Anais da Academia Brasileira de Ciências
ISSN: 0001-3765
aabc@abc.org.br
Academia Brasileira de Ciências
Brasil

NAVA, WILLIAM R.; MARTINELLI, AGUSTÍN G.
A new squamate lizard from the Upper Cretaceous Adamantina Formation (Bauru Group), São Paulo State, Brazil
Anais da Academia Brasileira de Ciências, vol. 83, núm. 1, marzo, 2011, pp. 291-299
Academia Brasileira de Ciências
Rio de Janeiro, Brasil

Anais da Academia Brasileira de Ciências (2011) 83(1): 291-299
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
www.scielo.br/aabc

A new squamate lizard from the Upper Cretaceous Adamantina Formation (Bauru Group), São Paulo State, Brazil

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Manuscript received on December 10, 2010; accepted for publication on January 24, 2011

ABSTRACT

The record of non-mosasaur squamates (Reptilia, Squamata) is sparse in the Cretaceus fossil record of Brazil a include six putative reports, three from the Aptian-Albian of the Araripe Basin (*Tijubina pontei* Bonfim-Júnior a Marques, *Olindalacerta brasiliensis* Evans and Yabumoto, and a lizard indet.) and three from the Upper Cretaceo of the Bauru Group (*Pristiguana brasiliensis* Estes and Price, Anilioidae gen. et sp. indet., and Squamata gen. et s indet.). In this contribution, a new genus and species of lizard, *Brasiliguana prudentis* gen. et sp. nov., is describ based on an isolated left maxilla with teeth. The material was discovered in an outcrop of the Upper Cretaceo Adamantina Formation (Bauru Group) located in the proximity of Presidente Prudente Municipality, São Paulo Sta Brazil. The new taxon is considered a basal non-Priscagamidae+Acrodonta iguanian based on the presence of a weak inclined anterior margin of the maxillary nasal process and maxillary tooth shape and tooth implantation similar to th of iguanians rather than of other lizard groups (e.g. teiids). This finding significantly increases the squamate liza diversity of South America, which is still poorly understood and sparsely represented in the fossil record.

Key words: Bauru Group, Brazil, Iguania, Late Cretaceous, Squamata.

INTRODUCTION

The record of squamate lizards (the term "lizard" is here informally used to the non-monophyletic non-mosasaur, non-amphisbaenian, non-serpentian squamates) in the Cretaceous of South America is scarce when compared with other regions, such as the United States and Asia (e.g. Alifanov 2004, Borsuk-Bialynicka and Moody 1984, Conrad and Norell 2007, Evans and Wang 2010, Gao and Norell 1998, 2000, Gilmore 1943, Nydam and Cifelli 2002, Nydam et al. 2000).

In South America, Cretaceous lizards have been reported in Argentina and Brazil. A putative record from

published (see Albino 2007:105). The findings fr gentina include a partial frontal bone of an ind nate iguanid from the Cenomanian Candeleros tion (Río Negro, Argentina; Apesteguía et al. 2 dentary fragment of an indeterminate lizard fr Campanian Anacleto Formation (Río Negro, Arg Albino 2002, 2007), and probable teiid remains, cited, from the Campanian-Maastrichtian Los tos Formation (Río Negro, Argentina; Albino 20 Brazil, the record of Cretaceous lizards is consi better represented, with findings in Lower and Cretaceous rocks. The Early Cretaceous taxa the species *Tijubina pontei* and *Olindalacerta br*

considered to represent basal squamatans (e.g. Bonfim-Júnior and Avilla 2002, Bonfim-Júnior and Rocha-Barbosa 2006, Martill 2007). Also, there is material of an indeterminate lizard from the Crato Formation (Evans and Yabumoto 1998) that has not been studied. The Late Cretaceous records include an articulated sequence of dorsal vertebrae and ribs from the Turonian-Santonian Adamantina Formation at the Municipality of Marília (São Paulo State) interpreted as an indeterminate lizard (Candeiro et al. 2009), and the lizard *Pristiguana brasiliensis* (Estes and Price 1973) from the Campanian-Maastrichtian Marília Formation at Peirópolis town (Municipality of Uberaba, Minas Gerais State). The affinities of *Pristiguana* are still debated. Originally, it was considered an iguanian (Estes and Price 1973), a hypothesis supported by other authors (Estes 1983, Estes and Báez 1985, Reynoso 1998), but other opinions suggest that *Pristiguana* possesses affinities with teiids (Borsuk-Bialynicka and Moody 1984). Non-lizard Cretaceous squamates of Brazil are also sparse and represented by a solely anilioid snake from the Adamantina Formation at Ribeirao Buriti (General Salgado Municipality, São Paulo State; Zaher et al. 2003) and Late Cretaceous mosasaur remains from the Pernambuco-Paraíba Basin (records of *Globidens*, *Mosasaurus*, and Plioplatecarpinae; Price 1953, 1957, Carvalho and Azevedo 1998), the Sergipe Basin (records of *Plioplatecarpus* and *Platecarpus*; Bengtson and Lindgren 2005), the São Luís Basin (Vilas Bôas and Carvalho 2001), and a doubtful record from the Acre Basin (see Bengtson and Lindgren 2005).

