

# First vertebrate assemblage of the Early Holocene from northeastern Argentina (Mesopotamian Region)

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# FIRST VERTEBRATE ASSEMBLAGE OF THE EARLY HOLOCENE FROM NORTHEASTERN ARGENTINA (MESOPOTAMIAN REGION)

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**Abstract.** In this contribution, we report and describe a microvertebrate fossil assemblage recovered from a Holocene fluvial unit located in Entre Ríos Province, northeastern Argentina (Mesopotamian Region). The analyzed stratigraphic section is on the left bank of Doll creek ( $32^{\circ} 18' 24''$  S,  $60^{\circ} 25' 41''$  W), southwestern Entre Ríos Province. The stratigraphic section was divided into three levels and a total of 36 samples were collected. Radiocarbon dating was obtained from gastropod shells from the base of the section, with a range of  $9,990 \pm 140$  BP (Early Holocene). It was possible to record fishes, such as eels and characids, anurans, reptiles, birds, and small-medium size mammals. Most of the identified taxa constitute the first fossil records from the Quaternary of the Mesopotamian Region and even from Argentina. The systematic, biostratigraphic, and taphonomical results show that the environmental conditions in this area at the beginning of the Holocene period were similar to the current ones: a temperate-humid climate with water availability. This contribution is the first study of a microvertebrate fossil assemblage from the Early Holocene from northeastern Argentina (Mesopotamian Region) and represents an important contribution to the knowledge of the Quaternary fossil vertebrates from Argentina.

**Key words.** Vertebrates. Holocene. Quaternary. Entre Ríos. Mesopotamia.

## Resumen. PRIMERA ASOCIACIÓN DE VERTEBRADOS DEL HOLOCENO TEMPRANO DEL NORESTE DE ARGENTINA (REGIÓN MESOPOTÁMICA).

En esta contribución reportamos y describimos un conjunto fósil de microvertebrados recuperado de una unidad fluvial holocena ubicada en la provincia de Entre Ríos, noreste de Argentina (región Mesopotámica). La sección estratigráfica analizada se encuentra en la margen izquierda del arroyo Doll ( $32^{\circ} 18' 24''$  S,  $60^{\circ} 25' 41''$  O), sudoeste de la provincia de Entre Ríos. La sección estratigráfica se dividió en tres niveles y se extrajeron un total de 36 muestras. Una datación  $^{14}\text{C}$  se obtuvo a partir de conchas de gasterópodos de la base de la sección, con un rango de  $9,990 \pm 140$  AP (Holoceno Temprano). Se registraron peces como anguilas y charácidos, anuros, reptiles, aves y mamíferos de tamaño pequeño-mediano. La mayoría de los taxones identificados constituyen los primeros registros fósiles del Cuaternario de la región Mesopotámica e incluso de Argentina. Los resultados sistemáticos, bioestratigráficos y tafonómicos permitieron inferir que las condiciones ambientales en esta área a comienzos del Holoceno eran similares a las actuales, con un clima templado-húmedo con disponibilidad de agua. Esta contribución es el primer estudio de un ensamblaje fósil de microvertebrados del Holoceno Temprano del noreste de Argentina (región Mesopotámica) y representa un importante aporte al conocimiento de los vertebrados fósiles cuaternarios de Argentina.

**Palabras clave.** Vertebrados. Holoceno. Cuaternario. Entre Ríos. Mesopotamia.

THERE HAS BEEN remarkable progress in the study of late Quaternary vertebrates in the south of the Argentinian Mesopotamian Region recently (Ferrero *et al.*, 2017, 2019, 2022; Peralta *et al.*, 2019; Peralta & Ferrero, 2022a, 2022b, 2023; Ferrero & Noriega, 2023). From a taxonomic, biostratigraphic, and biogeographic point of view, a wide diversity of Brazilian and Pampean lineages has been documented, as well as the coexistence of autochthonous and holarctic mammals, mainly from the Late Pleistocene

(Noriega *et al.*, 2004; Vucetich *et al.*, 2005; Ferrero *et al.*, 2007; Ferrero & Noriega, 2009; Ferrero, 2013; Ferrero & Alcaraz, 2013; Ferrero & Vezzosi, 2013; Holanda & Ferrero, 2013; among others).

In Entre Ríos Province, located in the south of the Mesopotamian Region, there are a large number of Quaternary vertebrate fossiliferous localities and most of them correspond to Pleistocene units located in the southwest of the province (Ferrero *et al.*, 2017). The aim of

these studies was to identify and describe mammals and, to a lesser extent, reptiles and birds (Ferrero *et al.*, 2019; Ferrero & Noriega, 2023).

Contributions to the knowledge of Holocene faunas (<11,000 years BP) in Entre Ríos are known from records at archaeological sites reported as Late Holocene (<3,000 years BP) in the center, west, and south of the province (Tonni *et al.*, 1985; Tonni, 2004; Bonomo *et al.*, 2010, 2014; Loponte *et al.*, 2012; Apolinaire *et al.*, 2015; Bastourre & Apolinaire, 2017; among others) and in upper Paraná Delta (Bonomo *et al.*, 2010, 2014; Bastourre, 2015; among others), an unpublished doctoral thesis reporting indeterminate fish remains from two localities in this province, La Picada and Molino Doll (Segovia, 2014), a recent communication on the remains in a paleontological collection conformed by mammals assigned to Holocene units of various fossiliferous localities in the east and center of this province (Peralta & Ferrero, 2022a), and new important contributions about vertebrate fossil remains from southwestern Entre Ríos (Peralta & Ferrero, 2022b, 2023).

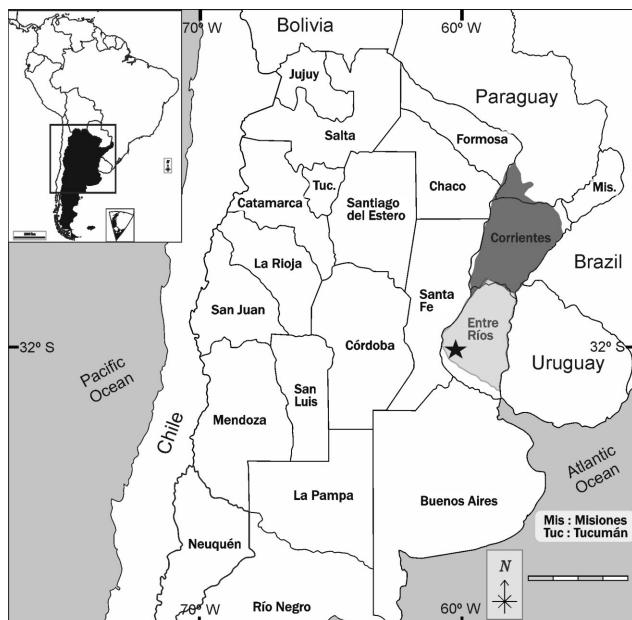
This contribution aims to report and describe the first fossil vertebrate assemblage from the Early Holocene in the southern Mesopotamian Region, northeastern Argentina, and to discuss the biostratigraphic, taphonomical, and paleoenvironmental inferences.

## GEOGRAPHICAL AND GEOLOGICAL SETTINGS

Mesopotamia is a region located in northeastern Argentina, which comprises 184,000 km<sup>2</sup>, and includes Misiones, Corrientes, and Entre Ríos provinces. It presents a smooth transition between a humid tropical climate in the north of Misiones and a humid subtropical climate in the south of Entre Ríos (Iriondo, 2010). Entre Ríos Province covers an area of 70,000 km<sup>2</sup> approximately, between the Paraná and Uruguay rivers, ranging between 28°–32° S and 58°–60° W. Currently, the climate is humid subtropical, with rainfalls around 1,200 mm/year in the east and 1,000 mm/year in the west (Iriondo, 2010) (Fig. 1).

The analyzed stratigraphic section is on the left bank of Doll creek, near Molino Doll locality (32° 18' 14" S; 60° 25' 24" W), in southwestern Entre Ríos Province, southern Mesopotamian Region, Argentina (Fig. 1). The Doll creek

bank presents several outcrops referable to the late Miocene–Holocene interval (Brunetto *et al.*, 2015; Fig. 2.1). The Holocene fossil-bearing unit is constituted by a lenticular sedimentary deposit interpreted as a channel deposit with a maximum thickness of 150 cm and a lateral extension of 400 cm (Fig. 2.1–2.2, Lower Holocene Unit). From base to top, three levels can be identified in the base of internal unconformities observed in the field. Level 1: at the base, consists of a 3 cm thick black silt layer; a 5 cm thick layer constituted by a matrix composed of small gastropod shells of *Heleobia* Stimpson, 1865 (Cochliopidae), and *Pomacea* Perry, 1810 (Ampullariidae) with clayey silt; a 30 cm thick blackish-gray silt layer with a lamination and some dispersed gastropod shells of the genus *Pomacea*, and at the top of this level, a 40 cm greenish-gray silt layer with abundant gastropod shells (*Pomacea* and *Heleobia*). Level 2: is at the base a 30 cm thick black silt-clay layer with abundant gastropod shells of the genus *Heleobia* (Cochliopidae) and *Biomphalaria* Preston, 1910 (Planorbidae), with an inter-layer of grey clay. Towards the top, gastropod shells become less abundant. Level 3: a base formed by a 15 cm thick black silt-clay layer with small (*Heleobia*, *Biomphalaria*) and big (*Pomacea*) gastropod shells, distributed homo-



**Figure 1.** Location of southern Mesopotamia (light gray) and northern Mesopotamia (dark gray) regions (modified from Ferrero *et al.*, 2017) and the Molino Doll fossil locality (black star). Scale= 400 km (map taken from D. Dalet/d-maps.com).

geneously and less abundantly than in the previous levels. At the top, there is a black silt layer with gastropod shells (Peralta & Ferrero, 2018, 2022b; Zilli *et al.*, 2019) (Fig. 2.2–3).

