The southernmost fossil record of Squamates

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Abstract. Squamates form a substantial part of the present-day South American herpetofauna, and their fossils constitute an indispensable evidence for understanding the origin and evolution of the main taxa. Squamates are relatively common in Miocene localities of Patagonia, especially in levels of the late early Miocene Santa Cruz Formation. In this contribution, remains of the three species of the extinct iguanid *Erichosaurus* Ameghino 1899 (*E. diminutus*, *E. bombimaxilla* and *E. debilis*) are redescribed, and new squamate specimens are reported for first time. The genus *Erichosaurus* is considered invalid. *Erichosaurus debilis*, *E. diminutus* and a new specimen are recognized as indeterminate species of the extant polichrotine *Pristidactylus*, whereas *E. bombimaxilla* remains as an indeterminate iguanid. Snakes are represented by an indeterminate colubrid. All these specimens, together with a tupinambine teiid previously described for the same formation, represent the southernmost fossil record of squamates in South America and indicate the occurrence of the iguanid *Pristidactylus*, the teiid *Tupinambis* and the colubrid snakes south to their present distribution as back as during the early Miocene.

Keywords: Colubridae, Iguanidae, Miocene, Patagonia, *Pristidactylus*.

Introduction

The complex history and diverse topography and climate of South America have produced an extraordinarily rich and diverse herpetofauna, among which squamates represent one of the most significant component. Nevertheless, Patagonia is a territory characterized by extremely dry environments and cold temperatures inhabited by a limited diversity of squamates, several of them confined to post-glacial refuges (Cei, 1986). The Patagonian paleontological record provides evidence on the origin and evolution of some South American groups of squamates, to better understanding their present diversity and distribution (Estes, 1983; Albino, 1996a, 2011; Albino and Brizuela, 2014).

In 1899, Florentino Ameghino erected the extinct iguanid genus *Erichosaurus* on the basis

of tooth-bearing remains recovered from sediments of the Santa Cruz Formation (late early Miocene) in the southeast of the province of Santa Cruz, Argentina. Ameghino (1899) recognized three species, *E. diminutus*, *E. bombimaxilla* and *E. debilis*, which Estes (1983) considered nomina dubia. Estes (1983) also reported that the holotype of *E. diminutus*, which is the type species of the genus, was lost. Although the descriptions given by Ameghino (1899) are brief and do not allow to ascertain the systematic affinities of the genus, *Erichosaurus* was repeatedly listed as a component of the Miocene herpetofauna (Báez and Gasparini, 1977; Estes and Báez, 1985; Gasparini, de la Fuente and Donadío, 1986; Albino, 1996a). Recently, Fernicola and Albino (2012) reported that all of the remains corresponding to the three species of *Erichosaurus* are housed in the Colección Nacional Ameghino at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN A). An initial examination of these remains demonstrates that the tooth crowns are labiolingually compressed and tricuspid, with a higher central cusp (Fernicola and Albino, 2012). These characters, emphasized in the original diagnosis of Ameghino (1899), are not appropriate for a definition of a particular genus

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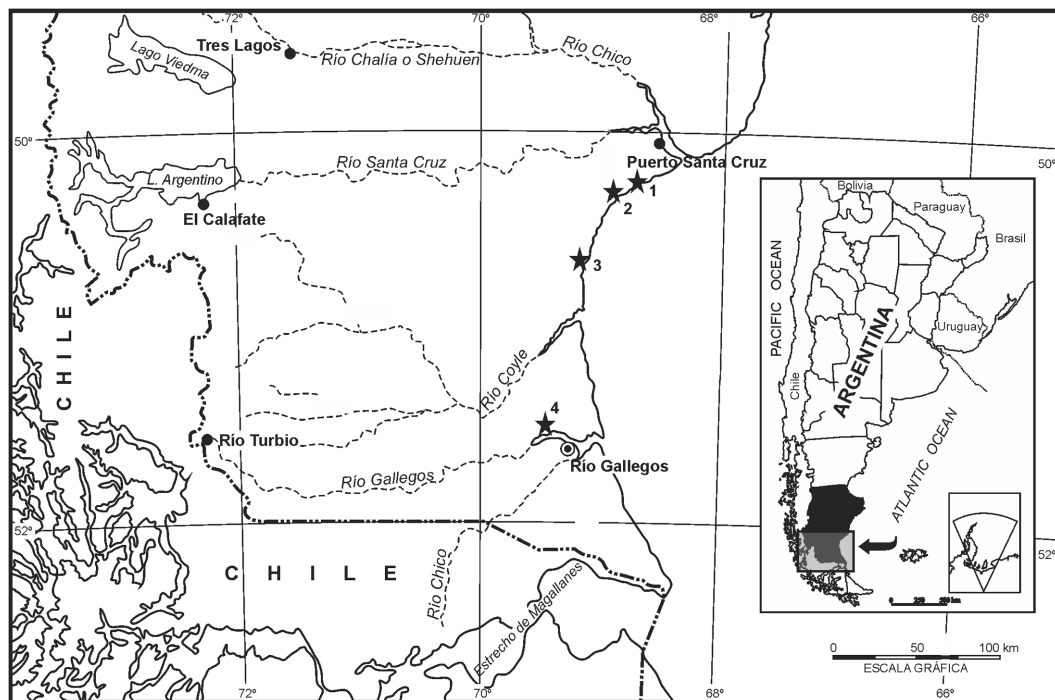
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Figure 1. Location map of the Miocene localities in southeastern Patagonia containing squamates. Monte León (1), La Cueva (2), Cañadón de las Vacas (3), Killik Aike Norte (4).

because tricuspid teeth with pleurodont implantation characterize the dentition of a large number of iguanid lizards.

In this contribution, the specimens studied by Ameghino (1899) are redescribed and exhaustively compared with extant iguanid genera, which permits a verifiable taxonomic assignment within Iguanidae. In addition, new remains of squamates recovered from the same formation during recent expeditions in different localities of Santa Cruz province are described here and discussed for first time.

