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NEW ELEMENTS OF THE PALEOHERPETOFAUNA OF THE PLEISTOCENE FROM MAR CHIQUITA COUNTY (BUENOS AIRES, ARGENTINA)

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Abstract. Fossils of amphibians and squamates are relatively common in Pliocene–Pleistocene sediments in the southeastern Atlantic coast of Buenos Aires Province (Argentina), particularly in the southern slope of the Tandilia mountain system. These taxa are less known in the northern slope, which in the county of Mar Chiquita are solely represented by one anuran record. Here, new herpetofaunal material is described from Mar Chiquita county in the northern slope of the Tandilia mountain system. These specimens, while few, present an interesting taxonomical and morphological diversity. From the Ensenadan outcrops, amphibians are represented by cf. *Rhinella.* On the other hand, *Stenocercus*, an indeterminate tropidurid, Colubroides, and an indeterminate snake account for the Ensenadan squamates. In the Bonaerian outcrops, squamates are represented by the viperid *Bothrops* and an indeterminate Pleurodont. These latter taxa are also present in the Lujanian with an indeterminate snake. These are the first fossil records of squamates from Mar Chiquita and together with the new and previous amphibian records constitute a herpetological assemblage (*Ceratophrys ornata*, cf. *Rhinella*, *Stenocercus*, and *Bothrops*) that suggests that the paleoclimatic conditions during the Pleistocene of the Pampean region would have been similar to those of the present day. This inference should be considered with caution, since it contradicts those suggested by the mammalian record, which is richer and presents taxonomic identifications that are more precise. Mammalian fossil records indicate a cold and dry glacial Pleistocene interspersed with short, warmer, and more humid periods.

Key words. Ensenadan. Bonaerian. Lujanian. *Rhinella*. *Stenocercus*. *Bothrops*.

Resumen. NUEVOS ELEMENTOS DE LA PALEOHERPETOFAUNA DEL PLEISTOCENO DEL PARTIDO DE MAR CHIQUITA (BUENOS AIRES, ARGENTINA). Fósiles de anfibios y reptiles escamosos son relativamente comunes en los sedimentos del Plioceno–Pleistoceno aflorantes en la costa atlántica de la provincia de Buenos Aires (Argentina), en particular en la ladera sur del sistema serrano de Tandilia. Estos grupos son menos conocidos en los sedimentos de la ladera norte, donde en el partido de Mar Chiquita están representados únicamente por un registro de anuro. Aquí se describen nuevos materiales de la herpetofauna del Pleistoceno de dicho partido. Estos materiales, restringidos a unos pocos especímenes, presentan una interesante diversidad anatómica y taxonómica. En el Ensenadense se reconoce la presencia del anfibio cf. *Rhinella*. A su vez, los reptiles escamosos del Ensenadense están representados por *Stenocercus*, un tropidúrido indeterminado, Colubroides y una serpiente indeterminada, mientras que en el Bonaerense fue posible reconocer al vipérido *Bothrops* y un Pleurodonta indeterminado. Estos últimos y una serpiente indeterminada están presentes en el Lujanense. Estos registros de reptiles escamosos fósiles son los primeros para el partido de Mar Chiquita y, en conjunto con los anfibios previamente y aquí descritos, constituyen un ensamble herpetológico (*Ceratophrys ornata*, cf. *Rhinella*, *Stenocercus* y *Bothrops*) que sugiere que las condiciones paleoclimáticas durante el Pleistoceno en la región Pampeana habrían sido similar a las actuales. Esta inferencia debe ser considerada con cautela, ya que contradice la visión de un Pleistoceno frío y seco intercalado con periodos cortos más cálidos y húmedos inferido a partir del registro de mamíferos, el cual es más abundante y presenta identificaciones más precisas.

Palabras clave. Ensenadense. Bonaerense. Lujanense. *Rhinella*. *Stenocercus*. *Bothrops*.

THE NEOGENE sediments of Buenos Aires Province have provided numerous herpetofaunal fossil records (for example see Albino & Brizuela, 2014a; Albino, 2020; Gómez & Turazzini, 2021; Báez & Desojo, 2022). Many of these fossils come from scattered localities, but there are two main exceptions from where several anuran and squamates fossils have been reported. These are Farola Monte Hermoso and the geographically more extended area of the southeastern coastal cliffs of Buenos Aires Province.

In the southern part of the Buenos Aires Province is the Farola Monte Hermoso area, where Late Miocene–Early Pliocene sediments of the Montehermosan stage are exposed (see Cione *et al.*, 2015). From these outcrops, several anuran amphibians have been recognized: *Ceratophrys* (*Ceratophrys ameghinorum*), *Lepidobatrachus* (*Lepidobatrachus australis* and *Lepidobatrachus* sp.), *Rhinella* cf. *dipcha*, and *Leptodactylus* sp. (Báez, 1986; Fernicola, 2001; Tomassini *et al.*, 2011; Gómez *et al.*, 2013; Nicoli, 2015). Squamates are represented in the Farola Monte Hermoso area by tupinambine teiids (*Callopistes bicuspidatus* and *Tupinambis* s.l. = *Salvator* and *Tupinambis*) (Albino *et al.*, 2009; Brizuela & Albino, 2017) and several snakes, the latter including a Boidae booid (?*Boa*) (Albino, 1992) and Caenophidia (Colubroids aff. *Bothrops*, and *Bothrops* aff. *alternatus*) (Albino, 1989, 1992; Aranciaga-Rolando *et al.*, 2021). The turtle ?*Chelonoidis australis* has also been recognized in Monte Hermoso (de la Fuente, 1997). Lastly, a younger (Pleistocene–Early Holocene) squamate assemblage (Liolaemidae, Gekkota, and Teiinae) has also been described from sediments of the south of Buenos Aires Province near Farola Monte Hermoso (Albino, 2005).

In the southeastern Atlantic coast of Buenos Aires Province, along the counties of Mar Chiquita, General Pueyrredon, and General Alvarado (Fig. 1), an important sequence of Pleistocene–Holocene sediments is exposed and has provided many herpetological fossil records. This area corresponds to the end of the Tandilia mountain system before reaching the ocean. There, on its coastal area, its northern and southern slopes can be differentiated at Mar del Plata city in General Pueyrredon county (Fig. 1). The sediments of the southern slope of the Tandilia mountain system represent a larger temporal range (Pliocene–Holocene) than those of the northern slope (Pleistocene–Holocene). Traditionally, the southern slope has received more attention with several amphibians and squamate remains described (Donadío, 1982; Albino &

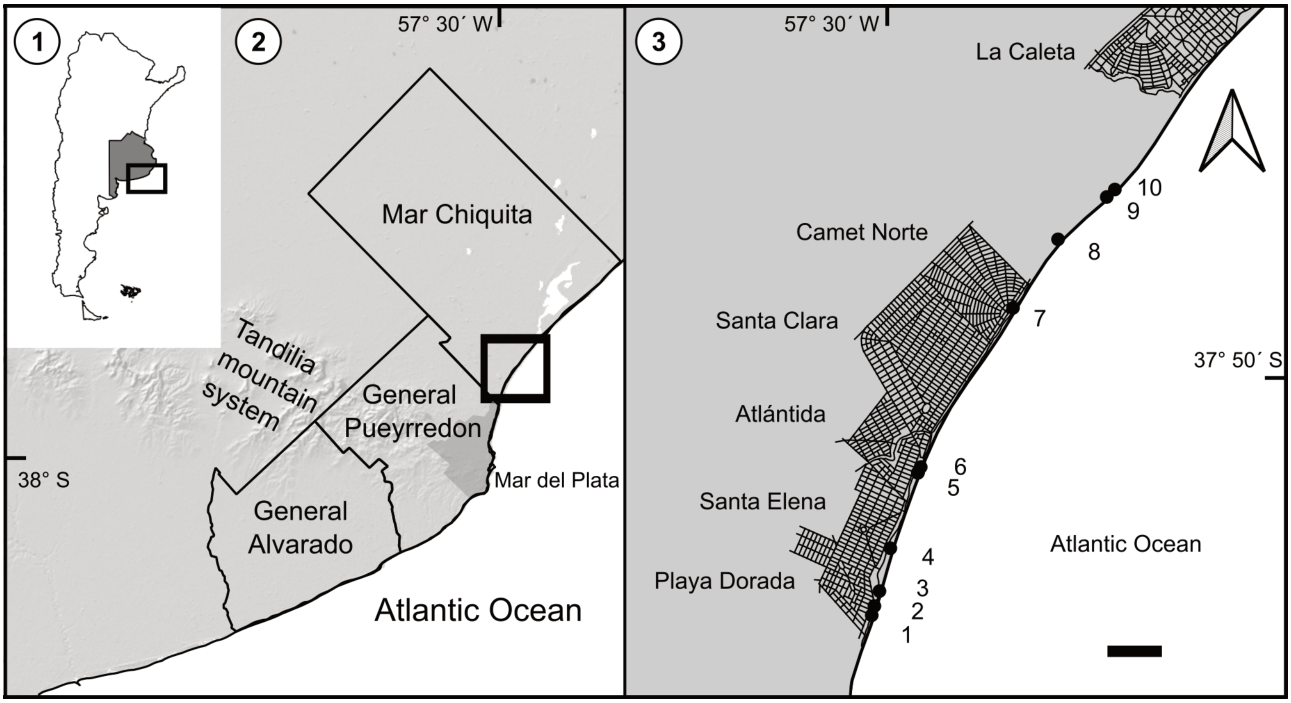

Figure 1. Location map. **1,** Argentina, Buenos Aires Province in gray; **2,** Close up of the Tandilia mountain system and Mar Chiquita, General Pueyrredon and General Alvarado counties. Map based on ESRI shaded relief; **3,** Atlantic coast of Mar Chiquita county and geographical occurrence of the specimens described. References: 1, **MMSCM 2017**; 2, **MMSCM 2023**; 3, **MMSCM 2027**; 4, **MMSCM 2029**; 5, **MMSCM 2037** and **2039**; 6, **MMSCM 2025**; 7, **MMSCM 2021**; 8, **MMSCM 2019**; 9, **MMSCM 2035**; 10, **MMSCM 2033**. Scale= 1 km.

Quintana, 1992; Albino, 1995; Fernicola, 2001; Scanferla *et al.*, 2005; Báez *et al.*, 2008; Brizuela & Albino, 2012; Pérez-Ben *et al.*, 2014, 2019a). Nonetheless, there are several anuran and squamates records from the northern slope. These include the anurans *Ceratophrys* (several forms) (Agnolin, 2005; Brizuela & Tassara, 2011; Gómez & Turazzini, 2021), *Odontophrynus* (*O.* aff. *americanus* or aff. *cordobae*) (Turazzini *et al.*, 2016), and many indeterminate anuran elements, all from General Pueyrredon north of Mar del Plata (Pardiñas *et al.*, 2004; Taglioretti *et al.*, 2009; Brizuela & Tassara, 2011). Squamates have also been reported in the Pleistocene of General Pueyrredon, like the legless lizard *Ophiodes* and an indeterminate colubroid (similar to *Erythrolamprus*) (Brizuela *et al.*, 2015; Brizuela & Tassara, 2016).

