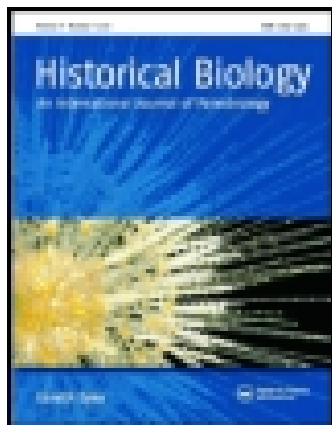


This article was downloaded by: [Adriana Albino]

On: 25 February 2015, At: 10:23

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Historical Biology: An International Journal of Paleobiology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ghbi20>

First Tupinambinae teiid (Squamata, Teiidae) from the Palaeogene of South America

S. Brizuela^a & A.M. Albino^a

^a Departamento de Biología, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina

Published online: 23 Feb 2015.



[Click for updates](#)

To cite this article: S. Brizuela & A.M. Albino (2015): First Tupinambinae teiid (Squamata, Teiidae) from the Palaeogene of South America, *Historical Biology: An International Journal of Paleobiology*, DOI: [10.1080/08912963.2014.993629](https://doi.org/10.1080/08912963.2014.993629)

To link to this article: <http://dx.doi.org/10.1080/08912963.2014.993629>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

First Tupinambinae teiid (Squamata, Teiidae) from the Palaeogene of South America

S. Brizuela* and A.M. Albino¹

Departamento de Biología, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina

(Received 4 November 2014; accepted 18 November 2014)

The Luján Formation in north-western Argentina is notable for preserving lizard remains from the Palaeogene of South America. In this paper, we offer a re-description and re-evaluation of the material belonging to the holotype of the teiid lizard *Lumbrerasaurus scagliai* (Donadío, 1985) recovered from sediments of the Luján Formation near Pampa Grande, Salta province, Argentina. *Lumbrerasaurus scagliai* is considered here as an extinct genus of Tupinambinae. These remains are the earliest record of teiid lizards and confirm the presence of tupinambine teiids in the South American Palaeogene.

Keywords: Squamata; Teiidae; Tupinambinae; Palaeogene; South America

Introduction

Palaeogene squamates of Argentina are represented by a number of snake vertebrae primarily from Patagonian localities (Simpson 1933, 1935; Hoffstetter 1959; Albino 1987, 1993, 1996, 2011, 2012); however, the Luján Formation has provided lizard remains from the north-west of the country (Figure 1) (Donadío 1985; Albino 1993). The lizard material from this formation was first described by Donadío (1985), who named a new genus and species of Teiidae, *Lumbrerasaurus scagliai*. Later, Sullivan and Estes (1997) suggested that *Lumbrerasaurus* is inadequately diagnosed and considered it as a *nomen dubium*. Nevertheless, nobody has studied the fossil remains since Donadío (1985). A re-description and re-evaluation of the remains belonging to *Lumbrerasaurus scagliai* are presented in this paper. They represent the only documented record of squamate reptiles from the Palaeogene of a non-patagonian site of Argentina.

Institutional abbreviation

AC, Cátedra de Anatomía Comparada, Departamento de Zoología, Universidad Nacional de Córdoba, Córdoba, Argentina; FML, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Argentina; MNHNC, Museo Nacional de Historia Natural, Santiago, Chile; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; QCAZR, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Pichincha, Ecuador; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, USA; UNMdP,

Colección Herpetológica Laboratorio de Vertebrados, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; UNMdP-O, Colección Herpetológica – Sección Osteología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; UNNE, Universidad Nacional del Nordeste, Resistencia y Corrientes, Argentina.

Materials and methods

The biochronological sequence of South American Land Mammal Ages (SALMAs of Pascual et al. 1996) for the early Cenozoic of South America was recently revised (Gelfo et al. 2009; Woodburne et al. 2013) and provides an up-to-date scheme for the record of early Cenozoic squamates. Squamate systematics follow Gauthier et al. (2012). Fossils were confronted with osteological specimens of different institutional collections (Appendix 1) and bibliography. Fossils and specimens were analysed using a stereoscope microscope and photographed with a digital camera; scanning electron microscopy was also used.

Vertebral terminology follows Hoffstetter and Gasc (1969), whereas cranial terminology is based on Oelrich (1956) with additions/modifications of Montero et al. (2004), Rage and Augé (2010), Smith (2006) and Smith and Gauthier (2013). Denton and O'Neill (1995, p. 240–241) describe a dual septum in the maxilla of *Prototeius stageri* and mentioned the distribution of this character among Teiidae and Polyglyphanodontia (= Borioteiioidea Nydam et al., 2007). Although *Prototeius stageri* was originally considered a Polyglyphanodontia, its relationship with these lizards is uncertain (Nydam et al. 2010).

*Corresponding author. Email: brizuela@mdp.edu.ar

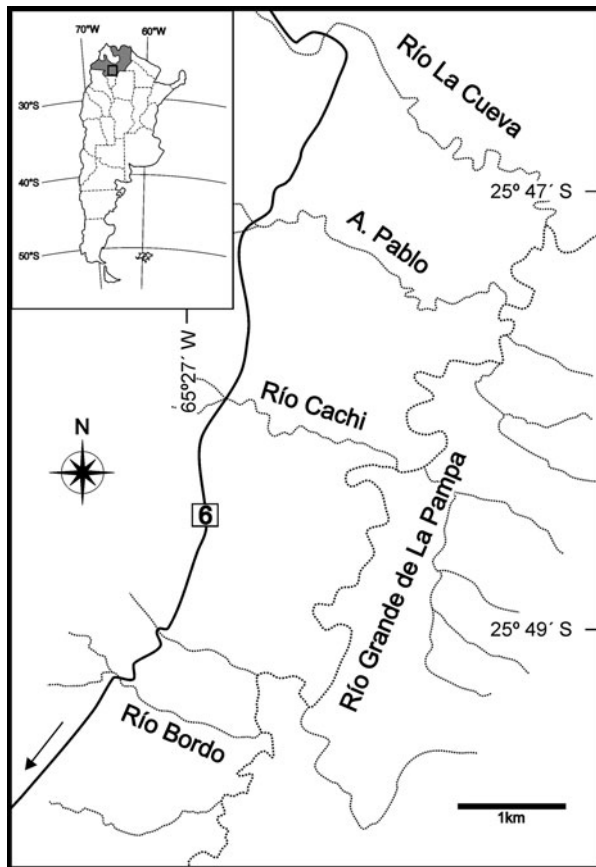


Figure 1. Location map of area from Lumbrera Formation from where fossils were recovered (modified from Carvajal et al. 1977). Salta Province in grey, square is the magnified area and arrow indicates the direction to Pampa Grande.

Independently, the dual septum has been recognised (i.e. coded in data matrix) in other Polyglyphanodontia (*Bicuspidon*, *Cherminosaurus*, *Gilmoretius*, *Polyglyphanodon*) and some Teiidae (*Callopietes*, *Dracaena*) (Denton and O'Neill 1995; Nydam et al. 2007). Denton and O'Neill (1995) do not name the anterior and posterior buttresses that constitute their dual septum. For teiids, our interpretation is that the first of these two structures would correspond (but much modified) to the *crista transversalis*, and the second to a previously unnamed vertical structure developed medially on the nasal process whose dorsal end continues posteriorly as the nasolacrimal ridge (lacrimal crest of Oelrich 1956 = *cresta semilunar* of Montero et al. 2004) (Figure 2). The septomaxilla largely articulates on the *crista transversalis* and extends posteriorly to the posterior buttress. The question on what is the anterior buttress of the Polyglyphanodontia (very developed *crista transversalis*, fused septomaxilla or something else) is out of the scope of this contribution.