## MATERIALS AND METHODS

The vertebrate fossils studied herein correspond to disarticulated and isolated remains obtained from the systematic sampling and sieving of sediments. These fossils are housed at Centro de Investigación Científica y Transferencia Tecnológica a la Producción (CICYTTP-CONICET- Prov.E.R.-UADER), in Diamante, Entre Ríos, Argentina.

A total of 36 sediment samples were extracted, 12 per established level. A sample of gastropod shells from the

base of the section was collected and sent to the Laboratorio de Tritio y Radiocarbono (LATYR) (CIG UNLP-CONICET) for radiocarbon dating. The shells were prepared at CICYTTP-CONICET-Gob.E.R.-UADER (Diamante, Entre Ríos) following the specific protocol provided by LATYR.

The fossils were extracted by wet screening using two superimposed sieves of 4 mm and 2 mm mesh, hand-picked, and counted using a magnifying glass. The specimens were photographed and measured under stereomicroscope LEICA S8 APO and digitized with a LEICA DFC295 camera (using LAS V3.8 software).

The systematics follow Mirande & Koerber (2020) for fishes, Vaira *et al.* (2012) and Frost (2024) for anurans, Avila *et al.* (2013) for amphisbaenians, Williams *et al.* (2021) for

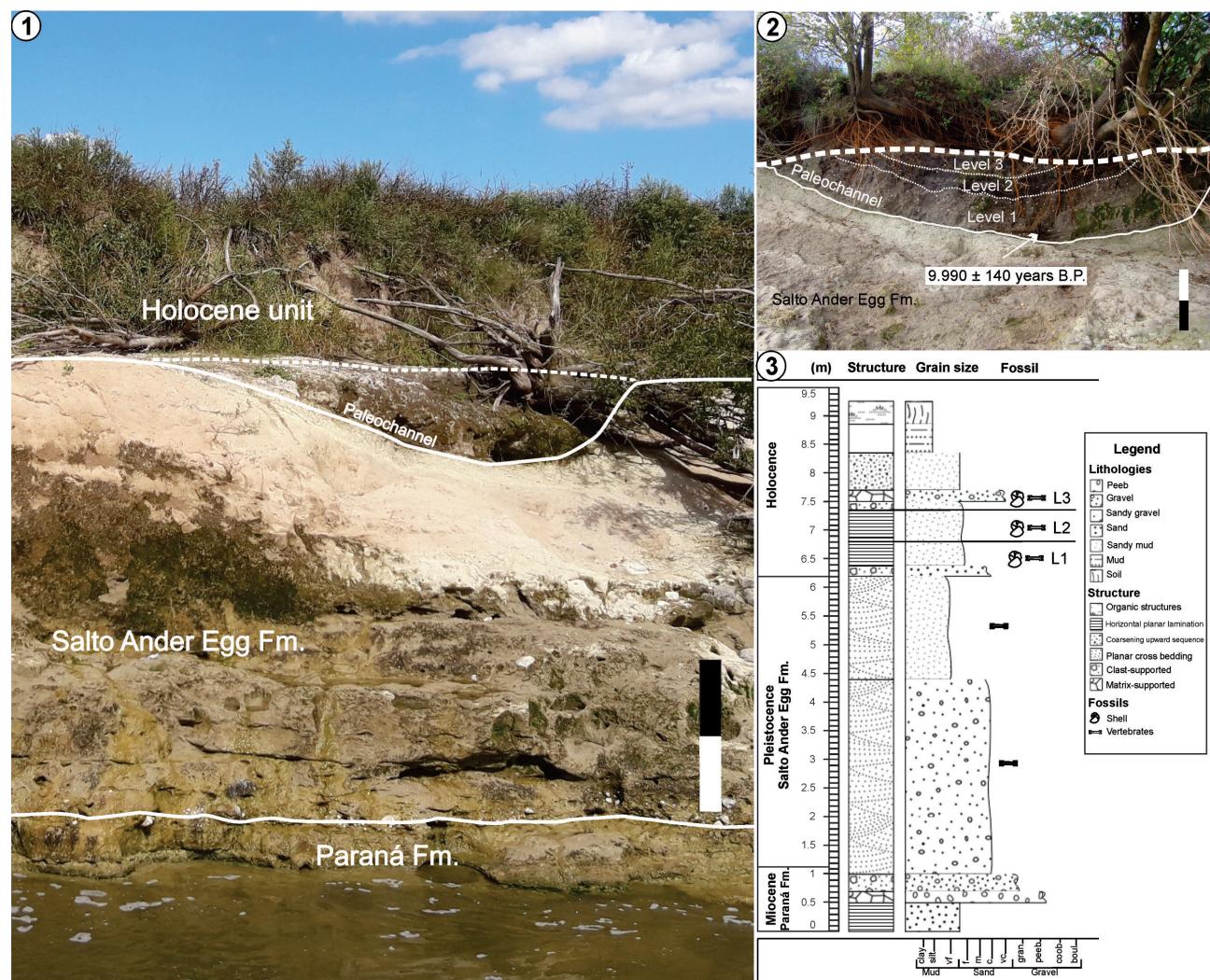


Figure 2. 1, Profile of left bank of the Doll creek at the Molino Doll locality; scale= 1 m. 2, Stratigraphic section of Holocene paleochannel unit; scale= 1 m. 3, Stratigraphic sequence of left bank in Doll creek; L1: level 1, L2: Level 2, L3: Level 3 (modified from Pedersen & Brunetto, 2020).

serpents, Remsen *et al.* (2023) for birds, and Teta *et al.* (2018) for mammals.

The osteological identification was done following Miquelarena (1986), Longenecker (2010), and Radu (2005) for fishes; Bailon (1999) and Turazzini (2020) for anurans; Auffenberg (1963), Hoffstetter & Gasc (1969), and Albino (1999) for reptiles; Baumel & Witmer (1993) for birds; Brown & Twigg (1969) and Reig (1977) for mammals. The remains were compared with the osteological collections deposited at the CICYTTP; Museo Provincial de Ciencias Naturales 'Florentino Ameghino' (MPCNFA), Santa Fe; Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Ciudad Autónoma de Buenos Aires; Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires (FCEyN- UBA), Ciudad Autónoma de Buenos Aires; Departamento de Biología, Universidad Nacional de Mar del Plata (UNMdP), Mar del Plata; Fundación de Historia Natural Félix de Azara (FFA), Ciudad Autónoma de Buenos Aires (Supplementary Data S1).

Ecological and environmental requirements and distribution patterns followed specialized literature (Del Hoyo *et al.*, 1992; Wilson *et al.*, 2017; among others) and websites (e.g., Frost, 2024 and <https://cma.sarem.org.ar/es>).

The taphonomical analysis was developed considering the diversity and frequency of the taxa, the number of specimens per level, geological characteristics based on field observations, and literature of the unit (see below). We assigned the category "indetermined" to those remains without clearly preserved taxonomic and anatomical features.

## RESULTS

### Chronological analysis

The assemblage of vertebrates from the analyzed stratigraphic section in Doll creek was dated by radiocarbon ( $^{14}\text{C}$ ) analysis from gastropod shells extracted from level 1 (LP-3060). An age of  $9,990 \pm 140$   $^{14}\text{C}$  years BP (9,680–9,280 cal. years BP) was determined, corrected by CALIB 7.0.0 software together with Stuiver & Reimer (1993), and SHCal13 curve for the Southern Hemisphere (Hogg *et al.*, 2013) (Supplementary data, Fig. S1).

### Number of recorded specimens

A total of 2,763 vertebrate fossil remains were

recovered from the section. Fish remains are the most frequent, with 2,072 specimens. Regarding other vertebrate groups, eight remains correspond to anurans, nine to reptiles, two to birds, and eight to mammals. The remaining 664 correspond to undetermined fragments (Tab. 1).

## SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERI Cope, 1871

Division TELEOSTOMORPHA Arratia, 2001

Subdivision TELEOSTEI *sensu* Nelson, 2016

Order SYNBRANCHIFORMES Gosline, 1983

Family SYNBRANCHIDAE Swaison, 1838

Genus *Synbranchus* Bloch, 1795

**Type species.** *Synbranchus marmoratus* Bloch, 1795. Early Holocene–Recent. Southern Mexico to northern Argentina (Kullander, 2003; Bogan *et al.*, 2012; Peralta & Ferrero, 2018; Peralta *et al.*, 2023).