Continuous and intensive prospecting of the coastal cliffs of Mar Chiquita, General Alvarado, and General Pueyrredon counties has produce many new fossils. Although the prospecting effort was put on small vertebrates, in a five year period (2018–2022) only a very small fraction of the recovered specimens were identified as herpetofaunal elements (75 specimens out of 1,943: 2.57% to amphibians and 1.34% to squamates). At the moment, it has not been justified nor have we tried to test intensive methods in the area. Despite these low proportions, the new fossils represent additions to the amphibian fauna previously described for Mar Chiquita county, as well as the first records of squamates for the county. Hence, the main objective of this contribution is to describe these herpetofaunal elements recovered from the Pleistocene sediments at Mar Chiquita county and integrate them with those previously described for the southeastern Atlantic coast of Buenos Aires Province (Mar Chiquita, General Alvarado, and General Pueyrredon counties).

MATERIAL AND METHODS

All fossils described are from Mar Chiquita county (Fig. 1) and are deposited at the Museo Municipal de Ciencias Naturales Pachamama (MMSCM) of Santa Clara del Mar. Reference specimens are from the Colección Herpetológica of the Universidad Nacional de Mar del Plata, Sección Osteología (UNMdP-O). Additionally, Digital Morphology online library (DigiMorph, 2022) specimens were consulted, as well as references from the literature. Specimens were either photographed or scanned at the Scanning Electron Microscope (SEM) at the Laboratorio de Microscopía Electrónica of the Universidad Nacional de Mar del Plata.

Squamate systematic follows Burbrink *et al.* (2020), while open nomenclature follows recommendations of Sigovini *et al.* (2016). Osteological terminology follows Oelrich (1956), Rage & Augé (2010), Smith & Gauthier (2013), and Auffenberg (1963), whereas dental nomenclature follows Bertin *et al.* (2018). Absolute tooth positions were indicated with Roman numbers, while relative positions were indicated with letters. When quantitative character definitions were used we followed LaDuke (1991) and the more recent work of Georgalis *et al.* (2021). Measures were taken with the image processing program Fiji (Schindelin *et al.*, 2012). We followed Cione *et al.* (2015) chronostratigraphic arrangement.

Abbreviations. asl, angulosplenial length; **cl,** centrum length; **conh,** condyle height; **conw,** condyle width; **cth,** cotyle height; **ctw,** cotyle width; **h,** vertebra height; **hw,** hypapophysis width; **ml,** maximum length; **mw,** maximum width; **naw,** neural arch width; **nawp,** neural arch width posterior to prezygapophyses; **nch,** neural canal height; **nh,** neural spine height; **nlu,** neural spine length at its dorsal edge; **pol,** postzygapophyseal length; **po-po,** postzygapophyseal distance; **po-pr,** interzygapophysial distance; **pow,** postzygapophyseal width; **pr-pr,** prezygapophyseal distance; **prl,** prezygapophysis process length (= APL, accessory process length of LaDuke, 1991); **prw,** prezygapophysis process width (= APD, accessory process diameter of LaDuke, 1991); **pzl,** prezygapophysis length (LPr length of prezygapophysis of LaDuke, 1991); **pzw,** prezygapophysis width (WPr, width of prezygapophysis of LaDuke, 1991); **skl,** skull length; **svl,** snout-vent length; **TL,** total length; **vr,** vaulting ratio; **z,** angle of zygosphene articulation facet; **zsh,** zygosphene height; **zsw,** zygosphene width; **zt,** zygosphene thickness; **zyp,** greatest distance between a lateral tangent to zygapophyses and neural arch.

GEOLOGICAL SETTING

The fossils presented here were recovered from the coastal cliffs of Mar Chiquita county, more specifically from the localities from Playa Dorada to north of Camet Norte, which are north of Mar del Plata city (Fig. 1). These sediments correspond the northern slope of the Tandilia mountain system where the Pleistocene sediments sink towards the north (Mar de Cobo) as suggested by paleomagnetic data and where the Brunhes/Matuyama reversal (0.78 Ma) is detected only south of Santa Clara del Mar (Bidegain *et al.*, 2005). Consistently, biostratigraphic data indicate the presences in the area of the Ensenadan, Bonaerian, and Lujanian stages (Pardiñas, 2004; Pardiñas *et al.*, 2004; Prevosti *et al.*, 2004; Isla *et al.*, 2015).

RESULTS

Ensenadan herpetofauna from Mar Chiquita county

The Ensenadan fossils described here were recovered in different localities within the base of Unit 3 of Bidegain *et al.* (2005) (Buenos Aires Formation, < 0.78 Ma, Mid–Late Pleistocene). Biostratigraphic (Verzi *et al.*, 2004) and paleomagnetic (Bidegain *et al.*, 2005) studies in the area allowed narrowing the age of these fossils between 0.4–0.78 Ma, Mid Pleistocene, Ensenadan stage.

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813
NEOBATRACHIA Reig, 1958
BUFONIDAE Gray, 1825

Genus ***Rhinella*** Fitzinger, 1826

Type species. *Rhinella proboscidea* Spix, 1824. Holocene, Amazon basin Brazil, Colombia, Ecuador, and Peru.

cf. ***Rhinella*** sp.
Figure 2

Referred material. MMSCM 2027, left angulosplenial; MMSCM 2039a, right radioulna and seven associated fragments which include a humeral head (MMSCM 2039b) and six autopodial elements (MMSCM 2039c–h).

Geographic occurrence. MMSCM 2027, Playa Dorada (37° 52′ 32.03″ S; 57° 30′ 53.21″ W) (= Los Cantiles of Isla *et al.*, 2015). MMSCM 2039, Atlántida (37° 51′ 17.2″ S; 57° 30′ 27.07″ W). Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Description. MMSCM 2027 is a large angulosplenial (ml= 24.82 mm) with a coronoid process extending for one fourth of the total length (Fig. 2.1–2.2). The coronoid process is simple (*i.e.*, lacks processes and notches), compressed, subrectangular/trapezoidal in outline, and relatively low and vertical (*i.e.*, blade-like). Anterior to the coronoid process, the angulosplenial is cylindrical, somewhat compressed anteriorly. The Meckelian groove is large, laterally exposed anteriorly and more dorsolaterally exposed posteriorly.

The radioulna MMSCM 2039 is large (ml= 23 mm; width at the base of olecranon= 6.35 mm) and robust, with a developed olecranon (Fig. 2.3–2.4). The distal epiphyses are not preserved. In anterior view the olecranon and the capitulum form an obtuse angle. Posteriorly, below this articulation, is a small, shallow subcircular depression

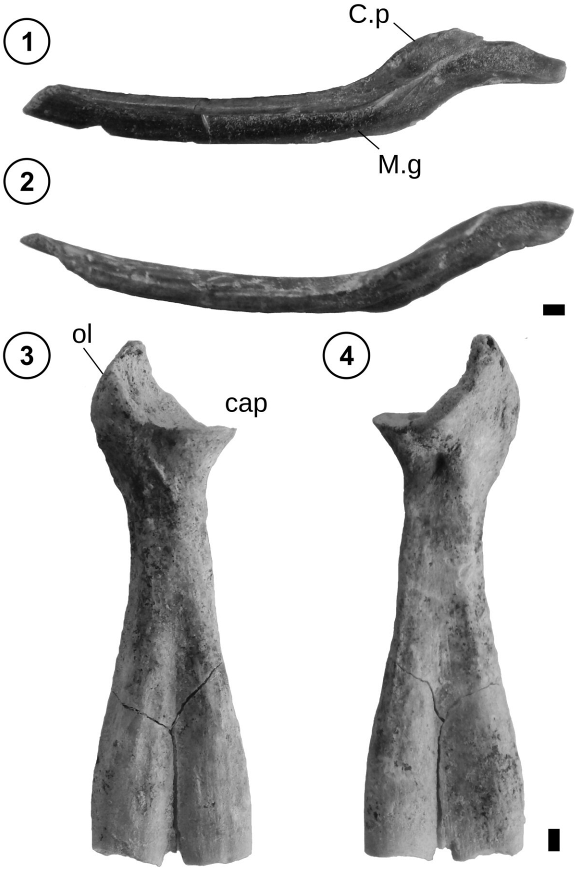

Figure 2. Ensenadan stage amphibian remains from Mar Chiquita county, Buenos Aires, Argentina. Cf. ***Rhinella***, **MMSCM 2027** angulosplenial in **1,** lateral and **2,** dorsal views; **MMSCM 2039** radioulna in **3,** anterior and **4,** posterior views. Abbreviations: **cap**, *capitulum*; **C.p**, coronoid process; **M.g**, Meckelian groove; **ol**, olecranon. Scale= 1 mm.

between the radial and ulnar areas. Below the humeral articulation, the radioulna is constricted and its components (radio and ulna) cannot be differentiated until the lower half of the bone where the *sulcus intermedius* becomes well-developed. At either side of the *sulcus intermedius* both elements of the radioulna are equally expanded. The ulnar component presents a marked proximodistal ridge. At the distal end, the section of the ulnar component is more depressed than that of the radial component.

Associated to the radioulna, seven additional small fragments were recovered, one representing a possible head of humerus and other elements of the autopodium.

Comments. The angulosplenial, compared to those of the available reference material, presents dimensions of a large anuran, between *Rhinella arenarum* (UNMdP-O 142, asl= 17.88 mm, svl= 59 mm), *Phyllomedusa sauvagii* (UNMdP-O 143, asl= 20.44 mm, svl= 81 mm), and *Rhinella diptycha* (UNMdP-O 144, asl= 32.29 mm, skl= 35.24 mm). The two most commonly used characters to describe the angulosplenial among anurans are the Meckelian groove morphology and topology and the coronoid process, both preserved in MMSCM 2027. The coronoid process in *Phyllomedusa* is small, short, compressed, and close to semi-spherical in shape (Ruiz-Monachesi *et al.*, 2016), unlike that of MMSCM 2027 which is trapezoidal as commonly observed in *Leptodactylus* and *Rhinella*, although shorter in the former (Perotti, 2001; Ponssa, 2006). The deep and open anterior Meckelian groove of the fossil is different form the sutured or fused to the dentary present in most Ceratophryidae (Gómez & Turazzini, 2021). The vertical condition of the coronoid process further differentiates MMSCM 2027 from *Ceratophrys* in which this process is horizontal (Gómez & Turazzini, 2021). Overall, the morphology of MMSCM 2027 resembles that of *Rhinella.*

Among anurans the radioulna presents a low anatomical information content (Bastir *et al.*, 2014; Nicoli, 2014; Pérez-Ben *et al.*, 2019b), as is also the case of the angulosplenial. The dimension of MMSCM 2039a is also of a large anuran, close in size to *Rhinella diptycha* (ml= 27.84 mm). The radioulna is elongated, differing from that of the Ceratophryidae whose radioulnar length is less than three times its width (Nicoli, 2014). Unfortunately, the main elements recovered are poorly informative. However, size and general morphology are consistent with *Rhinella.* Therefore, for the moment, they are assigned as cf. *Rhinella*.