Materials and methods

Geological context

The late early Miocene Santa Cruz Formation is widely distributed in the Austral geologic basin of Santa Cruz province, Argentina (fig. 1). It is composed of mudstones, tuffaceous sandstones, and tuffs, deposited in fluvial environments under the influence of intense pyroclastic input (Feruglio, 1949; Bown and Fleagle, 1993; Tauber, 1994, 1997; Matheos and Raigemborn, 2012; Fernicola et al.,

2014). The best-known exposures of this formation, especially notable for its abundance of fossil vertebrates, are located to the southeast of the Atlantic coast (Vizcaíno, Kay and Bargo, 2012). The localities Monte León and Cañadón de las Vacas (fig. 1) have already provided interesting squamate specimens, including teiid mandibles from the former (Brizuela and Albino, 2008a) and colubrid vertebrae from the latter (Albino, 1996c). According to Gasparini, de la Fuente and Donadío (1986), the locality where the remains of iguanid lizards studied by Ameghino (1899) were found is La Cueva (fig. 1); however, the exact location of this site is unknown. Marshall (1976) considered that it would be the same as Monte Observación (50°21′S, 68°57′W), which is a hill also named Cerro Monte Observación, located about 7 km south of Cerro Monte León, within the present Parque Nacional Monte León (Vizcaíno, Kay and Bargo, 2012). The fossils described herein for the first time come from the locality Killik Aike Norte, situated on the north margin of Río Gallegos, approximately at 51°34′S, 69°25′W (fig. 1). They comprise lizard and snake remains mostly found in a tephra level at the base of the exposure of the Santa Cruz Formation. Based on diverse radiometric dates and methods of tephrochronology, the age of the Santa Cruz Formation was estimated in about 18 to 16 Ma, corresponding to the late early Miocene (Perkins et al., 2012; Vizcaíno, Kay and Bargo, 2012).

Systematics and terminology

Systematic and taxonomy of Iguanidae follows Smith (2009), which is an osteological base study of the systematic relationships of the family. This decision is made because osteological characters are the ones applicable to evaluate paleontological specimens, and because Smith (2009) presents an adequate taxon sampling and is conservative in taxonomy. According to Smith (2009, who follows Schulte, Valladares and Larson, 2003) the Iguanidae (= Pleurodonta of Frost et al., 2001) are constituted by eight subfamilies (Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, Phrynosomatinae, Polychrotinae* and Tropidurinae*) distributed mainly in the New World. The number of clades, their Linnean rank, the phylogenetic relationships of these groups, and the monophyly of some of them are still controversial (Frost et al., 2001; Schulte, Valladares and Larson, 2003; Conrad, Rieppel and Grande, 2007; Smith, 2009; Nicholson et al., 2012). In particular regard, the monophyly of Tropudurinae* has been contested by some authors (Schulte, Valladares and Larson, 2003; Smith 2009). Perhaps even more problematic is the monophyly of the Polychrotinae*, which is recovered as monophyletic in some studies (e.g. Conrad, Rieppel and Grande, 2007) but paraphyletic in others (e.g., Pyron, Burbrink and Wiens, 2013; Reeder at al., 2015; Zheng and Wiens, 2016). Therefore, Polychrotinae*, and also Tropidurinae*, are considered as metataxa herein (denoted by an asterisk).

Concerning snakes, Colubridae is paraphyletic according to Zaher (1999). Taxonomy and systematics of fossil colubrids are based almost exclusively on vertebral morphology (Rage, 1984).

Osteological terminology for lizards follows mostly Oelrich (1956), with additional modifications from Bhullar and Smith (2008), Smith (2009), Rage and Augé (2010), and Smith and Gauthier (2013). The characters used for identifying colubrid vertebrae are discussed in Albino and Montalvo (2006). Small letters between parentheses were used to identify relative tooth positions in the broken fossil jaws; they do not imply an arranged tooth series along the jaw.

Specimens were examined using a stereomicroscope. Measurements are in millimetres.

Comparative osteological material

Comparisons of the fossils with osteological material of extant species were made to help fossil identification. The specimens used are listed below.

Lizards: *Anisolepis* sp (UNMdP-O 137), *Anisolepis grilli* (UNMdP-O 138), *Diplolaemus bibroni* (UNMdP-O 70, UNMdP-O 130), *Diplolaemus darwini* (UNMdP-O 71, UNMdP-O 131), *Enyalius iheringi* (UNMdP-O 139), *Iguana iguana* (UNMdP-O 29, UNMdP-O 30, UNMdP-O 37), *Leiosaurus* sp. (UNMdP-O 132), *Leiosaurus belli* (UNMdP-O 133, UNMdP-O 134), *Liolaemus argentinus* (UNMdP-O 86 a UNMdP-O 96), *Liolaemus bibroni* (UNMdP-O 107 a UNMdP-O 109), *Liolaemus boulengeri* (UNMdP-O 110), *Liolaemus darwini* (UNMdP-O 115, UNMdP-O 116), *Liolaemus elongatus* (UNMdP-O 97 a UNMdP-O 106), *Liolaemus gracilis* (UNMdP-O 118, UNMdP-O 119), *Liolaemus lineomaculatus* (UNMdP-O 111), *Liolaemus melanops* (UNMdP-O 112 a UNMdP-O 114), *Liolaemus multimaculatus* (UNMdP-O 76), *Liolaemus petrophilus* (UNMdP-O 119, UNMdP-O 120), *Liolaemus poecilochromus* (UNMdP-O 121, UNMdP-O 122), *Liolaemus rothi* (UNMdP-O 123), *Liolaemus sommuncurae* (UNMdP-O 124), *Phymaturus palluma* (UNMdP-O 67), *Phymaturus somuncurensis* (UNMdP-O 125, UNMdP-O 126), *Polychrus acutirostris* (UNMdP-O 73, UNMdP-O 129), *Pristidactylus achaliensis* (UNMdP-O 135), *Pristidactylus araucanus* (UNMdP-O 136), *Pristidactylus nigroiugulus* (UNMdP-O 68),), *Stenocercus* sp. (UNMdP-O 126, UNMdP-O 127), *Stenocercus pectinatus* (UNMdP-O 128), *Tropidurus sp* (UNMdP-O 125), *Tropidurus catamacensis* (UNMdP-O 69), *Tropidurus spinulosus* (UNMdP-O 21, UNMdP-O 77), *Urostrophus* sp (UNMdP-O 140).

Snakes: *Clelia rustica* (UNMdP-O 65), *Helicops leopardinus* (UNMdP-O 57), *Hydrodynastes gigas* (UNMdP-O 54), *Leimadophis poecilogyrus* (UNMdP-O 62), *Liophis anomalus* (UNMdP-O 61), *Lystrophis dorbigny* (UNMdP-O 59, UNMdP-O 60, UNMdP-O 63), *Oxyrhopus rhombifer* (UNMdP-O 58), *Phylodryas patagoniensis* (UNMdP-O 55, UNMdP-O 56, UNMdP-O 64).

Institutional abbreviations

DML: Digital Morphology Library; FMNH: Field Museum of Natural History, Chicago, USA; MACN A: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; MACN Pv: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional de Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; MPM PV: Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Santa Cruz Province, Argentina; UNMdP-O: Colección Herpetológica de la Universidad Nacional de Mar del Plata, Sección Osteología, Mar del Plata, Argentina.

