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# First record of squamate reptiles from the Oligocene of South America

ADRIANA MARÍA ALBINO and SANTIAGO BRIZUELA

5 ALBINO, A.M. & BRIZUELA, S., XXXX. First record of squamate reptiles from the Oligocene of South America. *Alcheringa* XX, xx–xx. ISSN 0311-5518.

10 Squamata have been known from South America since the Cretaceous, but their fossil record has an occurrence gap between the late Eocene and early Miocene. Fossils recovered from the Sarmiento Formation (Deseadan South American Land Mammal Age, late Oligocene) at Cabeza Blanca (45°S) partially fill this interval. The squamates recovered from Cabeza Blanca include both lizards (an indeterminate Iguanidae and a probable Iguaninae) and snakes (Madtsoiidae). If these taxonomic assignments are correct, the presence of an Iguaninae at such a latitude is unexpected because these lizards are presently absent from Argentine territory. The madtsoiid, here referred to *Madtsoia*, would extend the Cenozoic record of this genus back to around 16 Ma. The squamate fauna from Cabeza Blanca is compatible with warm and humid environments inferred for the Patagonian Deseadan.

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Key words: Oligocene, Squamata, Iguania, Iguanidae, Madtsoiidae, Argentina.

20 SQUAMATES of relatively high diversity are known from the Upper Cretaceous of South America (Albino 1996, 2007, 2011). Lower Paleocene to upper Eocene deposits have also yielded substantial remains (Simpson 1933, 1935, Hoffstetter 1958, 1959, Simpson *et al.* 1962, Rage 1981, 1991, 1998, 2001, 2008, Donadío 1985, Albino 1987, 1989, 1990, 1993, 2012, Carvalho 2001, Albino & Carlini 2008, Head *et al.* 2009, Brizuela 2010, Scanferla *et al.* 2013), but upper Eocene to lower Miocene rocks have provided scant records (Albino 1996, 2011, Albino & Brizuela *in press*). Thus far, Oligocene strata in South America have only produced an undescribed and unillustrated snake vertebral centrum found in an unidentified horizon at the Cabeza Blanca locality in the Chubut province of Argentina (Simpson 1933, p. 10). This fossil was not registered and is now presumed lost. Recent discoveries in the Sarmiento Formation at Cabeza Blanca have produced a late Oligocene vertebrate fauna including the only South American squamate specimens. We describe these fossils here and comment on their significance.

35 *Institutional Abbreviations.* MPEF-PV, Museo Paleontológico ‘Egidio Feruglio’, Argentina, Colección Paleontología Vertebrados; UNMdP, Universidad Nacional de Mar del Plata, Argentina, Colección Herpetológica; UNMdP-O, Universidad Nacional de Mar del Plata, Argentina, Colección Herpetológica, sección Osteología.

## Material and methods

45 The succession of South American Land Mammal Ages (SALMAs of Pascual *et al.* 1996), published by Gelfo *et al.* (2009), and the geochronology determined at Gran Barranca by Ré *et al.* (2010) have provided an improved stratigraphical framework for early Cenozoic squamate assemblages. All fossil remains studied here come from levels of the Sarmiento Formation at Cabeza Blanca (45°13’S; 67°28’W), Estancia El Molino, Escalante Department, 90 km northwest of Comodoro Rivadavia, Chubut province, Argentina (Fig. 1). The well-known fossil mammalian fauna derived from these beds characterizes the Deseadan SALMA. According to the most recent geochronological calibrations at Gran Barranca, Deseadan mammal assemblages could be as old as 29.2 Ma and as young as 26.3 Ma (Ré *et al.* 2010), a time span corresponding to the late Oligocene.

60 The fossil specimens reported in this article were deposited in the MPEF-PV. Comparisons were undertaken with extant osteological specimens from collections (UNMdP and UNMdP-O) at the Universidad Nacional de Mar del Plata, Argentina. Metataxa, or Linnaean taxa whose monophyly is in question based on the available evidence (Schulte *et al.* 2003), are denoted with an asterisk (\*) throughout the text. Unless stated otherwise, we follow the anatomical terminology of Hoffstetter & Gasc (1969) and Rage & Augé (2010), for vertebrae and tooth-bearing elements respectively. SVL means snout-vent length.

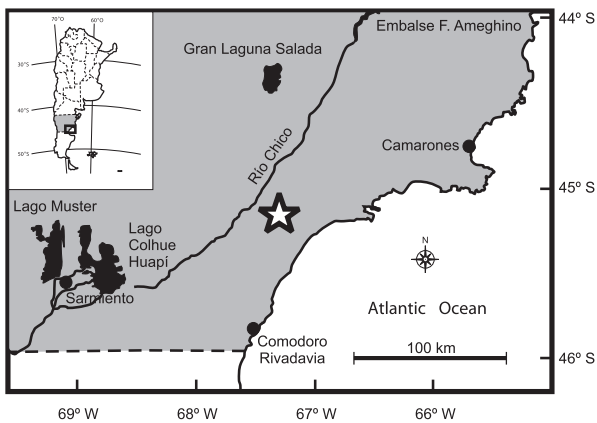


Fig 1. Map showing the Cabeza Blanca fossil locality (star: 45°13'S; 67°28'W): Chubut province in grey.