This record of cf. *Rhinella* is added to those of previously recognized anurans from the northern slope of the Tandilia mountain system, which include *Ceratophrys ornata* and *Ceratophrys* cf. *ornata* (Agnolin, 2005; Gómez & Turazzini, 2021), *Odontophrynus* (Turazzini *et al.*, 2016), and indeterminate anurans (Pardiñas *et al.*, 2004; Taglioretti *et al.*, 2009; Brizuela & Tassara, 2011). While there are no angulosplenials nor radioulnas among the anuran elements mentioned by Brizuela & Tassara (2011), the elements mentioned there are smaller than MMSCM 2027 and 2039a, suggesting a different smaller taxon.

SQUAMATA Oppel, 1811
IGUANIA Cope, 1864
PLEURODONTA Cope, 1864
TROPIDURIDAE Bell, 1843

Stenocercus Duméril & Bibron, 1837

Type species. *Stenocercus roseiventris* Duméril & Bibron, 1837. Holocene, Bolivia, Brazil, Peru, and northwest of Argentina.

Stenocercus sp.
Figure 3.1–3.4

Referred material. MMSCM 2017, right dentary with 19 tooth positions preserved (three missing and four broken teeth) with the anterior part of the surangular (TL= 9.12 mm) articulated; MMSCM 2025, partial left dentary with 21 tooth positions preserved (eight missing and four broken teeth) (TL= 9.42 mm).

Geographic occurrence. MMSCM 2017, Playa Dorada (37° 52′ 44.85″ S; 57° 30′ 57.99″ W) (= Los Cantiles of Isla *et al.*, 2015). MMSCM 2025, Atlántida (37° 51′ 13.74″ S; 57° 30′ 25.19″ W). Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Description. The dentaries are delicate, long, and overall shallow (*i.e.*, little dorsoventral development). Labially (Fig. 3.1, 3.3) they are smooth and unornamented, shallower anteriorly and with more dorsoventral development posteriorly. On the lateral surface, the slightly convex anterior area can be differentiated form the ventrolaterally orientated flat posterior area. The transition between these areas is a subtle medial fold that develops anteroventrally from the coronoid dorsal process articulation facet. Five (below tooth positions I, III, IV+V, VII, and IX) and four (II, V, VI–VII, and IX) mental foramina are present in MMSCM 2017 and MMSCM 2025, respectively. Posteriorly, ventral to the articulation facet for the coronoid dorsal process, the dentaries are smooth with no trace of an articulation facet for the anterolateral process of the coronoid.

Medially (Fig. 3.2, 3.4), Meckel's canal is closed and fused (up to tooth position XVI in both specimens), with a short anterior aperture (reaching tooth position IV or III in MMSCM 2017 and MMSCM 2025, respectively). The fusion of the upper and lower Meckelian lips establish a long and low "Meckelian cylinder" (= part of the canal closed, sutured or fused), with no crest on the suprameckelian lip's dorsal portion lingual to the dental series. No *sulcus dentalis* is evident either. Overall, in medial view, the Meckelian cylinder presents a parallel-subparallel outline, whereas the lateral parapet (= alveolar surface) gains height posteriorly reaching the maximum development at tooth position XVII (MMSCM 2025) and then decreasing rapidly towards the coronoid articulation. Posteriorly, the splenial articulation advances shortly to tooth position XVI (in both specimens), indicating the presence of a short splenial (close to 1/6 of the length of the dental series). In MMSCM 2017, ventral to the last two tooth positions (XVIII and XIX) and upon the suprameckelian lip is the articulation facet for the anteromedial process of the coronoid.

Dentaries preserve 19 (MMSCM 2017) and 21 (MMSCM 2025) functional tooth positions. Tooth implantation is pleurodont, with a developed lateral parapet to which teeth are attached from 1/2 to 2/3–3/4 of their height in an anteroposterior direction. In MMSCM 2017 teeth I, II, IV, and V are broken, while IX, XI, and XVII are missing. In MMSCM 2025 teeth I, II, IV, VI, XI, XIII, XIV, and XVIII are missing, whereas only the base of teeth III, V, VII, and VIII are preserved. The remaining teeth in both dentaries specimens are complete. Resorption zones, with different degrees of development, are present lingual to teeth III, V, VII, X, XII, and XV in MMSCM 2017 and V, VII, X, XII, and XIV in MMSCM 2025. In MMSCM 2017, where the dental series is more complete (Fig. 3.2), the anterior teeth (up to tooth XII) are lower than the posterior ones (although the last teeth are short but situated higher on the lateral parapet). Dentition is homodont, with tricuspid teeth. The base of the teeth are mesiodistally compressed and labiolingually developed, while the apical end is compressed with three mesiodistally aligned cusps. The central cusp is the dominant one, it is differentiated from the smaller mesial and distal cusps by evident intercuspidal grooves (that extend up to 1/3 of tooth height) which are observable on both labial and lingual views. These grooves are limited by two weak intercuspidal ridges, on the mesial and on distal sides of their respective grooves. These ridges are mostly vertically orientated blending with the lateral outline, although some may be inclined. The central cusp is triangular, low, and compressed. In labial view, this cusp is symmetrical and almost as wide as the tooth shaft. The accessory cusps are slightly divergent, nonetheless the overall lateral outline of the teeth present parallel-subparallel sides. Teeth enamel is smooth, with no ornamentation beyond the intercuspidal ridges.

MMSCM 2017 preserves part of the anterior process of the surangular articulated to the wall of Meckel's canal, upon and covering the inferior alveolar canal. The anterior process of the surangular is perforated (for the inferior alveolar nerve and internal mandibular artery) and extends anteriorly along the Meckel's canal.

Comments. The pleurodont implantation (geometry of implantation *sensu* Bertin *et al*., 2018) and the tooth resorption style (Edmund, 1960, 1969), the mesiodiastal tricuspid condition of the specimen with intercuspidal grooves observe both labial and lingually, as well as the fact that these dentaries did not extend laterally onto the coronoid constitute a set of characters that indicate affinities with pleurodont iguanian (Pleurodonta) lizards (Frost & Etheridge, 1989; Smith, 2009). One of the more informative character states of these dentaries is the absence of the anterolateral process of the coronoid. Many studies have evaluated the presence/absence of the anterolateral process of the coronoid among pleurodonts, with some differences based on their taxon sampling, but there is some agreement that this process is (generally) absent, as in the specimens described herein, in Polychrotidae, Corytophanidae, Leiosauridae, Opluridae, Phrynosomatidae, and Tropiduridae (Etheridge & de Queiroz, 1988; Frost & Etheridge, 1989; Smith, 2009; Gauthier *et al.*, 2012). All these families, except for Phrynosomatidae, also present a fused Meckel's canal (Etheridge & de Queiroz, 1988; Smith, 2009; S. Brizuela pers. obs.) as do these fossil dentaries. Polychrotidae teeth have evident striae (Smith, 2009) (*P. acutirostris*, UNMdP-O 73 and 129) which differ from the teeth of MMSCM 2017 and MMSCM 2025. The fossil taxon would have had a short splenial, as inferred from the articulation facets, very close to 1/6 of the dental series length, character state shared with the Tropiduridae (Frost & Etheridge, 1989) and that allows the exclusion of the specimens from the remaining families considered above. Among Tropiduridae we note some variation of the coronoid-dentary articulation in lateral view. This articulation is straight and horizontal in