Geological setting

The Lumbrera Formation corresponds to the upper unit of the Santa Barbara subgroup (Salta Group). del Papa (2006) recognised, based on facies associations, two sections in this formation: inferior and superior. Contact between the Inferior Lumbrera Formation and the Superior Lumbrera Formation is represented by an unconformity that separates two sedimentary cycles (del Papa 2006). Within the Inferior Lumbrera Formation, there are two green levels: the inferior Faja Verde I and the superior Faja Verde II. Only the former is continuous throughout the Inferior Lumbrera Formation (del Papa 2006).

The mammalian fauna of the Lumbrera Formation was initially referred to the Casamayoran SALMA (Carvajal et al. 1977; Pascual et al. 1978, 1981), which Kay et al. (1999), based on isotopic and magnetic polarity data from Patagonia, correlate with the late Eocene. More recently, Deraco et al. (2008), based on the presence of a leontiniid (Mammalia, Notungulata), consider the red levels above Faja Verde II, as 'Barrancan'–Mustersan (mid late Eocene). These authors consider the levels below the Fajas Verdes I and II as chronologically equivalent to the Patagonian Vaquian (early Casamayoran). However, the faunas from north-west of Argentina show strong endemism at the generic and specific level, complicating the correlation with other faunas, especially with those of Patagonia, on which the Casamayoran is sustained (Vucetich et al. 2007). Marshall et al. (1997) consider that the lower part of the Lumbrera Formation correlates with chrons 25n and 26n, and the Fajas Verdes (I and II) correlate with chron 24r. Therefore, an age of 58–55.5 Ma for the lower part of the Lumbrera Formation is inferred. This would put the Lumbrera Formation in the late Palaeocene. Some consideration must be taken into account regarding this age because the palaeomagnetic data from the Lumbrera Formation were analysed when laboratory techniques were less rigorous than those applied later (see Sempere et al. 1997, p. 725). In this paper, the more accepted criteria of Vucetich et al. (2007) are followed, according to which the Lumbrera Formation is early Eocene in age.

The material described here was collected in a joint expedition of MLP and MMP in 1979. It was retrieved 5 m below Faja Verde I in a canyon between rivers Bordo and Toro near Pampa Grande, Salta province (Donadío 1985). All elements were closely associated. Reference to Ruta Nacional 9 in Donadío (1985) and Carvajal et al. (1977) would correspond to Ruta Provincial 6 that connects the localities of Pampa Grande and La Viña, as inferred from course of the road and geographical coordinates provided in Carvajal et al. (1977) (Figure 1).

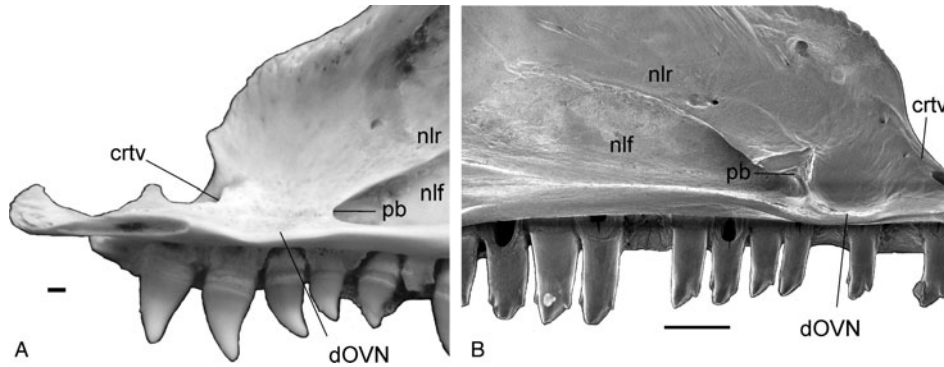


Figure 2. Antero medial anatomical features of Teiidae maxillae. (A) tupinambine *Tupinambis merianae* (UNMdP-O 75); (B) teiine *Ameiva ameiva* (UNMdP-O 27) crtv, crista transversalis; pb, posterior buttress; nlf, nasolacrimal fossa; nlr, nasolacrimal ridge; dOVN, depression for vomeronasal organ. Scale: 1 mm.

Systematic palaeontology

SQUAMATA Oppel, 1811

SCLEROGLOSSA Estes, de Queiroz and Gauthier, 1988

AUTARCOGLOSSA Wagler, 1830

SCINCOMORPHA Camp, 1923

TEIOIDEA Estes, de Queiroz and Gauthier, 1988

TEIIDAE Gray, 1827

TUPINAMBINAE Presch, 1974

Lumbrerasaurus scagliai Donadío, 1985

(Figure 3)

Holotype: MMP 1418, partial lizard skeleton, that includes fragments of an anterior (MMP 1418-1) and posterior (MMP 1418-2) left maxilla, the proximal end of a left epipterygoid (MMP 1418-3), three dorsal vertebrae (MMP 1418-4 a, 1418-6), one sacral vertebra (MMP 1418-7) and two caudal vertebrae (MMP 1418-8, 1418-9). All remains belong to a same specimen and were previously described by Donadío (1985).

Revised diagnosis: *Lumbrerasaurus scagliai* is a teiid lizard bearing a unique combination of characters but not those mentioned by Donadío (1985) as diagnostic. *Lumbrerasaurus scagliai* is distinguishable from Teiinae teiids (*Ameiva*, *Aspidoscelis*, *Cnemidophorus*, *Dicrodon* and *Kentropyx*) in presenting a low, vague posterior buttress, and vertebrae with narrow, thick zygosphene, triangular outline of the neural canal and weak sagittal crest. The amount of cementum at the base of the teeth in *Lumbrerasaurus* differs from the more abundant deposition in the tupinambines *Dracaena* and *Paradracaena*. *Lumbrerasaurus* further differs from *Dracaena*, *Paradracaena* and *Tupinambis* (except *Tupinambis quadrilineatus*) in presenting labiolingually compressed posterior teeth. Unlike other tupinambinae bearing labiolingually compressed teeth (*Crocodylurus* and *Tupinambis quadrilineatus*), those of *Lumbrerasaurus* are more compressed distally.

Re-description: The anterior and posterior maxillary fragments (MMP 1418-1, -2) show subpleurodont tooth implantation. Tooth positions are delimited by interdental septa (transverse walls from the parapet to the supradental shelf) of alveolar bone. Attachment of the teeth to the bone is mainly through their bases, which are, in turn, covered by abundant cementum. The latter only partially conceals both the interdental septa and *sulcus dentalis*.

Specimen MMP 1418-1 (Figure 3(A),(B)) is the anterior part of a left maxilla, where the anterior end of the premaxillary process is not preserved. The lateral surface is smooth, without ornamentation, and bears three labial foramina at tooth positions (b), (c) and one more posterior to this last. The posteroventral part of the fenestra exonarina is preserved. The facial process rises gradually in lateral view. Its dorsal surface is slightly convex and extends from the anterior superior alveolar foramen in an anterolabial direction as a weak *crista transversalis*. Medially and anteriorly on the palatal shelf, the articulation surface for the vomer is preserved. Posterior to this articulation surface, but dorsal on the palatal shelf, is the depression that dorsally housed the vomeronasal organ (VNO). This depression is limited laterally by a subtle step that as consequence of the distortion of the facial process forms a narrow and deep groove. Separating the depression for the VNO from the nasolacrimal fossa is possible to distinguish a faint, low and very short convexity, the posterior buttress. Only the anterior-most part of the nasolacrimal crest is preserved, which forms a relatively acute angle with the palatal shelf, and ends anteriorly at the posterior buttress. Only a small portion of the nasolacrimal fossa is preserved below the crest. The posteromedial border of the palatal shelf is not preserved. In ventral view, the maxilla is wide, with the parapet taller than the crest of the supradental shelf. Only three tooth positions are preserved, in which two teeth are present with their apical ends missing. The anterior-most tooth, (a), is tall and labiolingually compressed (i.e. suboval in