Measurements of snake vertebrae

cl, centrum length; cth, cotyle height; ctw, cotyle width; lpr-po, length of the neural arch between anterior edge of prezygapophysis and posterior edge of postzygapophysis of the same side; naw, neural arch width at interzygapophyseal constriction; wpo-po, width across postzygapophyses; wpr-pr, width across prezygapophyses; zh, zygosphene height; zw, zygosphene width.

Anatomical abbreviations

AIAF, anterior inferior alveolar foramen; AMF, anterior mylohyoid foramen; ASAF, anterior superior alveolar foramen; SAF, superior alveolar foramen; SNAF, subnarial arterial foramen.

Systematic paleontology (Iguania)

Squamata Oppel 1811

Iguania Cope 1864

Iguanidae Bell, 1825 (sensu Schulte, Valladares and Larson, 2003)

Leiosaurini Schulte, Valladares and Larson, 2003

Leiosaurae Schulte, Valladares and Larson, 2003

Pristidactylus Fitzinger, 1843

Pristidactylus sp. A (fig. 2)

Referred material.   MPM PV 4337, partial left hemimandible including splenial and toothed dentary.

Locality and horizon.   Killik Aike Norte (51° 34′S, 69°25′W), Güer Aike department, southeast Santa Cruz province, Argentina (fig. 1). Santa Cruz Formation (late early Miocene).

Description.   The specimen is an incomplete and small left dentary articulated with the partially preserved splenial (fig. 2). The dentary is anteriorly and posteriorly broken. It is relatively

Figure 2. *Pristidactylus* sp. A, MPM PV 4337, partial left hemimandible in labial (A) and lingual (B) views. Abbreviations: Aaf, angular articulation facet; aiaf, anterior inferior alveolar foramen; amf, anterior mylohyoid foramen; S, splenial; rz, resorption zone.

tall, and labially smooth and convex. Anteriorly, below teeth (b) and (c), there is a small, oval, and closed mental foramen. Posterior to the dental series, in lateral view, the suture with the coronoid (bone not preserved) is anteriorly vertical and, posteriorly, close to horizontal. This results in a right-angled morphology. There is no articulation surface for the anterolateral process of the coronoid indicating that this process was absent. Lingually, upon the weakly developed intramandibular lamella, there is an articulation surface for the anteromedial process of the coronoid. This surface extends anteriorly for more than three tooth positions, and lateral to the suprameckelian lip (not preserved). In lingual view, part of the splenial articulates with the dentary. Anteriorly to the splenial, there is a closed and fused Meckel's canal.

Only the last 13 tooth positions of the dental series are preserved. There are 11 complete teeth; tooth (h) and half of tooth (l) are missing. Teeth are tall, cylindrical, and pleurodont; with more than half of their height attached to the parapet. They are all of the same height and closely spaced. Apically, they are labiolingually compressed, tricuspid, and with slightly convergent lateral outlines. The central cusp is conical and higher than the accessory cusps, which are poorly developed, without well-defined intercuspidal grooves. Lingually, on tooth bases (c) and (f), there are two small resorption zones. A better developed resorption zone is present lingual to tooth (k).

Only the anterior half of the splenial is preserved. The fragment is slightly displaced (fig. 2B) and reaches anteriorly the tooth position (f) of the dentary. Considering that only the mid-section of the dentary is preserved, the splenial would probably have extended anteriorly between 25% and 50% of the total length of the dental series. The broken subdental shelf of the dentary exposes a broad articulation facet for the splenial, ventral to the dental series. Part of the articulation facet for the angular is preserved on the ventral face of the splenial; thus, the angular would have extended anteriorly on
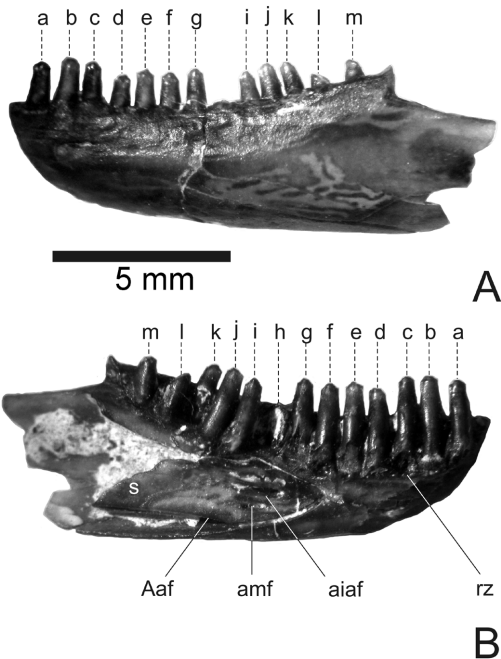
the dentary reaching the tooth position (i). On the anteriormost extremity of the splenial there are two large foramina that are entirely enclosed within the splenial. These foramina correspond to the large anterior inferior alveolar foramen (AIAF), and the smaller, and more ventrally placed AMF (anterior mylohyoid foramen of Oelrich, 1956). A third foramen, much smaller than the former, is located on the exposed articulation facet for the dentary. This foramen is considered a ramification of the inferior alveolar nerve/internal mandibulary artery that leads to the teeth. The dorsal articulation facet of the splenial is moderately inclined and sharply delimited by a low longitudinal crest (fig. 2B).

Comments. Tricuspid, pleurodont teeth with lingual resorption zones are present in all Iguanidae (Edmund, 1960, 1969; Frost and Etheridge, 1989; Smith, 2006, 2009). Within iguanids, Meckel's canal is closed and fused in Polychrotinae*, many Corytophaninae, Iguaninae, most Tropidurinae* and *Chalarodon* among Oplurinae (Frost and Etheridge, 1989; Smith, 2009, 2011). The following characters of the fossil only coexist within the Polychrotinae*: a weakly developed intramandibular lamella, a splenial that does not extend anteriorly beyond the 50% of the dental series length, and an angular surpassing anteriorly the ante-penultimate tooth (Frost and Etheridge, 1989; Conrad, 2008; Smith, 2009). The absence of a developed anterolateral process of the coronoid is a common condition in the Leiosaurae, and in *Anolis*, *Anisolepis* and *Polychrus acutirostris* (Frost et al., 2001). The specimen MPM PV 4337 differs from *Anolis* in having a splenial that has an anterior extension surpassing 25% of the dental series length (Frost et al., 2001) and posterior teeth without mesiodistal expansion of their bases (Smith, 2009). The fossil differs from *Polychrus* in not presenting the characteristic striae on the posterior teeth (Smith, 2009). Among the Leiosaurini, *Enyalius* presents parallel lateral tooth outlines with no apical convergence, whereas the splenial in *Anisolepis* and *Urostrophus* is more dorsoventrally restricted

than in the fossil specimen. Within Leiosaurae, *Diplolaemus* and *Leiosaurus* present robust and distally blunt teeth, without accessory cusps. Therefore, the fossil resembles most *Pristidactylus* species.