*Synbranchus* sp.

Figure 3.1

**Referred material.** Twenty vertebrae, CICYTTP-PV-P-3-103; two vertebrae, CICYTTP-PV-P-2-463.

**Stratigraphic provenance.** Level 2, CICYTTP-PV-P-3-103; level 3, CICYTTP-PV-P-2-463 (Fig. 2.2).

**Description.** Vertebrae with flat and subcircular anterior face with a small central orifice of the vertebral body (CICYTTP-PV-P-3-103). The posterior face is wider than the anterior one with a deep cavity. Parapophyses are well developed, originating close to the ventral surface of the vertebral body, and project ventrolaterally. They have walls that project anteroposteriorly to the ventral surface of the posterior face, forming a sheet. In some vertebrae, the neural spine is preserved and projects anteriorly. The neural canal is smaller than the anterior surface.

Specimen (CICYTTP-PV-P-2-463) with flat and subcircular anterior face with a small central orifice and posterior face of the vertebral body, wider than the anterior face, with a deep cone-shaped cavity. The neural arch is tall. The neural spine is not preserved in any specimen. The vertebrae (CICYTTP-PV-P-2-463) are smaller than

TABLE 1- Number of specimens of each taxon sampled from each level

|  | Level 1 | Level 2 | Level 3 |
|--|---------|---------|---------|
| <b>Fishes</b>                              |         |         |         |
| <i>Synbranchus</i> sp.                     | 0       | 20      | 3       |
| Characidae indet.                          | 18      | 2       | 2       |
| Characiformes                              | 60      | 3       | 10      |
| Cichlidae indet.                           | 3       | 1       | 0       |
| Teleostei indet.                           | 972     | 670     | 308     |
| <b>Amphibians</b>                          |         |         |         |
| cf. <i>Rhinella</i> sp.                    | 0       | 2       | 1       |
| cf. <i>Odontophrynus</i> sp.               | 0       | 0       | 1       |
| cf. <i>Physalaemus</i> sp.                 | 0       | 1       | 0       |
| Anura indet.                               | 3       | 0       | 1       |
| <b>Reptiles</b>                            |         |         |         |
| <i>Amphisbaena</i> sp.                     | 2       | 0       | 0       |
| Colubridae/Dipsadidae indet. morphotype I  | 1       | 0       | 0       |
| Colubridae/Dipsadidae indet. morphotype II | 1       | 3       | 1       |
| <b>Birds</b>                               |         |         |         |
| <i>Gallinula galeata</i>                   | 1       | 0       | 0       |
| <i>Nothura</i> cf. <i>maculosa</i>         | 0       | 1       | 0       |
| <b>Mammals</b>                             |         |         |         |
| <i>Dasypus hibridus</i>                    | 3       | 0       | 0       |
| <i>Ctenomys</i> sp.                        | 1       | 1       | 0       |
| <i>Calomys</i> sp.                         | 1       | 0       | 0       |
| <i>Necromys</i> sp.                        | 1       | 0       | 0       |
| Sigmodontinae indet.                       | 0       | 1       | 0       |
| Indet.                                     | 94      | 260     | 310     |
| Total                                      | 1163    | 963     | 637     |

CICYTTP-PV-P-3-103 and show different coloring, probably due to the taphonomical aspect.

**Comments.** According to Bogan *et al.* (2012), a platicellic vertebra with a vertebral body projected cranially and practically flat and a wider and profusely concave back are characteristics of precaudal vertebrae of Synbranchidae (Synbranchiformes). Only the genus *Synbranchus* is observed in South America (Nelson *et al.*, 2016), with three species represented, *S. marmoratus*, *S. lampreria*, and *S. madeirae*

(Froese & Pauly, 2023). In Argentina, only *S. marmoratus* is present (Mirande & Koerber, 2020) and its distribution is larger than other species of *Synbranchus* (*S. lampreria* and *S. madeirae*) (see Favorito *et al.*, 2005). However, molecular evidence suggests that the former corresponds to a species complex and its taxonomic status requires further study (Torres *et al.*, 2005). Consequently, the identification of the fossil specimens to a specific level is not currently possible.

In Argentina, *Synbranchus* is distributed throughout the

Paraguay, Paraná, Uruguay, and Río de la Plata rivers, in creeks with Atlantic slopes in Buenos Aires Province and creeks in Entre Ríos Province (Liotta, 2005; Arias *et al.*, 2013; Almirón *et al.*, 2015). It inhabits lentic and lotic environments with abundant floating vegetation and presents amphibian and fossorial habits (Favorito *et al.*, 2005; Perdices *et al.*, 2005; Almirón *et al.*, 2015).

Order CHARACIFORMES Fink & Fink, 1996

Family CHARACIDAE *sensu* Mirande, 2019

CHARACIDAE indet.

Figure 3.2

**Referred material.** Twenty-two isolated multicuspid teeth, CICYTTP-PV-P-2-465; three isolated multicuspid teeth, CICYTTP-PV-P-4-131; two isolated multicuspid teeth, CICYTTP-PV-P-4-148.

**Stratigraphic provenance.** Level 1, CICYTTP-PV-P-2-465; level 2, CICYTTP-PV-P-4-131; level 3, CICYTTP-PV-P-4-148 (Fig. 2.2).

**Description.** Small teeth, with the basal part of the crown rounded. The cusps are aligned, forming a serrated distal end. The central cusp is larger than the lateral ones.

**Comments.** The presence of well-developed multicuspid teeth is a characteristic of small characiforms commonly called "mojarras" (Characidae) (see Miquelarena, 1986; Almirón *et al.*, 2015; Nelson *et al.*, 2016). In the distal section of Paraná Basin (Entre Ríos Province), there are more than 60 species of characids (see Arias *et al.*, 2013). As the referred material corresponds to isolated teeth and Characidae comprises a great diversity, a more accurate taxonomic assignment is currently not possible.

CHARACIFORMES indet.

Figure 3.3

**Referred material.** Seventy-three isolated teeth, CICYTTP-PV-P-2-464; 16 isolated teeth, CICYTTP-PV-R-4-555; 11 isolated teeth, CICYTTP-PV-P-4-149.

**Stratigraphic provenance.** Level 1, CICYTTP-PV-P-2-464; level 2, CICYTTP-PV-R-4-555; level 3, CICYTTP-PV-P-4-149 (Fig. 2.2).

**Description.** Unicuspid teeth, labiolingually compressed with a subtriangular contour.

**Comments.** In some families of the order Characiformes, the presence of well-developed caniniform teeth is common (Nelson *et al.*, 2016). Miquelarena (1986) described this kind of teeth for the genus *Oligosarcus* (Characidae) and *Hoplias argentinensis* (= *H. malabaricus*; Erythrinidae). Considering the bibliography and comparative reference material available, we assigned them to Characiformes.

Order CICHLIFORMES Betancur-R *et al.*, 2013

Family CICHLIDAE Bonaparte, 1835

CICHLIDAE indet.

Figure 3.4

**Referred material.** Three pharyngeal jaws, CICYTTP-PV-P-2-469; upper pharyngeal jaw, CICYTTP-PV-P-3-104.

**Stratigraphic provenance.** Level 1, CICYTTP-PV-P-2-469; level 2, CICYTTP-PV-P-3-104 (Fig. 2.2).

**Description.** Three isolated and broken pharyngeal jaws without teeth (CICYTTP-PV-P-2-469). Two of them with only a part of the dentigerous area preserved, and the other one with the dentigerous area completely preserved, with the medial and lateral processes partially preserved. The alveoli of the dentigerous area are bigger in the posterior than in the anterior region.

A pharyngeal jaw is almost complete with 25 alveoli distributed in a dentigerous area (CICYTTP-PV-P-3-104). The dentigerous area with posterior alveolar bigger than anterior alveolars.

**Comments.** The morphology, size, and alveoli distribution are consistent with specimens assigned to Cichlidae observed in the osteological collections consulted and with illustrations in the literature (see Burres, 2015; Burres *et al.*, 2013, 2016). This family is commonly distributed in freshwater environments in South and Central America, Africa, and India (Nelson *et al.*, 2016). In Entre Ríos Province, there are 16 species that inhabit lentic and lotic environments, such as creeks, lagoons, and sporadic freshwater courses with abundant floating vegetation (Arias *et al.*, 2013; Almirón *et al.*, 2015).

TELEOSTEI indet.

Figure 3.5

**Referred material.** Two hundred and fourteen isolated teeth, CICYTTP-PV-R-2-459; 239 vertebrae, CICYTTP-PV-P-2-470; 350 fragments of scales, CICYTTP-PV-2-467; 169 fragments of spines, CICYTTP-P-2-466; 102 isolated teeth, CICYTTP-PV-P-4-135; 165 isolated vertebrae CICYTTP-PV-P-4-136; 324 fragments of scales, CICYTTP-PV-P-4-137; 79 fragments of spines, CICYTTP-PV-P-4-138; 92 isolated teeth, CICYTTP-PV-P-4-151; 52 vertebrae, CICYTTP-PV-P-4-152; 20 fragments of spines, CICYTTP-PV-P-4-153; 144 fragments of scales, CICYTTP-PV-P-4-154.