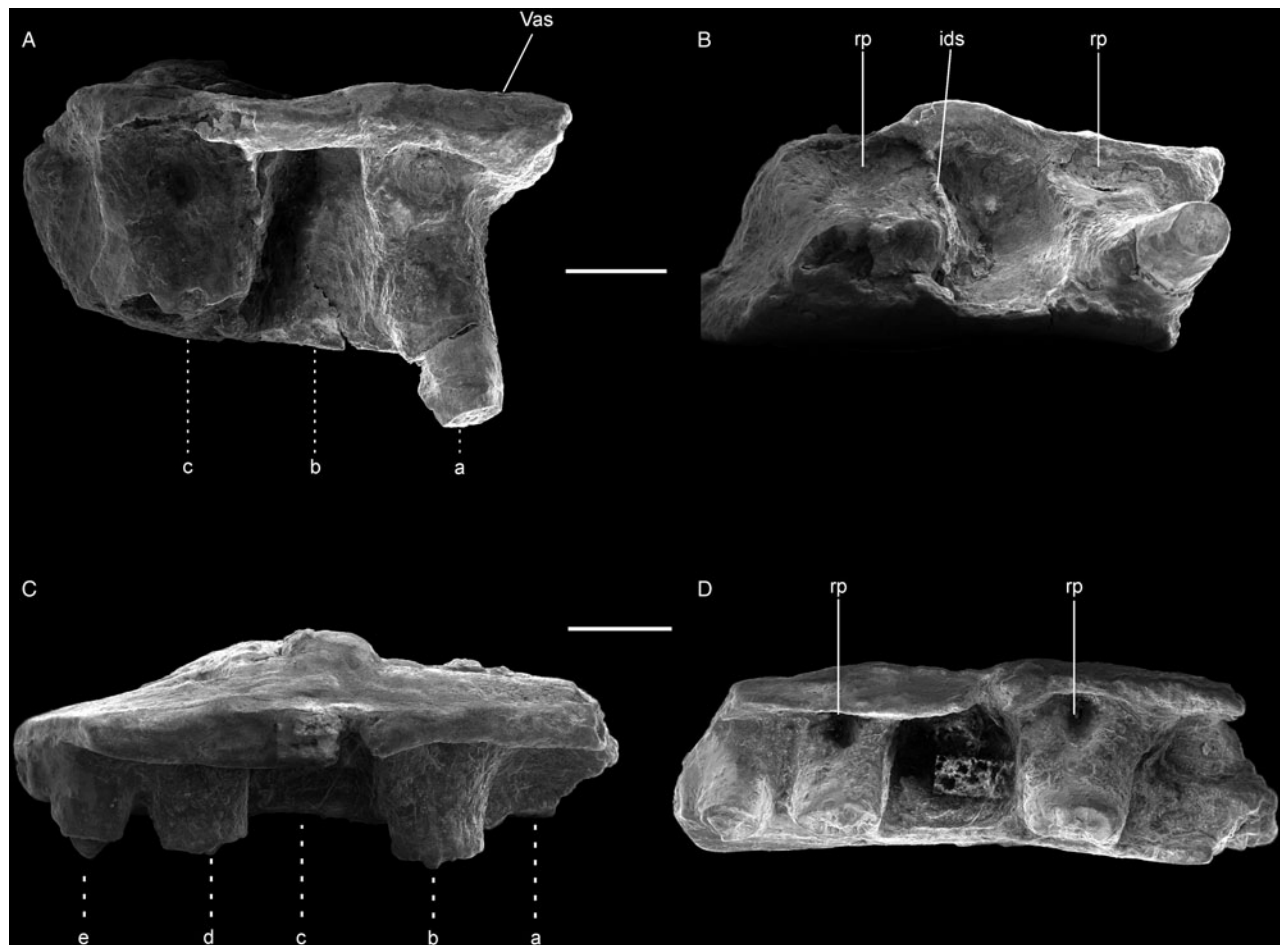


Figure 3. Cranial elements of the Tupinambinae *Lumbresasaurus scagliai*, from the early Eocene (Lumbrera Formation) of north-west Argentina. (A, B) Anterior fragment of a maxilla (MMP 1418-1) in medial (A) and ventral (B) views; (C, D) posterior fragment of a maxilla (MMP 1418-2) in medial (C) and ventral (D) views. ids, interdental septum; rp, resorption pit; Vas, vomer articulation surface. Scale: 2 mm.

section), compression that is more accentuated on the distal end of the tooth (Figure 3(A),(B)). A very thin and weak crest crosses the distal face of the tooth, from the base to the apex where it is more evident (Figure 3(B)). The base of tooth (c) is larger than that of tooth (a), and it is labiolingually compressed as in the last one. Resorption zones are located lingually at the base of the teeth, and they develop into deep, suboval pits excavated in the cementum.

Fragment MMP 1418-2 (Figure 3(C),(D)) represents the posterior end of the same left maxilla. Its lateral surface is straight and preserves the last labial foramen at tooth position (a). Dorsally, the preservation is poor, but the facial process border is distinguishable. Medially, the superior alveolar canal is exposed and filled with sediment. Posteriorly, and poorly defined, are the superior alveolar foramen medial to the groove that housed the maxillary process of the jugal; this groove extends anteriorly clearly reaching tooth (d). In medial view, a poorly preserved palatal shelf is observed, upon which the

articulation surfaces for the palatine and ectopterygoid are preserved posteriorly. Ventrally is the dental series, medial to which develops the *sulcus dentalis*. As in MMP 1418-1, the parapet is taller than the crest of the supraddental shelf. There are five tooth positions in which only three bases are preserved (positions b, d and e). Tooth bases are labiolingually compressed, more so distally. There is less cementum at the bases in this fragment than in MMP 1418-1. Two resorption pits are preserved lingual to teeth (b) and (d). The pits are more circular, somewhat smaller and deeper than those in MMP 1418-1.

MMP 1418-3 is a fragment of a long flat bone that probably corresponds to the ventral end of a left epipterygoid (Figure 4). The fragment is medially flat and laterally slightly convex. In lateral view, its ventral end is expanded, more pronounced anteriorly. The anterior lateral outline of this fragment is slightly concave. The posterior part of the lateral surface is higher, and we interpret it as the crest that crosses the epipterygoid dorsoventrally.

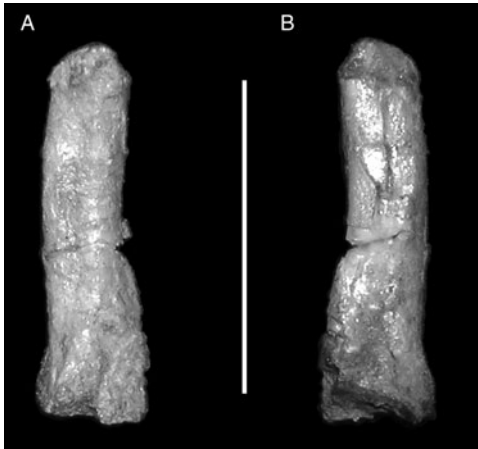


Figure 4. Epipterygoid fragment (MMP 1418-3) of the Tupinambinae *Lumbresasaurus scagliai*, from the early Eocene (Lumbrera Formation) of north-west Argentina. (A) lateral view; (B) medial view. Scale: 10 mm.

The dorsal vertebra MMP 1418-4 (Figure 5(A),(B)) is large and distorted. The latter resulted in the obliteration of the neural canal due to the collapse of the neural arch onto the vertebral centrum. The condyle is missing, while the left transverse process is only partially preserved. The prezygapophyses are anterolaterally oriented, and their articulation surfaces are oval and steeply inclined. The anteromedial end of the neural arch is not preserved. Nonetheless, from the thick proximal (right) part, an important anterior extension is inferred. Although distorted, the transition between the prezygapophyseal and zygosphenal articulation surfaces is continuous. The neural spine is broken anteriorly, though its mark on the neural arch is visible on the anterior part. Though well-developed, the neural spine was probably low. Laterally, posterior to the prezygapophyses, are the transverse processes that distally bear oval, vertically orientated synapophyses. The vertebral centrum has a triangular outline, with a poorly developed sagittal crest along its entire ventral length. On either side of the sagittal crest, there are small foramina, which are interpreted as subcentral foramina. The cotyle is oval, wider than high and oriented anteroventrally.