Pristidactylus casuhatiensis presents enlarged posterior teeth, whereas *P. achalensis* has clearly flared tooth outlines (Etheridge and Williams, 1985; Cei, 1986, 1993; Cabrera, 1992; Albino, 2008), differing from the fossil specimen. The AIAF located within the splenial is observed only in *Pristidactylus torquatus* (FMNH 206964 from DML), whereas it is dorsally limited by the dentary in *P. nigroiugulus* and *P. araucanus*. Nevertheless, the AIAF is located anterior to the AMF in *P. torquatus* but it is dorsal in the fossil specimen. Therefore, the fossil partial mandible is here considered belonging to a *Pristidactylus* species different from *P. torquatus*, *P. nigroiugulus*, *P. araucanus*, *P. casuhatiensis*, and *P. achalensis*. No other characters nor osteological material of the remaining species are available; hence, the specimen is considered an unknown species of *Pristidactylus*.

Pristidactylus sp. B (fig. 3)

Referred material. MACN A 5807, right dentary with teeth and fragment of the right surangular, previously described as the holotype of *Erichosaurus debilis* Ameghino, 1899 (Fernicola and Albino, 2012). A small separate untoothed fragment of a parapet associate to the dentary is not described.

Locality and horizon. La Cueva (50°21′S, 68°57′W), Corpen Aike department, southeast Santa Cruz province, Argentina (fig. 1). Santa Cruz Formation (late early Miocene).

Re-description. Fragment MACN A 5807 corresponds to an almost complete right dentary, articulated to a small piece of the surangular (fig. 3). The dentary is low and does not conserve its anterior extremity. Its labial wall is slightly convex and not ornamented. Four mental foramina are present below the horizontal
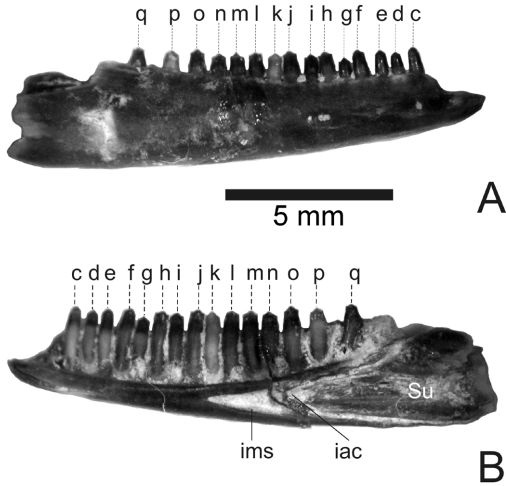
Figure 3. *Pristidactylus* sp. B, MACN A 5807, partial right dentary and surangular in labial (A), and lingual (B) views. Abbreviations: iac, inferior alveolar canal; ims, intramandibular septum; Su, surangular.

mid-line of the bone, at the level of tooth positions (a-b), (c), (e-f) and (h-i). The posterolateral region of the dentary, immediately below the dental series, does not present an articulation facet for the anterolateral process of the coronoid. Although poorly preserved, the suture with the coronoid is anteriorly vertical and posteriorly close to the horizontal. In dorsal view, the tapering shape of the dental series indicates that the coronoid articulated with the dentary posterior to the last preserved tooth position (q); therefore, the dentary would probably have extended posteriorly beyond the dorsal apex of the coronoid. The absence of clear reference points does not allow the quantification of its posterior extent. In lingual view, Meckel's canal is closed and fused. The anterior aperture of this canal starts at tooth position (d). Posteromedially, the dentary would have accommodated the splenial (not preserved) in an acute wedge. This wedge extends anterior to tooth position (k). The extension of the splenial along the dental series is approximately 45% of the dental series length. A facet for the articulation of the angular is not present in the preserved material. The missing splenial leaves a well-exposed intramandibular septum and a long intramandibular lamella. The

intramandibular septum extends posteriorly to tooth position (o), approximately 88% of the length of the dental series. A small anterior fragment of the surangular articulates posteromedially on the dentary. The overlap between these two bones is significant, with the surangular reaching anteriorly to the AIAF.

The teeth in specimen MACN A 5807 are pleurodont, of similar dimensions and closely packed. They are tricuspid, although accessory cusps tend to be more differentiated towards the posterior end of the dental series as seen from tooth (g), posteriorly. Seventeen tooth positions with 15 complete teeth are preserved. Teeth (a) and (b) are missing, and it is not possible to exclude the presence of another tooth anterior to them. Tooth (c) is cylindrical at the base, but apically it presents a slight labiolingual compression and a tricuspid condition, where the accessory cusps are reduced and poorly defined. The lateral outline of this tooth presents straight vertical and parallel mesial and distal borders, with a minor apical convergence. Morphology of the more posteriorly located teeth is similar, except that the accessory cusps are more evident. Five resorption zones are present on the bases of teeth (c), (e), (g), (i) and (l).

Comments. Tricuspid, pleurodont teeth with large resorption zones on the tooth bases are characters present in Iguanidae (Edmund, 1960, 1969; Frost and Etheridge, 1989; Smith, 2006). The closed and fused Meckel's canal, with a fusion that extends over more than 50% of the dentary length anterior to the splenial; an intramandibular septum that extends posteriorly over more than 75% of the length of the dental series; a weakly developed intramandibular lamella; and a splenial that extends anteriorly between 25%-50% of the dental series length, are features that coexist in Leiosaurini and *Polychrus* (Frost et al., 2001; Smith, 2009). Among the last ones, a coronoid without a developed anterolateral process is present in the Leiosaurae and *Anisolepis*. The lateral outline of the teeth in MACN A 5807 is similar to the condition seen in *Anisolepis* and *Pristidactylus* (except

P. achalensis and *P. casuhatiensis*, see above). The splenial in *Anisolepis* is very acute anteriorly, whereas in MACN A 5807 its anterior-end forms a larger angle, similar to that of *Pristidactylus*, supporting the inclusion of MACN A 5807 in this genus.