### Systematic palaeontology

SQUAMATA Oppel, 1811

IGUANIA Cuvier, 1817

IGUANIDAE Bell, 1825 (*sensu* Schulte *et al.* 2003)

Gen. et sp. Indet. (Fig. 2A)

*Referred material.* MPEF-PV 1460, tooth-bearing fragment (maxilla or dentary).

*Description.* Incomplete, poorly preserved tooth-bearing bone (maxilla or dentary), with a total length of 8.31 mm (Fig. 2A). The labial surface of the fossil is broken. There are six functional tooth positions preserved lingually, with four complete and two incomplete tooth bases. No complete teeth are preserved. Tooth bases are tall and firmly attached to the alveolar surface of the bone, in a pleurodont manner. In lateral view, the tooth bases evidence parallel mesial and distal faces. The transverse sections of the tooth bases are labiolingually oval, with a more pronounced mesiodistal constriction on the lingual face, resulting in a subtle lacrimiform cross-section. The tooth bases are tightly packed, separated by a thin deposit of cementum. The dental shelf is not preserved. A large, circular resorption zone is observed lingually on the third tooth base.

*Comments.* Edmund (1960) conducted an extensive revision of tooth replacement among reptiles. When considering Squamata, Edmund (1960, p. 61) recognized two main methods of tooth replacement, which he refers to as the 'iguanid' and 'varanid' methods. Replacement teeth in the 'iguanid' method (Gekkonidae, Iguanidae, Scincidae, Lacertidae, Xantusiidae and Cordylidae) are found lingual to functional teeth. As replacement teeth develop, the lingual wall of the functional tooth is resorbed, forming a large cavity where the replacement tooth continues developing. In contrast, replacement teeth in the 'varanid' method (Varanidae, Lanthanotidae, Helodermatidae and Serpentes) occur in an interdental position, and resorption is absent (or very reduced to an interdental

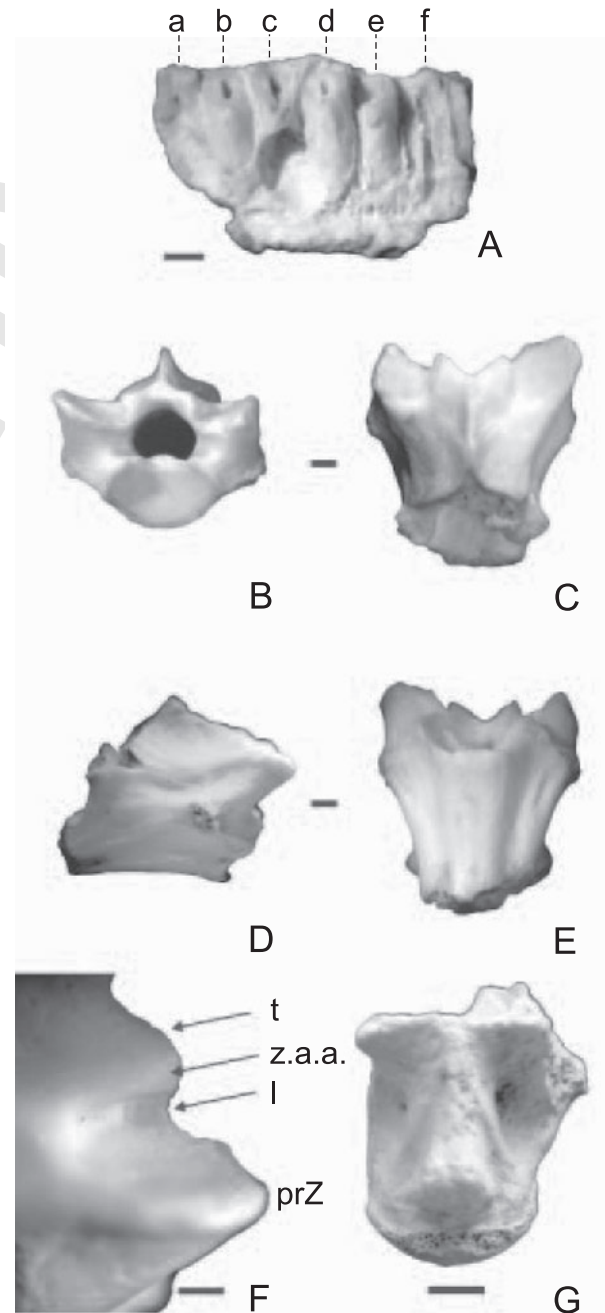


Fig 2. Squamates from the Cabeza Blanca locality. A, Iguanidae indet., tooth-bearing bone (MPEF-PV 1460). B–F, ?Iguaninae, vertebra (MPEF-PV 1463) in B, anterior, C, dorsal, D, lateral, and E, ventral views; F, detail of zygosphene. G, ?*Madtsioia*, vertebral centrum (MPEF-PV 1464) in ventral view. Abbreviations: l, lamina; t, tenon; prZ, prezygapophysis; z.a.a., zygosphene articulation area. Scale = 1 mm in all but G where it is 5 mm.

position). MPEF-PV 1460 shares the 'iguanid' method of tooth replacement, which, together with the unexpanded tooth bases and parallel outline of the mesial and distal faces, indicates iguanid affinities.