**Stratigraphic provenance.** Level 1, CICYTTP-PV-R-2-459, CICYTTP-PV-P-2-470, CICYTTP-PV-2-467, CICYTTP-P-2-466; level 2, CICYTTP-PV-P-4-135, CICYTTP-PV-P-4-136, CICYTTP-PV-P-4-137, CICYTTP-PV-P-4-138, CICYTTP-PV-P-4-139; level 3, CICYTTP-PV-P-4-151, CICYTTP-PV-P-4-152, CICYTTP-PV-P-4-153, CICYTTP-PV-P-4-154 (Fig. 2.2).

**Description.** CICYTTP-PV-R-2-459, CICYTTP-PV-P-4-135 and isolated unicuspid, bicuspid, and molariform teeth with a diameter less than 2 mm. Other specimens of the referred material are fragmentary.

**Comments.** The morphology of the teeth is similar to that of dentary, premaxillary, and pharyngeal jaw teeth of many Actinopterygii taxa observed in collections and described in the literature (e.g., Cichlidae; Burres *et al.*, 2016). The other specimens are clearly referable to Actinopterygii, but no other consideration is possible due to their fragmentary state.

Class AMPHIBIA Linnaeus, 1758

Order ANURA Fischer von Waldheim, 1813

Family BUFONIDAE Gray, 1825

Genus *Rhinella* Fitzinger, 1826

**Type species.** *Bufo (Oxyrhynchus) proboscideus* Spix, 1824. Late Oligocene–Recent. Southern USA to southern South America (Báez & Nicoli, 2004; Frost, 2023).

cf. *Rhinella* sp.

Figure 3.6–3.7

**Referred material.** Presacral vertebra II, CICYTTP-PV-AN-3-106; left coracoid, CICYTTP-PV-AN-3-105.

**Stratigraphic provenance.** Level 2, CICYTTP-PV-AN-3-105 and CICYTTP-PV-AN-3-106 (Fig. 2.2).

**Description.** A procelic presacral vertebra (CICYTTP-PV-AN-3-106) with the right transverse process absent and the distal section of the left one broken. The centrum is dorsoventrally flattened and smooth ventrally. In the anterior view, the cotyle is wider than longer, with an oval contour; the prezygapophyses are vertically oriented. In the posterior view, the condyle has an oval contour; the postzigapophyses have a subcircular contour and are ~45° oriented. In the dorsal view, the neural spine is located in the posterior margin of the neural arch and the transverse process preserved is laterally oriented and distally expanded.

The left coracoid (CICYTTP-PV-AN-3-105) is slightly curved with a sternal portion expanded and slightly broken. The glenoidal portion is expanded dorsoventrally. The articular glenoidal face has a semicircular contour. In ventral view, the anterior margin is more concave than the anterior one.

**Comments.** According to the characteristics of the specimens mentioned above, they can be assigned to Bufonidae (Pramuk, 2006; Araújo-Junior & Moura, 2014; Pérez-Ben *et al.*, 2019b). The specimens referred are indistinguishable from the genus *Rhinella* (see Supplementary Data S1). Considering that *Rhinella* is the most diverse genus of toads in Argentina (see Vaira *et al.*, 2012) and the fragmentary character of the referred material, the identification to a specific level is not possible.

Three species of the genus *Rhinella*, *R. arenarum*, *R. dorbignyi* (=*R. fernandezae*), and *R. diptycha* (=*R. scheneideri*) inhabit Entre Ríos Province (Vaira *et al.*, 2012; Frost, 2023). These species, with some variations, prefer open habitats and grasslands, living both in dry and humid environments, close to sporadic and permanent lagoons and creeks (Cei, 1980; IUCN SSC Amphibian Specialist Group, 2023a, 2023b, 2023c).

Family ODONTOPHRYNIDAE

Pyron & Wiens, 2011

Genus *Odontophrynus* Reinhardt & Lütken, 1862

**Type species.** *Odontophrynus cultripes* Reinhardt & Lütken, 1862. Middle Pleistocene–Recent. Southern and eastern South America (Turazzini *et al.*, 2016; Frost, 2023).

cf. *Odontophrynus* sp.

Figure 3.8

**Referred material.** Right femur, CICYTTP-PV-AN-2-468.

**Stratigraphic provenance.** Level 3 (Fig. 2.2).

**Description.** The femur is broken in its proximal and distal ends. It is relatively long, robust, and slightly sigmoid, with a long femoral crest and an incipient medial lamina.

**Comments.** This specimen and the specimens of the genus *Odontophrynus* share the presence of a long and simple femoral crest, an incipient medial lamina, and a slightly sigmoid body (Turazzini, 2020). The fragmentary state of the fossil prevents a more accurate taxonomic assignment.

In Argentina, the genus *Odontophrynus* is represented by six species, whereas only one of them, *Odontophrynus asper*, is found in Entre Ríos Province (Vaira *et al.*, 2012; Frost, 2023). This species is distributed in central and northern Argentina, Uruguay, southern Paraguay, and southeastern Brazil. It inhabits forests, savannahs, grasslands, and wetlands (Frost, 2023; IUCN SSC Amphibian Specialist Group, 2023d).

Family LEPTODACTYLIDAE Werner, 1896

Genus *Physalaemus* Fitzinger, 1826

**Type species.** *Physalaemus cuvieri* Fitzinger, 1826. Late Pleistocene –Recent. Northern and central Argentina; eastern Bolivia; Paraguay; Uruguay; Brazil and the Guianas; lowlands of southern Venezuela; and llanos of southeastern Colombia (Turazzini, 2020; Frost, 2023).

cf. *Physalaemus* sp.

Figure 3.9

**Referred material.** Left radio-ulnae, CICYTTP-PV-AN-2-461.

**Stratigraphic provenance.** Level 2 (Fig. 2.2).

**Description.** A robust left radio-ulnae with a well-developed olecranon process and with radio and ulnar processes well differentiated, each one with a slightly-developed crest.

**Comments.** This specimen and specimens of genus *Physalaemus* share the presence of a radio-ulnae with a

well-developed olecranon process and a robust body. Turazzini (2020) mentioned that the presence of crests developed in each epiphysis is present in the species *P. biligonigerus*. According to Vaira *et al.* (2012), the genus is represented by five species in Entre Ríos Province: *Physalaemus albonotatus*, *P. biligonigerus*, *P. henselii*, *P. riograndensis*, and *P. santafecinus*. As no other species inhabiting the area has been observed, we assigned this species to a genus level.

*Physalaemus* spp. inhabit grasslands, forests near watercourses, and wetlands in northeastern Argentina (Cei, 1980; Aquino *et al.*, 2004; Lavilla *et al.*, 2004; Silvano *et al.*, 2004; Kwet *et al.*, 2010; Frost, 2023).

ANURA indet.

Figure 3.10

**Referred material.** Presacral vertebrae, CICYTTP-PV-AN-3-107 (Fig. 3.10); humerus, CICYTTP-PV-AN-3-108; two isolated phalanges, CICYTTP-PV-AN-2-462.

**Stratigraphic provenance.** Level 1, CICYTTP-PV-AN-2-462 and CICYTTP-PV-AN-3-108; level 3, CICYTTP-PV-AN-3-107 (Fig. 2.2).

**Description.** An incomplete presacral vertebra (CICYTTP-PV-AN-3-107) with a smooth vertebral centrum, cotyle, and condyle dorso-ventrally flattened, and a well-defined precondilar constriction. Although transverse processes are not completely preserved, it is possible to observe that they are cylindrical in cross-section and posteriorly oriented. The postzygapophyses shows a rectangular contour. The specimen presents digestion signs.

