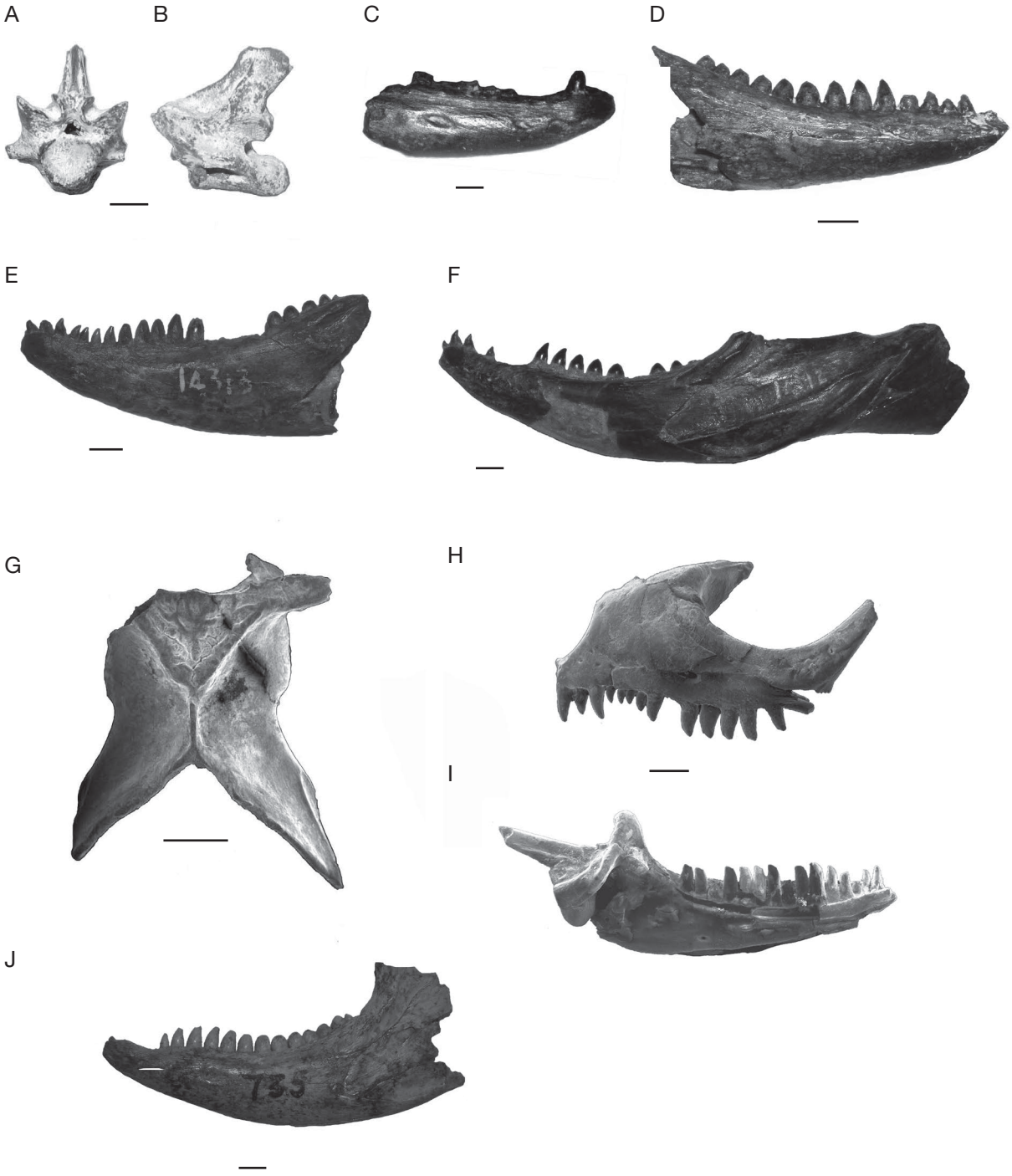

FIG. 3. — **A**, **B**, Huayquerian caudal vertebra of *Tupinambis* sp. (GHUNLPam 2313) in anterior (**A**) and lateral (**B**) views; **C**, Huayquerian right dentary of *Ameiva* Meyer, 1795 or *Kentropyx* Spix, 1825 (GHUNLPam 21745) in lateral view; **D**, Montehermosan right dentary of *Tupinambis* sp. (MACN 14311) in lateral view; **E**, Montehermosan left dentary of *Tupinambis* sp. (MACN 14313) in lateral view; **F**, Montehermosan left hemimadible of *Tupinambis* sp. (MACN 14312) in lateral view; **G**-**I**, Montehermosan *Callopistes bicuspidatus* (PVL 4818), frontal in dorsal view (**G**), partial skull in lateral view (**H**) and left hemimandible in medial view (**I**); **J**, Marplatan left dentary of *Tupinambis* sp. (MACN 17136) in medial view. Scale bars: A, B, D-F, J, 5 mm; C, 1 mm; G-I, 2 mm.

dae are the best-represented lizard family in the Pampean Region by the amount of remains and the amount of locations from where they have been collected. They include the genera *Callopistes*, *Cnemidophorus*, *Dracaena*, *Tupinambis*, and probably *Ameiva* or *Kentropyx*. Moreover, Iguanidae (*Liolaemus* and an indeterminate Polychrotinae*), Phyllodactylidae (*Homonota*), and Anguidae (*Ophiodes*) are also present in the fossil record of this region. From the detailed record, it is striking that the locality Camping Americano, in southern Buenos Aires province, is the unique site where more than two families and at least four species are undoubtedly represented. Until the moment, Gymnophtalmidae and Scincidae, which currently inhabit the Pampean Region, have no fossil representatives.

The teiid genus *Tupinambis* includes the largest living lizards confined to South America (east of the Andes, from Amazonia to northern Patagonia). It can be considered a relatively common squamate taxon for the Miocene-Holocene interval of the Pampean Region. The genus probably originated in the Eocene/Oligocene lapse (Giugliano *et al.* 2007) but its oldest record is in the early Miocene of Patagonia (Brizuela & Albino 2004). During the early-middle Miocene, the genus would have had the maximum southern extension, reaching latitude of 50°S (Brizuela & Albino 2008). Thus, the current distributional limit of *Tupinambis* at the 40ºS in northern Patagonia (Brizuela 2010) would represent a relic of a more widespread distribution in the past. According to the