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Abstract.—The Cerro Azul Formation of Argentina has yielded one of the highest diversities of squamate reptiles for the upper Miocene of South America including tupinambine teiids (*Tupinambis* sp.), "colubrids," and viperids. Here, we describe new remains of *Tupinambis* sp. and "Colubridae" from this Formation as well as the first records of teiine teiids and boid snakes. The teiine represents the oldest record of this subfamily in South America. The squamate assemblage of the Cerro Azul Formation is consistent with the mammalian fauna in supporting the interpretation of a Chacoan-type palaeoenvironment for the upper Miocene of Central Argentina.

Squamate remains are frequently recovered from South American Cenozoic localities. Their detailed morphological descriptions and taxonomic identifications, which are solidly supported, allow us to recognize past diversity, changes in the distribution of taxa through time, and historical evolution. Such information might also be used for calibration of molecular clocks and for inferring paleoenvironmental modifications.

The South American Miocene is an especially interesting period because the record of Cenozoic squamates shows a great diversity including representatives of Iguania, Teiidae, Scolecophidia, Boidae, "Colubridae," and Viperidae as well as the basal alethinophidian snake *Colombophis* (Albino, 1996a,b, 2008; Hecht and Laduke, 1997; Sullivan and Estes, 1997; Brizuela and Albino, 2004, 2008a,b, 2012; Albino et al., 2006; Albino and Montalvo, 2006; Head et al., 2006; Hsiou et al., 2009, 2010). Data on squamates from the upper Miocene of South America have increased significantly in recent years. Estes and Báez (1985) reported a vertebra from an undetermined boid in Venezuela, but the material was never described nor illustrated. Later, Head et al. (2006) described remains of snakes that they assigned to Aniliidae (*Colombophis*) and Boidae (genus and species indeterminate) from the same country. Upper Miocene deposits in the southwestern Amazonia of Brazil have recently yielded materials that include genera of the extinct tupinambine teiid *Paradracaena*, the basal alethinophidian snake *Colombophis*, boid specimens (*Eunectes* sp., aff. *Epicrates* sp. and *Waincophis* sp.), and two distinctive forms of snakes identified only to the level of family ("Colubridae") (Hsiou and Albino, 2009, 2010; Hsiou et al., 2009, 2010). In addition, the outcroppings of the Cerro Azul Formation in central Argentina have provided an abundant and taxonomically diverse squamate assemblage for the upper Miocene of southern South America. The teiid genus *Tupinambis* has been recognized in several localities of this formation (Albino et al., 2006), whereas snakes ("colubrids" and viperids) have only been reported from the Caleufú locality (Albino and Montalvo, 2006). Recent investigation of previously prospected and new outcroppings of the Cerro Azul Formation has resulted in the recovery of additional squamate specimens including formerly unreported taxa. We undertook the present study to provide descriptions of the new squamate material from the localities Cerro La Bota (37°22′S, 65°28′W), Cerro Patagua (37°08′S, 65°46′W), Estancia Ré (36°07′S, 64°59′W), Bajo Giuliani (36°43′S, 64°18′W), and Caleufú (35°41′S, 64°40′W) (Fig. 1A), and to ascertain whether this fossil material reinforces earlier interpretations from mammalian faunas with regard to paleoenvironments of central Argentina.

Materials and Methods

The discovery of fossil remains described in this paper is the result of fieldwork over the last 20 yr in upper Miocene outcrops of the Cerro Azul Formation in Argentina. All the paleontological sites were visited several times and exposed remains were collected at every opportunity. Square digging and sediment sieving were used only for the Cerro La Bota site. Exploratory analyses at other localities produced a few specimens, so these methodologies were not used. The faunal assemblages recovered from Cerro La Bota, Cerro Patagua, Bajo Giuliani, Estancia Ré, and Caleufú were composed mainly of mammals (Montalvo and Casadío, 1988; Goin et al., 2000; Montalvo et al., 2005; Verzi et al., 2008; Montalvo, 2011), whereas specimens assigned to other terrestrial vertebrates were very scarce (Albino et al., 2006; Albino and Montalvo, 2006; Cenizo et al., 2012).

A detailed description of the geology and stratigraphy of the Cerro Azul Formation can be found in Linares et al. (1980) and Goin et al. (2000). Goin et al. (2000) recognized three associated sedimentary facies in this formation, two of which have produced reptilian remains. These facies include eolian deposits with evidence of paleosoils (Cerro Patagua, Bajo Giulani, Estancia Ré, and Caleufú) and ephemeral fluvial deposits (Cerro La Bota) (Fig. 1B). We follow the biochronological sequence of South American Land Mammal Ages (SALMAs) of Pascual et al. (1996) for the record of Cenozoic squamates. According to this and to the proposed biochronological scheme of Verzi et al. (2008), the vertebrate fossils recovered from the Cerro Azul Formation in Cerro La Bota and Cerro Patagua localities contain a Chasicoan mammalian fauna, whereas the remaining localities are assigned to the Huayquerian SALMA, characterized by a somewhat younger mammal association. There are no data of numerical ages for these deposits. However, there are data of the type localities of the Chasicoan and Huayquerian SALMAs. The Late Miocene deposits exposed in the type locality of Chasicoan SALMA (Arroyo Chasicó in Buenos Aires province) were recently interpreted as fluvial deposits with three lithofacies associations (Zárate et al., 2007). These authors proposed that the lithofacies associations I and II would have been deposited between 9.43 Ma and 9.07 Ma, based on an impact event dated at 9.23 ± 0.09 Ma and on magneto-stratigraphy (Schultz et al., 2006). On the other hand, the type locality of Huayquerian SALMA (Huayquerías del Este in Mendoza province) was dated by Marshall et al. (1986) with an average age of 5.8 ± 0.1 Ma.