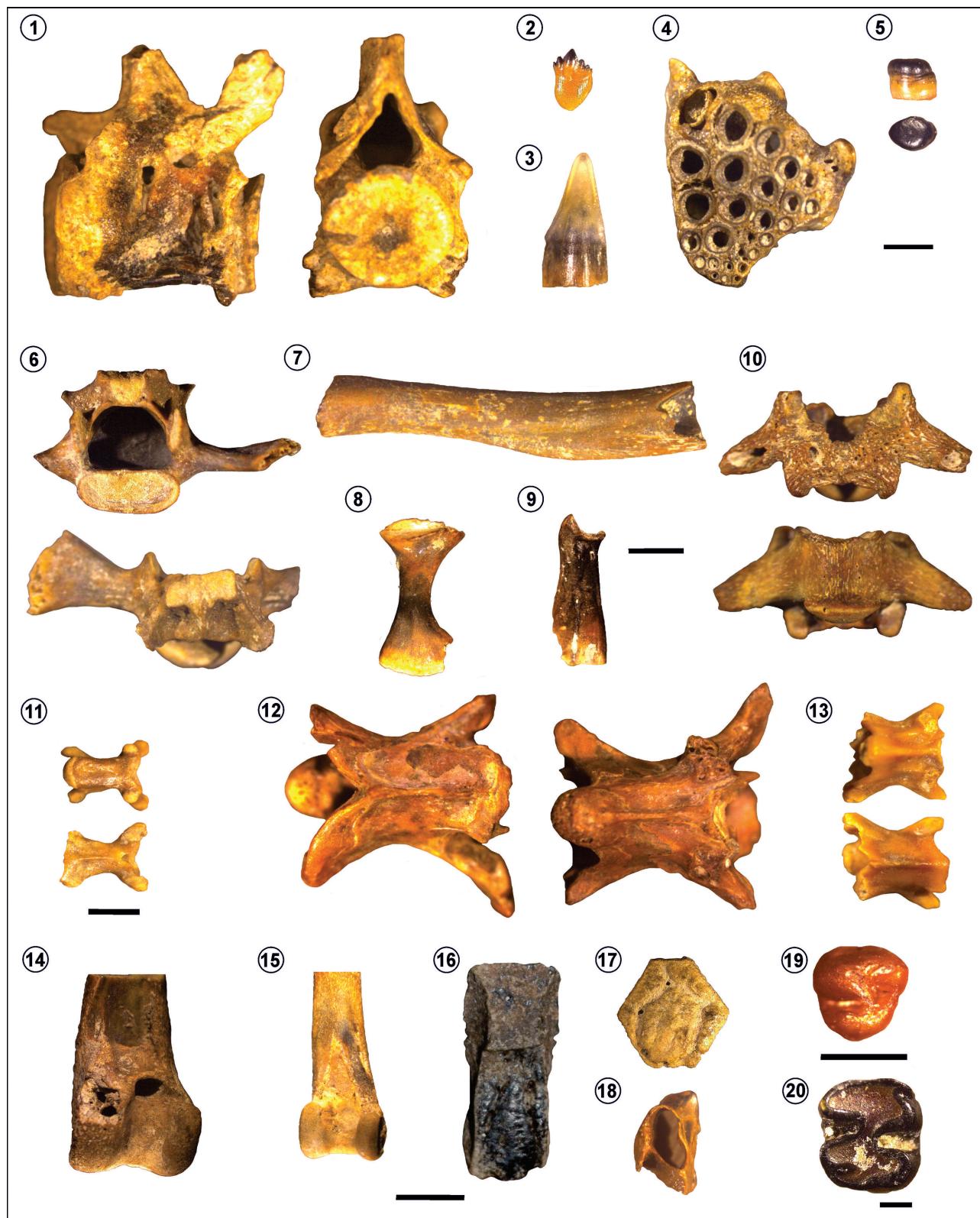
The specimen CICYTTP-PV-AN-3-108 corresponds to a fragment of a distal diaphysis of a humerus and CICYTTP-PV-AN-2-462 are two isolated phalanges, dorso-ventrally flattened, without diagnostic characteristics to mention.

**Comments.** The specimens described are referred to Anura, based on osteological comparison (Bailon, 1999; Turazzini, 2020). The fragmentary condition of the referred material does not allow a more accurate taxonomic assignment.

Class REPTILIA Laurenti, 1768

Superorder LEPIDOSAURIA Heckel, 1866

Order SQUAMATA Oppel, 1811



Infraorder AMPHISBAENIA Gray, 1844

Family AMPHISBAENIDAE Gray, 1865

Genus *Amphisbaena* Linnaeus, 1758

**Type species.** *Amphisbaena fuliginosa* Linnaeus, 1758. Early Pliocene–Recent. Panamá, west Antilles, and South America (Brizuela & Albino, 2012; Midtgaard, 2023; Uetz *et al.*, 2023).

*Amphisbaena* sp.

Figure 3.11

**Referred material.** Two posterior trunk vertebrae, CICYTTP-PV-R-3-109.

**Stratigraphic provenance.** Level 1 (Fig. 2.2).

**Description.** Two posterior trunk vertebrae (CICYTTP-PV-R-3-109), procelous, small, elongated, and slightly broken in the posterior margin of the neural arch. In the anterior view, the neural arch is low; the cotyle is dorsoventrally flattened, with an oval contour; the prezygapophyses are dorsally oriented. In the posterior view, the condyle is dorsoventrally flattened; the articulation zygantrum-zygosphene is absent. In the dorsal view, the prezygapophyses are anteriorly oriented, and have an oval contour; the prezygapophysial process is present; both specimens have an incipient neural spine. In the ventral view, the centrum is smooth, with two lateral foramina in the anterior part. In the lateral view, the synapophyses are subspherical.

**Comments.** The absence of the zygantrum-zygosphene articulation and the presence of a prezygapophysial process allow the assignment of CICYTTP-PV-R-3-109 to *Amphisbaenia* (Hoffstetter & Gasc, 1969). The specimens are procelous, with depressed cotyle and condyle and without precondilar neck. These characteristics are common in trunk vertebrae. The narrow neural spine is characteristic of anterior trunk vertebrae (Hoffstetter & Gasc 1969),

having a smooth and slightly concave dorsal surface of the neural arch, different from *Lepostemon* genus, which has a grooved surface and denticulated posterior margin of the neural arch (Kearney, 2003). Also, both specimens have sizes that exclude them from the genus *Anops* (Torres & Montero, 1998).

In Argentina, eight species of the genus *Amphisbaena* have been recognized: *A. angustifrons*, *A. bolivica*, *A. borelli*, *A. heterozonata*, *A. hiata*, *A. mertensi*, *A. plumbea*, and *A. prunicolor*. The only species of the genus in Entre Ríos Province is *A. angustifrons* (Avila *et al.*, 2013). It inhabits grasslands and savannahs in Buenos Aires, southern Santa Fe, Paraná Delta System, Córdoba, and eastern Jujuy provinces (Montero *et al.*, 2016).

Suborder SERPENTES Linneaus, 1758

Superfamily COLUBROIDEA Oppel, 1811

Family COLUBRIDAE Oppel, 1811 or

DIPSADIDAE Bonaparte, 1838

COLUBRIDAE/DIPSADIDAE indet.

Morphotype I

Figure 3.12

**Referred material.** A trunk vertebra, CICYTTP-PV-R-3-110.

**Stratigraphic provenance.** Level 1 (Fig. 2.2).

**Description.** A vertebra with a centrum longer than wider, the neural canal is high and a little wider than the cotyle. On both sides of the cotyle, the presence of paracotylar foramina is observed and the condyle is subcircular. The neural spine is incomplete, but it is possible to infer significant anteroposterior development starting behind the zygosphene and ending just at the posterior edge of the neural arch. The zygosphene is thin and the zygantrum has two well-developed zygomatic articular facets. The left

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**Figure 3. 1, CICYTTP-PV-P-3-103, right lateral and anterior views. 2, CICYTTP-PV-P-2-465, labial view. 3, CICYTTP-PV-P-2-465, labial view. 4, CICYTTP-PV-P-3-104, occlusal view. 5, CICYTTP-PV-R-2-459, lateral and occlusal views; scale 1–5= 1 mm. 6, CICYTTP-PV-AN-3-106, anterior and dorsal views. 7, CICYTTP-PV-AN-3-105, ventral view. 8, CICYTTP-PV-AN-2-468, medial view. 9, CICYTTP-PV-AN-2-461, medial view. 10, CICYTTP-PV-AN-3-107, dorsal and ventral views; scale 6–10= 2 mm. 11, CICYTTP-PV-R-3-109, ventral and dorsal views. 12, CICYTTP-PV-R-3-110, ventral and dorsal views. 13, CICYTTP-PV-R-3-111, ventral and dorsal views; scale 11–13= 1 mm. 14, CICYTTP-PV-A-2-457, anterior view. 15, CICYTTP-PV-A-2-458, anterior view. 16, CICYTTP-PV-M-2-452, dorsal view of movable plate. 17, CICYTTP-PV-M-2-452, fixed plate in dorsal view. 18, CICYTTP-PV-M-2-453, occlusal view; scale 14–18= 5 mm. 19, CICYTTP-PV-M-2-455, occlusal view; scale= 0.5 mm. 20, CICYTTP-PV-M-2-454, occlusal view; scale= 1 mm.**

prezygapophyseal process is broken. The right prezygapophyseal process is preserved, projected anterolaterally, and has an acute apex. The prezygapophyses have an oval and elongated contour and the postzygapophyses have an oval contour. The hemal keel is thin, well-defined along the entire centrum, and widened in the anterior part; the lateral margins are straight and the diapophyses and parapophyses are broken. Nevertheless, it is possible to determine that they were separated. There is no evidence of a well-defined precondylar constriction in the specimen.