? IGUANINAE Bell, 1825 (*sensu* Schulte *et al.* 2003)

Gen. et sp. Indet. (Fig. 2B–F)

*Referred material.* MPEF-PV 1463, isolated presacral vertebra.

*Description.* Medium-sized procoelous vertebra (conserved vertebral centrum length 6.4 mm), from which the condyle and posterior half of the neural arch (postzygapophyses and neural spine) are completely missing. The neural arch is wide and depressed. The base of the neural spine extends all along the preserved section of the neural arch. The neural canal is broad (5.2 mm), with a circular outline in anterior view. The height of the neural canal is similar to that of the cotyle. The floor of the neural canal bears a faint, longitudinal ridge in the middle. Between the prezygapophyses, the anterodorsal border of the neural canal projects anteriorly producing a thin and narrow tenon, when viewed in anterior and dorsal aspect respectively. The tenon is anteriorly notched in a wide V-shape. Each side of the tenon has an indistinct, small and vertically orientated articulation surface. These surfaces are separated from those of the prezygapophyses by a marked, plane and narrow bony lamina (Fig. 2F). The prezygapophyses are elevated, starting at the level of the dorsal half of the neural canal. Only the right prezygapophysis is completely preserved; it is large, anterolaterally orientated and inclined upward from the horizontal plane. It lacks a prezygapophyseal process. The articulation facets of the prezygapophyses are almost oval. In lateral view, a weak interzygapophyseal ridge (=margo lateralis) and a more distinct subcentral ridge (=margo ventralis) are evident. Anteriorly, below the prezygapophyses, there are relatively well preserved small transverse processes, which distally bear small, subcircular synapophyses. Short, marked ridges extend anteriorly from each synapophysis to the edge of the cotyle. The centrum is compressed dorsoventrally; its surface in ventral view is convex in cross-section with no sagittal ridge. It has a conical outline, where the subcentral ridges are slightly concave and diverge anteriorly. The cotyle is relatively deep, transversely oval, wider than the neural canal, and slightly inclined, facing anteroventrally. Its rim is broken dorsomedially.

*Comments.* Vertebrae of most squamate reptiles are procoelous as in the studied specimen. Amphicoelous vertebrae are known only in Gekkonidae, more specifically in some Diplodactylidae and most Eublepharidae (Hoffstetter & Gasc 1969, Conrad 2008), differing from the condition of the studied fossil vertebra. The absence of prezygapophyseal processes also excludes this fossil from extant Serpentes and Amphisbaenia, in which these processes are present (Hoffstetter & Gasc 1969). Further, the majority of snakes have well-developed zygosphenes and zyganchra unlike MPEF-PV 1463. The present specimen also lacks the anteromedial projection (knob of Hoffstetter & Gasc 1969) evident in the neural arch of Amphisbaenia, and the parallel subcentral ridges of these fossorial squamates. Although teiid lizards have a tenon, their vertebrae are characterized by: (1) a more triangular centrum outline in ventral view (at least in the last presacral vertebrae); (2) an oval (Teiinae) or

reduced and triangular (Tupinambinae) outline of the neural canal, not circular and wide as in MPEF-PV 1463; (3) a thicker tenon in anterior view (Tupinambinae); and (4) distinct zygosphenal articulation surfaces, continuous with the prezygapophyseal articulation facets through an arch of bone, not separated by the presence of a bony lamina as in MPEF-PV 1463. A bony lamina between prezygapophyseal and zygosphenal articulation surfaces is present in presacral vertebrae of most derived Iguaninae, but not in basal extant [(*Dipsosaurus* (Baird & Girard, 1852)] and extinct species (*Armandisaurus explorer* Norell & de Queiroz, 1991 and *Queironius praelapsus* Smith, 2011). Following de Queiroz's (1987) hypothesis that a continuous arch of bone uniting the prezygapophyseal and zygosphenal surfaces is plesiomorphic among Iguaninae, we cautiously consider MPEF-PV 1463 to be a derived iguanine.

The most notable feature of MPEF-PV 1463 is the structure between the prezygapophyses. The zygosphen-zyganchrum articulation is considered to have arisen several times within squamates (e.g., Estes *et al.* 1988) and varies significantly between taxa. This variation is not always reflected in the descriptive terminology. In order to better evaluate the taxonomic affinities of MPEF-PV 1463, we reviewed the morphology of the prezygapophyseal region in a sample of extant lizard taxa with procoelous vertebrae (Appendix 1). Our comparisons were made on the vertebra immediately anterior to the first sacral vertebra, or in its absence, on the available vertebra closest to it. This decision was made because the appearance of the small transverse process and subcircular synapophysis of MPEF-PV 1463 are present together in the posteriormost presacral vertebrae of lizards. Thus, vertebrae from the same intracolumnar position were compared (Fig. 3). We focused on various aspects, such as: (1) the presence/absence of zygosphenal articulation surfaces; (2) the definition of these surfaces (distinct/vague), when present. Other aspects considered are: (3) the transition between the prezygapophyseal articulation facets and the zygosphenal articulation surfaces (continuous/separated by a distinct, planar lamina of bone/interrupted, with no bone connection); (4) the anterior extension of the anterodorsal border of the neural canal (extended, constituting a tenon, greatly concealing the cotyle in dorsal view, or deeply notched, with the dorsal surface of the cotyle exposed in dorsal view, not constituting a tenon); (5) the width (in dorsal view); and (6) thickness (in anterior view) of the tenon, when present.