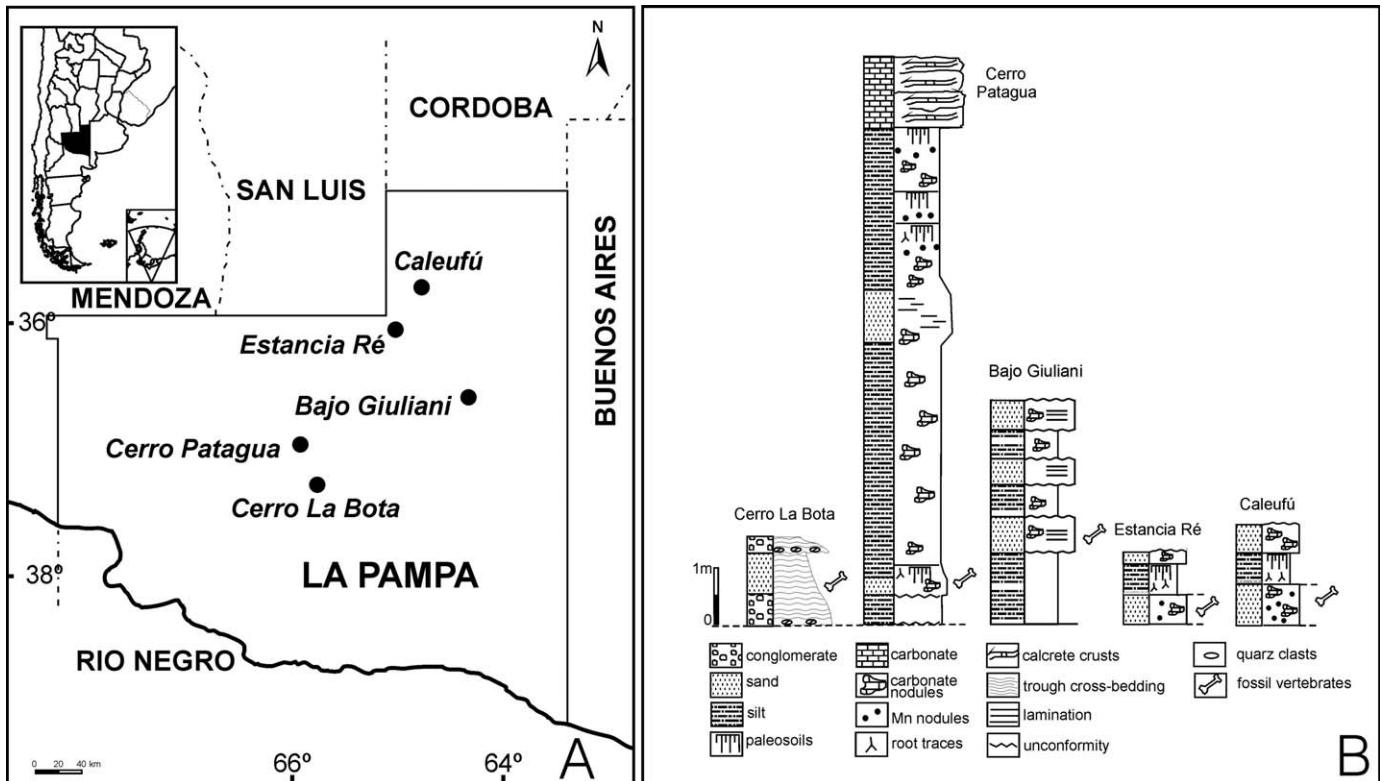[2]Corresponding author. E-mail: aalbino@mdp.edu.ar

Fig. 1. (A) Localities of the Cerro Azul Formation of Argentina cited in the text. (B) Stratigraphic profiles of these localities. Profiles from Cerro La Bota, Bajo Giuliani, and Caleufú modified from Verzi et al. (2008). (©2008 Elsevier Masson SAS. All rights reserved.) Used with permission.

The new fossil specimens described in this paper are deposited in the Paleontological Collection at the Facultad de Ciencias Exactas y Naturales of Universidad Nacional de La Pampa, Argentina (GHUNLPam).

Osteological specimens of extant squamates used for comparisons belong to the following collections (Appendix 1): Field Museum of Natural History, USA (FMNH); Fundación Miguel Lillo, Argentina (FML); Museo Nacional de Historia Natural de Santiago, Chile (MNHN); Museu da Zoologia, Universidade de São Paulo, Brazil (MZUSP); National Museum of Natural History, USA (NMNH); Universidad Nacional de Mar del Plata-Osteological Section, Argentina (UNMdP-O); Universidad Nacional del Noreste, Argentina (UNNE); and University of Michigan Museum of Zoology, USA (UMMZ).

Groups whose monophyly is questioned are denoted in quotes. "Cnemidophorinae" (i.e., non-*Teius* and *Dicrodon* Teiinae), although monophyletic, is an informal group and as such it is also written in quotes. The following anatomical abbreviations were used: cl, centrum length; naw, neural arch width at interzygapophyseal ridge; po-po, distance between postzygapophyses; pr-po, distance between pre- and postzygapophyses of the same side.

SYSTEMATIC PALEONTOLOGY
Squamata Oppel, 1811
Scincomorpha Camp, 1923
Teiidae Gray, 1827
Tupinambinae Presch, 1974
Tupinambis Daudin, 1802
Tupinambis sp.
Figure 2

Referred Specimens.—Bajo Giuliani Locality: GHUNLPam 22677, right dentary; GHUNLPam 2313, proximal caudal vertebra. Caleufú Locality: GHUNLPam 19874/42, articulated dorsal vertebrae. Estancia Ré Locality: GHUNLPam 4256, right maxilla.

Description.—Specimen GHUNLPam 22677 is the poorly preserved posterior half of a right dentary (Fig. 2A). Labial surface flat and smooth, preserving single mental foramen. Lingual surface with flat subdental shelf, which is the same height along its entire length. Ventral part of subdental shelf with wide surface for articulation with splenial. Meckelian groove incomplete but appears to have been open medially. Inferior alveolar canal exposed on posterior portion of Meckelian groove's roof. Five functional tooth positions preserved on dental groove. Tooth implantation subpleurodont. Basal cementum very abundant, covering the interdental septa and obscuring the sulcus dentalis. One tooth (c in Fig. 2A) complete but only the bases of remaining teeth were preserved. Teeth circular in cross section, although base of posteriormost tooth slightly compressed labiolingually. Tooth (c) robust, enlarged, straight, and ending in a blunt point. Base of tooth (d) slightly displaced towards the lingual side, which suggests it is a young tooth. Incipient resorption zones (i.e., replacement pits) present between teeth (a) and (b) and between (b) and (c).