**Comments.** The zygosphene-zigantrum articulation and well-developed prezygapophyseal processes are characteristics of snake vertebrae (Hoffstetter & Gasc, 1969). The centrum is longer than it is wider. The thin zygosphene, zygosphene-zigantrum joint, well-developed prezygapophyseal processes, differentiated diapophysis and parapophysis, and paracotylar foramina permit the assignment of this specimen to Colubroidea (Hoffstetter & Gasc, 1969; Albino & Montalvo, 2006). The absence of hypapophysis, haemapophyses, and lymphapophyses allow the assignment of the vertebra to a trunk region (Hoffstetter & Gasc, 1969). The absence of the hypoapophysis excludes the assignment of this specimen to Viperidae and Elapidae (Hoffstetter & Gasc, 1969; Albino & Montalvo, 2006). Thus, CICYTTP-PV-R-3-110 could be assigned to the Colubridae or Dipsadidae family, both present in Argentina (Williams *et al.*, 2021). Regarding diversity, there are 36 species registered in Entre Ríos Province belonging to the aforementioned families (Williams *et al.*, 2021).

COLUBRIDAE/DIPSADIDAE indet.

Morphotype II

Figure 3.13

**Referred material.** Trunk vertebra, CICYTTP-PV-R-4-553; three trunk vertebrae, CICYTTP-PV-R-3-111; trunk vertebra, CICYTTP-PV-R-3-858.

**Stratigraphic provenance.** Levels 1, CICYTTP-PV-R-4-553; level 2, CICYTTP-PV-R-3-111; level 3, CICYTTP-PV-R-3-858 (Fig. 2.2).

**Description.** All vertebrae are short and small, with the vertebral centrum longer than wider. The zygosphene is preserved in five specimens. It is thin, has a slightly straight

outline in the dorsal view, and is ventrolaterally oriented. The zygosphene-zigantrum joint is present in all specimens. The condyle and cotyle are circular and the cotyle projects caudally in all specimens. All vertebrae have an incipient precondylar constriction. In the ventral view, the hemal keel is prominent and well defined along the centrum, with subcentral grooves developed on each side of the hemal keel, and extending from the ventral margin of the cotyle to beyond the midline of the vertebral centrum. An anterior divergence of the vertebral centrum gives a slightly triangular outline. The neural canal is high and wider than the cotyle, the neural spines are broken in all vertebrae, but their base is uniform in width, and it extends from the posterior edge of the neural arch to behind the zygosphene. The vertebrae show paracotylar foramina on both sides of the cotyle and the prezygapophyseal process is not preserved. The prezygapophyses are only preserved in one specimen with an oval contour. The diapophyses and parapophyses are separated.

**Comments.** The presence of the zygosphene-zigantrum joint and zygosphenes ventrolaterally oriented indicate that CICYTTP-PV-R-4-553, CICYTTP-PV-R-3-111, and CICYTTP-PV-R-3-858 correspond to serpent vertebrae (Hoffstetter & Gasc, 1969; Conrad, 2008). According to Albino & Montalvo (2006), the Superfamily Colubroidea shows delicate vertebrae, thin zygosphene, differentiated diapophysis and parapophysis, paracotylar foramina, thin neural spine, and prezygapophyseal process. The presence of a hemal keel excludes the assignment to Viperidae and Elapidae (Hoffstetter & Gasc, 1969; Albino & Montalvo, 2006) and indicates that it corresponds to the trunk region of a taxon of Colubridae or Dipsadidae. These specimens present the same classification problem as CICYTTP-PV-R-3-110.

The specimens CICYTTP-PV-R-4-553, CICYTTP-PV-R-3-111, and CICYTTP-PV-R-3-858 are considerably smaller than CICYTTP-PV-R-3-110. For that reason, it can be inferred that the latter probably belongs to different taxa.

Class AVES Linnaeus, 1758

Order GRUIFORMES Bonaparte, 1854

Family RALLIDAE Refinesque, 1815

Genus *Gallinula* Brisson, 1760

**Type species.** *Gallinula chloropus* Linnaeus, 1758. Late Pleistocene–Recent. Southern USA to southern South America (Pampa Region) (Olson, 1977; Taylor, 1996).

*Gallinula galeata* (Linnaeus, 1758)

Figure 3.14

**Referred material.** Right tibiotarsus, CICYTTP-PV-A-2-457.

**Stratigraphic provenance.** Level 1 (Fig. 2.2).

**Description.** Fragment of a distal end of a right robust tibiotarsus. In the anterior view, a very wide supratendinal bridge is observed. The tendinal groove is deep, wide, and well-marked. The groove for *peroneus profundus* is well marked and begins just where the supratendinal bridge ends. The external condyle is big and approximately twice as wide as the internal condyle, which is broken at its proximal portion. The internal condyle shows a notch that extends to its midline. The anterior intercondylar fossa is deep but narrow, longer than wider, and between the supratendinal bridge and the external condyle, there is a well-developed triangularly contoured protuberance. In the posterior view, the posterior intercondylar sulcus is longer than wider. In the lateral view, the lateral condyle has a smooth impression.

**Comments.** According to Livezey (1998), a deep tendinal groove, a rounded lateral condyle, an internal condyle, slightly notched distally, a well-developed external ligamental prominence, a slightly-developed and caudally-rounded trochlea *cartilaginis tibialis*, an external condyle more cranially prominent than an internal condyle are characteristics of genus *Gallinula*. The fossil is indistinguishable from specimens of the species *Gallinula galeata* (see Supplementary Data S1).

*Gallinula galeata* is distributed throughout the central and northwestern region of Argentina, from Jujuy to the northernmost part of La Pampa provinces (Taylor, 1996) and it is the only species with South American distribution (Remsen *et al.*, 2023). It frequents a wide range of natural and artificial freshwater wetlands with lush emergent vegetation, rivers, streams, canals, lakes, ponds, and swamps. It is tolerant to a wide variety of climatic conditions but vulnerable to freezing temperatures (Taylor, 1996).

Order TINAMIFORMES Huxley, 1872

Family TINAMIDAE Gray, 1840

Genus *Nothura* Wagler, 1827

**Type species.** *Tinamus boraquira* Spix, 1825. Late Miocene–Recent. Eastern and central South America, occupying the Center-South of Brazil, Uruguay, and up to the northern limits of Patagonia, Argentina (Cabot, 1992; Cenizo *et al.*, 2012).

*Nothura* cf. *maculosa*

Figure 3.15

**Referred material.** Left tibiotarsus, CICYTTP-PV-A-2-458.

**Stratigraphic provenance.** Level 2 (Fig. 2.2).

**Description.** In the anterior view of the tibiotarsus, the distal end shows the tendinal groove in medial position. The external condyle is slightly wider and larger than the internal condyle. In the lateral view, the external condyle is oval and the internal condyle has a rounded contour. The anterior intercondylar fossa is well marked and wide. In the lateral view, a well-developed crest along the entire edge of the medial condyle is noticeable. The supratendinal bridge is not preserved. The epicondyle is developed and exposed in anterior view.

**Comments.** The external condyle, larger than the internal one, and the tendinal groove in medial position are characteristics of Tinamidae (Bertelli, 2002). The internal condyle, slightly larger than the external one, indicates that the specimen does not belong to the genera *Crypturellus*, *Rhynchotus*, *Eudromia*, or *Tinomotis*, for which this condition is more conspicuous (Bertelli, 2002). The first of the aforementioned conditions is present in the genus *Nothura*, a common genus represented in the north and east of Argentina by *N. maculosa* and *N. darwinii* (see Remsen *et al.*, 2023). CICYTTP-PV-A-2-458 was compared with the available comparative material (*N. maculosa*) and resulted indistinguishable. As the specimen is incomplete, it can be tentatively assigned as *N. maculosa*.

*Nothura maculosa* is distributed in the east of Brazil, Uruguay, Paraguay, and from almost all the north of Argentina to the northern limits of Patagonia. It has a subtropical distribution and inhabits temperate areas, lowlands, grasslands, savannahs, and semi-arid environments (Cabot, 1992).

Class MAMMALIA Linnaeus, 1758

Superorder XENARTHRA Cope, 1889

Order CINGULATA Illiger, 1811

Family DASYPODIDAE Gray, 1821

Genus *Dasypus* Linnaeus, 1758

**Type species.** *Dasypus novemcinctus* Linnaeus, 1758. Pleistocene–Recent. Southern Paraguay, southern Brazil, Uruguay, and north-eastern Argentina including Entre Ríos and Corrientes provinces, and the southwest of the province of Buenos Aires (Vizcaino *et al.*, 1995; Abba & Superina, 2016; Abba *et al.*, 2019).

*Dasypus hybridus* Desmarest, 1804

Figure 3.16–3.17

**Referred material.** A movable and two fixed osteoderms, CICYTTP-PV-M-2-452.

**Stratigraphic provenance.** Level 1 (Fig. 2.2).

**Description.** The movable osteoderm is antero-posteriorly elongated, with a central figure delimited by two diverging sulci with three glandular foramina conferring a lageniform shape. On the posterior edge, there are four piliferous foramina. It is 14 mm long and 5 mm wide.

One of the fixed osteoderms is complete. It is hexagonal in shape with a subcircular central figure that occupies almost the entire surface. This figure is surrounded by five peripheral figures, with small perforations in the intersections of the figure grooves. The second fixed osteoderm is hexagonal in shape and partially broken. The central figure occupies almost the entire surface, and it is surrounded by four peripheral figures. In the grooves between the peripheral figures and the central figure, there are four glandular foramina. The dimensions of the fixed osteoderm (based on the complete specimen) is 6 mm long and 5 mm wide.