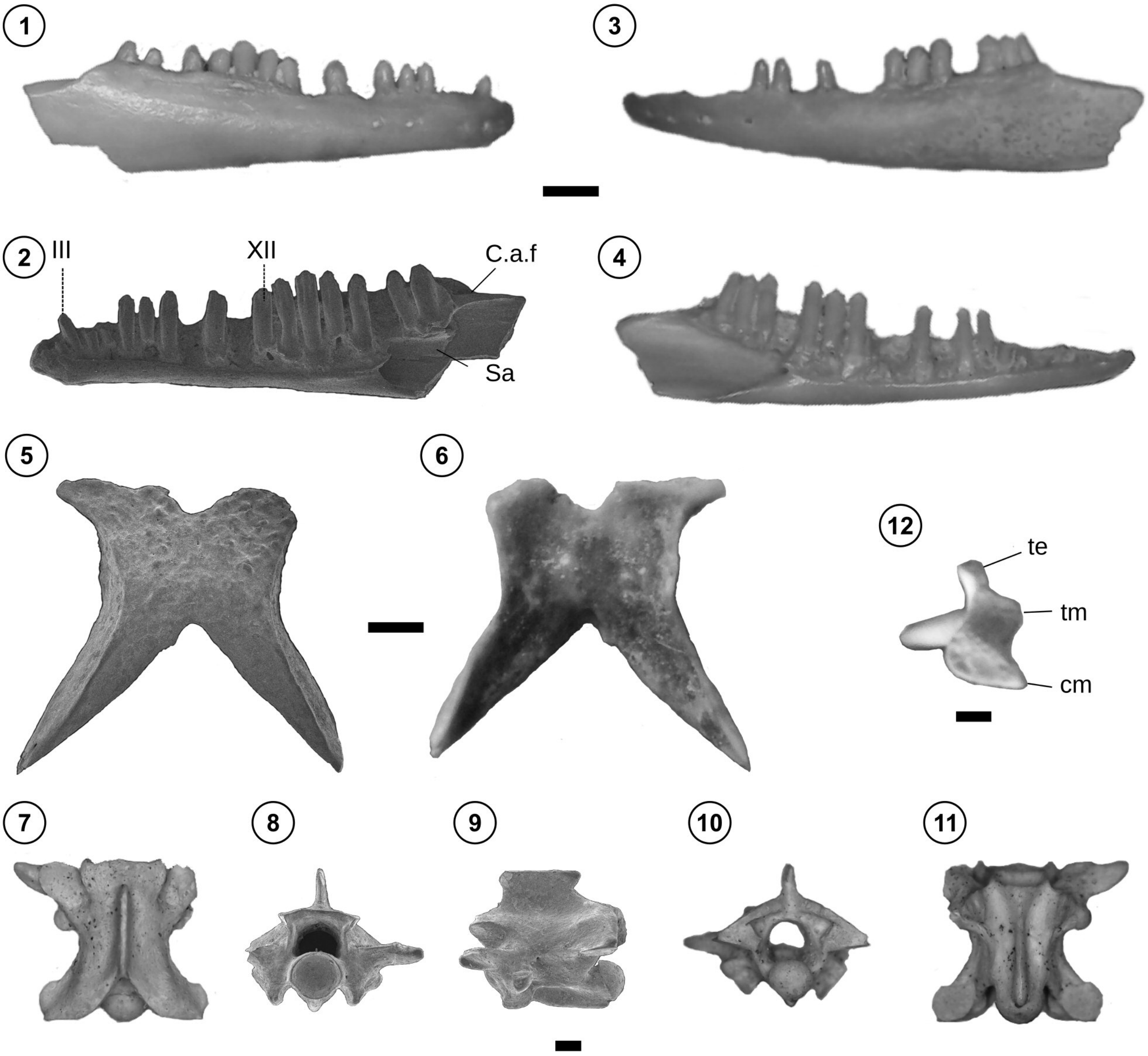

Figure 3. Ensenadan stage squamate remains from Mar Chiquita county, Buenos Aires, Argentina. ***Stenocercus*** sp., **MMSCM 2017** right dentary in **1,** lateral and **2,** medial views; **MMSCM 2025** left dentary in **3,** lateral and **4,** medial views. Tropiduridae, **MMSCM 2023** parietal in **5,** dorsal and **6,** ventral views. Colubriformes, **MMSCM 2029** vertebra in **7,** dorsal, **8,** anterior, **9,** lateral, **10,** posterior, and **11,** ventral views. Serpentes indet., **MMSCM 2037** rib in **12,** articular view. Abbreviations: **C.a.f**, coronoid articulation facet; **cm**, rib capitulum; **Sa**, surangular; **te**, rib tubercle; **tm**, rib tuberculum. Scale= 1 mm.

Plica (FMNH 81451; DigiMorph, 2022), *Tropidurus* (*T. spinulosus* UNMdP-O 21 and 77; *T. catalanensis* UNMdP-O 69), and *Uranoscodon* (YPM 12871; DigiMorph, 2022). In *Microlophus* there is variation. The articulation is nearly vertical anteriorly and later close to horizontal in *Microlophus atacamensis*, whereas in *Microlophus quadrivittatus* it is sinusoidal (convex then concave) anteriorly and much later horizontal (Vidal & Ortiz, 2004). In *Stenocercus* (*e.g.*, *S. pectinatus* UNMdP-O 128) it is anteriorly concave and posteriorly straight and horizontal, as in these specimens. The condition in *Eurolophosaurus*, *Strobilurus*, and *Uracentron* could not be evaluated. Additionally, Frost (1992) noted variation of the alveolar ridge (= subdental shelf) among Tropiduridae, reflected in the Meckelian cylinders outline from a parallel borders state to concave dorsal outline of the cylinder. According to Frost (1992), among Tropiduridae the parallel borders as observed in the specimens are only present in *Stenocercus*. Among *Stenocercus* species, Torres Carvajal (2003) noted that the coronoid of *Stenocercus guentheri* has a small labial process (anterolateral process) that overlaps the dentary, a different condition than that observed in *Stenocercus pectinatus* (UNMdP-O 128) and *Stenocercus dumerilii* (Hernández-Ruz & Ávila-Pires, 2008). No evidence of such labial process overlapping the dentary is observed in these specimens. These dentaries share with *S. pectinatus* the medial fold of the posteroventral portion. Furthermore, the range of tooth count in the specimens are compatible with the number observed in *S. pectinatus* (21 teeth, UNMdP-O 128) as well as the number of mental foramina (four foramina for *S. pectinatus*, UNMdP-O 128).

Therefore, the following combination of characters allow the assignation of MMSCM 2017 and MMSCM 2025 to *Stenocercus*: closed and fused Meckel's canal with a very short anterior aperture; extension of the fused Meckel's canal is more than half of the splenial-symphysis distance; the splenial anterior extent is 1/6 of the dental series length; medial wall of Meckel's canal (or Meckelian cylinder in medial view) with straight parallel borders in outline; the medial fold of the posteroventral part of the dentary; dental series with 20 (mean) functional teeth; teeth with parallel outlines; dental series with tricuspid teeth with mesiodistally aligned cusps; wide and conical central cusp flanked by shorter accessory cusps, differentiated by intercuspidal grooves and ridges (Frost & Etheridge, 1989; Frost, 1992; Torres Carvajal, 2003; Smith, 2009).

Albino *et al.* (2020) described a dentary from another Pliocene site of Buenos Aires Province very similar to those presented here, which they assigned to *Stenocercus*. As in this case, no specific assignation was made. All these specimens assigned to *Stenocercus*, including Albino *et al.* (2020), differ from *S. dumerilii*, which has a more extended anterior aperture of Meckel's canal, embracing six tooth positions (Hernández-Ruz & Ávila-Pires, 2008). The specimens also differ from *S. guentheri*, which presents a small labial process on the coronoid. At the moment, these are the only know *Stenocercus* records.

TROPIDURIDAE indet.

Figure 3.5–3.6

Referred material. MMSCM 2023 parietal, missing the right anterolateral process.

Geographic occurrence. Playa Dorada (37° 52′ 39.21″ S; 57° 30′ 56.40″ W), Santa Clara del Mar, Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Description. MMSCM 2023 is a small parietal (ml with supratemporal processes= 5.37 mm; mw= 8.12 mm). The outline of the parietal table is that of an isosceles trapezoid, with the more develop side on the frontoparietal suture. On the sagittal plane, the frontoparietal suture is interrupted by the parietal foramen which is markedly concave in outline. This suture continues laterally on a developed anterolateral processes, of which only the left is preserved. The posterior part of the parietal table is straight, with a relative narrow nuchal fossa. The dorsal surface of the parietal table is rugose, with numerous poorly defined protuberances of different dimensions, which are more evident in the anterior end of the parietal. The adductor musculature does not advance dorsally onto the parietal. In lateral view, the parietal develops ventrally along the parietal table and below the supratemporal processes as well. Ventral to the parietal table, part of this projection, the descending processes, are only slightly developed. The supratemporal processes are robust and as long as the parietal table. Posteriorly, along the ventral side of the supratemporal processes, the lateroventral articulation facets for the supratemporals are elongated. The dorsal part of each articulation surface is more lateral, while the ventral part curves slightly ventrally. The articulation facets extend at about 2/3 the supratemporal length but do not reach the parietal notch. Dorsally, the supratemporal processes present marked longitudinal crests (= adductor crests), which delimit relatively large medial and lateral surfaces. In ventral view (Fig. 3.6), the parietal table presents two (left and right) evident concavities. No fossa for the cartilage of the pineal organ is present. Posteriorly is a marked parietal fossa (*ressesus processi ascendentis*) in terminal position.

Comments. Most squamates present a fused parietal like MMSCM 2023, with the exception of some Gekkota (Pygopodidae and Sphaerodactylidae, Diplodactylidae, Carphodactilidae) and few scattered species (Gauthier *et al.*, 2012) of other groups. The adductor musculature is exposed in dorsal view, in both the parietal table and supratemporal processes (not to be confused with the advance of the musculature on the parietal), a condition observed among Iguania and Teiidae (Gauthier *et al.*, 2012). However, the latter groups along with Gymnophthalmidae and Lacertidae present ventral lappets (Gauthier *et al.*, 2012) which are lacking in the present specimen, indicating that this is an iguanian parietal. The trapezoidal outline of the parietal table is shared with most pleurodonts, with the exception of Corytophanidae, Dactyloidae, and *Iguana iguana*, which is Y-shaped (Smith, 2009). The parietal foramen on the frontoparietal suture is the most common condition among pleurodonts (Etheridge & de Queiroz, 1988; Smith, 2009; Gauthier *et al.*, 2012), with variation in the main position on the frontal or parietal, except Corytophanidae and some Iguanidae (*Dipsosaurus* and *Armandisaurus explorator*), where it is completely within the frontal. According to Smith (2009), the terminal parietal fossa (located at or just under the posterior margin of the parietal) is present in Crotaphytidae, Hoplocercidae, Opluridae, Tropiduridae, Leiocephalidae, and many Iguanidae and Phrynosomatidae. Hoplocercidae present an overgrowth of the parietal covering the nuchal fossa (Gauthier *et al.*, 2012), unlike MMSCM 2023. Among the mentioned taxa, only Tropiduridae and Phrynosomatidae present a ventrolateral articulation for the supratemporal (Gauthier *et al.*, 2012), as the specimen here. However, unlike Phrynosomatidae (except *Sceloporus undulatus*) (Smith, 2009; *S. variabilis* FMNH 122866; DigiMorph, 2022) which present a strongly developed adductor crests, those of the specimen resemble the weaker crests of Tropiduridae. Therefore, from all of the above, MMSCM 2023 is considered as an indeterminate Tropiduridae. This is consistent with the tropidurid (*Stenocercus*) dentaries from the same sediments, but there are no elements that would allow allocating this specimen to the same taxon.

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
CAENOPHIDIA Hoffstetter, 1939
COLUBROIDES Zaher *et al.*, 2009
COLUBRIFORMES Zaher *et al.*, 2009
COLUBRIFORMES indet.
Figure 3.7–3.11

Referred material. MMSCM 2029, mid-posterior trunk vertebra.

Geographic occurrence. Santa Elena (37° 52′ 3.95″ S; 57° 30′ 49.06″ W), Santa Clara del Mar, Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Measurements (in mm). cl= 5.027; conh= 1.864; conw= 1.66; cth= 1.811; ctw= 1.939; h= 5.078; naw= 2.832; nawp= 3.001; nch= 1.402; nh= 1.470; nlu= 2.885; pol= (1.230, 1.281) 1.256; po-po= 5.374; po-pr= 5.077; pow= (1.468, 1.646) 1.557; prl= 0.862; pr-pr= 7.2 (inferred); prw= 0.681; pzl= 1.475; pzw= 1.225; vr= 1.278/(5.374/2) = 0.48; z= (44°, 63°) 53.5°; zsw= 2.763; zt= 0.152; zyp= (1.176, 1.078) 1.127.