Specimen GHUNLPam 4256 is a posterior fragment of a right maxilla (Fig. 2B). Only part of the sulcus dentalis and tooth series are preserved, with four whole teeth and incomplete remains of two teeth. Tooth implantation subpleurodont. Teeth robust, blunt, and with a large cross section; heavy deposits of cementum at the bases, covering the interdental septa and obscuring the sulcus dentalis. Sulcus dentalis preserved lingually to teeth (b), (c), and (d). Tooth height decreasing
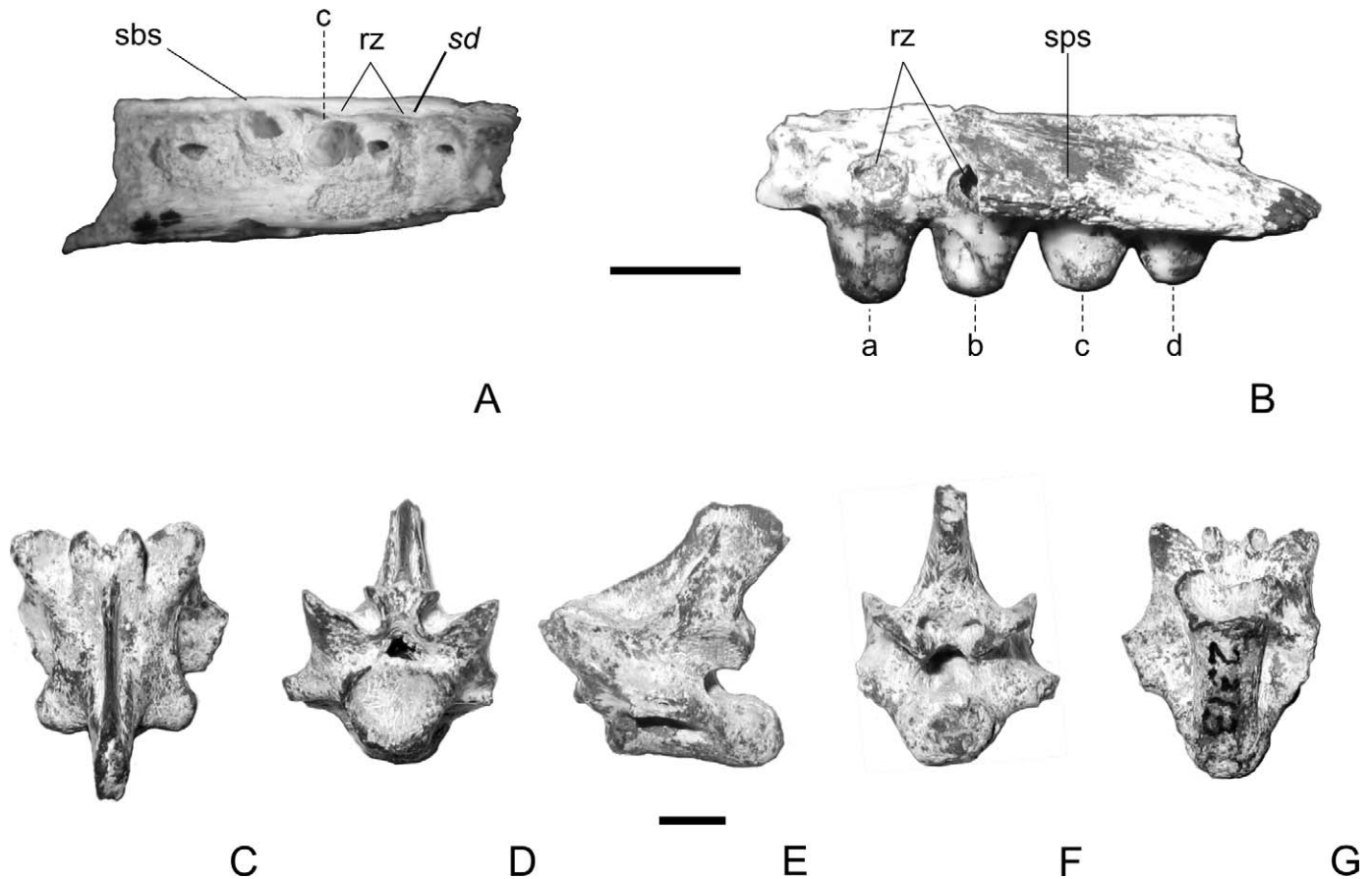
FIG. 2. *Tupinambis* sp., (A) right dentary in oclusal view (GHUNLPam 22677); (B) right maxilla in lingual view (GHUNLPam 4256); (C–G) caudal vertebra (GHUNLPam 2313) in dorsal (C), anterior (D), lateral (E), posterior (F), and ventral (G) views. Letters (a) to (d) indicate relative tooth positions. Abbreviations: rz, resorption zone; sbs, subdental shelf; sd, sulcus dentalis; sps, supradental shelf. Scale = 5 mm.

backwards. Tooth crowns bearing a central protuberance with a thin mesiodistal apical ridge and with labial and lingual striae that converge at the apex (see Brizuela and Albino, 2010).

Specimen GHUNLPam 19874/42 consists of two incomplete articulated vertebrae. Only the posterior part of the anterior vertebra is preserved, articulating with the anterior half of the next vertebra whose posterior half is missing. Neural spines missing from both vertebrae. Zygosphene and zygantrum well-developed. Prezygapophyses short, slightly inclined from the horizontal plane and oriented anteriorly. Prezygapophyseal process absent. Transverse processes lie ventral to prezygapophyses of the posterior vertebra; relatively short and with moderate dorsoventral development, bearing the synapophyses at the distal end. Vertebral centrum ventrally conical and posteriorly truncated bearing a broad, poorly defined sagittal ridge. Cotyle and condyle transversally oval. Condyle preceded by a well-defined precondylar neck and with minor axis inclined from the vertical.

The vertebra GHUNLPam 2313 is almost completely preserved (Fig. 2C–G). Large, high, and long vertebra, broader anteriorly than posteriorly. Neural spine tall, proximally long, but anteriorly thin and posteriorly thick. Distally, it becomes shorter and strongly inclined posteriorly so as to surpass the posterior margin of neural arch, reaching level of condyle. Neural canal small and triangular. Neural arch long, with low roof. Zygosphene well-developed, narrower than cotyle; with an anterior margin strongly notched at the middle and articular surfaces oriented anteriorly and inclined with respect to the

horizontal. Zygantra small but quite distinguishable from one another. Prezygapophyses arise in a very elevated position, at level of the dorsal half of neural canal. Prezygapophyses well inclined with respect to the horizontal plane with their ends slightly surpassing level of zygosphene roof. Prezygapophyseal surfaces large and oriented anterolaterally. Prezygapophyseal process absent. Postzygapophyses smaller than prezygapophyses, strongly inclined with respect to the horizontal plane and oriented laterally. Vertebral centrum cylindrical, long and narrow, with almost parallel sides and flat ventral surface. Precondylar neck present, but eroded. Cotyle and condyle large and almost circular. Cotyle clearly exposed ventrally. Smaller axis of condyle strongly inclined with respect to the transverse plane, being little visible in ventral view. Transverse processes, as inferred by proximal portions, well developed and dorsoventrally compressed. Distal ends of transverse processes not preserved.