The dorsal vertebra MMP 1418-5 (Figure 5(C),(D)) is also dorsoventrally distorted and somewhat smaller than the previous one. In this vertebra, the neural canal is displaced to the left of the centrum. The right prezygapophysis and postzygapophysis and the transverse processes are missing. The left prezygapophysis is large and anterolaterally oriented. Its articulation surface is poorly preserved. Medial to the prezygapophyses is the proximal part of the zygosphenon, which is poorly preserved. The broken base of the neural spine extends along the entire dorsal surface of the neural arch. The

articulation surface of the left postzygapophysis is oval and posterolaterally oriented. The ventral outline of the vertebral centrum is triangular, ending in a marked precondylar constriction. The ventral surface of the centrum is similar to that described for vertebra MMP 1418-5 with a small subcentral foramen on the right. The cotyle is deep, transversally oval and ventrally inclined. The condyle is similarly oval and inclined.

The dorsal vertebra MMP 1418-6 is only partially preserved but includes the left side of the zygosphenon (Figure 5(E),(F)). It extends anteriorly covering the cotyle in dorsal view, with the anterior margin notched. Due to distortion, the zygosphenal articulation surface is horizontal and parallel to that of the prezygapophysis. Transition between these surfaces is continuous as in MMP 1418-4. Only the anterior part of the neural spine is preserved, which is bent laterally because of distortion. The left prezygapophysis is large, orientated anterolaterally and bears a large, subcircular articulation surface. Posterior to the prezygapophysis is a well-defined interzygapophyseal crest. The transverse process is short and bears a vertically oriented, rectangular synapophysis. The cotyle is much deformed, but clearly deep.

Sacral vertebra MMP 1418-7 (Figure 5(G),(H)) does not preserve its dorsal part, except for the left prezygapophysis and the anterodorsal surface of the left pleurapophysis. The prezygapophysis is small and anteriorly orientated. Its articulation surface is subtriangular and almost vertically orientated because of distortion. In ventral view, the vertebral centrum is anteroposteriorly short and rectangular. A marked precondylar constriction precedes the condyle. At both sides of the centrum, there are the proximal parts of the pleurapophyses. These are strong and depressed. Ventrally they show shallow longitudinal grooves, but no ventral foramina are observed.

Caudal vertebra MMP 1418-8 preserves part of the left side and the vertebral centrum. The latter is long, cylindrical and constricted at the middle, with a well-developed precondylar constriction. Posterior to the cotyle, there are two subcentral foramina, of which the right one is larger. In lateral view, upon the neural arch, is a well-defined interzygapophyseal ridge. Between the neural arch and vertebral centrum is the mark of the transverse process/pleurapophysis, which was anteroposteriorly long and strongly depressed.

The caudal vertebra MMP 1418-9 preserves the right side and the vertebral centrum but not the condyle. The centrum is short but more robust than the one previously described. All other aspects are as in MMP 1418-8.

Fragment MMP 1418-10 could correspond to the posterior part of a dorsal vertebra. Part of the condyle is inferred as well as the right posteroventral border of the neural arch.

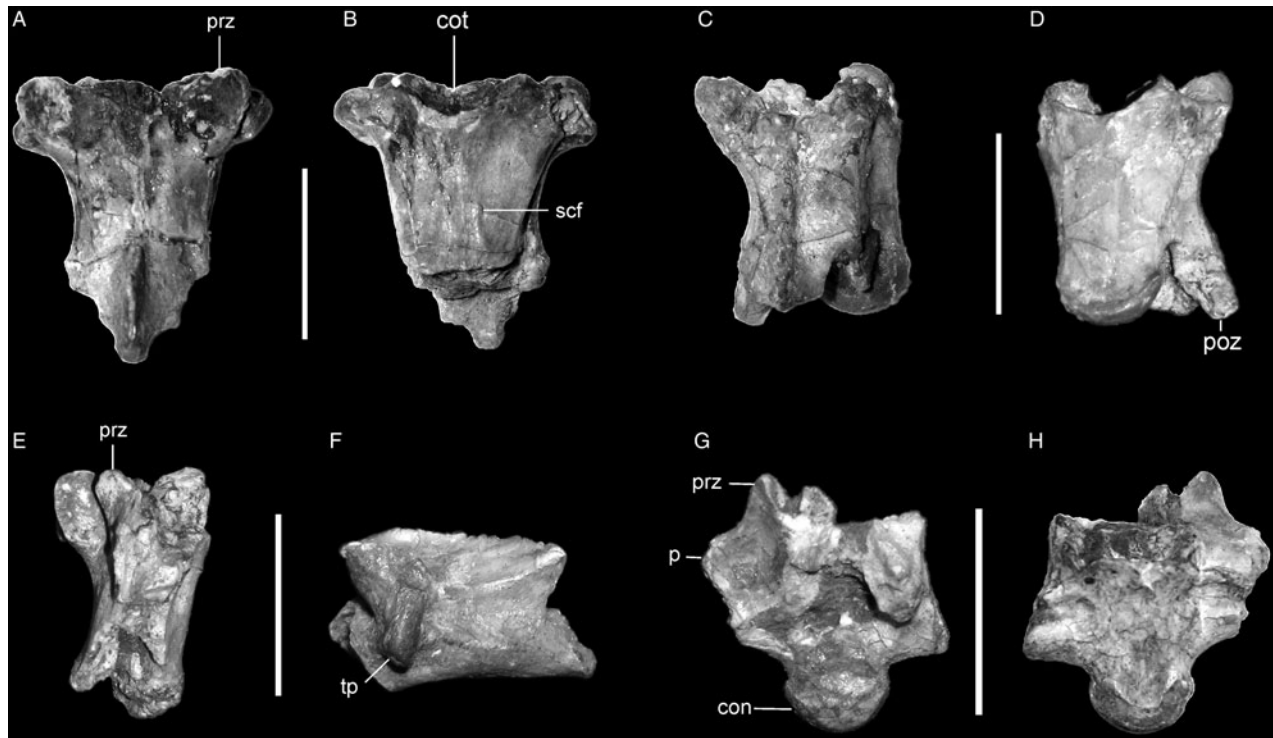


Figure 5. Vertebrae of the Tupinambinae *Lumbrerasaurus scagliai*, from the early Eocene (Lumbrera Formation) of north-west Argentina. (A, B) Dorsal vertebra (MMP 1418-4) in dorsal (A) and ventral (B) views; (C, D) dorsal vertebra (MMP 1418-5) in dorsal (C) and ventral (D) views; (E, F) dorsal vertebra (MMP 1418-6) in dorsal (E) and lateral (F) views; (G, H) sacral vertebra (MMP 1418-7) in dorsal (G) and ventral (H) views. con, condyle; cot, cotyle; p, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis; scf, subcentral foramen; tp, transverse process. Scale: 10 mm.

Comparisons

From the observations of the articulation surface for the vomer on the maxilla MMP 1418-1, it is possible to affirm that maxilla and vomer meet at the anterior margin of the fenestra exochoanalis, which is a squamate synapomorphy (Rieppel et al. 2008; Gauthier et al. 2012). The nasolacrimal fossa, ventral to the nasolacrimal ridge, as observed in the fossil maxilla MMP 1418-1 is a synapomorphy of Autarchoglossa (Gauthier et al. 2012). The anteriorly extended maxillary process of the jugal (relative to the tooth row), as inferred from MMP 1418-2, allows the exclusion of the fossils from most Xantusiidae (except *Lepidophyma flavimaculatum*), Rhineuridae and the clade *Aiolosaurus oriens* + Varanoidea (Gauthier et al. 2012). The presence of a jugal can further exclude the fossils from the Krypteia because they lack this bone (Gauthier et al. 2012).