The fossil dentary MACN A 5807 resembles those assigned to *Pristidactylus* sp. form the early Miocene of Patagonia (Gaiman, Chubut province, Argentina) described by Albino (2008), which has a similar tooth count (17 in MACN A 5807 and 18 in most fossils from Gaiman). All these specimens differ from *Pristidactulus* sp. A described above in: (1) their smaller dimensions, (2) a splenial that ends anteriorly in a more acute angle, and (3) lesser anterior extent of the angular. Thus, they are interpreted representing as distinct species.

Pristidactylus sp. indet. (fig. 4)

Referred material. MACN A 2272, right maxilla with teeth, previously described as the holotype of *Erichosaurus diminutus* Ameghino, 1899 (Fernicola and Albino, 2012).

Locality and horizon. La Cueva (50°21′S, 68°57′W), Corpen Aike department, southeast Santa Cruz province, Argentina (fig. 1). Santa Cruz Formation (late early Miocene).

Re-description. The maxilla is short and delicate. It does not preserve the facial process (= facial lamina), the last portion of the posterior process, and the anteriormost part of the premaxillary process (fig. 4). Labially, it is smooth; a series of seven labial foramina demarcates two sections: a ventral, convex section, and a dorsal, flat section (fig. 4A). The labial foramina are preserved above tooth positions (d), (e-f), (f), (g), (h-i), (j) and (k). Dorsally to the second (e-f) and seventh (k) labial foramina, two additional smaller foramina are present. The fenestra exonarina is posteromedially bordered by a tall and distinct *crista transversalis*. In a midlingual position, upon the *crista transversalis*, it is possible to see the opening of the ASAF. At the medial end of the *crista*
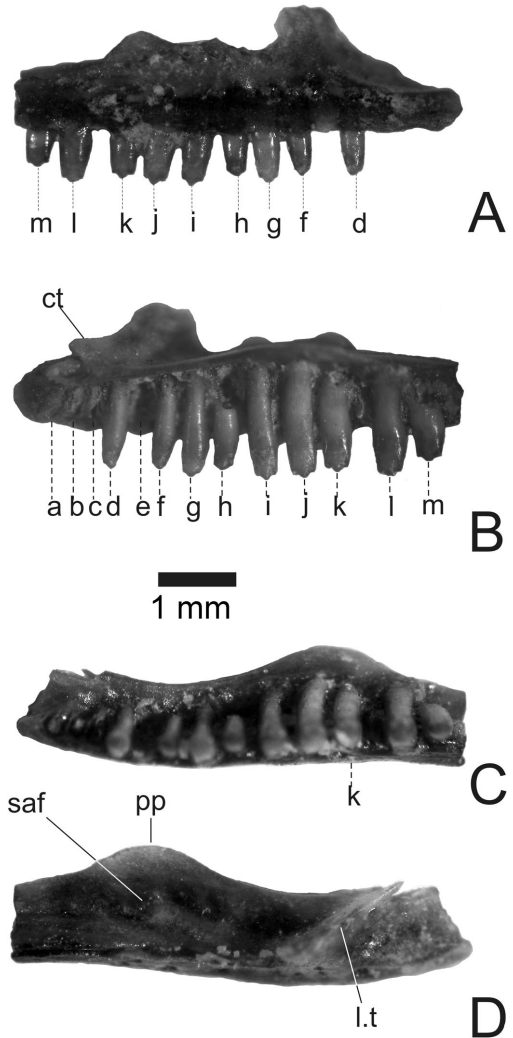

Figure 4. *Pristidactylus* sp., MACN A 2272, right maxilla in labial (A), lingual (B), ventral (C) and dorsal (D) views. Abbreviations: ct, crista transversalis; pp, palatine process; saf, superior alveolar foramen.

transversalis there is a notch interpreted as part of the SNAF. An additional foramen is observed on the posterior face of the *crista transversalis*. In occlusal view, the outline of the palatal shelf is anteriorly concave, followed by a convex and weakly developed palatine process. Dorsally, at tooth position (k), the palatine process bears the SAF, which is not preceded by a marked groove. There is a subtle depression medial to the SAF, whereas there is a jugal articulation suface laterally to it, which is deep and extends anteriorly to tooth position (k).

The dental series is well preserved and almost complete, with 13 preserved tooth positions. The teeth are pleurodont and most of them are tricuspid. Only the slightly mesiodistally compressed bases of teeth (a), (b) and (c) are preserved. The first complete tooth is (d), which is attached to the parapet with more than half of its height. This poorly preserved tooth is conic, with a blunt tip and slight labiolingual compression. Tooth (e) is missing. Tooth (f) is similar to tooth (d), although it presents two minute accessory cusps (mesial and distal). The lateral outline of this tooth presents straight mesial and distal borders, with a hint of apical convergence. The subsequent teeth are similar to tooth (f), but with more differentiated accessory cusps. This differentiation is on the account of the development of the accessory cusp since the intercuspidal gutters are only weakly developed. The accessory cusps are of similar dimension, always smaller and shorter than the main central cusp. Two large resorption zones are present lingual to teeth (h) and (m), whereas an incipient resorption zone is observed lingual to tooth (k).

Comments. The maxilla described above presents pleurodont, tricuspid teeth with large and lingual resorption pits and a symmetric palatine process, which represent a combination of characters present in Iguanidae (Edmund, 1960, 1969; Smith, 2009). Smith (2009) recognized as a synapomorphy of Iguanidae the presences of two foramina on the premaxillary process of the maxilla, for the passage of the subnarial artery and the anterior inferior alveolar nerve. Upon the transverse lamina of the described maxilla there is one foramen (ASAF) and part of the second (SNAF), supporting its affinity with iguanids. Character-states present in the studied specimen constituting a suite of features found in Polychrotinae* are (Smith, 2009; Daza et al., 2012): (1) a weakly developed palatine process, (2) a dorsally shallow premaxillary process, (3) absence of an elongated depression for the posterior process with no jugal buttress, (4) plane maxilla above posterior

teeth (i.e., absence of an offset), and (5) posterior teeth showing lateral outlines with parallel borders and a slight apical convergence. The fossil maxilla differs from those of the polychrotid *Anolis* in not presenting mesiodistally expanded posterior teeth (Smith, 2009). The fossil also lacks a dorsally concave premaxillary process, limited by developed *cristae transversalis* and *crista lateralis* as in *Polychrus*, from which it further differentiates in not having striated marginal teeth (Smith, 2009). Most Anisolepae have a similar tooth outline as the fossil, although *Enyalius* does not have the slight apical convergence. The fossil maxilla differs from *Anisolepis* and *Urostrophus* in the presence of a less developed palatal process. Tooth morphology allows the exclusion from the Leiosaurae *Diplolaemus*, *Leiosaurus*, and *Pristidactylus casuhatiensis* because all have enlarged, robust teeth. It also differs from *Pristidactylus achalensis*, which has flared tooth outlines (Etheridge and Williams, 1985; Cei, 1986, 1993; Cabrera, 1992). Therefore, MACN A 2272 is assigned to the genus *Pristidactylus*. Dimensions of the maxilla are not equivalent to those of the other *Pristidactylus* species from the Santa Cruz Formation (*Pristidactylus* sp. A and sp. B), but this could be because it corresponds to a younger individual of one of these species.