The results of our observations indicate that in Anguillidae (represented in this case by *Ophiodes* Wagler, 1828) the neural arch does not extend anteriorly beyond the base of the prezygapophyses, i.e., there is no tenon (Fig. 3A). Therefore, in dorsal view, the cotyle is visible beneath the wide V-shaped anterior border of the neural arch. In anterior view, the anterodorsal border of the neural canal is thin. No articulation surfaces are

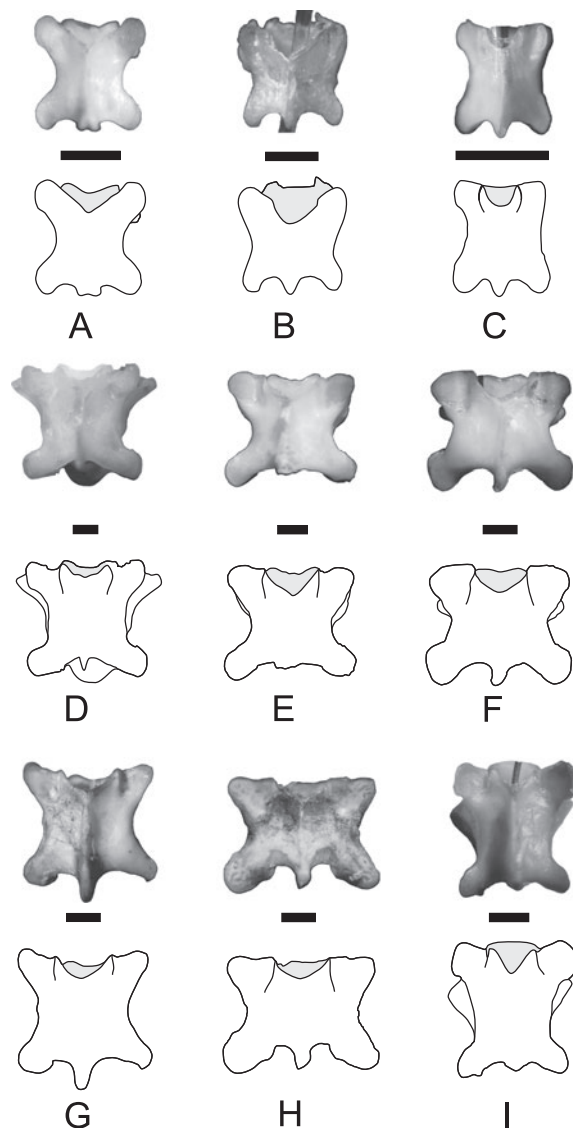


Fig 3. Dorsal view and outline of lumbar vertebrae of various lizard taxa. **A**, *Ophiodes vertebralis* (Anguillidae, UNMdP-O 66); **B**, *Mabuya frenata* (Scincidae, UNMdP 1599); **C**, *Cercosaura schreibersii* (Gymnophthalmidae, UNMdP-O 72); **D**, *Ameiva ameiva* (Teiidae, UNMdP-O 27); **E**, *Tropidurus spinulosus* (Iguanidae, UNMdP-O 77); **F**, *Phymaturus palluma* (Iguanidae, UNMdP-O 67); **G**, *Pristidactylus nigroiugulus* (Iguanidae, UNMdP-O 68); **H**, *Diplolaemus bibroni* (Iguanidae, UNMdP-O 57); **I**, *Polychrus acutirostris* (Iguanidae, UNMdP-O 73). Scale = 1 mm.

evident medial to the prezygapophyses. Contrary to these observations, Conrad (2008, C. 235) recorded the presence of a zygosphene with a dorsolateral orientated articulation facet in *Ophiodes*, although this author used an unidentified specimen of the genus. The morphology of the anterodorsal edge of the neural arch in the Scincidae [here typified by *Mabuya* (Fitzinger, 1826)] is the same as that described for *Ophiodes*, but with a somewhat deeper V-shaped anterior outline (Fig. 3B). In all other lizards with a procoelous centrum that we studied (Appendix 1) there are zygosphenal articulation surfaces with a different degree of development and/or definition. In Gymnophthalmidae (e.g., *Cercosaura* Wagler, 1830) the anterodorsal end of the neural arch