Description. This is an elongated (cl/naw= 1.78; *sensu* LaDuke, 1991), slightly depressed, and almost complete mid-posterior vertebra, missing only the right prezygapophysis and prezygapophyseal process. In dorsal view (Fig 3.7), the zygosphene is crenate, with oval, inclined (≈ 53.5°) articulation facets. The pre- and postzygapophyses are horizontal and they do not protrude laterally (zyp/cl= 1.127/5.027= 0.22; *sensu* LaDuke, 1991) although they are orientated ≈ 47° in dorsal view. The left prezygapophysis presents a circular-oval articulation facet, under which an acute prezygapophyseal process develops. This process is relatively thick (prw/pzw= 0.56; *sensu* LaDuke,

1991) and well developed (prl/pzl= 0.58 *sensu* LaDuke, 1991) but not long, and more laterally orientated than the prezygapophysis. Also in dorsal view, the articulation facets of the postzygapophyses are observed below the respective processes. In ventral view, these facets are circular. Posteriorly, on the postzygapophyses, there are small epizygapophysial spines.

In anterior view (Fig. 3.8), the neural arch is relatively low, with a subquadrangular neural canal which has similar dimensions as the cotyle. Above the neural arch is a uniformly thin neural spine. The cotyle is circular (cth/ctw= 0.93) and well developed. At both sides of the short paracotylar processes are paracotylar foramina.

In lateral view (Fig. 3.9) is the medium height (nh/nlu= 0.51; *sensu* LaDuke, 1991) blade-like neural spine. The neural spine bears two short overhangs (*sensu* Auffenberg, 1963): a convex anterior one and a more triangular posterior one. The interzygapophysial ridge (= *margo lateralis*) is evident, below which are the lateral foramina. The paradiapophyses presents semispherical diapophyses, differentiated from the low, flat, and oval parapophyses. Diapophyses and parapophyses are almost separated by a wide posterior notch. The paracotylar processes are short like the hemal keel. The subcentral ridges (= *margo ventralis*) are not evident. Posteriorly, there is an oblique condyle.

Posteriorly (Fig. 3.10), the vertebra is vaulted (vr= 0.48) with straight neural arch laminae. The condyle and the cotyle are circular (conh/conw= 1.12).

Ventrally (Fig. 3.11), the centrum is elongated, conical, with evident subcentral grooves lateral to the hemal keel, were there are tiny subcentral foramina. The hemal keel is long, oblanceolate, and relatively developed in lateral view. The cotyle is differentiated from the centrum by a condylar neck.

Comments. Colubroides are distinguished by several morphological synapomorphies, none of which correspond to the axial skeleton (Zaher *et al.*, 2009). Nonetheless, there are several characters historically recognized in colubroidean vertebrae that are present in MMSCM 2029: an elongate centrum; developed prezygapophyseal processes; a uniformly thin blade-like neural spine that extends onto the zygosphene; dia- and parapophysis differentiated; and the presence of paracotylar foramina, among others (Zaher *et al.*, 2019).

The specimen differs from the Xenodermidae, which present zygapophyses and neural spines with broad lateral expansions (Zaher *et al.*, 2009) and blade like prezygapophysis accessory processes (Zaher *et al.*, 2019). Colubriformes, as Colubroides, are not characterized by any particular vertebral characteristic, although many of its members present a hemal keel and do not a develop hypapophysis in the mid–posterior trunk vertebrae as in MMSCN 2029. A developed hypapophysis throughout the trunk vertebrae is a character present in Homalopsidae, Viperidae, Elapidae, Pseudoxyrhophiidae, Cyclocoridae, some Lamprophiidae (*e.g.*, *Boaedon fuliginosus*) and among Colubroidea: Sibynophiidae, many Natricidae, and some Dipsadidae (*e.g.*, *Synophis lasallei*, *Nothopsis rugosus*, and *Helicops angulatus*) (Zaher *et al.*, 2009, 2019; Smith, 2013; Georgalis *et al.*, 2019; Carrillo-Briceño *et al.*, 2021). Given that the fossil specimen lacks hypapophysis, it is excluded from these taxa. No lower assignation for MMSCM 2029 is possible at present.

The oldest South American record of a colubroid is from the Early–Mid Miocene of Patagonia (Albino & Brizuela, 2014a), and there are many late Cenozoic colubroid records in Buenos Aires Province. The oldest of these records are of indeterminate Colubroides (Colubridae before Zaher *et al.*, 2009), aff. *Bothrops*, and *Bothrops* cf. *alternatus* from the Montehermosan stage (Late Miocene–Early Pliocene) at Monte Hermoso (Albino, 1989; Albino & Montalvo, 2006; Aranciaga-Rolando *et al.*, 2021). MMSCM 2029 is similar to the Montehermosan non-viperid colubroid (MLP 87-II-25-2; see Albino, 1989). Although MMSCM 2029 differs from the montehermosan colubrid in lacking zygantral foramina, in the shape the zygosphene (straight–convex in the montehermosan vertebra), as in other characters that could vary intracolumnarly (as a more developed hemal keel). Geographically and temporally closer are indeterminate colubroids recovered from the Chapadmalalan (Pliocene) (Los Lobos and Las Palomas beaches) and Vorohuense (Late Pliocene–Early Pleistocene) (Punta Vorohué) (Albino & Quintana, 1992). Of those, the ones that can be compared with show more differences (zygosphene morphology, longer prezygapophyses) than similarities with the Montehermosan vertebra. Scanferla (2006) recognizes

Paraphimophis (Pseudoboini) in the Ensenadan (Pleistocene) in the north of Buenos Aires, which presents a short, tall neural spine that differs from MMSCM 2029. This same characteristic differentiates MMSCN 2029 from the *Xenodon* vertebra of the Bonaerian (Pleistocene) of Centinela del Mar (*Lystrophis* in Scanferla *et al.*, 2005). Brizuela *et al.* (2015) described an indeterminate colubroid from the Bonaerian of Mar del Plata, with similarities to the vertebrae of *Erythrolamprus* (Brizuela & Tassara, 2016) and to MMSCM 2029. The youngest non-viperid colubroids of Buenos Aires Province are those from the archaeological site of Cuva Tixi, where fossil vertebrae have been assigned to *Philodryas* and *Paraphimophis* (Albino, 1999). These are wider and more depressed or with a shorter and taller neural spine respectively, differing in their condition to that of MMSCM 2029.

SERPENTES indet.
Figure 3.12

Referred material. MMSCM 2037, proximal end of a left rib.

Geographic occurrence. Atlántida (37° 51′ 13.74″ S; 57° 30′ 25.19″ W), Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Description. The specimen corresponds to the proximal end of a large unicapitate, biarticular rib. The outline of the articular surface is bold c-shape. The "tuberculum" (see Capano, 2020 regarding homology) is concave, circular, and limited posteriorly by the caudal ridge. Posterodorsally, a robust tubercle develops. The "capitulum" is shallow and slightly cuneiform.

Comments. Unicapitate biarticular ribs are characteristic of Serpentes (Capano, 2020). At the moment, we can only consider it as of an indeterminate Serpentes of small–medium size.

Bonaerian stage Squamates from Mar Chiquita county

All Bonaerian specimens described were recovered from the upper member of the Santa Clara Formation (Schnack *et al.*, 1982). According to paleomagnetic data of the Camet Norte locality (Gómez Samus *et al.*, 2014), these fossils are younger than 0.78 Ma, indicating an upper Pleistocene age, Bonaerian stage. The Bonaerian stage is confirmed by the presence of *Megatherium americanum* (MMSCM 1575).

SQUAMATA Oppel, 1811
IGUANIA Cope, 1864
PLEURODONTA Cope, 1864
PLEURODONTA indet.
Figure 4.1

Referred material. MMSCM 2033, right dentary fragment with 12 tooth positions with functional teeth and replacements.

Geographic occurrence. Northeast of Camet Norte (37° 48′ 20.27″ S; 57° 28′ 23.48″ W), Santa Clara del Mar, Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Description. This specimen is poorly preserved and broke during a SEM session. It is labially smooth, without ornamentation, and with a long conversational fissure across the specimen. Meckel's canal is closed and fused. The dental series was preserved in a moment of active tooth replacement. Twelve dental positions are preserved, all with teeth except in tooth position d, where no tooth is preserved. In tooth position k both functional and a well-developed replacement are present. Dentition is as in MMSCM 2017 and MMSCM 2025.

Comments. There is a set of character states in MMSCM 2033 (shared with MMSCM 2017 and MMSCM 2025) that, as mentioned above, allow its placement among Pleurodonta. These characters are: pleurodont tooth implantation, an iguanian style of tooth replacement, and the presence of mesiodistally tricuspid teeth with intercuspidal grooves (Edmund, 1960, 1969; Frost & Etheridge, 1989; Smith, 2009). As already mentioned, among Pleurodonta a fused Meckel's canal is present in Polychrotidae, Dactyloidae, Leiosauridae, Iguanidae, Tropiduridae, some Opluridae (*Chalarodon*), and some Liolaemidae (except in some *Eulaemus*). Polychrotidae, Dactyloidae, and Iguanidae differ in tooth characters, as do some Leiosauridae (*Diplolaemus*, *Leiosaurus*, *Pristidactylus achalensis*, and *P. casuhatiensis*) (Etheridge & Williams, 1985; Cei, 1986, 1993; Cabrera, 1992; S. Brizuela per. obs.). This specimen is less complete than MMSCM 2017 and 2025, therefore there are less elements to achieve a better taxonomic assignation.

SERPENTES Linnaeus, 1758
COLUBROIDES Zaher *et al.*, 2009
COLUBRIFORMES Zaher *et al.*, 2009
VIPERIDAE Oppel, 1811

Bothrops Wagler, 1824

Type species. *Bothrops lanceolatus* Bonnaterre, 1790. Holocene, Martinique, Lesser Antilles.

Bothrops sp.
Figure 4.2–4.6

Referred material. MMSCM 2035a and b, two (mid posterior trunk) precloacal vertebrae.

Geographic occurrence. Northeast of Camet Norte (37° 48′ 24.09″ S; 57° 28′ 26.86″ W), Santa Clara del Mar, Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Measurements (in mm). cl= 4.787; conh= 1.555; conw= 2.004; cth= 1.771; ctw= 2.269; h= 4.658; hw= 1.683; nh= 1.133; nlu= 1.696; naw= 3.503; ; nawp= 4.068; nch= 1.545; pol= (1.090, 1.183) 1.137; po-po= 6.090; pow= (1.327, 1.452) 1.389; pr-pr= 6.782 (inferred); po-pr= 5.287; prl= 0.297; prw= 0.396; pzl= 1.311; pzw= 1.639; vr= 0.716/(5.707/2) 0.25; z= (54°, 47°) 50.5°; zsw= 3.215; zt= 0.113; zyp= (1.206, 1.331) 1.2685. (MMSCM 2035a).