Comments.—The more recent phylogenetic analyses of Squamata (e.g., Gauthier et al., 2012) do not recover synapomorphies from the mandible of Tupinambinae or Teiinae Teiidae. Nonetheless, in more-circumscribed analyses (Nydam et al., 2007), Teiidae subfamilies are characterized at the dentary level. In the studied fossil dentary, the large articular surface for the splenial, which extends well anteriorly to the entrance foramen of the lower alveolar canal, indicates the presence of a hypertrophied splenial. This character, together with the presence of abundant basal cementum on the teeth and the deep subcircular resorption zones observed on both dentary
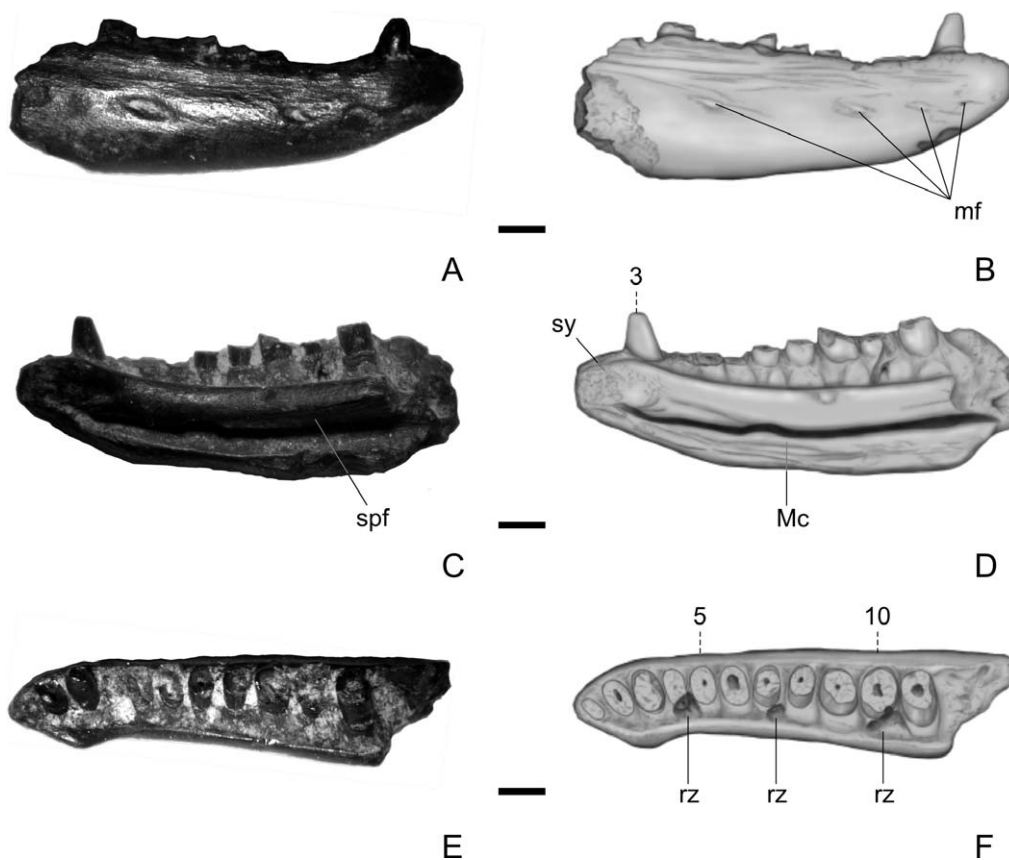
Fig. 3. "Cnemidophorinae," right dentary (GHUNLPam 21745), in labial (A,B), lingual (C,D), and occlusal (E,F) views. Numbers indicate absolute tooth positions. Abbreviations: Mc, Meckel's groove; mf, mental foramen; rz, resorption zone; spf, splenial articulation facet; sy, symphysis. Scale = 1 mm.

and maxilla, is characteristic of both Borioteiioidea and Teiidae (Nydam et al., 2007). Both clades have been traditionally considered closely related (e.g., Estes 1983). However, the Borioteiioidea (=Polyglyphanodontia, Estes, 1983) have more recently been placed phylogeneticaly further away from the Teiioidea (Gymnophthalmidae + Teiidae) (Nydam and Caldwell, 2008; Gauthier et al., 2012), hence the similarities among them are more likely to be convergences.

Among Teiidae, the amount of basal cementum observed in the studied fossils is similar to the condition present in the Tupinambinae genera *Crocodilurus* and *Tupinambis* (Nydam and Cifelli, 2002; S. Brizuela, pers. obs.). Robust and large teeth that are blunt and broad in cross section (i.e., molariform) occur in *Tupinambis* (Brizuela and Albino, 2010). Smoothly grooved teeth with grooves converging onto a central protuberance and a mesiodistal ridge on the occlusal surface, as in specimen GHUNLPam 4256, is characteristic of large specimens of this genus (Brizuela and Albino, 2010). With respect to species identification, it is only possible to exclude *Tupinambis longilineus* and *Tupinambis quadrilineatus* because they lack molariform dentition (Ávila-Pires, 1995; Brizuela and Albino, 2010).

The vertebrae share with members of the family Teiidae the possession of well-developed zygosphene-zygantrum articulation, deeply notched anterior margin of zygosphene, absence of prezygapophyseal process, and well-defined precondylar neck (Hoffstetter and Gasc, 1969). The dorsal vertebrae of teiids are characterized by having conical and posteriorly truncated centrum and oval, dorsoventrally compressed cotyle and condyle, as observed in specimen GHUNLPam 19874/42. In

the caudal vertebrae the centra are cylindrical and the cotyle and condyle are approximately circular, as in specimen GHUNLPam 2313. The lack of an autotomy plane indicates that this last vertebra corresponds to the proximal caudal region. Among members of the family Teiidae, only species of the subfamily Tupinambinae have a weakly developed sagittal ridge on the ventral surface of the dorsal vertebrae, such as in specimen GHUNLPam 19874/42. When we compared our new material to recent material (Appendix 1), both vertebrae are only consistent with the morphology and size of *Tupinambis* vertebrae from the respective column regions.