environmental requirements of actual *Tupinambis* species and associated fossil mammalian fauna, the paleoenvironmental conditions in the early and middle Miocene of Patagonia would have been subtropical, warmer, and more humid than today (Brizuela & Albino 2004, 2008). During the late Miocene, open environments and more arid conditions characteristic of a Chaco biome (an environment nowadays typical of northern Argentina), would have been established in central Argentina (Goin *et al.* 2000). The association of squamates found in these levels includes *Tupinambis*, an indeterminate teiid (probably corresponding to *Ameiva* or *Kentropyx*), a boid snake, a viperid and colubrids, which is as a whole compatible with this interpretation.

Molecular data indicate *Callopistes* would have diverged during the Paleocene and the two extant species (*C. flavipunctatus* Duméril & Bibron, 1839 and *C. maculatus* Gravenhorst, 1838) diverged during the Oligocene (Giugliano *et al.* 2007); thus, *Callopistes* would have had a long evolutionary history in South America. The current distribution of the genus, restricted to the west of the Andes from Ecuador to Chile, contrasts with the record of the extinct species *C. bicuspidatus* in the Atlantic coast of Argentina. This suggests that the Pliocene record could have been a representative of ancestral populations with widespread distribution including cis-Andean areas (Brizuela & Albino 2017). The major uplift of the mountain system would have caused divergence of the species at both sides of the Andes, and unknown processes would have produced the extinction of the cis-Andean species; thus, the present distribution of the genus would be relictual (Brizuela & Albino 2017). This was recently corroborated by the presence of another extinct species of the genus (*C. rionegrensis* Quadros, Chafrat & Zaher, 2018) in the lower Miocene of northern Patagonia, which is the oldest record of the genus and allows estimating its age at least between 21.1 and 20.1 Mya (Quadros *et al.* 2018). Moreover, the paleoenvironmental conditions inferred from the accompanying vertebrate fauna for the early Pliocene in the Pampean Region, and the records of *Tupinambis* and a boine snake in the same locality Farola Monte Hermoso, suggest that *C. bicuspidatus* exploited more humid conditions than the living species of the genus, which inhabits very dry environments (Brizuela & Albino 2017).