Description. These are relatively square vertebrae (pr-pr/po-pr= 1.28) with the centrum somewhat longer than the neural arch width (cl/naw= 1.28) and constricted between zygapophyses. In dorsal view (Fig. 4.2), the zygosphenal roof is wide and crenate and the zygosphenal articulation facets are delimited by a long marked border. Posterior to the zygosphene is a thin neural spine (broken in MMSCM 2035b) that does not extend beyond the postzygapophyseal outline. The zygapophyses do not protrude (zyp/cl= 1.2685/4.787= 0.265, *sensu* LaDuke, 1991). The prezygapophyses are anterolaterally orientated and present large and oval-reniform articulation facets. On the prezygapophyses are short, stout, and obtuse (*sensu* Auffenberg, 1963) prezygapophyseal process. Posteriorly, the postzygapophyses are posterolaterally orientated and the anterior part of the articulation facet is anteriorly exposed.

In anterior view (Fig. 4.3), the cotyle is circular (ctw/cth= 1.09) with a marked rim and a paracotylar foramen at both sides. The parapophyseal processes are well-developed, half the height of the cotyle and anteriorly inclined. The prezygapophyses articulation facets are slightly elevated from the horizontal plane (≈ 15°). The hypapophysis is slightly longer than the cotyle height.

In lateral view (Fig. 4.4), the neural spine is low and as tall as the neural canal. The neural spine distal end is as long as its base. The interzygapophysial ridge is more evident than the subcentral ridge, which is only evident in the anterior portion of the centrum. Below the interzygapophysial ridge, at the posterior end of short shallow grooves and posterior to the diapophysis, are the lateral foramina. The paradiapophyses are dorsoventrally elongated, differentiated in a semispherical dorsal diapophysis and anteroventral flat-convex parapophysis. Anterior to the condyle an important hypapophysis develops. The hypapophysis is proximally wide, poorly differentiated from the condyle from which it extends posteroventrally. The condyle is inclined and preceded by a condylar neck.

Posteriorly (Fig. 4.5), the vertebra is low vaulted (vr= 0.25) with low slight convex laterally neural arch laminae. The condyle as the cotyle is slightly oval (conh/conw= 0.78). There are very small paired foramina on the postzygapophyses of MMSCM 2025b. The zygantrum is deep and presents zygantral foramina.

Ventrally (Fig 4.6), the centrum is weakly conical. The parapophyseal processes extend anteriorly beyond the condylar rim and prezygapophyseal processes. Posteriorly on the sagittal plane develops the hypapophysis, which does not extend beyond the condyle. The condyle is preceded by a condylar neck. The postzygapophyseal facets are large and oval-reniform in outline.

Comments. These vertebrae possess a set of characters previously mentioned and observed in colubroids (see above), particularly they present a developed hypapophysis which is developed in the mid and posterior trunk vertebrae of Homalopsidae, Viperidae, Elapidae, Pseudoxyrhophiidae, Cyclocoridae, Sibynophiidae, many Natricidae, and some Lamprophiidae and Dipsadidae (Zaher *et al.,* 2009; Smith, 2013; Georgalis *et al.*, 2019; Carrillo-Briceño *et al.*, 2021). In addition, the anteroventral orientated paracotylar processes are a synapomorphy of Viperidae (Szyndlar, 1984; Zaher *et al.*, 2009), also present in some natricids (Auffenberg, 1963; Zaher, 1999). Unlike the hypapophyses of natricids, those of viperids are thicker, more ventrally directed, and generally straight (Szyndlar, 1984; Albino & Montalvo, 2006) as in specimens MMSCM 2035a and b. Other characters indicative of Viperidae affinities of MMSCM 2035 are: the condyle poorly differentiated from the base of the hypapophysis; the subcentral ridges present only on the anterior portion of centrum; and the dorsoventral developed paradiapophysis (Szyndlar, 1984; Albino & Montalvo, 2006).

Among the Argentine Viperidae MMSCM 2035 shares several characteristics with *Bothrops* that allow its differentiation from *Crotalus*. These are: crenate anterior edge of zygosphene (not straight or concave), relatively low neural spine (Hsiou *et al*., 2012), and a divergent, less curved parapophyseal process (Aranciaga-Rolando *et al*., 2021). Among the more widely distributed Argentine *Bothrops* (*B. alternatus*, *B. ammodytoides*, and *B. diporus*) (see Carrasco *et al*., 2019 regarding *B. diporus* in Argentina), and according to data figured in Aranciaga-Rolando *et al.* (2021), MMSCM 2035 resembles *B. ammodytoides.* This latter species, like the specimens, presents a lower neural spine than *B. alternatus* and *B. diporus* and a more posteriorly inclined hypapophysis. The size of these fossil vertebrae (cl= 4.797 mm, ctw= 2.269) is also somewhat smaller than those of *B. alternatus* (UNMdP-O 78) and those fossils assigned to the species (Aranciaga-Rolando *et al*., 2021). While size and some of the mentioned characters could be indicative of similarities with *B. ammodytoides*, these traits seem to vary along the vertebral column, at least in *B. alternatus* (UNMdP-O 78). Hence, for the moment we refer MMSCM 2035 to *Bothrops* sp.

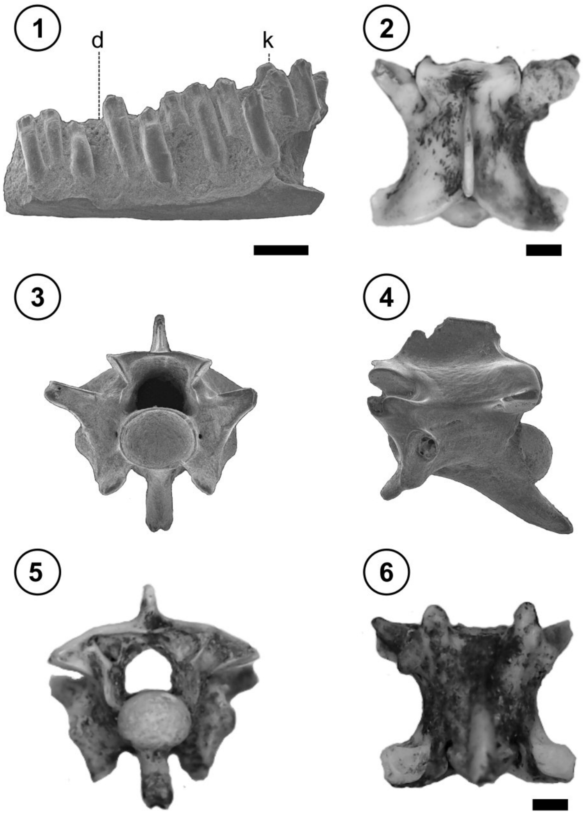

Figure 4. Bonaerian stage squamates from Mar Chiquita county, Buenos Aires, Argentina. **1,** Pleurodonta indet., **MMSCM 2033** dentary in medial view; ***Bothrops*** sp., **MMSCM 2035a** vertebra in **2,** dorsal, **3,** anterior, **4,** lateral, **5,** posterior, and **6,** ventral views. Note that d and k indicate the relative tooth position. Scale= 1 mm.

The oldest Argentine Viperidae fossil is an isolated vertebra of an indeterminate form from the Huayquerian (Late Miocene) of La Pampa Province (Albino & Montalvo, 2006). In Buenos Aires Province, isolated (Albino, 1989) and articulated (Aranciaga-Rolando *et al.*, 2021) vertebra of aff. *Bothrops* and *Bothrops* cf. *alternatus*, respectively, have been recovered from the Montehermosan (Late Miocene–Early Pliocene). Albino (1995) described another isolated vertebra of an indeterminate Viperidae from the Sanandresian (Early Pleistocene) of the Atlantic coast of Buenos Aires between Mar del Plata and Miramar. From Early–Middle Pleistocene sediments near La Plata city, north of Buenos Aires Province, an isolated compound bone has been assigned to *Bothrops* sp. (Scanferla & Nenda, 2005). Several Pleistocene–Holocene vertebrae and a pterygoid have been recovered from an archaeological site in the Tandilia mountain system and assigned to *B. alternatus* (Albino, 1999, 2001). Albino (1999) also identified, at that same site, small vertebrae that could not be assigned to either *B. alternatus* or *B. ammodytoides*, referring them to *Bothrops* sp.

Lujanian stage Squamates from Mar Chiquita county

Al Lujanian fossils described were recovered from Units B (MMSCM 2021) and C (MMSCM 2019) of the Camet Norte facies (Fasano *et al*., 1984). Absolute dating of the top and lower units allow to set a time rage of 24,550±600 (Pardiñas *et al*., 1998) to 21,000±7,000 years BP (Bigazzi *et al*., 1995). Late Pleistocene, Lujanian stage.

SQUAMATA Oppel, 1811
IGUANIA Cope, 1864
PLEURODONTA Cope, 1864
PLEURODONTA indet.
Figure 5.1–5.5

Referred material. MMSCM 2021, isolated presacral vertebra.

Geographic occurrence. Camet Norte (37° 49′ 33.20″ S; 57° 29′ 22.61″ W), Santa Clara del Mar, Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Description. Small, delicate, procoelic vertebra. In dorsal view (Fig. 5.1), it is close to squared in outline. Anteriorly, the dorsomedial part of the neural arch presents a V-shape indent, below which the cotyle is exposed. The prezygapophyses are well developed, antero-anterolaterally orientated (≈ 40°) and inclined (≈ 45°). The prezygapophyseal articulation facets are separated from the neural arch by evident grooves. Immediately medial to those grooves, on the lower part of the neural arch there are weak and poorly defined dorsolateral orientated zygosphenal articulation facets. The distally broken neural spine originates posterior to the prezygapophyses. It is low and extends posteriorly beyond the postzygapophyses posterior outline. There is no evident constriction between the pre and postzygapophyses.

In lateral view (Fig. 5.3), the interzygapophysial ridge is evident, more than the subcentral ridge, which shows a smooth transition to the ventral part of the centrum. The centrum in ventral view (Fig. 5.5) is short and wide, from which the condyle extends. A subcentral foramen is present to the left of a poorly differentiate subcentral crest. In anterior view, the neural canal is larger than the cotyle, with an inverted hart outline. Both cotyle and condyle are oval and vertically orientated (Fig. 5.2, 5.4).