The subpleurodont tooth implantation is characteristic of the Teiidae, although it is known in members of other groups (e.g. the scincid *Tiliqua rugosa*, the amphisbaenian *Rhineura hatcherii*) (Gao and Fox 1996; Zaher and Rieppel 1999; Kearney et al. 2005; Nydam et al. 2007). The maxilla also shows lingual resorption zones, which corresponds to the iguanid method of tooth replacement

observed in most Scincomorpha, among others (see Edmund 1960, 1969). Resorption zones in Teiidae are not always lingual: they are sometimes found in a distolingual position (Edmund 1960, 1969). This variation is found at different levels, from generic, species, individual and even within the same specimen (Edmund 1960). Resorption pits of the fossils do not extend apically beyond the cementum. This type of 'low' resorption pit is observed among Teiidae. This contrast with the more apical developed pits observed in some pleurodont iguanids (e.g. *Tropidurus*) and seems to be related to implantation types.

The articulation surface for the palatine and ectopterygoid is wide, undifferentiated and embracing all the posterior end of the fossil maxilla MMP 1418-2. This allows the inference that the maxilla was excluded from the suborbital fenestra (Donadío 1985). This condition has long been recognised among Teiidae (although not exclusively) by various authors (e.g. Estes et al. 1988), further supporting affinity with them.

The Polyglyphanodontia, a Cretaceous Laurasian radiation of lizards, has for a long time been considered related to Teiidae (e.g. Estes 1983). This relationship between extinct Polyglyphanodontia and extant Teiidae (Teiidae and Gymnophthalmidae) [note the difference in

spelling, from the original of Estes et al. (1988) and emended in Gauthier et al. (2012)] is now considered to be more distant (e.g. Nydam et al. 2007; Nydam and Caldwell 2008; Gauthier et al. 2012). As mentioned before, Denton and O'Neill (1995) described a dual septum in the *Prototeius* (and noted in some Polyglyphanodontia) that limits anteriorly and posteriorly the depression for the VNO (on the palatal shelf). The anterior buttress is evident and medially expanded in Polyglyphanodontia (e.g. *Bicuspidon* see figure 2(A),(B) in Nydam and Cifelli 2002), whereas in the Teioidea, it is much reduced to the *crista transversalis*. Furthermore, the posterior buttress is located in different position among Teiidae and Gymnophthalmidae. While in Teiidae it is located posterior to the fenestra exonarina (in lingual view) (Figure 2), in Gymnophthalmidae, it is found just below, or much closer, to this fenestra (Bell et al. 2003, figure 4; Brizuela 2010). The morphology of the posterior buttress varies among Teiidae. In Teiinae the posterior buttress is marked, generally more developed dorsally (where it receives the septomaxilla), whereas in Tupinambinae, it is a low and vague ridge (Figure 2) (Brizuela 2010, figure 89). The morphology of the posterior buttress of MMP 1418-1 more closely resembles that of Tupinambinae. The dorsal morphology between the *crista transversalis* and posterior buttress, with a medial depression and a more lateral step, all much thinner than the posterior part of the palatal shelf, is also observed in tupinambine teiids (Figure 2(A)).

Regarding the postcranial elements, the morphology observed among the fossil vertebrae is like in extant Teiidae, although not exclusively (Hoffstetter and Gasc 1969). The shared characters are: procoelia, large size, well-developed zygosphenes–zygantrum system with a developed tenon and notched anterior zygosphenal border, no prezygapophysial process, triangular vertebral centrum (in outline), dorsoventrally compressed cotyle and condyle, and marked precondylar constriction. Among Teiidae, several differences have been observed at subfamilial level (Donadío 1985; Brizuela 2010; Albino and Brizuela 2014). In Tupinambinae there is a low, wide and vague ventral sagittal crest unlike the well-defined sagittal crest observed in Teiinae. In Tupinambinae, the neural canal is small and triangular in cross section, but it is relatively larger and oval in Teiinae. Finally, the zygosphenes of adult Tupinambinae is narrower (in dorsal view) and thicker (in anterior view) than in Teiinae. The fossil shares the same characters observed in Tupinambinae. The large size of fossil vertebrae also favours Tupinambinae relationships. Small, subcentral foramina are observed on the dorsal vertebra (MMP 1418-4, contra Donadío 1985). These are smaller than those of the caudal vertebra (MMP 1418-8). Small foramina are common among dorsal vertebrae of extant teiids, although irregularly present. Donadío (1985) considered that the presence/absence of these foramina (on dorsal and caudal

vertebrae) and the shape of the articulation surfaces of the zygapophyses have systematic value. These characters were later dismissed as non-diagnostic by Sullivan and Estes (1997). The variability present in these vertebral structures observed in the referred specimens (see Appendix 1), and the distortion of the fossils, support Sullivan and Estes's (1997) claim.

The maxilla fragments were originally recovered without the apical end of the teeth. Nonetheless, and based on the cross section of the preserved tooth bases, Donadío (1985) inferred a heterodont dentition in the fossil species. It could be argued that the subtle differences in the shape of the resorption pits could also correspond to a heterodont dentition. Unfortunately, the absence of the apical ends of functional or replacement teeth and the similarity of the tooth bases along the dental series make it impossible to verify Donadío's statement. Other aspects of the dentition are noteworthy. The suboval outline of the tooth bases, with a more marked distal constriction, is a character absent in other teiids, extant or extinct. This character was also dismissed by Sullivan and Estes (1997), but it seems unlikely to be an artefact because it is observed in all preserved tooth bases (Figure 3). The suboval outline of the fossil teeth differs from the more circular outline present in the tupinambines *Dracaena* and adult *Tupinambis* (except *Tupinambis quadrilineatus*). The subtle, but clear distal crest of tooth (a) of MMP 1418-1, seems to accompany this distal compression and would argue against artefactual compression. The dental characteristics of the fossils could be interpreted as similar to those observed in 'taxon 5' described by Carvalho (2001) for the Palaeogene of Itaboraí (Brazil) (Itaboraian SALMA early Eocene: Vucetich et al. 2007). 'Taxon 5' is referred by Carvalho (2001) to an unnamed new genus and species of Teiidae similar to the extant *Crocodylurus*. This fossil taxon is characterised by its heterodonty, which is composed of uni-, bi- and tricuspid teeth with cusps mesiodistally arranged. The particularity of this dentition is that the first accessory cusp that develops is the distal one, not the mesial one. Although Carvalho (2001) does not make reference to the cross section of the teeth, they appear to be oval based on his figures (Carvalho 2001, figures 24 and 25). The first appearance of the distal cusp could imply a more marked labiolingual constriction of the distal end of the tooth section, resulting in an outline similar to that of fossils studied here. However, in view of the insufficiency of the material from the Lumbreira Formation and the lack of a formal description of 'taxon 5', study of their possible relationships would be speculative.

Unlike Sullivan and Estes (1997), we feel that the Tupinambinae assignment of the studied specimen is supported by both cranial (subpleurodont implantation, lingual replacement zones with 'low' resorption pits and maxilla excluded from the suborbital fenestra) and

vertebral characters (developed zygosphenes–zygantrum, precondylar constriction, among others), and that there is no justification to consider *Lumbrerasaurus scagliai* as a *nomen dubium* because it is characterised by a unique combination of characters.