The record of an iguanid specimen with Polychrotinae* affinities from the late Pliocene of the Atlantic coastal areas of Buenos Aires province is interesting since Polychrotinae* are currently absent in this location (Brizuela *et al.* 2011). Polychrotinae* are known since the early Miocene of Patagonia (*Pristidactylus* Fitzinger, 1843) together with Tropidurinae* specimens assigned to the extant genus *Liolaemus* (Albino 2008; Albino *et al.* 2017). Unfortunately, the assignation of Polychrotinae* from the Pliocene of the Pampean Region is not as precise to interpret the record but it supports the opinion about an early diversification of iguanids in South America.

Concerning the geckos, Agnolin & Jofré (2011) indicate that the genus *Homonota*, in association with the amphisbaenid *Anops* Bell, 1833 and the iguanid *Liolaemus*, do not presently occur in northern Buenos Aires province. These three genera are currently found together at the Partido de Balcarce, a locality at more than 600 km south of the fossiliferous locality of Mariano Acosta; thus, this reptile assemblage reinforces previous suggestions based on fossil mammals about an arid and colder climate at the lowermost portion of the upper Pleistocene of Buenos Aires province (Agnolin & Jofré 2011).

The presumption that the extant teiid *Dracaena* is recorded in the Late Pleistocene of southern Brazil (Quadros *et al.* 2018) contrasts with its present distribution in tropical environments of Amazonas, Maranhao, Amapa, Acre and Matto Grosso, and would suggest warmer conditions in the past, but additional evidence concerning paleoenvironmental changes in the area is unknown.

Concerning the south of Buenos Aires province, *Liolamus multimaculatus*, *L. darwini* and *Cnemidophorus* were recognized exploiting the sandy beaches of the southeastern Buenos Aires province (Kacoliris *et al.* 2006), whereas *Homonota* is recongnized living in rocky outcrops of the Ventania system, around 130 km from Camping Americano (Avila *et al.* 2012). The lizard assemblage from the Camping Americano fossil locality is found in southeastern Río Negro province where the climate is cooler and dryer than that of the Pampean Region (Albino 2005). Dryer climatic conditions suggested by the associated fauna at the fossil locality could explain the occurrence of *Homonota* in this area during the late Pleistocene-early Holocene. These lizards may have disappeared locally as a consequence of the climate change increasing humidity (Albino 2005).

The above-mentioned fossil record indicates that at least most fossil lizards from the Pampean Region can be assigned to extant genera. According to combined molecular and paleontological evidences, some of these genera would have differentiated as early as the Paleogene or early Neogene (*Callopistes*, *Tupinambis, Liolaemus*). Other South American squamate taxa would also originated at the beginning of the Neogene or previously (the iguanian *Pristidactylus*, the boid snakes *Boa* Linnaeus, 1758*, Corallus* Daudin, 1803, *Epicrates* Wagler, 1830 and *Eunectes* Wagler, 1830; Albino & Brizuela 2014), suggesting that some typical components of the modern Neotropical herpetofauna would be already well established at least since the Miocene.