Comments. Procoelic vertebrae are common to most extant Squamata, with the exception of some Diplodactylidae and most Eublepharidae gekkotans (Hoffstetter & Gasc, 1969; Conrad, 2008; Daza *et al.*, 2014). The absence of prezygapophyseal processes is indicative that this specimen does not correspond to Serpentes or Amphisbaenia. From the latter it can be further excluded since Amphisbaenia also lacks developed neural spines in precloacal/trunk vertebrae (Hoffstetter & Gasc, 1969; Augé, 2012). The fact that vertebrae are the most polyvalent part of the skeleton (Hoffstetter & Gasc, 1969) and the scarce knowledge of extant lizard vertebrae morphological diversity is a major problem for precise taxonomic assignation of these elements. Albino & Brizuela (2014b) present a basic evaluation of the vertebral anatomy of some members of extant Argentine lizards families. In that framework, this fossil vertebra can be excluded from Anguidae and Scincidae, since these taxa lack zygosphenal articulation facets (*i.e.*, there are no articulation medial to those of the prezygapophyses). Furthermore, the absence of a distinct tenon for the zygosphenal articulation excludes the specimen from Teiidae, as well as some Pleurodonta (Hoffstetter & Gasc, 1969; Albino & Brizuela, 2014b). Unlike Gymnophthalmidae, the zygosphenal articulation facets are dorsolateral and lack the crest limiting the zygosphenal articulation facets (Albino & Brizuela, 2014b). Also, MMSCM 2021 presents poorly developed and dorsolateral orientated zygosphenal articulation facets. The development and orientation of these facets is highly diverse among Pleurodonta taxa and along the vertebral column of an individual specimen (Albino & Brizuela, 2014b). Therefore, at present, MMSCM 2021 can only be considered as an indeterminate Pleurodonta.

SERPENTES Linnaeus, 1758
SERPENTES indet.
Figure 5.6–5.10

Referred material. MMSCM 2019a–f, series of six associated caudal vertebrae.

Geographic occurrence. Camet Norte (37° 48′ 51.67″ S; 57° 28′ 51.08″ W), Santa Clara del Mar, Mar Chiquita county, Buenos Aires, Argentina (Fig. 1.3).

Measurements (in mm). cl= 2.382; conh= 0.583; conw= 0.606; cth= 0,526; ctw= 0.562; h= 1.719; naw= 1.025; nawp= 1.174; nch= 0.466; nh= 0.438; nlu= 1.746; pol= (0.493, 0.611) 0.552; po-po= 1.612; po-pr= 2.607; pow= (0.324, 0.302) 0.313; prl= (0.093, 0.091) 0.092; pr-pr= 1.756; prw= (0.155, 0.127) 0.141; pzl= (0.649, 0.641) 0.645; pzw= (0.338, 0.345) 0.342; vr= (0.342/(po-po/2) = 0,42; z= (52°, 56°) 54°; zsw= 1.035; zsh= 0.06; zyp= (0.284, 0.334) 0.309.

Description. The description and measurements correspond to the largest and anterior-most vertebra of the series MMCSM 2019a. The remaining vertebrae are morphologically similar but smaller. In dorsal view (Fig. 5.6), the zygosphene is crenated and developed. The neural spine starts after the zygosphenal roof and does not extend posteriorly beyond the postzygapophyseal notch. The prezygapophyses slightly surpass anteriorly the zygosphene and are anterolaterally orientated (≈ 28° in dorsal view) with obovate–oval articulation facets. There are reduced, short, and obtuse prezygapophyseal processes. The postzygapophyses are posterodorsally orientated, with the condyle exposed between them.

In anterior view (Fig. 5.7), the zygosphene is thin and straight. The zygosphene is located above a large, square neural canal. The condyle is circular, deep, not inclined, and narrower than the neural canal. At either side of the cotyle are paracotylar foramina. The pleurapophyses are simple (*i.e.*, not forked), well-developed, long, and ventrolaterally orientated.

In lateral view (Fig. 5.8), vertebra MMCSM 2019a is elongated and depressed (cl/naw= 2.32), with a low neural arch. The interzygapophysial ridges are not marked and ventrally is a small lateral foramen. The zygosphenal articulation facets are elongated, rectangular, and inclined, while the prezygapophyses are close to horizontal. The keeled-shaped pleurapophyses curve anteriorly and extend beyond the prezygapophyses. Posterior to the pleurapophyses develops a marked and short (less than half the centrum length) subcentral ridge. Posteriorly on the centrum are elongated, unfused haemapophyses, which are blade-like with rectangular lateral outline.

As in anterior view, in posterior view (Fig. 5.9) the neural canal is large. The condyle is circular, not inclined, and of smaller dimensions than the neural canal.

In ventral view (Fig. 5.10), the centrum is cylindrical and elongated. The condyle is clearly differentiated from the centrum by a marked condylar neck.

Comments. These vertebrae with non-forked pleurapophyses and haemapophyses are of the postcloacal

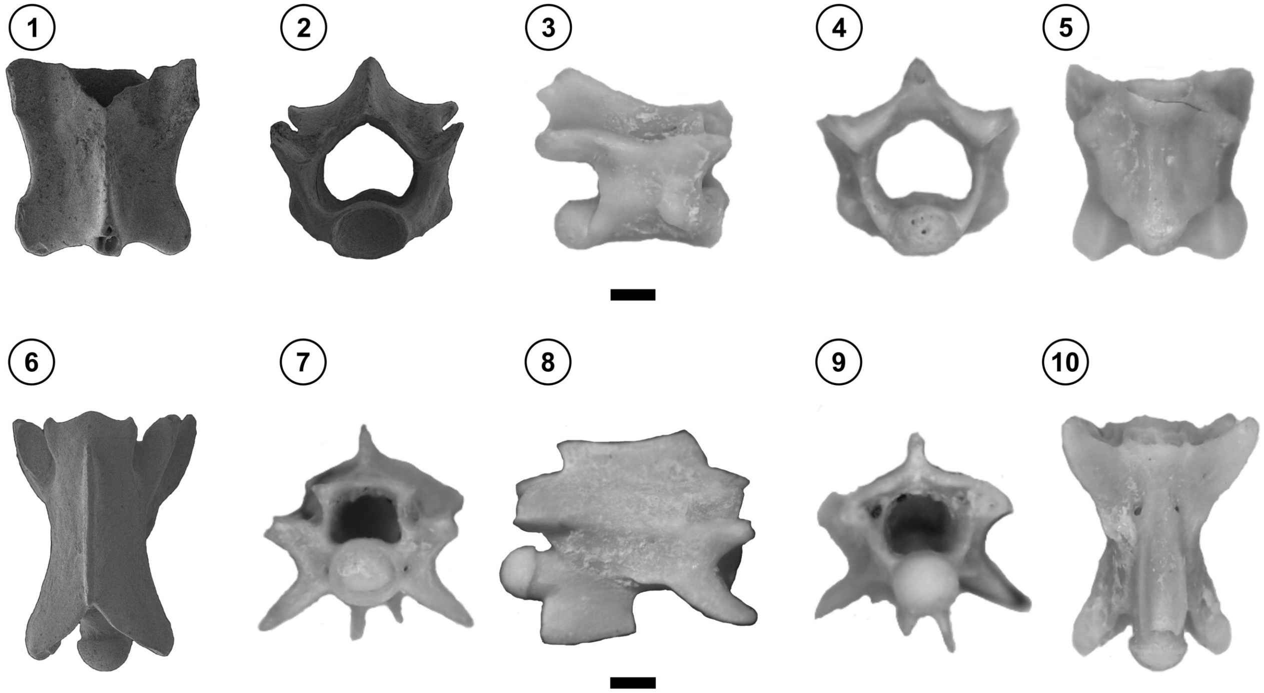

Figure 5. Lujanian stage squamates from Mar Chiquita county, Buenos Aires, Argentina. **1–5,** Pleurodonta indet., **MMSCM 2021** vertebra in **1,** dorsal, **2,** anterior, **3,** lateral, **4,** posterior, and **5,** ventral views; **6–10,** Serpentes indet., **MMSCM 2019** in **6,** dorsal, **7,** anterior, **8,** lateral, **9,** posterior, and **10,** ventral views. Scale= 1 mm.

caudal region of the axial skeleton of a snake (Hoffstetter & Gasc, 1969). Fossil snake vertebra systematics are based mainly on precloacal vertebral morphology, although caudal vertebrae have been occasionally used (Jasinski & Moscato, 2017). At the moment, we cannot allocate this specimen to any particular group of snakes.

DISCUSSION

As mentioned above, amphibian and squamate fossils are relatively rare at the northern slope of the Tandilia mountain system in the coastal area of Buenos Aires Province. Despite being just a few, the specimens presented in this contribution represent an interesting morphological and taxonomical diversity. Furthermore, the squamates described here represent the first records of the clade for Mar Chiquita county, which together with the new and previously described amphibians depict the Pleistocene herpetofaunal assemblage (Ensenadan, Bonaerian, and Lujanian) for this particular area (Fig. 6).

From the Ensenadan outcrops, we were able to identify a large anuran which by its morphology and size is regarded as cf. *Rhinella*. This is the second large anuran recovered in a particular site, Playa Dorada, along with *Ceratophrys ornata* (Agnolin, 2005; Gómez & Turazzini, 2021). *Ceratophrys* (*C. ornata* and other species, see Gómez & Turazzini, 2021) is also present in the Ensenadan of General Pueyrredon, north of Mar del Plata city, indicating a widespread regional presence of this genus during the Ensenadan at the northern slope of the Tandilia mountain system. Agnolin (2005) states that *Ceratophrys* wide distribution does not contribute relevant data for paleoenvironmental inferences. This is also true for *Rhinella*, a specious genus (more than 90 spp.) found throughout a great diversity of environments and ecoregions (Pereyra *et al.*, 2021; Frost, 2023). Therefore, it is difficult to characterize paleoclimatic and paleoenvironmental conditions from these generic taxonomic identifications. Nonetheless, both *Rhinella* (*R. arenarum and R. dorbignyi*) and *C. ornata* currently present a sympatric distribution in the Pampean region (Vaira *et al.*, 2012; Pérez-Ben *et al.*, 2019b). The Playa Dorada anurans suggest that Ensenadan paleoclimatical conditions would have been similar to the present ones. Similar inferences have been proposed for a similar but younger (Lujanian) anuran assemblage (*C. ornata* and *R. arenarun*) from another Pampean locality (Pérez-Ben *et al.*, 2019b).