Teiinae Presch 1974
"CNEMIDOPHORINAE"
Genus and species indeterminate
Figure 3

Referred Specimen.—Cerro La Bota Locality: GHUNLPam 21745, incomplete right dentary.

Description.—The fossil specimen is the anterior half of a right dentary (Fig. 3). Low dentary, with smooth labial face bearing four mental foramina. Subdental ridge moderately developed, bearing articular surface for splenial. Dorsal and ventral margins of dentary almost parallel from anterior tip to the level of the sixth tooth position. Meckelian groove opened medially and extended anteriorly ventral to the symphysis. Exposure of Meckelian groove not very wide in the preserved portion. Anterior ventral margin of dentary curved medially, further restricting Meckelian groove in this area. Dental series limited
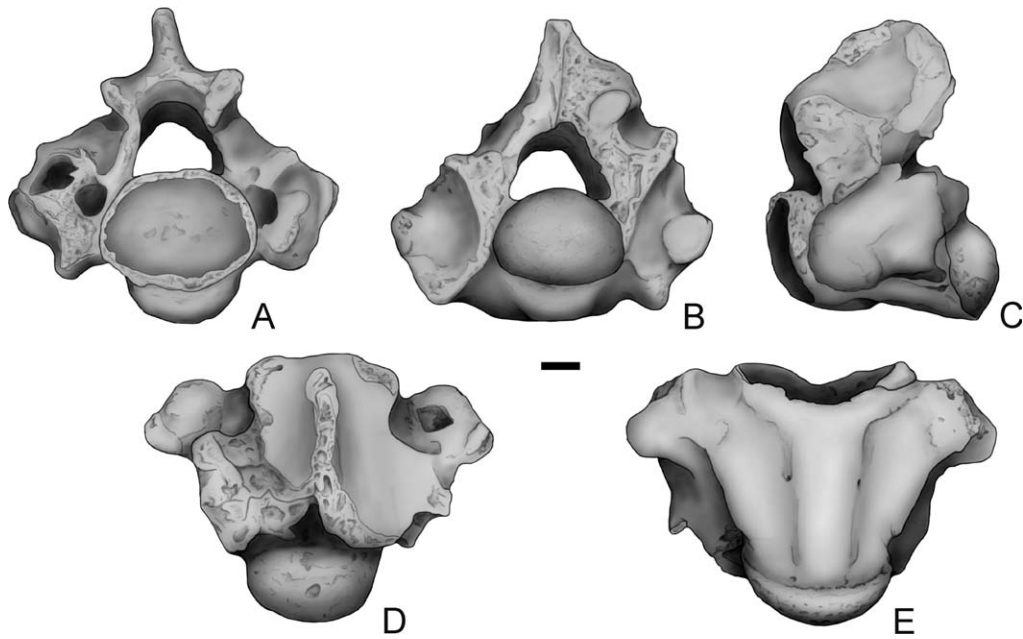
FIG. 4. Boidae, vertebra (GHUNLPam 8888/1) in anterior (A), posterior (B), lateral (C), dorsal (D), and ventral (E) views. Scale = 1 mm.

lingually by a poorly defined sulcus dentalis. Eleven functional tooth positions preserved. Third tooth almost completely preserved while only bases of remaining teeth are present. Teeth show subpleurodont implantation and basal deposition of cementum, which does not obscure the interdental septa. Tooth bases closely spaced; six anterior tooth bases slightly compressed mesodistally whereas posterior bases more circular in cross section. Third tooth unicuspidate, large, robust, and straight, with its tip broken. Three deep, subcircular, and empty resorption zones present.

Comments.—The anteriorly extended splenial, inferred from the articulation surface of the dentary in addition to the deep subcircular resorption zones and the subpleurodont implantation, are characteristics observed in both Teiidae and Borioteiioidea (Nydam et al., 2007). According to other authors and our own observations, members of the subfamily Teiinae differ from those of the subfamily Tupinambinae by having an anteriorly restricted Meckelian groove (Denton and O'Neill, 1995; Nydam and Cifelli, 2002; Nydam et al., 2007), as in the case of the specimen studied here. Furthermore, the Meckelian groove of the specimen continues ventrally to the mandibular symphysis, as observed in members of the subfamily Teiinae, whereas in Tupinambinae this groove ends at the symphysis itself. Though the anterior restriction of the Meckel's groove and the ventral extension of the symphysis might be plesiomorphies, they have not been observed in Tupinambinae specimens. Unfortunately, Teiinae have not been characterized by any synapomorphy in the anterior end of the dentary (e.g., Gautier et al., 2012); hence, the assignation of the dentary here described to Teiinae is based on the former stated features and overall similarity with the available extant specimens here compared.

The teeth of the fossil specimen have a moderate deposit of basal cementum. Among Teiinae, this condition is similar to that occurring in the informal group of the "cnemidophorines" ("*Ameiva*," *Aspidoscelis*, "*Cnemidophorus*," and *Kentropyx*), whereas the other genera of this subfamily (*Teius* and *Dicrodon*) have a much greater amount of cementum that completely covers the interdental septa (pseudothecodont condition of Denton and

O'Neill, 1995; Nydam and Cifelli, 2002; Nydam et al., 2007). In addition, the terminal portion of Meckelian groove in this specimen is ventrally limited by the medial curvature of the dentary. This condition is shared by the majority of "cnemidophorines." It is not possible to assign the fossil to any "cnemidophorine" genus; however, in the comparison with available material of living "cnemidophorine" genera (Appendix 1), the size of the dentary is compatible with those of the species of "*Ameiva*" and *Kentropyx*.

SERPENTES Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Macrostomata Müller, 1831
Boidae Gray, 1825
Boinae Gray, 1825
Genus and species indeterminate
Figure 4

Referred Specimen.—Cerro Patagua Locality: GHUNLPam 8888/1, isolated trunk vertebra.