Discussion

Previous reports concerning South American Palaeogene squamates include a great diversity of lizards and snakes from Brazil (Albino 1990; Rage 1998, 2001, 2008; Carvalho 2001), few representatives from Bolivia and Peru (Rage 1981, 1991), a marine palaeopheid snake from Ecuador (Hoffstetter 1958), a giant boid from Venezuela (Head et al. 2009) and a number of snakes from Argentina mainly distributed in Patagonian localities (Simpson 1933, 1935; Hoffstetter 1959; Albino 1987, 1993, 1996, 2011, 2012; Albino and Carlini 2008). The notable diversity of Palaeogene snakes from Patagonia, with at least one genus of madtsoiid (*Madtsoia*) and three genera of boids (*Boa*, *Chubutophis* and *Waincophis*), contrasts with the absence of lizards during the same period (Albino 2011). A similar pattern is observed in Patagonian Mesozoic deposits, where snakes are represented by more than six genera and continental lizards only by two taxa (Albino 2007, 2011). However, Cretaceous lizards from non-Patagonian localities are represented by interesting and diverse remains from various localities of Brazil (Estes and Price 1973; Evans and Yabumoto 1998; Candeiro et al. 2009; Nava and Martinelli 2011; Simões 2012; Simões et al. 2014). Also, the diverse but undescribed Itaboraian lizard fauna of Brazil (Carvalho 2001) demonstrates that the principal clades of lizards probably were diversified in South America at least by the early Eocene (Albino 2011). These deposits are also rich in snakes (Albino 1990; Rage 1998, 2001, 2008). In southern mid-latitudes, the fauna from Tiupampa in Bolivia (early Palaeocene, Gelfo et al. 2009) has provided a possible iguanian lizard and diverse snake taxa (de Muizon et al. 1983; Rage 1991). Early Eocene deposits of the Lumbra Formation in north-western Argentina provide remains of a teiid lizard, corroborating that lizards and snakes were present in the Palaeogene of South America outside of Patagonia. It is not possible to know at present the reason for the disparity between Patagonian and non-Patagonian Palaeogene lizard occurrence. It could reflect the lack of lizards in southernmost Palaeogene environments, poorer samplings of small remains in Patagonian Palaeogene deposits, or insufficient conservation of fossil specimens for recognition as lizards.

As stated above, the South American Palaeogene includes a possible teiid lizard from the early Eocene of Brazil, although the material remains unpublished (Carvalho 2001). Teiid remains described in this paper suggest that this lizard group may have been broadly distributed from north-western Argentina to the Atlantic

coast of Brazil during the early Cenozoic. Also, the presence of tupinambine teiids in the Eocene indicates that the divergence of the two subfamilies of Teiidae (Teiinae and Tupinambinae) had already occurred at the beginning of the Cenozoic. This palaeontological conclusion is consistent with the molecular data indicating that the most basal tupinambine lineage (i.e. *Callopiestes*) would have diverged during the Palaeocene (Giugliano et al. 2007).

Quattrocchio (2006) identified in the Lumbra Formation a subtropical vegetation including elements of temperate regions. The teiid lizard studied in this paper, as well as the presence of sebecid crocodiles and pelomedusid turtles in the same sediments (Gasparini 1984; Gasparini et al. 1986), is consistent with these assumptions. Today, *Tupinambis rufescens* is the unique tupinambine teiid living in the area of Pampa Grande of the Salta province (Ceï 1993).

Acknowledgements

We thank A. Dondas (MMP) and F. Scaglia (MMP) for allowing the study of the Lumbra fossils. We are grateful to the following people who facilitated, in one way or another, reference material for this study: M. Cabrera (AC), E.R. Heyer (USNM), S. Kretzschmar (FML), H. Núñez (MNHNC), G. Schneider (UMMZ), M.E. Tedesco (UNNE), O. Torres Carvajal (QCAZR), L.E. Vega (UNMDP) and H. Zaher (MZUSP). We also thank the reviewers J.D. Daza, R.L. Nydam and K.T. Smith for their valuable comments on the manuscript and F. Tricárico (Museo Argentino de Ciencias Naturales) for the helping us with the scanning electron microscope images.

Funding

This work was partially supported by the Consejo Nacional de Investigaciones Científicas y Técnicas [grant number PIP-CONICET 112-200901-00176].

Note

1. Email: aalbino@mdp.edu.ar

References

- Albino AM. 1987. Un nuevo Boidae (Reptilia: Serpentes) del Eoceno temprano de la provincia del Chubut, Argentina [A new Boidea (Reptilia: Serpentes) from the early Eocene of Chubut province, Argentina]. *Ameghiniana*. 24(1–2):61–66.
- Albino AM. 1990. Las serpientes de Sao José de Itaboraí (Edad Itaboraiense, Paleoceno medio), Brasil [Snakes from São José de Itaboraí (Itaboraian Mammal Age, Middle Paleocene), Brazil]. *Ameghiniana*. 27(3–4):337–342.
- Albino AM. 1993. Snakes from the Paleocene and Eocene of Patagonia (Argentina): paleoecology and coevolution with mammals. *Hist Biol.* 7:51–69.
- Albino AM. 1996. Snakes from the Miocene of Patagonia (Argentina). Part I: the Booidea. *N Jb Geol Paläontol Abh.* 199(3):417–434.
- Albino AM. 2007. Lepidosauromorpha. In: Gasparini Z, Salgado L, Coria RA, editors. *Patagonian Mesozoic reptiles*. Bloomington, IN: Indiana University Press; p. 87–115.