In this contribution, an isolated left maxilla with teeth is described and adscript to a new genus and species of lizard, interpreted as having non-Priscagamidae+Acrodonta iguanian affinities (*sensu* Conrad 2008). The specimen, housed at the Museu Nacional, Rio de Janeiro (Rio de Janeiro State, Brazil), was discovered in 2005 in the proximity of Presidente Prudente Municipality, São Paulo State (Brazil; Fig. 1), from outcrops of the Adamantina Formation (Turonian-Santonian, Upper Cretaceous). Presidente Prudente and surrounding localities (e.g., Álvarez Machado, Pirapozinho, Presi-

nomically diverse material such as invertebrates, turtles, crocodyliforms, and dinosaurs (e.g. Bertini et al. 1993, Dias-Brito et al. 2001, Kellner and Azevedo 1999, Kellner and Campos 1999, 2000, Price 1945). Since 2004, prospecting and excavations carried out at the Presidente Prudente region by the staff of the Museu de Paleontologia de Marília (São Paulo State) recovered several small vertebrate remains that include fishes and anurans remains, titanosaur and abelisaur teeth, diverse types of coprolites, enantiornithe birds (Alvarenga and Nava 2005), and the lizard specimen here described.

The new taxon presented here represents the third lizard record from the Bauru Group (Fernandes and Coimbra 1996) and the sixth from the Cretaceous of Brazil as a whole. The presence of tiny fossil material in the Late Cretaceous outcrops of Brazil can increase our current knowledge about groups rarely represented in the fossil record (Kellner and Campos 1999).

SYSTEMATIC PALEONTOLOGY

LEPIDOSAURIA Heackel 1866
SQUAMATA Oppel 1811
IGUANOMORPHA Sukhanov 1961
(*sensu* Conrad 2008)
IGUANIA Cuvier 1817 (*sensu* Conrad 2008)

Brasiliguana gen. nov.

Etymology: *Brasil*, in reference to its provenance from the Late Cretaceous of Brazil; *iguana*, from the South American and Caribbean aboriginal language Arawakan *iguana*,*iwana*, which refers to the local name for lizard.

Diagnosis: As for the type and only known species.

Type species: *Brasiliguana prudentis*.

Brasiliguana prudentis sp. nov.

Holotype: MN 7230-V (Coleção de Paleovertebrados, Museu Nacional, Rio de Janeiro, Rio de Janeiro State, Brazil) consists of an isolated left maxilla with partially preserved teeth (Figs. 2 and 3).

Etymology: *Prudentis*, in reference to Presidente Prudente Municipality, São Paulo State (Brazil), where the