**Comments.** According to Soibelzon *et al.* (2015), fixed osteoderms with hexagonal contours with a large central figure occupying almost the entire surface and small peripheral figures, and movable osteoderms with a central figure delimited by two diverging sulci towards the back, with a lageniform appearance are characteristics of species of the subfamily Dasypodinae, currently represented by the genus *Dasypus* (Teta *et al.*, 2018). In north-western Argentina, there are currently two species: *D. hybridus* and *D. novemcinctus* (Abba *et al.*, 2019; Varela *et al.*,

2019). In the latter, the movable osteoderm is proportionally more elongated than in *D. hybridus* (see Vickaryous & Hall, 2006; Soibelzon *et al.*, 2015; Fig. 5). In addition, the measurements obtained of the elements here described are similar to those of *D. hybridus* (Soibelzon *et al.*, 2015). The fixed osteoderms are similar to the posterior ones in the *D. hybridus* carapaces observed, thus, it can be inferred that this specimen could correspond to this part of the carapace.

*Dasypus hybridus* is distributed from southern Paraguay, southern Brazil, Uruguay, and north-eastern Argentina including Entre Ríos and Corrientes provinces, to the southwest of the Buenos Aires Province. It inhabits grasslands in temperate-humid areas (Abba & Superina, 2016; Abba *et al.*, 2019).

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOMORPHA Brandt, 1855

Superfamily OCTODONTOIDEA Waterhouse, 1839

Family CTENOMYDAE Lesson, 1842

Genus *Ctenomys* de Blainville, 1826

**Type species.** *Ctenomys brasiliensis* de Blainville, 1826. Pliocene–Recent. The genus is distributed from Peruvian highlands and the Brazilian state of Rondônia in the north (11°S) to Tierra del Fuego Province in the south, and from the Atlantic to the west coast (Bidau, 2015; Maestri & Patterson, 2021).

*Ctenomys* sp.

Figure 3.18

**Referred material.** Fragment of left mandible, CICYTTP-PV-M-2-453; right pelvic girdle, CICYTTP-PV-M-3-112.

**Stratigraphic provenance.** Level 1, CICYTTP-PV-M-2-453; level 2, CICYTTP-PV-M-3-112 (Fig. 2.2).

**Description.** The fragment of the left mandible preserves an alveolus kidney-shaped of p4 (CICYTTP-PV-M-2-453).

A right pelvic girdle fragment (CICYTTP-PV-M-3-112) with part of the ilium, the horizontal ramus, and part of the descending ramus is preserved. The acetabulum is subcircular. The border of the acetabulum in the pubis is broken. The iliac tubercle is low and poorly developed.

**Comments.** The kidney-shaped alveolus of CICYTTP-PV-M-2-453 allows the assignment to the genus *Ctenomys* (see Ortiz *et al.*, 2011, fig. 2; 2012, fig. 9; Scheifler *et al.*, 2012,

fig. 2; Udrizar Sauthier *et al.*, 2020). The poorly-developed iliac tubercle and the size of the specimen are consistent with specimens of the genus *Ctenomys* observed in the available comparative material. The fragmentary state of the specimens and the diversity of the genus prevents a more specific assignment.

*Ctenomys* is distributed from the south of Perú to the south of Argentina, including northern Tierra del Fuego, Antártida e Islas del Atlántico Sur Province, and from sea level to 4,000 meters (Freitas, 2016; Maestri & Patterson, 2021). In Entre Ríos Province there are two species of *Ctenomys*, *C. rionegrensis* and *C. pearsoni* (Tomasco & Caraballo, 2019a, 2019b). These inhabit sandy patches distributed among grasslands, forests, and dunes. Only *C. rionegrensis* inhabits southwestern Entre Ríos Province (Tomasco & Caraballo, 2019a).

Order CRICETIDAE Fischer, 1817

Suborden MYOMORPHA Brants, 1855

Superfamilia MUROIDEA Illiger, 1811

Subfamily SIGMODONTINAE Wagner, 1843

Genus *Calomys* Waterhouse, 1837

**Type species.** *Mus bimaculatus* Waterhouse, 1837. Early Pleistocene –Recent. Inhabits dry vegetation areas and has a wide distribution in southern South America, from the Venezuelan Llanos to the southern limit of the Argentinian Chaco, southern Brazil, and, in northern South America, in the Llanos of Colombia and Venezuela and islands of the Venezuelan coast (Pardiñas *et al.*, 2002; Almeida *et al.*, 2007; Salazar-Bravo, 2015).

*Calomys* sp.

Figure 3.19

**Referred material.** An isolated left m3, CICYTTP-PV-M-2-455.

**Stratigraphic provenance.** Level 1 (Fig. 2.2).

**Description.** In the occlusal view, it has a subcircular outline. Metaconid and protoconid are opposite. The entoconid and hypoconid are fused. The molar has three roots preserved and two are complete.

**Comments.** The specimen described shows a circular occlusal contour, similar to that of the *Calomys* specimens observed in collections and in the literature (Ortíz *et al.*,

2012; Pardiñas *et al.*, 2014). The isolated condition of the specimen does not allow the assignment to a species level.

The genus has a wide distribution in Argentina, from southern Patagonia in northern Tierra del Fuego, Antártida e Islas del Atlántico Sur provinces to northern Jujuy Province. Three species inhabit Entre Ríos Province: *Calomys laucha*, *C. musculinus*, and *C. callidus*. Only *C. laucha* and *C. musculinus* are present in the northwest of Entre Ríos (Gómez Villafañe *et al.*, 2019).

Genus *Necromys* Ameghino, 1889

**Type species.** *Necromys conifer* Ameghino, 1889. Pleistocene–Recent. Inhabit open areas north and south of Amazonia and in Andean grasslands (D'Elía *et al.*, 2008; Teta *et al.*, 2013; Stutz *et al.*, 2017; Boroni *et al.*, 2020).

*Necromys* sp.

Figure 3.20

**Referred material.** An isolated right m2, CICYTTP-PV-M-2-454.

**Stratigraphic provenance.** Level 1 (Fig. 2.2).

**Description.** An isolated and worn right m2. In occlusal view, it shows a rectangular outline. The molar cusps are alternated. The hypoflexid and mesoflexid are well marked and deep. The posterior cingulum is well developed and is parallel to hypoconid and entoconid, with a well-marked and deep mesolophid.

**Comments.** The specimen described shows a circular occlusal contour, similar to that of the *Necromys* specimens observed in collections and in the literature (Teta *et al.*, 2013; Stutz *et al.*, 2017; Boroni *et al.*, 2020). The isolated condition of the specimen does not allow the assignment to a species level.

In Argentina there are six species, *Necromys amoenus*, *N. lactens*, *N. lasiurus*, *N. lenguarum*, *N. lilloi*, and *N. obcurus* (Bauni *et al.*, 2021) and they are characteristic of grasslands. Particularly, the species close to the study area, *N. lasarius* and *N. obcurus*, also frequent gallery forests and areas near lagoons and water courses (Pardiñas *et al.*, 2017).

In Argentina, the fossil record of the genus *Necromys* covers the northeast of the country (Tucumán Province) and center (Buenos Aires Province), from the Late Pleistocene–

Late Holocene period (Teta *et al.*, 2013; Pardiñas *et al.*, 2015). The specimen described here correspond to the first fossil record of the genus in a paleontological site in Entre Ríos Province. Furthermore, it is a contribution to the paleobiogeography of the genus.

SIGMODONTINAE indet.

**Referred material.** Isolated left m2, CICYTTP-PV-M-2-456.

**Stratigraphic provenance.** Level 2, CICYTTP-PV-M-2-456 (Fig. 2.2).

**Description.** A left m2 with a rectangular outline. The molar cuspids are opposite. The posterior cingulum is short, with an oval contour and a well-developed posterolophid.

**Comments.** The shape and size of the specimen indicate that they can be assigned to Sigmodontinae (see Ortíz *et al.*, 2011, 2012; Udrizar Sauthier *et al.*, 2020). The isolation of the specimens prevents a more specific assignment.

## DISCUSSION

### Paleontological remarks on the Molino Doll locality

Before this study, there have been no Quaternary ichthyological records in paleontological sites from Entre Ríos Province (see Ferrero *et al.*, 2017, 2019). There have been records only of siluriform and characiform fishes in archaeological sites, dated >3,000  $^{14}\text{C}$  years BP (Late Holocene) (Bonomo *et al.*, 2010; Ottalagano *et al.*, 2015; Bastourre & Apolinaire, 2017; among others). These remains correspond mainly to Siluriformes and Characiformes fishes that were consumed as part of the diet of aboriginal groups in the area (Bonomo, 2012). The Quaternary fossil records of synbranchids in Argentina are scarce, represented by few fossil remains from the Late Pleistocene in Buenos Aires Province and the Early Holocene in Formosa Province (Bogan *et al.*, 2012 and references therein). The remains described here and assigned to *Synbranchus* sp. constitute the first fossil record from Quaternary in Entre Ríos and contribute to the knowledge of its paleodistribution during the Early Holocene, extending it to the southern Mesopotamian Region of Argentina (northwestern Entre Ríos Province). The other fish taxa studied and described correspond to Characidae, Cichlidae, Characiformes, and other indeterminate Teleostei and constitute the first

non-archaeological paleoichthyological record of these taxa from Quaternary in Mesopotamian Region.