- Albino AM. 2011. Morfología vertebral de *Boa constrictor* (Serpentes: Boidae) y la validez del género mioceno *Pseudoepicrates* Auffenberg, 1923 [Vertebral morphology of *Boa constrictor* (Serpentes: Boidae) and the validity of the Miocene genus *Pseudoepicrates* Auffenberg, 1923]. *Ameghiniana*. 48(1):53–62.
- Albino AM. 2012. First snake record from the Sarmiento Formation at La Gran Hondonada (Chubut Province, Argentina). *Ameghiniana*. 49(2):230–235.
- Albino AM, Brizuela S. 2014. First record of squamate reptiles from the Oligocene of South America. *Alcheringa*. 38(3):412–421.
- Albino AM, Carlini AA. 2008. First record of *Boa Constrictor* (Serpentes, Boidae) in the Quaternary of South America. *J Herpetol*. 42(1):82–88.
- Bell CJ, Evans SE, Maisano JA. 2003. The skull of the gymnophthalmid lizard *Neusticurus eupleopus* (Reptilia: Squamata). *Zool J Linn Soc*. 139:283–304.
- Brizuela S. 2010. Los lagartos continentales fósiles de la Argentina (excepto Iguania) [The continental fossil lizards of Argentina (except Iguania)] [Ph.D. dissertation] La Plata: Universidad Nacional de La Plata.
- Camp CL. 1923. Classification of the lizards. *Bull Am Mus Nat Hist*. 48: 289–481.
- Candeiro CRA, Navas CA, Martinelli AG, Forasiepi AM, Scanferla CA, Muzzopappa P. 2009. New lizard record (Diapsida, Lepidosauria) from the Upper Cretaceous Adamantina Formation, Brazil. *Bull Geosci*. 84(3):573–576.
- Carvajal E, Pascual R, Pinedo R, Salfity J, Vucetich MG. 1977. Un nuevo mamífero de la Formación Lumbra (Grupo Salta) de la Comarca de Carahuasi (Salta, Argentina). Edad y correlaciones [A new mammal from the Lumbra Formation (Salta Group) from the Carahuasi (Salta, Argentina) region. Age and correlations]. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia'*. 2:148–163.
- Carvalho AB. 2001. Estudo taxonomico dos 'lagartos' fósseis (Lepidosauria: Squamata) da Bacia de Sao José de Itaboraí (Paleoceno), Estado do Rio de Janeiro [Taxonomic study of the fossil "lizards" (Lepidosauria: Squamata) from the São José de Itaboraí basin (Paleocene), Rio de Janeiro state] [Ph.D. dissertation] Rio de Janeiro: Universidade Federal do Rio Janeiro.
- Cei JM. 1993. Reptiles del Noroeste, Nordeste y Este de la Argentina. *Herpetofauna de las selvas subtropicales, Puna y Pampas* [Reptiles from the northwest, northeast and east of Argentina. Herpetofauna of the subtropical jungles, Puna and Pampas]. Torino: Museo Regionale di Scienze Naturali. Monografía XIV.
- de Muizon C, Gayet M, Lavenu A, Marshall LG, Sigé B, Villarroel C. 1983. Late Cretaceous vertebrates, including mammals, from Tiupampa, South Central Bolivia. *Geobios*. 16(6):747–753.
- del Papa CE. 2006. Estratigrafía y paleoambientes de la Formación Lumbra, Grupo Salta, noroeste argentino [Stratigraphy and paleoenvironments of the Lumbra Formation, Salta Group, northwestern Argentina]. *Rev Asoc Geol Argent*. 61(3):313–327.
- Denton, Jr, RK, O'Neill RC. 1995. *Prototeius stageri*, gen. et sp. nov., a new teiid lizard from the upper Cretaceous Marshalltown Formation of New Jersey, with a preliminary phylogenetic revision of the Teiidae. *J Vertebr Paleontol*. 15(2):235–253.
- Deraco MV, Powell JE, Lopez G. 2008. Primer leontínido (Mammalia, Notoungulata) de la Formación Lumbra (Subgrupo Santa Bárbara, Grupo Salta-Paleógeno) del noroeste argentino [First leontiniid (Mammalia, Notoungulata) from the Lumbra Formation (Santa Bárbara Subgroup, Salta Group-Paleogene) of Northwestern Argentina]. *Ameghiniana*. 45(1):83–91.
- Donadío OE. 1985. Un nuevo Lacertilo (Squamata, Sauria, Teiidae) de la Formación Lumbra (Eoceno temprano) Provincia de Salta, Argentina [A new lizard from the Lumbra Formation (early Eocene) (Squamata, Sauria, Teiidae) Salta province, Argentina]. *Ameghiniana*. 22(3–4):221–228.
- Edmund AG. 1960. Tooth replacement phenomena in the lower vertebrates. *Roy Ontario Mus Life Sci Div Contrib*. 52:1–190.
- Edmund AG. 1969. Dentition. In: Gans C, Bellairs Ad'A, Parsons TS, editors. *Biology of the Reptilia*. Vol. 1. New York, NY: Academic Press; p. 117–200.
- Estes R. 1983. Sauria Terrestria, Amphisbaenia. Stuttgart: Gustav Fischer. 249 pp. (Handbuch der Paläoherpetologie [Encyclopedia of Paleoherpetology] 10A).
- Estes R, de Queiroz K, Gauthier J. 1988. Phylogenetic relationships within Squamata. In: Estes R, Pregill G, editors. *Phylogenetic relationships of the lizard families, Essays commemorating Charles L Camp*. Stanford, CA: Stanford University Press; p. 119–281.
- Estes R, Price LI. 1973. Iguanid lizard from the upper Cretaceous of Brazil. *Science*. 180:748–751.
- Evans SE, Yabumoto Y. 1998. A lizard from the Early Cretaceous Crato Formation, Araripe Basin, Brazil. *Neues Jahrb Geol P-A*. 1198(6): 349–364.
- Gao K, Fox RC. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bull Carnegie Mus Nat Hist*. 33:1–107.
- Gasparini Z. 1984. New Tertiary Sebecosuchia (Crocodylia: Mesosuchia) from Argentina. *J Vertebr Paleontol*. 4(1):85–95.
- Gasparini Z, de la Fuente MS, Donadío OE. 1986. Los Reptiles Cenozoicos de la Argentina: implicancias paleoambientales y evolución biogeográfica [The Cenozoic reptiles of Argentina: paleoenvironmental implications and biogeographic evolution]. In: IV Congreso Argentino de Paleontología y Bioestratigrafía. Vol. 2. Mendoza. p. 119–130.
- Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bull Yale Peabody Mus*. 53(1): 3–308.
- Gelfo JN, Goin FJ, Woodburne MO, de Muizon C. 2009. Biochronological relationships of the Earliest South American Paleogene mammalian faunas. *Palaeontology*. 52(1):251–269.
- Giugliano LG, García Collevatti R, Colli GR. 2007. Molecular dating and phylogenetic relationships among Teiidae (Squamata) inferred by molecular and morphological data. *Mol Phylogenet Evol*. 45: 168–179.
- Head JJ, Bloch JJ, Hastings AK, Bourque JR, Cadena EA, Herrera FA, Polly PD, Jaramillo CA. 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature*. 457(7230):715–717.
- Hoffstetter R. 1958. Un serpent marin du genre *Pterosphenus* (*P. sheppardi* nov. sp.) dans l'Éocène Supérieur de l'Équateur (Amérique du Sud) [A sea serpent of the genus *Pterosphenus* (*P. sheppardi* nov. sp.) from the Upper Eocene of Ecuador (South America)]. *B Soc Geol Fr*. 6. 8:45–50.
- Hoffstetter R. 1959. Un dentaire de *Madtsoia* (serpent géant du Paléocène de Patagonie) [A dentary of *Madtsioia* (giant snake from the Paleocene of Patagonia)]. *B Mus Natl Hist Nat Ser*. 2(31): 379–986.
- Hoffstetter R, Gasc JP. 1969. Vertebrae and ribs of modern reptiles. In: Gans C, Bellairs A, Parsons TS, editors. *Biology of the Reptilia*. Vol. 1. London: Academic Press; p. 201–310.
- Gray JE. 1827. A synopsis of the genera of saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. *Ann Philos*. 2(2):58–54.
- Kay RF, Madden RH, Vucetich MG, Carlini AA, Mazzoni MM, Re GH, Heizleri M, Sandeman H. 1999. Revised geochronology of the Casamayoran South American Land Mammal Age: climatic and biotic implications. *Proc Nat Acad Sci*. 96(23):13235–13240.
- Kearney M, Maisano JA, Rowe T. 2005. Cranial anatomy of the extinct amphisbaenian *Rhineura hatcherii* (Squamata, Amphisbaenia) based on high-resolution X-ray computed tomography. *J Morphol*. 264:1–33.
- Marshall LG, Sempere T, Butler RF. 1997. Chronostratigraphy of the mammal-bearing Paleocene of South America. *J South Am Earth Sci*. 10(1):49–70.
- Montero R, Abdala V, Moro S, Gallardo G. 2004. Atlas de *Tupinambis rufescens* (Squamata: Teiidae). Anatomía externa, osteología y bibliografía [Atlas of *Tupinambis rufescens* (Squamata: Teiidae). External anatomy, osteology and references]. *Cuad herpetol*. 18(1): 17–32.
- Nava WR, Martinelli AG. 2011. A new squamate lizard from the Upper Cretaceous Adamantina Formation (Bauru Group), São Paulo State, Brazil. *An Acad Bras Cienc*. 83(1):291–299.
- Nydam RL, Caldwell MW. 2008. Laurasian versus Gondwanan origins of the Teiioidea. In: III Congreso Latinoamericano de Paleontología de Vertebrados [III Latin American Congress of Vertebrate Paleontology]. Neuquén. p. 179.