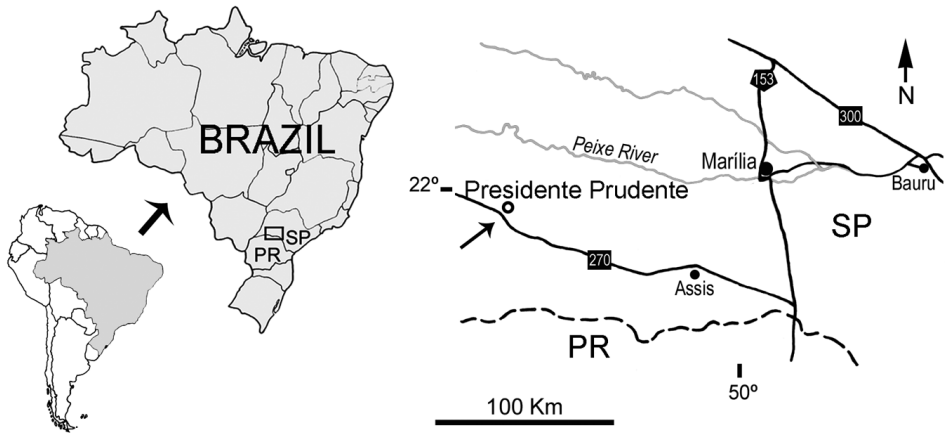


Fig. 1 – Map showing the locality where *Brasiliguana prudentis* was discovered (arrow), in the vicinities of Presidente P
São Paulo State, Brazil. Abbreviations: PR, Paraná State; SP, São Paulo State.

São Paulo State, southeast Brazil. The outcrop belongs to the Adamantina Formation, Bauru Group; Turonian-Santonian, Upper Cretaceous (Fernandes and Coimbra 1996).

Diagnosis: *Brasiliguana prudentis* differs from other squamatans in the association of the following features: triangular shaped unornamented maxilla with a high nasal process located in the anterior half of bone; weakly inclined anterior margin of the maxillary nasal process; long and thin maxillary jugal process; four conspicuously aligned foramina well above the dental margin; last five teeth placed posterior to the level of the orbital margin; teeth with labial pleurodont implantation; heterodont dentition; mid-maxillary teeth with noticeable constriction of the crown relative to the shaft as occurs in some Tropiduridae and Phrynosomatidae; mid-maxillary teeth with main bulbous cusp and very small accessory mesial and distal cusps, smaller than in Tropiduridae and Phrynosomatidae, not flared; and posterior sub-conical teeth with backwardly projecting crown.

DESCRIPTION

The holotype MN 7230-V of *Brasiliguana prudentis* consists of an isolated left maxilla with ten partially preserved teeth and space for at least four others. The

tion of the nasal process and the anteriormost
of the premaxillary process partially broken (
The labial surface of the maxilla is flat to slight
cave, unsculptured, with a shallow anteroposteri
at mid-height that is pierced by four main nu
foramina. These prominent foramina are locate
level of the second, fifth, eight and tenth teeth po
respectively (Fig. 2). The anteriormost foramen
largest and, immediately posterodorsal to it, the
additional very small foramen. The second and
foramina are similarly sized, and the third is the
est, with a circular shape. The second foramen
cular, laterally opened, and the fourth is drop-s
facing posteriorly. Near the dorsal broken edge
nasal process there are two other foramina, small
the others. The dental margin of the maxilla
tively straight, curving slightly dorsally after t
tooth. In the anterior portion, the maxilla exh
rounded, slightly concave edge interpreted as th
terior border of the external nares. The contr
of septomaxilla could not be evaluated. The p
illary process is anteriorly broken, but based up
narial and dental edges, it was likely thin, long a
izontal rather than dorsally curved. The base
nasal process is wide and located in the anteri
of the maxilla. The dorsal border of this process