Iguanidae indet. (fig. 5)

Referred material. MACN A 2283 includes three fragments of toothed bones (MACN A 2283a, b and c) presumably corresponding to a right dentary of a single individual, and previously described as the holotype of *Erichosaurus bombimaxila* Ameghino, 1899 (Fernicola and Albino, 2012).

Locality and horizon. La Cueva (50°21′S, 68°57′W), Corpen Aike department, southeast Santa Cruz province, Argentina (fig. 1). Santa Cruz Formation (late early Miocene).

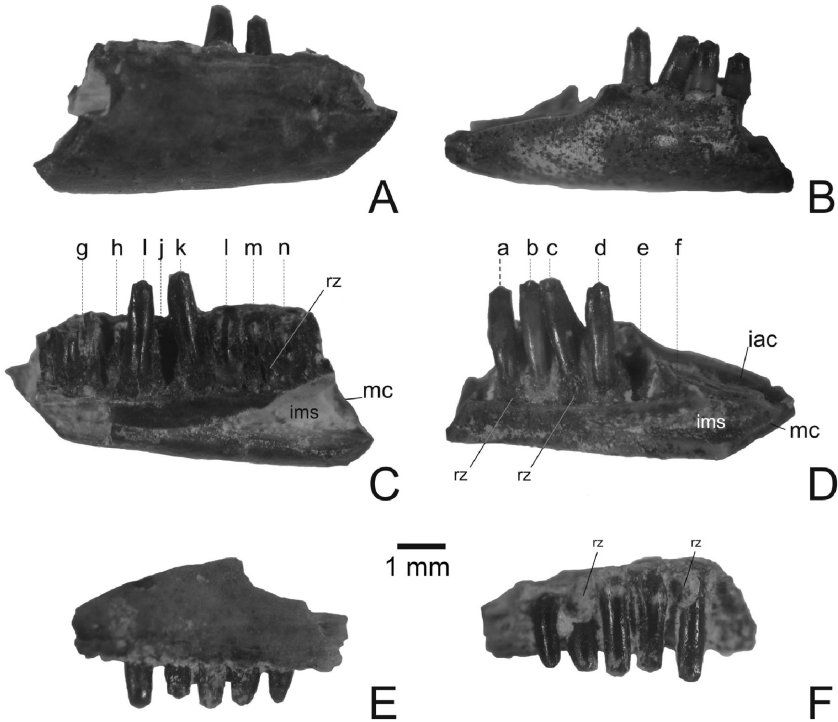*Description.* Fragments MACN A 2283-a and MACN A 2283-b are considered belong to the

Figure 5. Indeterminate Iguanidae, MACN A 2283a and MACN A 2283b are considered as of the same right dentary and presented correspondingly. MACN A 2283b (A) and MACN A 2283a (B) in labial views; MACN A 2283b (C) and MACN A 2283a (D) in lingual views; MACN A 2283c in labial (E) and lingual (F) views. Abbreviations: iac, inferior alveolar canal; ims, intramandibular septum; mc, Meckel's canal; rz, resorption zone.

same individual's right dentary, although they do not fit together (presumably due to missing fragments). Fragment MACN A 2283-a corresponds to the anterior midsection and is relatively shallow, whereas MACN A 2283-b has a much more dorsoventrally developed posterior part. Labially, both fragments are convex and smooth; they contain mental foramina at tooth positions (c) and (h). The Meckel's canal is considered closed and fused. However, this condition is only preserved in the anterior-most part of MACN A 2283-a, because the Meckel's canal region is broken in the other fragments. The intramandibular septum is present in both fragments. MACN A 2283-a preserves six tooth positions (a-f), with four complete teeth (a-d), whereas MACN A 2283-b preserves eight tooth positions (g-n), with two complete teeth (c, e). All teeth are pleurodont, high and tricuspid. The tooth bases are mesiodistally compressed and

labiolingually developed. Their labial and lingual faces are vertical and obliquely oriented, respectively. The lingual face is somewhat compressed near the base, but not so near the apex. The lateral outline of the teeth presents vertical mesial and distal borders, with a slight apical convergence. The main (central) cusp is conical and labiolingually compressed; the accessory cusps are poorly developed, with no intercuspidal grooves. Resorption zones are present lingually to teeth (a), (c), and (m).

MACN A 2283-c does not preserve enough features that could allow its anatomical identification. It bears five slightly tricuspid pleurodont teeth, which are as those described for MACN A 2283-a and MACN A 2283-b. Large resorption zones are present lingual to tooth (a) and (d).

Comments. In the brief description of *Erichosaurus bombimaxilla*, Ameghino (1899)

states that this taxon is of similar size to *E. debilis* (*Pristidactylus* sp. B in the present paper), but it can be distinguished by the structure of the dentary, which increases in height more abruptly from front to back and has a very convex external face. It is from this statement, and osteological correspondence, that MACN A 2283-a and MACN A 2283-b are referred to the same dentary (it is believed the specimen was broken after Ameghino studied it). Although there are not enough elements to associate MACN A 2283-c with MACN A 2283-a and MACN A 2283-b, tooth morphology suggests that it belongs to the same taxon. Dentition characters, such as pleurodont implantation, tricuspid teeth with large, lingual resorption zones indicate that these remains correspond to an Iguanidae (Edmund, 1969; Smith, 2009). Among iguanids, a closed and fused Meckel's canal is characteristic of many Corytophaninae, Iguaninae, Polychrotinae*, Oplurinae (*Chalarodon*), and most Tropidurinae* (Frost and Etheridge, 1989; Conrad, 2008; Smith, 2009, 2011). Except for Iguaninae, most Corytophaninae and several Tropidurinae*, in which posterior tooth outlines are distinctly flared, Polychrotinae*, and most Oplurinae and Tropidurinae* have outlines with almost parallel mesial and distal borders (Smith, 2009, 2011), as in the studied specimens. Thus, the combination of these two characters (Meckel's canal closed and fused, and tooth lateral outline not distinctly flared) are present in the

Polychrotinae*, some Tropidurinae*, the Oplurinae *Chalarodon madagascariensis*, and the Corytophaninae *Laemanctus longipes* (Smith, 2009). A subfamily designation based only on these characters would be too speculative.