does not project anteriorly; therefore, there is no tenon. In dorsal view, the anterior outline of the neural arch varies from U-shaped to V-shaped, and the exposure of the cotyle is smaller than that observed in *Ophiodes* and *Mabuya* (Fig. 3C). Anteriorly, to each side of the anterodorsal end of the neural arch, there are distinct zygosphenal articulation surfaces opposed to the prezygapophyses. They are ventrolaterally orientated and clearly defined dorsally where there is a somewhat enlarged rim. The zygosphenal facets are united to the prezygapophyseal facets by a continuous arch of thin bone. Ossification of this arch is weak posteriorly. In teiine vertebrae (Teiidae), the anterodorsal end of the neural arch extends anteriorly, constituting a tenon that covers the cotyle when viewed dorsally (Fig. 3D). In dorsal view, the tenon is wide at the base, whereas in anterior view it is thin. Variation is evident in the anterior outline of the tenon in dorsal view: from straight to wide and shallow U-shaped notch. The distinct zygosphenal articulation surfaces are well delimited dorsally by a weak rim. Zygosphenal and prezygapophyseal articulation surfaces are united by a continuous arch of bone. In small/young specimens of the tupinambine teiid *Tupinambis* Daudin, 1802 (UNMdP-O 26: SVL = 117 mm; UNMdP-O 36: SVL = 169 mm), the morphology is similar to that of teiines. However, it changes in larger specimens (UNMdP-O 33: SVL = 315 mm; Montero *et al.* 2004) where the base of the zygosphene, in dorsal view, is constricted (i.e., shorter than the distance between its articulation surfaces), and the zygosphene is markedly thick in anterior view. Regarding the Iguanidae, the anterodorsal end of the neural arch in *Tropidurus spinulosus* (Cope, 1862) (Tropidurinae\*) does not extend anteriorly beyond the base of the prezygapophyses, so there is no tenon (Fig. 3E). However, there are vague, poorly developed, vertically orientated, small articulation surfaces. These surfaces are separated from those of the prezygapophyses by a weak, thin rectangular lamina of bone. In *T. spinulosus* there is a marked variation throughout the vertebral column. The lamina tends to become larger and the zygosphenal articulation smaller (even disappearing anteriorly) in the more anterior vertebrae. Moreover, both structures tend to lie on the same plane, making it impossible to differentiate them in anterior vertebrae. Therefore, the anterior vertebrae do not have the laminar morphology. In *Tropidurus catalanensis* Gudynas & Skuk, 1983, the anterodorsal end of the neural canal has a short anterior extension, and the distinct zygosphenal articulations are ventrolaterally orientated, unlike *T. spinulosus*. Other characteristics are similar to those evident in *T. spinulosus*, and there is significant variation throughout the vertebral column, as described for this latter species. In *Phymaturus palluma* (Molina, 1782) (Tropidurinae\*), there is no anterior projection of the anterodorsal end of the neural canal (Fig. 3F). The prezygapophyseal articulation surfaces are medially flanked by a relatively

wide groove that curves dorsally towards the mid-line of the vertebra. This arrangement ultimately constitutes a vertical–dorsolateral articulation zone. A similar condition is evident in *Liolaemus multimaculatus* (Duméril & Bibron, 1837) (Tropidurinae\*, Liolaemini), where there is no tenon, and the anterodorsal end of the neural arch has a wide V-shaped dorsal outline. In *L. multimaculatus*, vague zygosphenal articulation areas are dorsolaterally orientated and continuous with the prezygapophyseal articulation facet. In *Pristidactylus nigroiugulus* Cei *et al.*, 2001 (Polychrotinae\*), the anterodorsal end of the neural arch does not extend anteriorly far beyond the base of the prezygapophyses; thus, there is no marked tenon (Fig. 3G). In dorsal view, the anterodorsal end of the neural arch has a wide U-shaped outline, whereas it is thin in anterior view. Medial to the prezygapophyses there are indistinct zygosphenal articulation surfaces, which are small and vertically orientated. The dorsal border of the zygosphenal surfaces are delimited by marked crests. The transition between the zygosphenal and prezygapophyseal articulation surfaces is via a faint groove. There is significant variation throughout the vertebral column. There is a trend in the zygosphenal articulation surface to become dorsolaterally orientated on the anterior vertebrae, in the same plane as the faint separation groove, which is always distinguishable (in some cases with difficulty). In these anterior vertebrae, the dorsal outline of the anterodorsal end of the neural arch is subquadrangular, not concave as in the posterior vertebrae. In other polychrotines (*Diplolaemus bibroni* Bell, 1843 and *D. darwini* Bell, 1843), there is no anterior extension of the anterodorsal end of the neural arch (Fig. 3H) and the prezygapophyseal articulation facets are medially flanked by indistinct, vertically orientated zygosphenal articulation surfaces. Prezygapophyseal articulation facets are slightly elevated from a shallow weak groove (more evident in *D. bibroni*) that separates them from the zygosphenal articulation surfaces. This groove is not evident in more anterior vertebrae, where the dorsal outline of the anterodorsal end of the neural arch is subquadrangular and narrow because of the dorsolateral orientation of the zygosphenal articulation surfaces. *Polychrus acutirostris* Spix, 1825 (Polychrotinae\*) does not have a developed tenon (Fig. 3I). Nevertheless, the narrow anterodorsal end of the neural arch extends anteriorly and forms a significant V-shaped notch. In this case, the cotyle is greatly exposed in dorsal view, but unlike other species available to us, this is because of an apparent anterior extension of the centrum. The distinct zygosphenal articulation surfaces are small, very inclined and parallel to those of the prezygapophyses, from which they are disconnected (i.e., there is no bone between them). Only vertebrae from small/young specimens of Iguaninae [*Iguana iguana* (Linnaeus, 1758)] were available for our assessment. In these examples, the anterodorsal border of the neural canal extends a little beyond the base of the

prezygapophyses and has a straight or V-shaped outline in dorsal view. The zygosphenal articulation surfaces are indistinct. They are vertically orientated and continuous to the prezygapophyseal articulation facet. A marked crest delimits these areas dorsally. From these observations we infer that *I. iguana* presents ontogenetic change in the transition of the articulation areas because adults have a lamina between them (de Queiroz 1987) and a thick tenon (Hoffstetter & Gasc 1969, fig. 41).