The Ensenadan squamate assemblage in Mar Chiquita includes both lizards and snakes. Some of the more informative elements allowed recognizing the tropidurid lizard *Stenocercus* (MMSCM 2017 and 2025). *Stenocercus* is a specious South American genus (Torres Carvajal, 2007) represented in Argentina by six species (*S. azureus*, *S. caducus*, *S. doellojuradoi*, *S. marmoratus*, *S. pectinatus*, and *S. roseiventris*). *Stenocercus pectinatus* presents the southernmost distribution of the genus (Cei, 1993; Abdala *et al.*, 2012) exploiting grassland and coastal dune environments in southeastern Atlantic coast (Isacch *et al.*, 2016). When compared with other sand-dwelling lizards of the area (*e.g.*, *Liolaemus multimaculatus, Liolaemus gracilis, Liolaemus weigmannii*), *Stenocercus pectinatus* is known to exploit more vegetated areas (Vega, 2010). Given the wide distribution of the genus and the absence of a species level assignation, it does not allow a particular paleoclimatic and/or paleoenvironmental inference. The dentaries reported here are the first Pleistocene record of the genus. Prior to these (MMSCM 2017, 2025), *Stenocercus* was only known from a partial, isolated dentary from the Montehermosan of southern Buenos Aires Province (Albino *et al.*, 2020). Another Ensenadan lizards fossil (parietal MMSCM 2023), taxonomically less informative, could ultimately be assigned to *Stenocercus* with the acquisition of new data. Regarding Ensenadan colubroids, these fossils are the first records for Mar Chiquita. Unfortunately, they could not be assigned at lower taxonomical levels but they are clearly different from the only known Ensenadan colubroid (*Paraphimophis*; Scanferla, 2006). The poor knowledge of vertebrae morphology variation, the apparent similarity to the Buenos Aires taxa, and lack of vertebral synapomorphies for lower level taxa remains an important impediment for the study of these and other squamates.

The Bonaerian indeterminate pleurodont dentary MMSCM 2033 is very similar to those from the Ensenadan referred to *Stenocercus,* although there are no preserved characters that would allow this assignation. On the other hand, the Bonaerian snakes vertebrae are much more informative, allowing their assignation to *Bothrops.* This is the first record of *Bothrops* for the southeastern Atlantic coast of Buenos Aires Province. The oldest known argentinean *Bothrops* (and aff. *Bothrops*) are from the Montehermosan of southern Buenos Aires (Albino, 1989; Aranciaga-Rolando *et al.*, 2021), while in the southeastern Atlantic coast of Buenos Aires Province only a Marplatan (Sanandresian) Viperidae record is known (Albino, 1995). The presence of *Bothrops* in the Bonaerian is within its current distribution, since in the area *B. alternatus* and *B. ammodytoides* are currently recorded (Giraudo *et al.*, 2012; Povedano, 2022). Previously described anuras for the Bonaerian of the northern slope include *Odontophrynus* (Turazzini *et al.*, 2016), *Ceratophrys* (*C. ornata* and *Ceratophrys* cf. *ornata*) (Gómez & Turazzini, 2021) and many indeterminate elements from General Pueyrredon (Pardiñas *et al.*, 2004; Taglioretti *et al.*, 2009; Brizuela & Tassara, 2011). Squamates have also been reported in the Bonaerian of General Pueyrredon including *Ophiodes* and an indeterminate colubroid (similar to *Erythrolamprus*) (Brizuela *et al.*, 2015; Brizuela & Tassara, 2016). Lastly, the younger Lujanian stage elements of Mar Chiquita are not informative beyond indeterminate pleurodonts and serpentes.

Considering all the herpetological fauna of the late Neogene southeastern Atlantic coast of Buenos Aires (Fig. 6), we must first note that outcrops from the southern slope of the Tandilia mountain system represent a larger temporal range (Pliocene–Holocene) than those of the northern slope and the distribution of its known herpetofaunal assemblage comes largely from its older sediments. The records present a gap during the Barrancalobian and an absence of fossils in the southern slope Ensenadan stage, both most likely due to historical factors. Also, there are some differences between the amphibian and squamate records. While among anurans there are extant (*R. arenarum*) and extinct (*e.g.*, *C. ameghinorum*, *R. loba*) species described, among squamates only extant genera are recognized, with no species level assignation achieved so far. Furthermore, squamate fossils belong to taxa currently distributed in the Pampean region, whilst pipid anurans are now distributed at lower and tropical-subtropical latitudes in South America (Báez *et al.*, 2012). It is also worth noting that the *Ceratophrys*-*Rhinella* association, registered in the Chapadmalalan and Bonaerian stages, is probably present since the Chapadmalalan. Among squamates, *Tupinambis* s.l., *Amphisbaena*, and colubroids are the main components of the Pliocene–Early Pleistocene squamate fauna, although iguanians are the main lizards in Ensenadan and younger sediments.

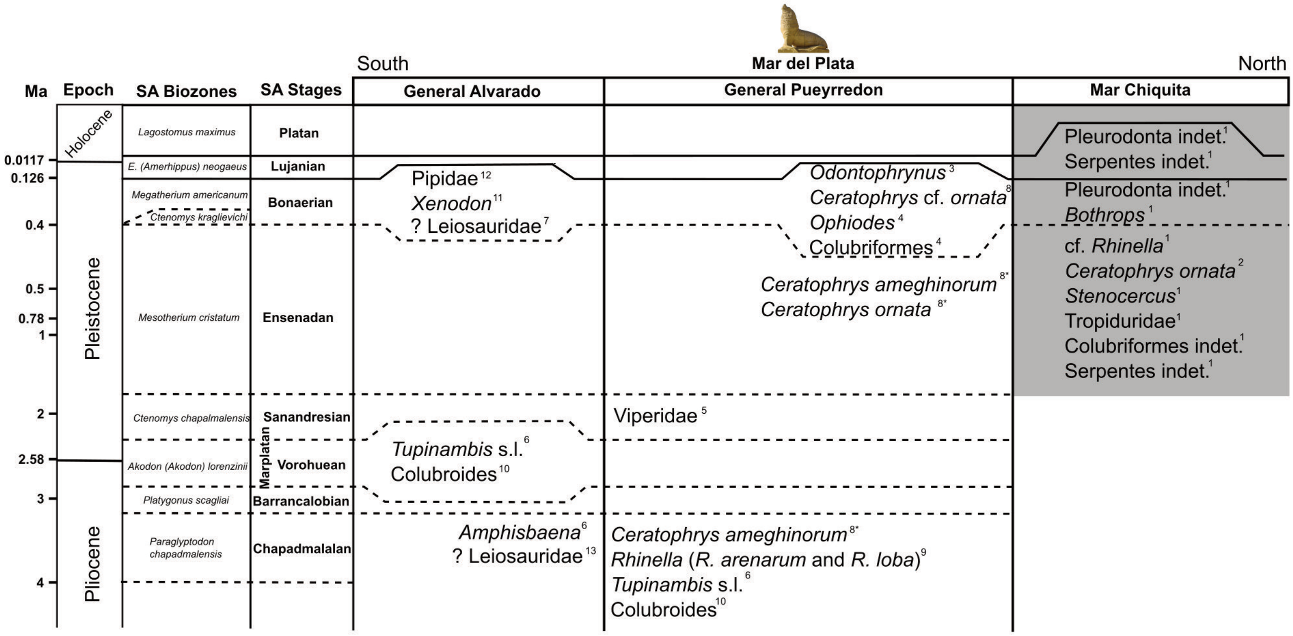

Figure 6. Simplified herpetofaunal elements from the Neogene of the southeastern Atlantic coast of Buenos Aires (Mar Chiquita, General Alvarado, and General Pueyrredon counties). References: 1, this study; 2, Agnolin (2005); 3, Turazzini *et al.* (2016); 4, Brizuela *et al.* (2015); 5, Albino (1995); 6, Brizuela & Albino (2012); 7, Brizuela *et al.* (2022); 8, Gómez & Turazzini (2021); 9, Pérez-Ben *et al.* (2014, 2019a); 10, Albino & Quintana (1992); 11, Scanferla *et al.* (2005); 12, Báez *et al.* (2008, 2012); 13, Brizuela *et al.* (2011). Asterisk denotes several morphotypes.

Further data is needed to evaluate if this a natural trend or, most likely, a preservational/recovery bias.

Albino (2020) considered that the paleoenvironmental hypothesis for lizards should be based using assemblages rather than isolated records. The same is true for paleoclimatic inferences. The herpetological assemblage from the Pleistocene of Mar Chiquita (cf. *Rhinella*, *Ceratophrys ornata*, *Bothrops*, and *Stenocercus*) includes taxa which are currently distributed in the Pampean region. This region is characterized by a temperate-subtropical humid climate with average temperatures oscillating between 13 and 18 °C and precipitations ranging from 600 to 1.200 mm/year (Prado *et al.*, 2021). Thus, the fossil herpetological assemblage suggests that during the Pleistocene climatic conditions would have been similar to those of today. Geological data indicates that the northern slope of the Tandilia mountain system lacked a marked slope, enabling the deposition of lacustrine and palustrine sediments in a general environment with permanent meandering canals (Isla *et al.*, 2015) that would have allowed the presence of this assemblage. Pardiñas (2004) found that the Ensenadan mammalian assemblage southwest of the Santa Elena stream (Complejo Ferroviario) is currently sympatric with the fitogeographic Monte province, suggesting a cooler and more arid condition than the Pampean region. Pardiñas (2004) also recognized *Clyomys* in that assemblage, a Brazilian taxa interpreted as a relict taxon of more benign paleoclimatical conditions. This is consistent with the general hypothesis of a cold, dry glacial Pleistocene climate for the Pampean region, with interspersed short, warmer, more humid interglacial events inferred from other mammalian fossils (Cione *et al.*, 2015; Soibelzon *et al.*, 2019; Prado *et al.*, 2021). One of these short interglacial events is registered in a Lujanian mammalian assemblage in Cament Norte, where arid-semiarid paleoclimatic conditions have been inferred (Pardiñas *et al.*, 1998; Prevosti & Pardiñas, 2001). However, the presence of *Sarcoramphus papa* (Noriega & Areta, 2005) in the same assemblage is contradicting this hypothesis, since this vulture is currently distributed in humid tropical-subtropical climates in the northern part of Argentina.

Therefore, the herpetological fossil record of the southeastern Atlantic coast of Buenos Aires indicates that the general squamate fauna composition was established in the region since the Pliocene. The main problem for these records is the lack of lower, more precise taxonomic assignation. The better-resolved anuran record indicates that during the Late Pliocene–Pleistocene extant, extinct and now displaced extant taxa were present in this area. Anurans would have presented different reactions to the changing paleoclimatic-paleoenvironmental conditions that occurred during the Pliocene–Pleistocene in this area. These changes, as stated by Rabassa *et al.* (2005), were of recurrent cold-warm cycles during the Ensenadan to late Lujanian. Those changes are not evident from the fossil herpetofaunal assemblage (cf. *Rhinella*, *Ceratophrys ornata*, *Bothrops* and *Stenocercus*) from Mar Chiquita, suggesting similar climatic conditions as today. But these inferences are in conflict with those from the mammal fossil record, which is more abundant and with better (specific) taxonomic assignations. This particular discrepancy with the Mar Chiquita herpetological assemblage could correspond either to different responses to climatic-environmental changes between cold and warm blooded animals or the lack of information due to low taxonomic assignation (in particular for squamates). Further data is needed to consider either hypothesis.

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