The taxon represented by MACN A 2283-a, MACN A 2283-b and MACN A 2283-c is characterized by teeth with lateral outlines of parallel mesial and distal borders, with a slight apical convergence and poorly developed accessory cusps. The tooth bases are labiolingually developed and mesiodistally compressed, which differ from other fossils from the same site (MACN A 2272 and MACN A 5807). The difference in depth and convexity of the labial wall of the dentary, noted originally by Ameghino (1899), further differentiates this lizard from MACN A 5807.

Systematic paleontology (Serpentes)

Squamata Oppel 1811
 Serpentes Linnaeus 1758
  Alethinophidia Nopcsa 1923
   Caenophidia Hoffstetter 1939
    Colubroidea Oppel 1811
    Colubridae Oppel 1811
     Colubridae indet. (fig. 6)

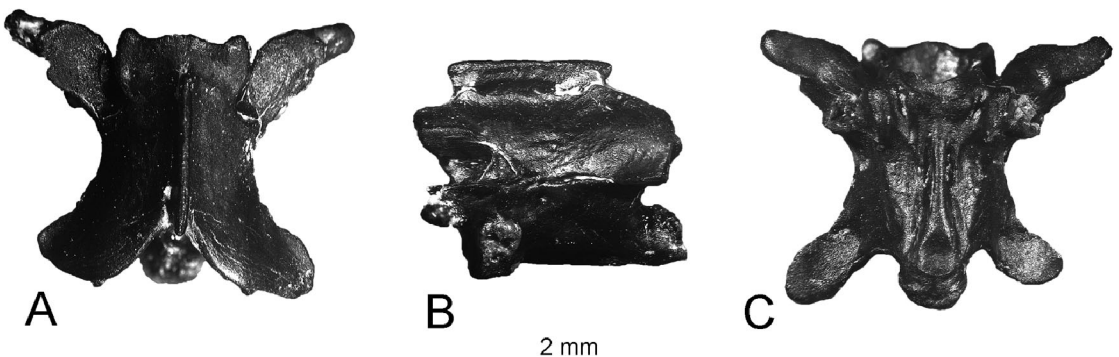*Referred material.*   MPM PV 4338, isolated precloacal vertebra.

Figure 6. Colubridae indet., MPM Pv 4338, isolated precloacal vertebra in dorsal (A), lateral (B) and ventral (C) views.

Locality and horizon. Killik Aike Norte (51° 34′S, 69° 25′W), Güer Aike department, southeast Santa Cruz Province, Argentina (fig. 1). Santa Cruz Formation (late early Miocene).

Description. The specimen is a nearly complete precloacal vertebra, lacking only part of the condyle and the synapophyses. It is a small, long, wide, and low vertebra. The neural arch is long and depressed, widened toward the prezygapophyses and postygapophyses, and constricted in the middle. The interzygapophyseal constriction is long and well defined. The notch on the posterodorsal border of the neural arch is deep, leaving exposed most of the condyle in dorsal view. The lateral walls of the neural arch are long and bear lateral foramina immediately below the interzygapophyseal ridges. The neural spine is long, low, and very thin, extending from the zygosphenal roof to the posterior notch of the neural arch. The zygosphene is very thin and broader than the cotyle. In anterior view, its dorsal margin is slightly convex in the middle. In dorsal view, the anterior margin is sinuous, with a broad and weak convexity in the middle, and with prominent lateral projections corresponding to the articular facets. In lateral view, the zygosphenal facets are long, narrow and with the main axis anteriorly oriented. The zygantrum is large and deep, with articular surfaces slightly protruding from the posterior surface of the neural arch. Adjacent to the zygantrum, there are some small foramina (no parazygantral fossae). The zygapophyses are well developed. The prezygapophyses arise from the level of the ventral half of the neural canal and are anterolaterally oriented in dorsal view. In anterior view, they are scarcely inclined in relation with the horizontal plane. The articular surfaces are long, narrow and oval. The prezygapophyseal processes are well developed, robust, and anterolaterally oriented with respect to the main axis of the prezygapophyseal surface. The postzygapophyses are slightly inclined on the horizontal and posterolaterally oriented. The neural canal is large, high and wide. The vertebral centrum is long and narrow, with

subcentral ridges well developed but not very divergent anteriorly, and less well defined posteriorly. There are two small projections anterolaterally located on each side and ventral to the cotyle, and well separated from the synapophyses by deep constrictions. These projections are interpreted as ventrolateral processes. In ventral view, the ventrolateral processes are evident at the basis of the cotyle on each side of the centrum. The haemal keel is well developed. It is narrow anteriorly and wider posteriorly. Although the haemal keel is partially broken in the most distal margin, it does not show any sign of developing of a hypapophysis. Additionally, the haemal keel is well separated from the condyle base by a short smooth surface. The precondylar constriction is weakly defined. On the ventral surface of the centrum, weakly developed ridges run longitudinally at both sides of the haemal keel, between the later and the subcentral ridges. The subcentral foramina are located between the haemal keel and these longitudinal ridges. The cotyle is round, small, very deep and with a marked border. In anterior view, relatively large paracotylar foramina are present on deep depresions at each side of the cotyle. The condyle is partially broken, although it is possible to infer that it was small and round. The synapophyses are small; they are placed adjacent to the cotyle, and are well separated from the prezygapophyseal articular surfaces. Although the synapophyses are broken, a convex and prominent diapophyseal surface is distinct from the wide and smooth parapophyseal surface. The last one surpasses the level of the ventral border of the cotyle, from which it is separated by a well-marked constriction.

Measurements. cl = 3.56, ctw = 1.10, cth = 1.10, pr-po = 4.56, naw = 2.56, wpo-po = 4.70, wpr-pr = 5, zgh = 0.22, zgw = 2.14.