Description.—Poorly preserved trunk vertebra lacking zygapophyses and with posterior half of neural arch and spine missing (Fig. 4). Vertebra robust, although small, wide, short, and high. Anterior part of neural spine shows that it was relatively low. Neural arch mostly broken but high in lateral and posterior view, bearing lateral foramen on both sides. Interzygapophyseal ridge well defined. Zygosphene moderately high, almost as wide as the cotyle, with its roof slightly elevated in the middle in anterior view and the anterior margin straight in dorsal view. Neural canal relatively large, high, and triangular in cross section. Vertebral centrum short (cl/naw < 1) and widened anteriorly. Subcentral ridges well defined and anteriorly divergent. Subcentral foramina small, located at both sides of a broad, flat, and poorly defined haemal keel. Precondylar constriction well developed. Cotyle and condyle large, transversely oval. Paracotylar foramina absent. Syna-
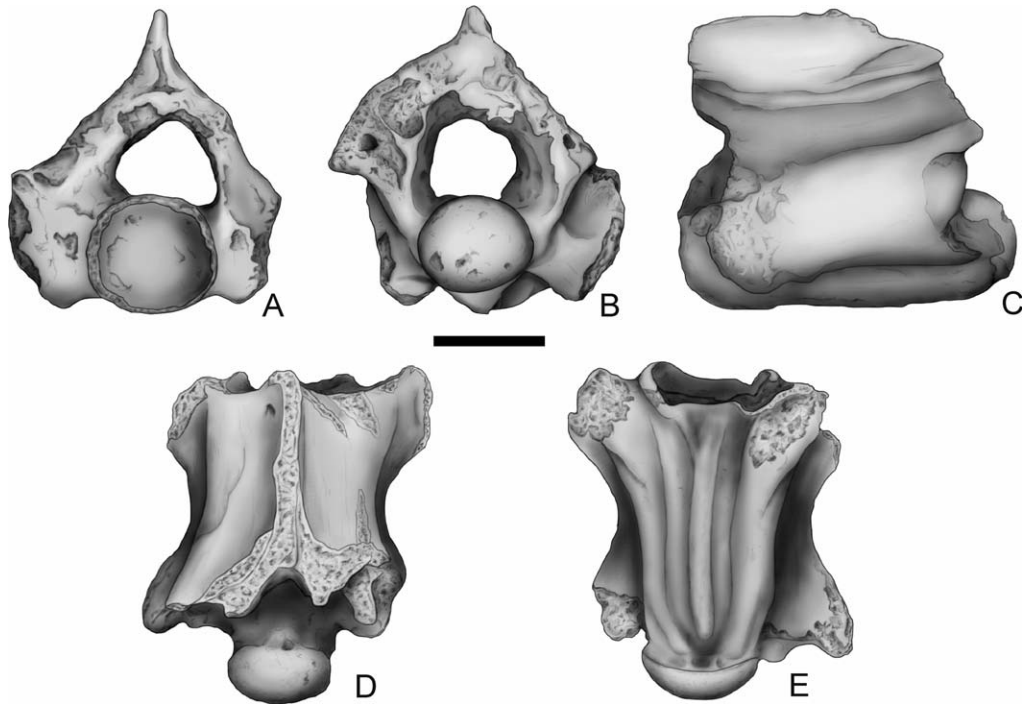
Fɪɢ. 5. "Colubridae," vertebra (GHUNLPam 6732–2) in anterior (A), posterior (B), lateral (C), dorsal (D), and ventral (E) views. Scale = 1 mm.

pophyses elevated, not surpassing lower margin of cotyle and with distinct diapophyseal and parapophyseal surfaces.

Comments.—The combination of features observed in this vertebra is entirely consistent with middle and posterior vertebrae of boid snakes (Rage, 1984, 2001; Holman, 2000; Lee and Scanlon, 2002): it is short, wide, and high, massively built; the neural arch was nondepressed; the lateral and subcentral foramina are present; the ventral surface of the centrum lacks hypapophysis; the precondylar constriction is well developed; and the vertebral centrum is shorter than the width of the neural arch. Trunk vertebrae of Erycinae are distinguished from those of other boids because the neural arches are depressed (Rage, 1984), which contrasts with the studied specimen. Trunk vertebrae of boas and pythons are homogeneous in overall morphology (Rage, 2001; Szyndlar and Rage, 2003). However, paracotylar foramina are absent in all pythons and in the extant boine genera *Eunectes*, *Epicrates*, and most *Corallus* species (Kluge, 1991; Hsiou and Albino, 2009) but they are always present in *Boa*. Therefore, the fossil vertebra can be exclude from this last genus. Zygosphene without a vertical median ridge, forming a distant prominence in dorsal view, absence of small parazygantral foramina, haemal keel not well defined and not protected below centrum in the posterior part, and small size of the vertebrae clearly argue against an assignment to Pythoninae (Scanlon and Mackness, 2001). Among the Neotropical boas, the vertebra differs from those of *Eunectes*, *Epicrates*, and *Corallus* by its smaller size, higher position of the synapophyses that do not surpass the lower margin of the cotyle, and zygosphene without median anterior process. Although it is closest in size to *Epicrates*, the lack of a well-developed haemal keel in the fossil vertebra has only been observed in some specimens of *Corallus*. Nevertheless, the vertebra also differs from this genus by a greater differentiation of the diapophyseal and parapophyseal surfaces of the synapophyses. Unfortunately, the poor preservation of the specimen hinders adequate comparison with other fossil boines.

Cᴀᴇɴᴏᴘʜɪᴅɪᴀ Hᴏꜰꜰsᴛᴇᴛᴛᴇʀ, 1939
Colubroidea Oppel, 1811
"Colubridae" Oppel, 1811
Genus and species indeterminate
Figure 5

Referred Specimens.—Caleufú Locality: GHUNLPam 21888/17, a series of articulated trunk vertebrae. Cerro La Bota Locality: GHUNLPam 6732-1 and GHUNLPam 6732-2, two isolated trunk vertebrae.

Description.—GHUNLPam 21888/17 consists of one isolated vertebra and a block comprising a total of six articulated vertebrae in two sections of three vertebrae each. Dorsally, between the two sections, a rib is partially preserved. Isolated vertebra badly preserved, small, elongate, with depressed neural arch. Spine mostly broken, but probably low. Lateral foramen present. Neural canal very large and high. Only the left postzygapophysis is preserved, showing posterolateral orientation. Vertebral centrum long, scarcely widened anteriorly, with well-developed haemal keel that is mostly thin, but widened and flattened posteriorly. Subcentral foramina small and close to the midline. Cotyle small and approximately circular. Paracotylar foramen very small. Synapophyses broken, but ventrally surpassing the lower margin of cotyle; convex diapophyseal surface very prominent in lateral view and distinct from the flat parapophyseal surface. Parapophyseal process absent.