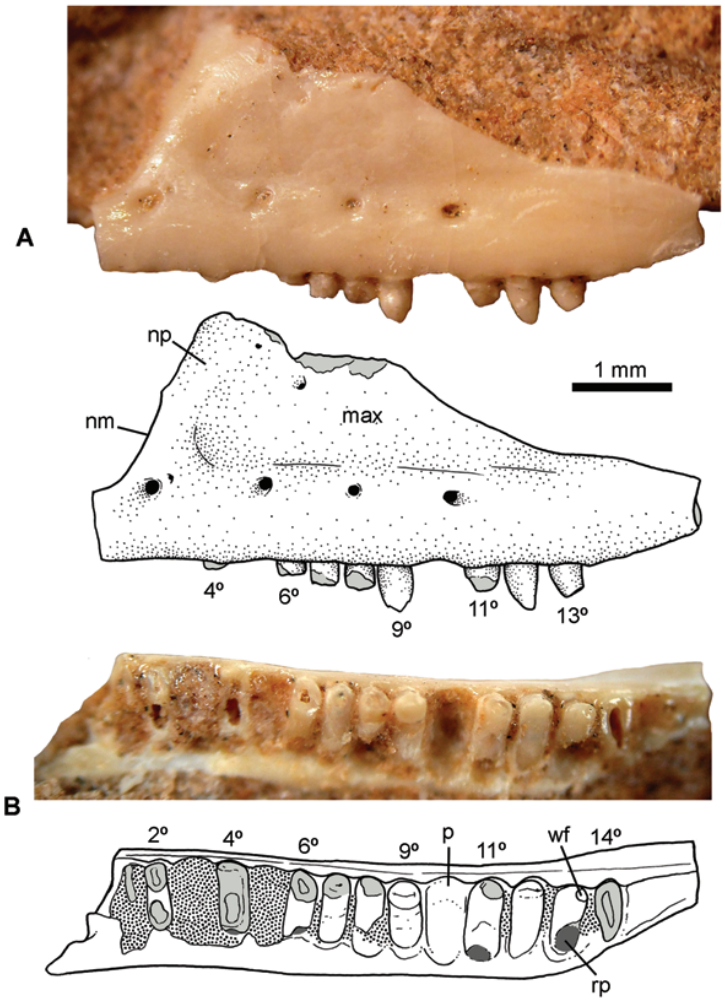


Fig. 2 – *Brasiliguana prudentis* gen. et sp. nov. Holotype MN 7230-V, left maxilla in lateral (A) and ventral (B) views with accompanying drawings. Light grey indicates broken bone and teeth. Dark grey indicates replacement pits. Regular dotted surfaces indicate main portions with sandstone. Abbreviations: **max**, maxilla; **nm**, narial margin; **np**, nasal process of the maxilla; **p**, pleura of the maxilla; **rp**, replacement pit; **wf**, wear facet. Numbers refer to teeth positions.

bones could not be discerned. This border is slightly concave and sub-parallel to (i.e., posteriorly convergent to) the dental margin (Fig. 2). The jugal process is long and thin, decreasing in height posteriorly from the level of the eighth tooth. Based on these features, at least five teeth are placed posterior to the level of the anterior border of the orbit. In ventral view, the palatine process (or palatine flange) of the maxilla does not possess

teen teeth possibly correspond to the total upper tooth count for this species. All teeth are synostotically ankylosed to the lingual surface of the pleura of the maxilla, and the teeth are tightly packed without distinctive interdental ridges. This type of tooth implantation, i.e., labial pleurodonty (*sensu* Zaher and Rieppel 1999), is characteristic of many lizard, groups but absent in varanoids, snakes, acrodonts, and acrodont amphisbaenians

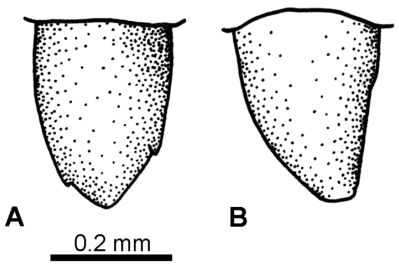
The first (1st) and second (2nd) preserved teeth are broken and were apparently smaller than the following ones, which maintain a similar size along the tooth row. The spaces for the third (3rd) and fifth (5th) teeth, respectively, are full of sediment. The forth (4th) tooth is badly preserved, with only a remnant of the crown and the shaft. At the base of this tooth, there is a depression that possibly corresponds to a replacement pit. The sixth (6th) to eighth (8th) teeth have their crowns broken at the level of the dental margin. The ninth (9th) tooth is the best preserved (Figs. 2 and 3). It is circular in cross section at the level of the dental margin and transversely oval through the shaft. It has a large main cusp with anterior and posterior blunt crests that hold very small mesial and distal accessory cusps. The mesial accessory cusp is placed higher than the distal cusp. The tip of the main cusp is sharp and slightly posteroventrally projected. There is no neck on the shaft. In lateral view, the exposed crown represents about 1/3 of the total tooth height. In lateral view, the mesial and distal outlines are slightly divergent to the base, resulting in a narrower crown. Noticeably, the labial surface of the crown is more convex than the lingual surface. This tooth is apparently a new element due to the lack of wear and the absence of a replacement pit at its base (Fig. 2).