Some aspects of significance of the zygosphene are also revealed by our review. Hoffstetter & Gasc (1969, p. 250) considered the zygosphene-zygantrum articulation as ‘... a condition in which an anteriorly facing tenon, situated between the prezygapophyses and provided by articulation facets, is engaged by a posteriorly facing mortise between the postzygapophyses of the preceding vertebra’. Within the examined specimens, we only recognized a developed tenon (as defined by us) in the Teiidae. In all other studied specimens, the anterodorsal end of the neural arch does not extend far beyond the base of the prezygapophyses, leaving the cotyle greatly exposed in dorsal view. Therefore, a more adequate definition seems to be that of Hoffstetter (1943, p. 5), who stated ‘...[a] true zygosphene, that is to say, an anterior projection of the neural arch provided with articulation facets’. Rage & Augé (2010, p. 256) gave a compatible description for the structure we found in extant iguanids: ‘... it approaches the morphology of true zygosphenes in having a roof which connects the two articular facets; however, the extent of the roof is strongly reduced by a large notch’. Rage & Augé (2010) referred to this morphology as a pseud-zygosphene, though, it must be noted that it is not present in all iguanids. For example, the iguanines *Iguana iguana* (adult) and *Queironius praelapsus* have a tenon as does MPEF-PV 1463. The term pseud-zygosphene for this structure, suggested by Rage & Augé (2010), was used earlier by Hoffstetter (1968) to refer to a different structure present in the vertebrae of the extinct Varanidae *Saniwa* Leidy, 1870. In this genus, the anterodorsal end of the neural canal has a pair of rudimentary elevations, with no articulation surfaces, associated to the intervertebral ligaments (Hoffstetter 1968, Holmes *et al.* 2010); hence this is not homologous to the zygosphene. Therefore, the central issue seems to be the presence of articulation surfaces defining a zygosphene. McGuire (1996, p. 27) further differentiated weak to developed zygosphenes according to the orientation of the zygosphenal surfaces: ‘... in the weak form, the facet of the zygosphene faces dorsolaterally, while in the moderately developed form, the facet faces either laterally or ventrolaterally. The most strongly developed form of zygosphene is characterized by a ventrolaterally facing facet with a notch separating this facet from the prezygapophysis’. This arrangement seems to be valid for iguanines but should be further evaluated in other lizards. In short, based on these



assessments and our own observations, Anguidae and Scincidae do not possess a zygosphenon based on the studied specimens, whereas all other taxa do. Among the latter, a distinct tenon is lacking in most of the species available to us; only Teiidae and some Iguaninae (*Iguana iguana* and *Queironius praelapsus*) have a marked tenon (Hoffstetter & Gasc 1969, Smith 2011). The tenon is thick in tupinambine teiids and adult *Iguana*, whereas it is thin in *Queironius praelapsus* and teiid teiids.

SERPENTES Linnaeus, 1758  
MADTSOIIDAE Hoffstetter, 1961

?*Madtsoia* Simpson, 1933 (Fig. 2G)

*Referred material.* MPEF-PV 1464, isolated prelocaal vertebral centrum.

*Description.* The incomplete vertebral centrum comes from a mid- or posterior snake trunk vertebra. It is large, short and wide. Only the condyle and the ventral surface of the centrum are completely preserved. It is a procoelous centrum, with concave anterior cotyle and hemispherical posterior condyle. The centrum length from the ventral tip of the cotyle to the most distal point of the condyle is 19.18 mm. The condyle is large, wider than taller (width = 13.14 mm, height = 10.40 mm). Although the cotyle is partially broken, it is large, deep, wider than higher and defined by a thin edge. Because the articular surfaces of both condyle and cotyle are moderately inclined, some of the condylar surface is visible in dorsal view, and some of the cotylar surface is visible in ventral view. In ventral view, only the left, well-defined subcentral ridge (= *margo ventralis*) is preserved. The ventral surface of the centrum is widened anteriorly. Moderately deep subcentral fossae are present on both sides of the hemal keel. They have subcentral foramina located on the anterior half. The hemal keel is moderately developed but posteriorly it has a bulging expansion that forms laterally paired projections separated from the ventral edge of the condyle by a well-defined groove circumscribing a condylar 'neck'. These projections constitute a bifid hemal process. In lateral view, the bifid, posterior part of the keel projects below the level of the condyle. A lateral foramen is visible on the left side where the lateral wall of the neural arch is somewhat preserved.