Comments. The characters of the studied vertebra which are known to occur in colubroid mid-trunk vertebrae are: vertebra longer

than wide (cl > naw); delicately build; zygosphene slender, with anterior edge sinuous in dorsal view; neural spine thin; zygapophyses not strongly inclined medially on the horizontal plane; prezygapophyseal processes well developed; paracotylar foramina present; condyle round in posterior outline; and diapophyses and parapophyses differentiated (Rage, 1984; Lee and Scanlon, 2002). The presence of hypapophyses on mid- and posterior trunk vertebrae varies among colubroids. Well-developed hypapophyses are found in boodontines, xenodermatines, pseudoxyrhophiines, homalopsines, natricines, elapids, and viperids, whereas very reduced or absent hypapophyses occur in atractaspidids, most colubrines, xenodontines, dipsadines, pareatines, and calamariines (Zaher, 1999). Except for the elapids, atractaspidids and viperids, all other colubroids are included into the family Colubridae (Zaher, 1999); hence, the absence of hypapophysis on the ventral surface of the centrum supports assigning the specimen MPM PV 4338 to the Colubridae. Considering that colubrid vertebrae are notoriously difficult to identify to genus or species level (Rage, 1984), and that the number of extant colubrid species is very high (1861 species according to Uetz, Freed and Hošek, 2016), with few skeletonized specimens available for comparison, we cannot identify the specimen beyond this taxonomic level.

Discussion

The squamate material described in this paper corroborates the presence of iguanid lizards and colubrid snakes in the late early Miocene Santa Cruz Formation of southern Patagonia (Ameghino, 1899; Albino, 1996c; Fernicola and Albino, 2012). Together with specimens of teiids from the same Formation (Ameghino, 1893; Brizuela and Albino, 2008a), they represent the southernmost fossil records of squamates in South America. In addition, the partially coeval Pinturas Formation (∼19 to 14 Ma, Perkins et al., 2012) exposed in northwestern Santa Cruz province has also provided squamate specimens, including colubrids and iguanids (Albino, 1996c; pers. obs.). Among early Miocene localities of southern Patagonia, those from the Santa Cruz and the Pinturas formations have not been as prolific in squamate specimens as those from the older Sarmiento Formation at Gaiman (= Bryn Gwyn, approximately 43°21′S, 65°27′W), in Chubut province. The taxa shared by the three formations are iguanids and colubrid snakes (Albino, 1996c; 2008a, b; this paper), whereas tupinambine teiids (*Tupinambis* sp.) are only present in the Sarmiento and Santa Cruz formations (Brizuela and Albino, 2004, 2008a). Nevertheless, boids are relatively common in Miocene levels of the Sarmiento Formation (Albino, 1996b) but completely absent in localities of the Santa Cruz and Pinturas formations. At the moment, it is impossible to determine whether boids were distributed in the southernmost areas of Patagonia during Miocene times (as tupinambine teiids and colubrids), but their fossils remain to be discovered, or they not reached such high latitudes, around 50°S.

The presence of tupinambine teiids and colubrids in sediments of the Santa Cruz Formation at latitudes around 50°S (Albino, 1996c; Brizuela and Albino, 2004, 2008a; this paper) indicates a wider distributional range during the early Miocene. Tupinambines are now restricted to the north of 40°S, whereas colubrids inhabit vast regions of Patagonia, but are currently absent south of the 44°S parallel (Albino, 2011). Several other taxa recovered from the Santa Cruz Formation or in nearby penecontemporaneous levels (e.g. palm trees, the frog *Calyptocephalella*, the anteater *Protamandua*, and the primate *Homunculus*) strongly indicate that the climate was much warmer and wetter than today (Kay, Vizcaíno and Bargo, 2012). Mammalian species suggest that the overall rainfall was in the range of 1000 to 1500 mm per annum, whereas the occurrence of calcaneous root cast in paleosols indicates high seasonality in rainfall with cool wet winters and

dry warm summers (Kay, Vizcaíno and Bargo, 2012). Thus, the early Neogene climatic conditions, with temperatures warmer than today, permitted the distribution of tupinambine teiids and colubrids south of their current range of distribution (Albino, 2011).

Among iguanids, the Sarmiento and Santa Cruz formations share the occurrence of Polychrotinae* but not Tropidurinae* (Albino, 2008; this paper). The presence of the polychrotine* genus *Pristidactylus* occurs in both formations represented by many remains that correspond to more than one species, whereas the tropidurine* *Liolaemus* is only represented by few remains in the Sarmiento Formation (Albino, 2008; this paper). The evolutionary history of both genera probably began during the earliest Neogene (Albino, 2008).

Pristidactylus is presently distributed in central and southern Argentina, and central Chile, with 10 valid species, some that have very restricted distributions (Cei, Scolaro and Videla, 2004). In Argentina, six species are distributed in disjunct areas over a 29° to 45°S latitudinal range (Minoli and Avila, 2011). Thus, the late early Miocene distribution of *Pristidactylus* in south Santa Cruz province reported in the present paper implies a wider past range of dispersion probably due to favorable climatic conditions developed in southernmost territories of Patagonia, and an early diversification of the genus, with at least two different species. Morando et al. (2015), based on the recognition of *Pristidactylus* sp. from the early Miocene Sarmiento Formation at Gaiman (Albino, 2008), suggested that the Leiosaurae originated in South America ∼18 my ago. The Sarmiento Formation, from where these *Pristidactylus* remains were recovered, contains a mammal fauna correlating with the Colhuehuapian South American Land Mammal Age, which was recently dated as older than previously thought (∼20-21 Ma, Dunn et al., 2013). The identification of the genus in the Santa Cruz Formation (this paper) corroborates the early Miocene occurrence of *Pristidactylus* in

Patagonia. Furthermore, Morando et al. (2015) consider that the various extant species of *Pristidactylus* in Argentina originated relatively late, during the early-middle Pliocene (∼4 my ago) in central Argentina. Thus, the Patagonian Miocene *Pristidactylus* from Chubut and Santa Cruz provinces would have been representatives of an ancestral, old stock from where later species diverged in both Argentina and Chile. *Pristidactylus* would have responded in the same way that snakes and *Tupinambis* did to the environmental changes of the early Neogene (Pascual, Ortiz-Jaureguizar and Prado, 1996; Ortiz Jaureguizar and Cladera, 2006), retreating to the North. Following Morando et al. (2015), *Pristidactylus* suffered new diversification and reentered Patagonia during the Pliocene.

A diverse fauna of lizards was present in southern Patagonia during the early Miocene, with representatives of two early diverging groups, Scleroglossa and Iguania (Gauthier et al., 2012). Patagonian Miocene Scleroglossan lizards are represented by the teiid *Tupinambis*, whereas iguanians are exemplified by two subfamilies of iguanids, the Tropidurinae* and Polychrotinae* (Albino, 2008; Brizuela and Albino, 2004, 2008a, b; this paper). It is noteworthy that these families/subfamilies are the most taxonomically rich lineages of extant lizards in Argentina (Abdala et al., 2012), suggesting not only that the basic stock of the living lizards was present in Argentina since the beginning of the Neogene, but also that it already included some living lizard genera (*Tupinambis*, *Pristidactylus*, *Liolaemus*).

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