The articulated vertebrae shows the same morphology as the isolated vertebra. Elongated and broad vertebrae, with vertebral centrum longer than width of neural arch (cl/naw $\sim$ 1.2). Neural arch depressed, wider than long (po-po > pr-po), with deep, well-defined interzygapophyseal ridge. Posterior margin of neural arch strongly notched medially in dorsal view. Neural spines broken in all vertebrae but spine bases thin and long, extending from the beginning of the zygosphene to the posterior notch of neural arch. In the anteriormost vertebra, neural spine looks low. Zygosphene wider than cotyle, very thin, and with its

anterior margin slightly convex in dorsal view. Zygapophyses well developed. Prezygapophyseal process broken in almost all the vertebrae; long, clearly visible in dorsal view, and projecting laterally when preserved. One lateral foramen on each lateral wall of neural arch. Neural canal large and high. Vertebral centrum long, narrow, and widened anteriorly. Haemal keel thin but becomes posteriorly wider and flatter, and ends before the base of the condyle. Two more or less defined lateral tuberosities (ventrolateral processes) present anteriorly, ventral to the cotyle. Cotyle almost circular. Synapophyses small and slightly surpassing the ventral margin of cotyle. Convex diapophyseal surface very prominent and parapophyseal surface flat; both separated by a strong constriction.

The material for GHUNLPam 6732-1 is an incomplete vertebra with missing prezygapophyses, postzygapophyses, synapophyses, and zygosphene and with a partially broken neural spine. Very small, delicate, and elongate vertebra, with vertebral centrum much longer than the width of the neural arch (cl/naw = 1.5), narrow, and slightly divergent anteriorly. Cotyle and condyle small and circular. Haemal keel well developed. Moderately developed precondylar constriction. Neural canal relatively large. Well preserved neural spine long, rather low, and thin.

The vertebra of GHUNLPam 6732-2 is small, delicate, with missing left prezygapophysis, right postzygapophysis, neural spine, condyle, and synapophyses (Fig. 5). Neural arch high and long. Large deep foramen present on posterior surface of neural arch, next to the left zygantrum. Section corresponding to this foramen seen on the right side. Zygosphene extremely thin, very wide, surpassing width of cotyle, elevated medially, and with small articular surfaces. Anterior margin of zygosphene slightly sinuous in dorsal view. Prezygapophysis little inclined from the horizontal plane and oriented more anteriorly than laterally. Prezygapophyseal process long, robust, and quite extended laterally beyond the prezygapophyseal surface. Neural canal very large, wide, and high. Vertebral centrum long, narrow, scarcely divergent anteriorly. Haemal keel is like the one in specimen GHUNLPam 6732-1. Cotyle small and round. One paracotylar foramen preserved.

Comments.—Features that characterize colubroids are observed in all the described specimens (Rage, 1984; Holman, 2000; Lee and Scanlon, 2002): vertebrae longer than wide; build delicate; zygosphene slender and with its anterior margin straight or slightly sinuous; neural spine thin; paracotylar foramina present; zygapophyses not strongly inclined from horizontal; prezygapophyseal process prominent; condyle round in posterior outline; cotyle with ventrolateral processes; precondylar constriction moderate; and ventral surface of centrum with a single haemal keel. Within Colubroidea, the condition of very reduced or absent hypapophyses on mid- and posterior trunk vertebrae occurs in paraphyletic "Colubridae."

Considering the difficulty in identifying "colubrid" vertebrae to the genus or species level (Rage, 1984), the great number of species presently inhabiting the Neotropical region, the lack of comparative osteological collections of South American "colubrids" to represent this diversity, and the poor preservation of the material reported here, we cannot identify these specimens beyond family level. However, we note that the specimens in GHUNLPam 6732 are much smaller than the articulated vertebrae (GHUNLPam 21888/17), have a higher neural arch, a more-developed and better-defined haemal keel, and shorter prezygapophyseal process. In addition, these vertebrae have a foramen on the posterior surface of the neural arch near the

zygantrum that is not interpreted here as homologous with the parazygantral foramen. We consider these specimens to represent a taxon different from GHUNLPam 21888/17. Interestingly, they come from a different locality than the rest of "colubrid" remains from the Cerro Azul Formation (see Albino and Montalvo, 2006). On the other hand, the vertebrae of GHUNLPam 21888/17 show no differential characters with respect to "Colubridae" remains described earlier by Albino and Montalvo (2006) from the same locality and stratigraphic level (GHUNLPam 19612/9, GHUNLPam 19937, GHUNLPam 19938).

DISCUSSION

Previous reports about the presence of squamates in the Miocene of South America are numerous and have been revised and expanded recently. These include records from Argentina (Albino et al., 2006; Albino and Montalvo, 2006; Albino, 2011), Colombia (Hecht and LaDuke, 1997; Sullivan and Estes, 1997; Hsiou et al., 2010), Venezuela (Head et al., 2006; Hsiou et al., 2010), and Brazil (Hsiou and Albino, 2009, 2010; Hsiou et al., 2009, 2010). The teiid genus *Tupinambis* is recorded from the lower Miocene onwards, especially in Patagonia (see Albino, 2011). The present report confirms the presence of *Tupinambis* in the upper Miocene of central Argentina (Albino et al., 2006), where the genus is currently represented only by the species *Tupinambis rufescens*. Regarding the Teiinae, the oldest records correspond to findings of "*Cnemidophorus*" in the Miocene of the United States (Estes, 1983). Several species of this genus have been described (see Estes, 1983), but at present the only taxon occurring in North America is the genus *Aspidoscelis*, now separated from "*Cnemidophorus*" (Reeder et al., 2002). The identifications of several of the North American fossils are based on subtle differences in tooth morphology, number of teeth, and bone size, which suggests that a revision is in order. Molecular dating and biogeographical analysis indicate that all extant genera of "cnemidophorines" (except *Aspidoscelis*) evolved in isolation in South America and that most extant genera diversified during the Paleocene, coinciding with the expansion of savannas on this continent (Giugliano et al., 2007). The finding of a "cnemidophorine" in the Cerro Azul Formation of Argentina represents the oldest record of the Teiinae in South America and agrees with the above-mentioned hypothesis. At present, the "cnemidophorines" are diverse and widely distributed in Argentina, including the La Pampa province (Cei, 1986, 1993).