- Nydam RL, Cifelli RL. 2002. A new Teiid from the Cedar Mountain Formation (Albian-Cenomanian boundary) of Utah. *J Vertebr Paleontol.* 22(2):276–285.
- Nydam RL, Caldwell MW, Fanti F. 2010. Borioteioid lizard skulls from Kleskun Hill (Wapiti Formation; upper Campanian), west-central Alberta, Canada. *J Vert Paleontol.* 30(4):1090–1099.
- Nydam RL, Eaton JG, Sankey J. 2007. New taxa of transversely-toothed lizards (Squamata: Scincomorpha) and new information on the evolutionary history of teiids. *J Paleontol.* 81(3):538–549.
- Oelrich TM. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc Publ Mus Zool Univ Mich.* 94:1–122.
- Oppel M. 1811. Die ordnungen familien und Gattungen der Reptilien, als Prodrom einer Naturgeschichte derselben [The orders, families and genera of reptiles as a prodrome of a natural history itself]. München: Joseph Lindauer.
- Pascual R, Bond M, Vucetich MG. 1981. El Subgrupo Santa Bárbara (Grupo Salta) y sus vertebrados. Cronología, paleoambientes y paleobiogeografía [The Santa Bárbara Subgroup (Salta Group) and its vertebrates. Chronology, paleoenvironments and paleobiogeography]. In: VIII Congreso Geológico Argentino. Vol. 3. San Luis. p. 743–758.
- Pascual R, Ortiz Jaureguizar E, Prado JL. 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. *Münchner Geowissenschaftliche Abhandlungen A.* 30:265–320.
- Pascual R, Vucetich MG, Fernandez J. 1978. Los primeros mamíferos (Notoungulata, Henricosborniidae) de la Fm. Mealla (Grupo Salta, Subgrupo Santa Bárbara) [The first mammals (Notoungulata, Henricosborniidae) from Mealla Formation (Salta Group, Santa Bárbara Subgroup). Their phylogenetical, taxonomic and chronological implications]. *Sus implicancias filogenéticas, taxonómicas y cronológicas.* *Ameghiniana.* 15(3–4):366–390.
- Quattrocchio ME. 2006. Palynology and palaeocommunities of the paleogene of Argentina. *Rev Bras Paleontol.* 9(1):101–108.
- Rage J-C. 1981. Les continents péri-atlantiques au crétacé supérieur: Migrations des faunes continentales et problèmes paléogéographiques [The peri-Atlantic continents in Upper Cretaceous: migration of continental faunas and paleogeographic problems]. *Cretaceous Res.* 2(1):65–84.
- Rage JC. 1991. Squamate reptiles from the Early Paleocene of the Tiupampa area (Santa Lucia Formation). Bolivia. *Rev Téc YPFB.* 12:503–508.
- Rage J-C. 1998. Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata.* 27:109–144.
- Rage J-C. 2001. Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part II. Boidae. *Palaeovertebrata.* 30:111–150.
- Rage J-C. 2008. Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part III. Ungaliophiinae, Booids incertae sedis, and Caenophidia. Summary, update, and discussion of the snake fauna from the locality. *Palaeovertebrata.* 36:37–73.
- Rage J-C, Augé ML. 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. *Geobios.* 43(2):253–268.
- Rieppel O, Gauthier J, Maisano JA. 2008. Comparative morphology of the dermal palate in squamate reptiles, with comments on phylogenetic implications. *Zool J Linn Soc.* 152:131–152.
- Sempere T, Butler RF, Richards DR, Marshall LG, Sharp W, Swisher, III, CC. 1997. Stratigraphy and chronology of Upper Cretaceous-lower Paleogene strata in Bolivia and northwest Argentina. *Geol Soc Am Bull.* 109(6):709–727.
- Simões TR. 2012. Redescription of *Tijubina ponteii*, an Early Cretaceous lizard (Reptilia; Squamata) from the Crato Formation of Brazil. *An Acad Bras Cienc.* 84:79–94.
- Simões TR, Caldwell MW, Kellner AWA. 2014. A new Early Cretaceous lizard species from Brazil, and the phylogenetic position of the oldest known South American squamates. *J Syst Palaeontol.* 1–14. DOI:10.1080/14772019.2014.947342.
- Simpson GG. 1933. A new fossil snake from the *Notostylops* beds of Patagonia. *Bull Am Mus Nat Hist.* 67:1–22.
- Simpson GG. 1935. Early and middle Tertiary geology of the Gaiman region, Chubut, Argentina. *Am Mus Novit.* 775:1–29.
- Smith KT. 2006. A diverse new assemblage of Late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. *Palaeontol Electron.* 9(2):1–44.
- Smith KT, Gauthier JA. 2013. Early Eocene Lizards of the Wasatch Formation near Bitter Creek, Wyoming: diversity and paleoenvironment during an interval of global warming. *Bull Yale Peabody Mus.* 54(2):135–230.
- Sullivan RM, Estes R. 1997. *Paradracaena colombiana* (Estes, 1961) new genus (Squamata, Teiidae): A reassessment of the Tupinambinae from the Miocene Honda Group of Colombia. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ, editors. *Vertebrate paleontology in neotropics.* Washington, DC: Smithsonian Institution Press; p. 100–112.
- Vucetich MG, Reguero MA, Bond M, Candela AM, Carlini AA, Deschamps CM, Gelfo JN, Goin FJ, López GM, Ortiz Jaureguizar E, et al. 2007. Mamíferos continentales del Paleógeno argentino: las investigaciones de los últimos cincuenta años [Paleogene continental mammals from Argentina: the last fifty years of investigations]. *Archangelsky S, Sánchez T, Tonni EP, editors Ameghiniana Publicación Especial.* 11:239–255.
- Wagler J. 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur vergleichenden Zoologie* [Natural system of amphibians, with leading classification of mammals and birds. A contribution to comparative zoology]. München: J.G. Cotta Buchhandlung.
- Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, López GM, Iglesias A, Zimicz AN. 2013. Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. *J Mammal Evol.* 21:1–73.
- Zaher H, Rieppel O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. *Am Mus Novit.* 3271:1–19.

Appendix 1. Reference specimens consulted for this study.

ANGUIDAE: '*Ophiodes vertebralis*', UNMdP 162. IGUANIDAE: '*Pristidactylus nigroiugulus*', UNMdP-O 68; '*Tropidurus spinulosus*', UNMdP-O 77; '*Tropidurus catalanensis*', UNMdP-O 69. SCINCIDAE: '*Mabuya frenata*', UNMdP 1599. GYMNOPTHALMIDAE: '*Anadia bogotensis*', UMMZ 192802; '*Bachia dorbignyi*' UMMZ 172147; '*Cercosauria schreibersii*', UNNE 8285, AC C119, C182, C253, C316, C318, C255, C081, C137, C155, C180, C181, C292; UNMdP-O 72, UNNE 8284, '*Vanzosaura rubricauda*', UNMdP 649. TEIIDAE: '*Ameiva ameiva*', UMMZ 149442, 176270, UNMdP 796, 1235, UNMdP-O 27, UNNE 1374, 1365, USNM 257529, 257530, 2414, 292419, 290898, '*Ameiva bifrontata*', UMMZ 149443, 149444, 150782, 149449; '*Ameiva exsul*', UMMZ 149448, 200865; '*Aspidoscelis cadilipes*' UMMZ 149550, 149457, 149459, 149460; '*Aspidoscelis communis*' UMMZ 149574; '*Aspidoscelis cozumela*', UMMZ 149464; '*Aspidoscelis deppii*', UMMZ 149551, 149552; '*Aspidoscelis exsanguis*' UMMZ 138822, 149569; '*Aspidoscelis gularis*', UMMZ 149553; '*Aspidoscelis sexlineata*', UMMZ 149576, USNM

313460; '*Callopietes maculatus*' USNM 4112, 4113; '*Cnemidophorus lacertoides*', UNMdP-O 80; '*Cnemidophorus lemniscatus*', UMMZ 189452, '*Cnemidophorus longicauda*' UNMdP-O 51, 52, 81; '*Cnemidophorus ocelifer*', UMMZ 149522; '*Cnemidophorus serranus*', AC C371, UNMdP-O 82; '*Cnemidophorus tergoaevigatus*', UNMdP-O 83; '*Crocodilurus amazonicus*', MZUSP 8526, 12624, 92074; '*Dracaena guianensis*', MZUSP 40082, USNM 220278; '*Dracaena paraguayensis*', MZUSP 62849; '*Dicrodon guttulatum*', QCAZR 2139; '*Kentropyx viridistriga*', UNNE 4647, 1062; '*Kentropyx calcarata*', MZUSP 81580, 82978, USNM 292412; '*Teius teyou*', UNMdP-O 15, 16, 22, 23, AC C365, UNNE 1398, 8715; '*Teius oculatus*', AC C360, C368, C369, UNMdP-O 53, UNNE 4464, 4462; '*Teius suquiensis*', AC C366, C367, UNMdP-O 84, 85; '*Tupinambis* sp.', MZUSP 43042, 73309; '*Tupinambis duseni*', MZUSP 92131; '*Tupinambis merianae*', UMMZ 190109, UNMdP-O 1–14, 17–20, 24–26, 28, 32, 33, 35; '*Tupinambis quadrilineatus*', MZUSP 84921, 84928; '*Tupinambis rufescens*', FML 7545, 7547, 1336, 2560, MZUSP 93082, 93083, 93084, UNMdP-O 36, USNM 342486; '*Tupinambis teguixin*', MZUSP 92087, 92149, USNM 220279.