The fossil record indicates significant chorological changes where genera, which occurred in specific locations of the Pampean Region during the lapse Miocene-Holocene, are currently absent from these places. In some cases, the genera

inhabit regions distant to their fossil occurrences whereas in others they live relatively close to the places where the fossils come from. For example, the presence of the genus *Callopistes* in the Pliocene of the Atlantic coast contrasts with its current distribution 3000 km away and to the west of the Andes. In the past, *Homonota* had populations in northern (Mariano Acosta) and southern Buenos Aires province (Camping Americano), whereas presently it is restricted to the stony environments of the Balcarce, Tandilia and Ventania hills as endemic forms adapted to arid environments (Avila *et al.* 2012). *Liolaemus* inhabited northern Buenos Aires province (Mariano Acosta) although presently it occupies the Atlantic coastal tract of the province and the rocky grounds of the Tandilia System.

The absence of diagnostic characters at species level in the records presented here has allowed only assignment to genus level in most cases; thus, the possibility that these records could be new species with ecological requirements different from those of living species cannot be excluded. A good example of this case is the record of the extinct species *Callopistes bicuspidatus* in the Pliocene of the Pampean Region, which would have dwelled under different climatic conditions than those present in the area of distribution of the living species of the genus.

Therefore, paleoenvironmental hypothesis based on fossil lizards should be better performed using the whole available evidence and taking into account faunal assemblages more than isolated records. Under this perspective, it is possible to propose that the Neogene and Quaternary climatic-environmental changes that affected dramatically the mammalian and avian faunas of the Pampean Region (Pascual *et al.* 1996; Tambussi 2011) also influenced significantly the biogeographical history of the herpetofauna.

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ANNEXE 1. — Material revised in this study.

Anguidae:
Ophiodes Wagler, 1828: MMP 5194-1 (Constitución).

Phyllodactylidae:
Homonota Gray, 1845: MRJP P556 (Mariano Acosta); MMH 85-1-1-b-24 to MMH 85-1-1-b-46, MMH 85-1-1-b-47 to MMH 85-1-1-b-52, MMH 85-1-1-b-53 (Camping Americano).

Iguanidae:
Liolaemus multimaculatus (Duméril & Bibron, 1837): MMH 85-1-1-b-01 (Camping Americano);
Liolaemus darwini (Bell, 1843): MMH 85-1-1-b-02 to MMH 85-1-1-b-11 (Camping Americano);
Liolaemus Wiegmann (1834): MRJP P722 (Mariano Acosta); MMH 85-1-1-b-12 to MMH 85-1-1-b-14 (Camping Americano); Iguanidae indet.: UNSGH 606 (Dique Paso Piedras); MMP 5142 (San Eduardo del Mar); MMP 2304 (Constitución); MMH 85-1-1-b-15 to MMH 85-1-1-b-23 (Camping Americano).

Teiidae:
Callopistes bicuspidatus Chani, 1976: FML 4618 (Farola Monte Hermoso);
Tupinambis Daudin, 1803: GHUNLPam 2340, 2396, 5413, 5493, 8550, 2274, 21712, 5494, 22677, 2313 (Bajo Giuliani); GHUNLPam 19608, 19610, 19854,19856, 19914,19855, 19609, 19612/4, 19865/30, 19874/42 (Caleufú); GHUNLPam 4256 (Estancia Ré); GHUNLPam14283, 14284 (Loventué); GHUNLPam 9674 (Quehué); GHUNLPam 21669 (Telén): MACN Pv 14310 14311, 14312, 14313, 14314, 14338, 14344, MD-FM 95-3, 08-01-a, 08-01-b, MMH-FMH 82-2-19, 84-1-3, 84-1-4, 86-4-3, 76-6-22 (Farola Monte Hermoso); MACN Pv 10247, 19394 (Chapadmalal); MACN Pv 17136 (Barranca Parodi);
Dracaena Daudin, 1802: MCN-PV 2184 (Uruguaiana);
Cnemidophorus Wagler, 1830: MMH 85-1-1-b-54 to MMH 85-1-1-b-56 (Camping Americano); *Ameiva* Meyer, 1795 or *Kentropyx* Spix, 1825: GHUNLPam 21745 (Cerro La Bota); Teiidae indet.: MACN Pv 16831, 16831-3, 16831-4, 16831-5, 16831-1/2, 17452, 16791, 16815 (Chapadmalal).