Following the ninth tooth (9th), there is an empty cavity (for 10th tooth). The eleventh (11th) tooth is intensely worn out apically and labially with an oblique wear surface facing ventrolateraly. In this tooth, there is no clear evidence of accessory cusps. At the base of the eleventh tooth there is a circular pit. The twelfth (12th) tooth has a relatively well preserved crown (Figs. 2 and 3). It is sub-conical, with the sharp tip slightly curved posterolingualy, thus differing from the condition observed in the ninth tooth. The crown surface is poorly preserved and the presence of accessory cusps could not be evaluated with confidence. Also, the crown seems to be less globose than in the ninth tooth. The thirteenth (13th) tooth is slightly smaller than the preceding one and the tip is strongly worn (Fig. 2). As in the previous tooth, the crown is sub-conical and the portion of preserved crown is posteriorly inclined. At

ference in the crown morphology between the ni
the twelfth-thirteenth teeth (Fig. 3) suggests some
of heterodonty, as occurs in other lizards (e.g. B
and Albino 2010, Estes et al. 1988, Frost 1992
tanucci 1968).

COMPARISONS AND DISCUSSIONS

Brasiliguana prudentis constitutes the second
species from the Late Cretaceous of Brazil ba
cranial material. The holotype and only known
imen of *Pristiguana brasiliensis* (Divisão de G
e Mineralogia, Rio de Janeiro, DGM-552; Est
Price 1973) from the Marília Formation at Pei
locality (Uberaba, Minas Gerais State) includes
dentary with teeth, right surangular, fused fronta
pterygoid, left humerus, and an indeterminate fra
Unfortunately, the lack of homologous element
pers detailed comparisons between the two Br
fossils. Nonetheless, the teeth of both species
some features that support their distinctiveness
sidering that upper and lower dental morpholog
a similar pattern, the tricuspid teeth of *Pristigua*
hibit relatively larger accessory cusps and higher
and roots than in *Brasiliguana* (largest tooth of
liguana: 0.9 mm high; larger tooth of *Pristi*
1.3 mm high). The teeth are more tightly pac
Brasiliguana than in *Pristiguana*, and the posteri
ical and curved teeth of *Brasiliguana* are not
in the lower dentition of *Pristiguana* (Estes an
1973). In *Pristiguana*, the teeth are columnar w
allel sides, whereas in *Brasiliguana* (considering
preserved tooth) the crowns are constricted rela
the shafts, giving the appearance of bulbous teeth



The 9th tooth of *Brasiliguana* exhibits a noticeable constriction of the crown relative to the shaft (Fig. 3), similar to the teeth of the tropidurids *Uranoscodon superciliosus*, *Tropidurus thresiae*, *Stenocercus guentheri*, *Microlophus atacamensis*, *M. quadrivittatus* and the phrynosomatid *Cophosaurus texanus* (see Etheridge and de Queiroz 1988, Frost 1992, Torres-Carvajal 2003, Vidal and Ortiz 2004). This differs from other iguanians that usually possess flared crowns (e.g. Etheridge and de Queiroz 1988, Frost 1992, Montanucci 1968). Despite the morphological similarity of the teeth to the teeth of some Tropiduridae and Phrynosomatidae, the accessory cusps are relatively less prominent in *Brasiliguana*. Some tropidurids, such as *Leiocephalus*, have recurved crowns (Frost 1992), as occurs in the posteriormost teeth of *Brasiliguana* (Fig. 3).

The lack of flared crowns in the tricuspid teeth of *Brasiliguana* is possibly a primitive feature within iguanians due to the occurrence of flared crowns with better developed cusps in more derived forms (e.g., Etheridge and de Queiroz 1988). This is also concordant with the morphology observed in some phrynosomatids (see above), which are nested as basalmost iguanians (e.g., *sensu* Conrad 2008).

Despite other lizard groups with tricuspid teeth, such as the teiids *Ameiva*, *Kentropyx*, and *Cnemidophorus* (Presch 1974), the general morphology of the crowns of *Brasiliguana* is more reminiscent to iguanians than to teiids.

The presence of replacement pits at the base of the 4th, 6th, 11th, and 13th teeth of *Brasiliguana* (Fig. 2), rather than interdental placement, suggests tooth replacement typical of iguanians, gekkotans, various scincomorphs, and some anguids (Edmund 1969, Estes et al. 1988, Rieppel 1978).