*Comments.* Monophyly of Madtsoiidae is accepted provisionally on the basis of vertebral characters (Scanlon 1992, 2005, Rage 1998). Short, laterally paired projections on the posterior extremity of the hemal keels are considered a distinctive apomorphy of some of the Madtsoiidae (Scanlon 1992, 2005, Albino 1996, LaDuke *et al.* 2010). In spite of its fragmentary preservation, MPEF-PV 1464 is characterized by this state. The large (centrum length > 18 mm) excludes it

from affinity with the smaller-bodied madtsoiid genera *Alamitophis* Albino, 1986, *Patagoniophis* Albino, 1986, *Rionegrophis* Albino, 1986, *Herensugea* Rage, 1996, *Nanowana* Scanlon, 1997, *Menarana* LaDuke *et al.*, 2010 and *Nidophis* Vasile *et al.*, 2013. The extremely large vertebrae of *Gigantophis* Andrews, 1901 (precondylar centrum length = 3.06 cm) is considered an autapomorphy of this genus (Mohabey *et al.* 2011) and the vertebrae substantially exceed the dimensions of MPEF-PV 1464. Also, MPEF-PV 1464 has a more depressed condyle than in *Gigantophis* and *Madtsoia madagascariensis* Hoffstetter, 1961. The triangular process on the hemal keel reported in *Madtsoia pisdurensis* Mohabey *et al.*, 2011 differs from the condition of the bifid hemal keel of MPEF-PV 1464. The typical rhombic termination of the hemal keel of *Madtsoia camposi* Rage, 1998 distinguishes this species from our specimen. Conversely, the short, wide centrum, and transversally expanded condyle and cotyle, together with the morphology of the paired projections of the hemal keel, are consistent with *Madtsoia bai* Simpson, 1933, but also in two large Australian madtsoiids: the Miocene *Yurlungur* Scanlon, 1992 and Pleistocene *Wonambi* Smith, 1976 (Simpson 1933, Hoffstetter 1961, LaDuke *et al.* 2010). These latter genera have a series of small parazygantral foramina lateral to the zygantrum, whereas *Madtsoia* usually have a single, large foramen recessed in a distinct fossa (LaDuke *et al.* 2010). Unfortunately, the poor preservation of the vertebra prevents further comparison of this character, and the assignment to *Madtsoia* is, therefore, tentative.

## Discussion and conclusions

The iguanid and madtsoiid specimens described here constitute the first record of squamates for the Deseadan SALMA, and expand the known distribution of South American squamates during the Paleogene.

Iguanians have a poor South American fossil record, with the earliest examples from the Cenomanian–Turonian of Argentina (Apesteguía *et al.* 2005) and late Maastrichtian of Brazil (Estes & Price 1973). The iguanian taxonomic affinities of the Maastrichtian *Pristiguanana brasiliensis* Estes & Price, 1973 have been questioned (Borsuk-Bialynicka & Moody 1984), and a recent phylogenetic analysis places it in a basal position among Iguanomorpha together with *Huehucuetzpalli mixtecus* Reynoso, 1998 from the Early Cretaceous of Mexico (Daza *et al.* 2012). Cenozoic records of iguanians date back to the Paleocene of Bolivia (de Muizon *et al.* 1983, Rage 1991) but elements have also been reported from the early Paleogene of Itaboraí, in Brazil. Estes (1970) mentions the presence of at least eight taxa from Itaboraí, a number that has been revised to five or six in later contributions (Báez & Gasparini 1979, Estes 1983). Based on the remains observed by Estes (1970, 1983), Carvalho (2001) only recognized *Iguania incertae sedis*, and thus the Brazilian early Paleogene

material requires further description. There is a substantial gap between the Eocene and later Cenozoic records. Ameghino (1899) described the extinct iguanian *Erichosaurus* from the early–middle Miocene of Patagonia, but the diagnostic characters presented do not sustain the validity of the genus (Fernicola & Albino 2012). Albino (2008) reported the presence of the iguanian *Liolaemus* Weigmann, 1834 (Tropidurinae\*) and *Pristidactylus* Fitzinger, 1843 (Polychrotinae\*) from the early Miocene of Patagonia, both representing the earliest occurrences of these extant genera. Two lizard fossils were also found in Pliocene strata of Argentina: a probable Polychrotinae\* (Brizuela *et al.* 2011) and *Uquiasaurus heptanodonta* Daza *et al.*, 2012, which would be basal to the Tropidurinae\*. In addition, iguanians are recorded from the late Pleistocene of Ecuador and Argentina, where *Iguana* (Iguaninae) and *Leiosaurus belli* Duméril & Bibron, 1837 (Polychrotinae\*, Leiosaurini) have been identified respectively (Hoffstetter 1970, Van Devender 1977). The iguanian material described in this paper, therefore, constitutes the first record from the Oligocene of South America.