With respect to the snakes, recent phylogenetic analysis indicates that Boinae, in the sense of Kluge (1991), does not constitute a monophyletic group although the Neotropical boas, comprising *Boa*, *Corallus*, *Epicrates*, and *Eunectes* genera are a well-supported clade (Noonan and Chippindale, 2006). However, a number of extinct snakes (known mostly from isolated precloacal vertebrae) have been included in the Boinae, although their affinities with extant booids remain unresolved (see Szyndlar and Rage, 2003). The fossil boid reported here is assigned to the same lineage as the extant Neotropical boas, although the lack of diagnostic vertebral characters exclusive of Boinae (Kluge, 1991) casts doubts on its relationships.

Despite the limitations of the taxonomy, the specimen from Cerro Patagua is significant because it is the first boid recorded in the Cerro Azul Formation and for the upper Miocene of Argentina. Boids have been represented widely in South America since the Paleocene, including extant genera (Rage,

2001; Albino, 2011). In Argentina, most of the Paleocene records come from Patagonian localities, where large and medium-sized boids were recognized (Albino, 1993). In contrast, Miocene Patagonian records all correspond to small snakes, suggesting a temperature drop (Albino, 2012), which is in line with known changes in mean global annual temperatures reported for this epoch (Zachos et al., 2001). At present, no boids occur at the latitude of the La Pampa province because they are confined to the north of 34°S (Giraudo and Scrocchi, 2002). Therefore, the finding in the Cerro Azul Formation in La Pampa province implies that the distribution of boids during the upper Miocene extended further south than its current limit. The posterior retraction to the north would be correlated with the global cooling event (Zachos et al., 2001), which would be expected to cause many ectothermic species to be confined to low latitudes.

The presence of "colubrids" in levels of the Cerro Azul Formation outcropping at Caleufú had already been documented (Albino and Montalvo, 2006). The material reported here includes the distribution of this group in the locality of Cerro La Bota, where it is represented by an undetermined taxon clearly different from the one identified previously in Caleufú. This finding confirms the presence of the group in the late Miocene of central Argentina, with a diversity of at least two different genera. "Colubrids" have been found in South America since the lower Miocene (see Albino, 2011) and, therefore, this record supports the hypothesis of their entrance into South America before the formation of the Isthmus of Panama (Albino, 1989; Albino and Montalvo, 2006). No viperid remains were found among the new material, although they were present in the Cerro Azul Formation at Caleufú (Albino and Montalvo, 2006).

In conclusion, the association of squamates found in the upper Miocene of La Pampa province includes the tupinambine *Tupinambis*, a "cnemidophorine" probably corresponding to "*Ameiva*" or *Kentropyx*, an undetermined boid, undeterminated "colubrids," and a viperid (Albino et al., 2006; Albino and Montalvo, 2006; this paper). Montalvo and Verzi (2004) considered the presence of the mammals Echimyidae (Rodentia) and *Protabrocoma* (Rodentia: Abrocomidae) in most of the faunal associations from the Cerro Azul Formation in La Pampa to suggest that environmental conditions were similar to those of the current Chacoan biogeographical province. These records would be related with the expansion of open environments during the late Miocene (Ortiz Jaureguizar and Cladera 2006, and literature therein). The squamate association listed above is wholly compatible with these interpretations. That is, the taxa that lived in central Argentina during the late Miocene currently inhabit the Chacoan environment. Especially, the recognition of a boid in the late Miocene at higher latitudes than they occur at present day is significant because it is the only taxon currently absent from La Pampa province but represented in the Chaco biome.

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APPENDIX 1—SPECIMENS EXAMINED

Snakes: *Boa constrictor* (FMNH 22362, 211926, 22353; UNMdP-O 44, 45, 46, 47, 49, 50). *Candoia carinata* (FMNH 217065). *Clelia rustica* (UNMdP-O 65). *Corallus caninus* (FMNH 223192). *Corallus cookii* (FMNH 212337). *Epicrates cenchria* (UNMdP-O 42, 43). *Eryx colubrinus* (FMNH 223196). *Eryx johni* (FMNH 31319). *Eunectes murinus* (FMNH 212710). *Eunectes notaeus* (UNMdP-O 48). *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, 60, 63). *Oxyrhopus rhombifer* (UNMdP-O 58). *Phylodryas patagoniensis* (UNMdP-O 55, 56, 64).

"Lizards": *Ameiva ameiva* (NMNH 257529, 257530, 292414, 292419, 290898; UMMZ 149442, 176270). *Ameiva bifrontata* (UMMZ 149443, 149444, 150782). *Ameiva exsul* (UMMZ 292424). *Aspidoscelis calidipes* (UMMZ 149457, 149459, 149460). *Aspidoscelis communis* (UMMZ 149574). *Aspidoscelis cozumela* (UMMZ 149464). *Aspidoscelis deppei* (UMMZ 149551). *Aspidoscelis exsanguis* (UMMZ 149569). *Aspidoscelis sexlineatus* (NMNH 313460). *Ameiva ameiva* (UNNE 1365, 1374). *Ameiva bifrontata* (UMMZ 149444, 149449). *Ameiva exsul* (UMMZ 200865). *Callopistes maculatus* (MNHN-cl-4112, 4113). *Cnemidophorus lacertoides* (UNMdP-O 80). *Cnemidophorus lemniscatus* (UMMZ 189452). *Cnemidophorus longicauda* (UNMdP-O 81). *Cnemidophorus ocellifer* (UMMZ 149522). *Cnemidophorus serranus* (UNMdP-O 82). *Cnemidophorus tergolaevigatus* (UNMdP-O 83). *Dracaena guianensis* (NMNH 220278). *Kentropyx calcarata* (MZUSP 81580, 82978; NMNH 292412). *Kentropyx viridistriga* (UNNE 4647, 1062). *Teius oculatus* (UNNE 4464, 4462). *Teius suquiensis* (UNMdP-O 84, 85). *Teius teyou* (UNNE 1398, 8715). *Tupinambis rufescens* (NMNH 342486). *Tupinambis teguixin* (NMNH 220279; MZUSP 92087, 92149; UMMZ 190109). *Tupinambis duseni* (MZUSP 92131). *Tupinambis merianae* (UMMZ 190109; UNMdP-O 01 to 13, 17 to 20, 25, 32, 33, 35). *Tupinambis quadrilineatus* (MZUSP 84921, 84928). *Tupinambis rufescens* (FML 7545, 7547, 1336, 6859, 2559, 2560; MZUSP 93082, 93083, 93084; NMNH 342486; UNMdP-O 36).