Unfortunately, none of the synapomorphies of the clade Iguania listed by Estes et al. (1988) and by Conrad (2008) could be evaluated in *Brasiliguana* due to the fragmentary nature of the holotype. Nonetheless, *Brasiliguana* possesses a synapomorphy of the Iguania clade (exclusive of phrynosomatids) *sensu* Conrad (2008): the presence of a weakly inclined anterior margin of the 2000), in Serpentes, and in Varanoidea (e.g. Conrad 2008). Differing from *Brasiliguana*, the priscagamid lizards have acrodont dentition and exhibit dermal sculpturing on the maxilla (Conrad 2008, Gao and Norell 2000). Consequently, the presence of this character-state in *Brasiliguana* plus the type of tooth implantation indicates strong evidence for its inclusion within the Iguania as a non-Priscagamidae+Acrodonta taxon (*sensu* Conrad 2008). In other words, following the phylogenetic hypothesis of Estes et al. (1988; see also, for example, Smith 2009), *Brasiliguana* could be considered as a member of the Iguania clade positioned closer to the traditional "Iguanidae" (a paraphyletic assemblage of non-acrodont lizard groups; also called Pleurodonta, see Frost et al. 2001, Evans and Jones 2010) than to acrondont lizards.

The shape of the premaxillary and nasal processes, the row of labial nutritious foramina and their placement with regard to the dental margin, and the shape of the orbital contribution of the maxilla is similar to the condition of other fossil iguanians such as the Late Cretaceous Mongolian *Saichangurvel davidsoni* (Conrad and Norell 2007), *Temujinia ellisoni* (Gao and Norell 2000), *Ctenomastax parva* (Gao and Norell 2000), the Miocene *Armandisaurus exploratory* (New Mexico, USA; Norell and de Queiroz 1991), and the current *Tropidurus* and *Tapinurus* (Frost 1992). Despite the similar morphology of the maxillary, the teeth of *Brasiliguana* differ from these taxa in the lack of flaring and complex crowns (see above). The unornamented surface of the maxilla of *Brasiliguana* is also similar to the condition of most iguanians and different from the condition of others lizards such as cordyloideans and teiids (e.g. Conrad 2008), in which the maxillae are ornamented.

Due to the fragmentary nature of the only known material of *Brasiliguana*, the phylogenetic placement of the Brazilian fossil within lizards is only partially resolved. The above mentioned resemblances of the maxilla and dentition with members of the basal clade Iguania (e.g. Estes et al. 1998, Conrad 2008) may suggest that *Brasiliguana* is likely a plesiomorphic non-Priscagamidae+Acrodonta iguanian. Iguanians of Late

ent from the condition of *Brasiliguana*, possibly supporting its basal position. Moreover, the morphology of the teeth of *Brasiliguania* is similar to that present in members of the basal family phrynosomatid and in some tropidurids.

New materials from rich fossiliferous localities of Late Cretaceous age in southeast Brazil will be necessary for more precise taxonomic discussions and for a better understanding of the origin and diversity of Mesozoic squamatan lizards in South America and their bearing in Squamate phylogeny.

ACKNOWLEDGMENTS

We especially thank H.M.F. Alvarenga (Museu de História Natural de Taubaté, SP) for the preparation of the material and J.J.W. Sertich (Department of Anatomical Sciences, Stony Brook University, New York) for suggestions and English corrections. Two anonymous reviewers and the Editor A.W.A Kellner made several suggestions that greatly improved the Ms. A.G.M. is supported by a Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq/Brazil) scholarships under the direction of V.P.A. Teixeira (CCCP/UFTM).

RESUMO

Os achados de escamados (Reptilia, Squamata) são escassos no Cretáceo do Brasil, incluindo cinco registros pontuais, dois do Aptiano-Albiano da Bacia do Araripe (*Tijubina pontei* Bonfim-Júnior e Marques e *Olindalacerta brasiliensis* Evans e Yabumoto), e três do Cretáceo Superior do Grupo Bauru (*Pristiguana brasiliensis* Estes and Price, Anilioidae gen. et sp. indet., Squamata gen. et sp. indet.). Nesta contribuição apresentamos um novo gênero e espécie de lagarto, *Brasiliguana prudentis*, baseado numa maxila esquerda com dentição. O material provém de depósitos da Formação Adamantina aflorantes próximos a cidade de Presidente Prudente, Estado de São Paulo, Brasil. O novo táxon é considerado um iguanídeo não-Priscagamidae+Acrodonta baseado na presença de uma margem anterior do processo nasal do maxilar pouco inclinada e na morfologia maxilar e dentaria mais semelhante à de outros iguanideos que a outros grupos de lagartos (ex. teiídeos). A presente descoberta aumenta a diversidade de lagartos escama-

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