Extant Iguaninae are distributed from southwestern United States through Central America and the Caribbean reaching southern Brazil and Paraguay. They also experienced important dispersal events through the Caribbean, to the Galapagos and to Fiji and Tonga (de Queiroz 1987, Keogh *et al.* 2008). Their southernmost continental range reaches the 28°S parallel (de Queiroz 1987). The American geographic area of distribution of iguanines coincides mainly with the Caribbean and Amazonic Biogeographic Domains (Cabrera & Willink 1980). This last biogeographic unit is little represented in Argentina where iguanines are currently absent (Cei 1993). If the identification of the fossil specimen described in this paper is correct, the presence of an iguanine in Patagonia during the Oligocene, at a latitude around 45°S, greatly exceeds the present range of distribution. Nevertheless, it is not totally surprising. First, crown group iguanines are known from the late Eocene of North America at similar mid-latitudes (46°N; Smith 2011). Second, the global Late Oligocene Warming event occurred during the late Oligocene (Zachos *et al.* 2001, Ortiz Jaureguizar & Cladera 2006) potentially extending the environmental conditions that most Iguaninae require to sites as far south as Cabeza Blanca in Patagonia.

With respect to snakes, Madtsoiidae represents a mainly Gondwanan group with a fossil record beginning in the Late Cretaceous and known from all major Gondwanan landmasses except Antarctica (LaDuke *et al.* 2010). Madtsoiids were formerly considered to have disappeared from the fossil record in the mid-Paleogene across most Gondwanan continents, except in Australia where several genera are known from the Miocene and, at least two of them, persisted to the Pleistocene (Scanlon 2005, LaDuke *et al.* 2010). The South American record of madtsoiids includes taxa from the Late Cretaceous of Argentina (*Alamitophis*,

*Patagoniophis* and *Rionegrophis*) (Albino 1986, 1994, 2000, 2007, 2011, Martinelli & Forasiepi 2004) and the early to late Eocene of Argentina and Brazil (*Madtsoia*, *Herensugea*; Simpson 1933, Hoffstetter 1959, 1961, Albino 1993, Rage 1998). Following the present biochronological sequence of mammal faunas (Gelfo *et al.* 2009), Paleocene deposits include only a possible Madtsoiidae (or Boidae) from Bolivia (Rage 1991). The record reported here indicates that madtsoiids persisted in South America until the late Oligocene. Four valid species of *Madtsoia* are currently recognized (LaDuke *et al.* 2010), of which only two are from South America. These are *M. bai* from the Riochican SALMA (Hoffstetter 1959, Albino 1993), currently regarded as early Eocene to middle–late Eocene Casamayoran SALMA (Simpson 1933, Albino 1993) in Argentina, and *M. camposi* from the early Eocene Itaboraian SALMA of Brazil (Rage 2001). The hypothesized origin of the genus is 100 Ma in Gondwana, with its last appearance in the Casamayoran of Argentina *ca* 45–47 Ma (LaDuke *et al.* 2010); but this could be slightly younger (*ca* 42–44 Ma) following the current estimated age for the earliest subage of the Casamayoran SALMA (Gelfo *et al.* 2009). This implies at least a 50 million year history of madtsoiids in South America, and if the systematic allocation of the Deseadan specimen is correct, the survival of *Madtsoia* would be extended by around 16 million years.

Lastly, the Deseadan SALMA is characterized by a modernization of the mammal assemblages that mainly exploited extensive temperate grasslands, although arboreal communities were also present (Pascual *et al.* 1996). The existence of iguanine lizards and large snakes such as the madtsoiids is compatible with such a mixed environmental regime and implies climatic conditions that were significantly warmer and more humid than experienced today.

## Acknowledgments

We thank Eduardo Ruigómez from the Museo Paleontológico ‘Egidio Feruglio’, who loaned us the material studied here. We also thank K. Smith for providing photographs of *Queironius praelapsus* for comparison. We further thank the reviewers, J.C. Rage, M. Augé and Z. Szyndlar, and the editors, S. McLoughlin and B. Kear, for their helpful suggestions and comments. This research was supported by PIP-CONICET # 112-200901-00176.

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## Appendix 1 List of extant reference specimens

- Anguidae: *Ophiodes vertebralis* (UNMdP-O 66, UNMdP 162).
- Scincidae: *Mabuya frenata* (UNMdP 1599).
- Gymnophthalmidae: *Cercosaura schreibersii* (UNMdP-O 72).
- Teiidae: Tupinambinae: *Tupinambis merianae* (UNMdP-O 14, 24, 26, 28, 32, 33, 75), *Tupinambis rufescens* (UNMdP-O 36, 74); Teiinae, *Teius teyou* (UNMdP-O 15, 16, 22), ‘*Ameiva*’ *ameiva* (UNMdP-O 27).
- Iguanidae: Tropidurinae\*, *Liolaemus multimaculatus* (UNMdP-O 76), *Phymaturus palluma* (UNMdP-O 67), *Tropidurus catalanensis* (UNMdP-O 69), *Tropidurus spinulosus* (UNMdP-O 21, 77); Polychrotinae\*, *Pristidactylus nigroingulus* (UNMdP-O 68), *Polychrus acutirostris* (UNMdP-O 73), *Diplolaemus bibroni* (UNMdP-O 70) *Diplolaemus darwini* (UNMdP-O 71); Iguaninae, *Iguana iguana* (UNMdP-O 29, 37).

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