In South America, the anuran fossil records are among the most incomplete and sporadic among vertebrates, characterized by disarticulated and fragmentary remains (Barcelos & dos Santos, 2022). In Argentina, the Quaternary fossil records are mainly in Buenos Aires Province and correspond to hyperossified cranial and postcranial bones of Bufonidae and Ceratophryidae, and other groups less represented as Hylidae, in sediments from Middle and Late Pleistocene (Turazzini, 2020; Barcelos & dos Santos, 2022; and references therein). The genus *Rhinella* is recorded in the Early–Late Pliocene and the Early–Late Pleistocene of Buenos Aires Province, the Pliocene of Córdoba Province, and Late Pliocene of Jujuy Province (Ortíz *et al.*, 2012; Pérez-Ben *et al.*, 2014, 2019a, 2019b; Cruz *et al.*, 2017; Turazzini, 2020). Thus, the specimens described and tentatively assigned in this work represent the first ones for the Entre Ríos Province and also the first ones for the Early Holocene in Argentina. Regarding the genus *Odontophrynus* and *Physalaemus*, they are recorded in the Middle–Late Pleistocene and in the Late Pleistocene of Buenos Aires Province, respectively (Turazzini *et al.*, 2016; Turazzini, 2020). Thus, the specimens reported and described herein are the first records of these taxa for Entre Ríos Province and for the Early Holocene in Argentina. In this context, these records constitute an important contribution to the paleoherpetological Quaternary knowledge of the anuran diversity that inhabited the region (southern Mesopotamian, Argentina). Besides, it is important due to the scarce fossil anuran reports from the beginning of the Holocene (see Barcelos & dos Santos, 2022).

In Argentina, the fossil records of *Amphisbaena* were reported for the Pliocene to Late Pleistocene (Torres & Montero, 1998; Scanferla *et al.*, 2006; Brizuela & Albino, 2012), all of them in Buenos Aires Province. Other amphisbaenid remains, assigned to *Anops kingii*, were recovered from the Late Pleistocene in northwestern Buenos Aires Province (Agnolin & Jofré, 2011). Regarding Holocene records, *Amphisbaena* was recorded from an archaeological site in northwestern Argentina (Kligman & Albino, 2007 in Agnolin & Jofré, 2011). Thus, the record of *Amphisbaena* sp. reported here is the first one for Entre

Ríos Province and constitutes a contribution to the paleobiogeographic distribution of the genus with scarce fossil records, extending it to the southern Mesopotamian Region.

There are numerous fossil records of snakes in the Pampean Region (Albino & Brizuela, 2014). The oldest records of colubrids come from the Pliocene (Albino & Quintana, 1992; Scanferla & Agnolin, 2016). Several Early to Middle Pleistocene records were also obtained (Scanferla *et al.*, 2005, 2009; Scanferla, 2006; Brizuela & Albino, 2012; Brizuela *et al.*, 2015). Holocene snake fossil records come from archaeological sites such as the Cueva Tixi (Buenos Aires Province), corresponding to the Late Pleistocene–Early Holocene period (Albino, 1999). Thus, the fossils reported here constitute the first Quaternary fossil record of colubrids outside of Buenos Aires Province. Also, these specimens contribute to the Quaternary herpetological fossil record knowledge of Entre Ríos, restrictive to Testudines at present (see Ferrero *et al.*, 2019, 2022).

The bird's fossil records in Entre Ríos Province come from Neogene units corresponding to the Late Miocene (Diederle & Noriega, 2013; Schmidt *et al.*, 2020), from the Salto Ander Egg Formation (Late Pleistocene) (Noriega & Tonni, 2007; Ferrero *et al.*, 2017) and from archaeological sites (Bonomo *et al.*, 2011; Bastourre & Apolinaire, 2017; among others). The specimens described here constitute the first records of birds from the Holocene in Entre Ríos Province in a non-archaeological context.

Concerning the mammalian fossil records, remains of *Dasypus hybridus* are commonly recovered in archaeological sites near the Paraná river and tributaries in Entre Ríos Province (Vizcaíno & Bargo, 1993; Bonomo *et al.*, 2010). Regarding the genus *Ctenomys*, it is recorded in Entre Ríos Province from the Late Pleistocene (Ferrero *et al.*, 2017) and Late Holocene (Bastourre & Apolinaire, 2017). With regard to *Calomys* and *Necromys*, they are the first fossil record of these genus in the province. In this framework, all mammals described here are first records from the Early Holocene in Entre Ríos Province.

#### **Faunistic composition and taphonomical remarks**

The richness, with at least 15 identified taxa to or below family level, and the abundance of small vertebrates found

in the stratigraphic section sampled make this a unique microvertebrate fossil assemblage in comparison with other fossiliferous Quaternary fluvial units outcropping in the area (see Ferrero *et al.*, 2017; Ferrero & Noriega, 2023). The analyzed levels in the stratigraphic section of the Molino Doll locality are mainly silty and present fossils of the five major vertebrate groups (fishes, anurans, reptiles, birds, and mammals) (Tab. 1). Level 1 shows the greater number of identified taxa with all the major vertebrate groups represented and the largest number of specimens. A similar case is observed for level 2, but with a lower richness of taxa and abundance of remains recovered. Level 3 shows the lowest number of taxa and specimens, with only three groups represented (fishes, anurans, and reptiles). Birds and mammals are represented at levels 1 and 2. Birds are the least represented group with only two taxa recorded in the stratigraphic section (Tab. 1). In summary, we noticed that the richness of taxa decreases from the base to the top (Tab. 1). Likewise, the number of fish specimens decreases from level 1 to 3.

Taphonomical aspects, such as the number of fossils and the taxonomic structure, the high degree of fracture and erosion, and the lack of evidence of digestion (see descriptions in the Systematic Paleontology section) indicate that the fossil assemblage in the Early Holocene unit analyzed in the Doll creek was the result, at least in part, of water transportation and subsequent accumulation within fluvial units (Badgley, 1986). Furthermore, the fragmented and isolated condition of the specimens could be attributed to sediment compaction, erosion resulting from surface exposure and water transport, as well as extraction and sieving methodologies.

Considering field observations, the fossiliferous unit was formed by the sedimentary infilling of the alluvial valley in this area, and the structures and architecture suggest channel belts. In this sense, the water was the principal transport and selector agent of the fossil assemblage of the analyzed Holocene unit at the Molino Doll locality.

In this work, the sedimentary unit is interpreted as a channel–fill where most of the specimens are autochthonous (Behrensmeyer, 1988). The presence of fishes indicates a death site in the channel or a short-distance transportation, while the record of the other groups of small

vertebrates (anurans, reptiles, birds, and rodents) indicate sporadic water flowing and reworking of banks and bedload sediments (Behrensmeyer, 1988). This inference is consistent with the ecological and paleoenvironmental requirements of mollusk faunal assemblage recovered from the unit, e.g., *Pomacea* and *Heleobia*, and fossil diatoms, e.g., *Diploneis* sp., *Navicula peregrina*, *Synedra* sp., *Nitzchia* sp., among others, which inhabit lagoons and semipermanent streams with abundant floating vegetation (Pérez Pincheira *et al.*, 2018; Zilli *et al.*, 2019). The scarcity of medium-size specimens (*sensu* Araújo-Júnior & Porpino, 2011 in Araújo-Júnior *et al.*, 2013) in samples might have been due to a low-load capacity of the fluvial system to transport bigger ones, commonly associated with that kind of environments. The only medium-size taxon found in the assemblage corresponds to *Dasypus hybridus*, represented only by small osteoderms. In this regard, probably the quantitative and taxonomic differences between the levels (see Tab. 1) were established by the transport capacity of the system over time and not by their absence in the area. In this context, we highlight the need to increase sampling efforts in these stratigraphic sections and to continue geo-stratigraphic studies.

#### Comparative aspects between the analyzed assemblage from the Molino Doll locality and previous Holocene records

The fauna found in the analyzed stratigraphic section at the Doll creek presents differences with those in Holocene archaeological sites in southern Mesopotamia. However, genera such as *Dasypus* and *Ctenomys* are recorded in both (see Bastoure & Apolinaire, 2017). Most of the taxa identified in the archaeological sites near the studied area belong to medium and large-sized vertebrates, mainly mammals and fishes, which provided more resources (e.g., food and skins) to aboriginal groups (Bonomo *et al.*, 2011; Politis *et al.*, 2011). The poor coincidence between the fauna registered in archaeological sites and the paleochannel studied is conditioned, in the first place, by the collecting action of hunter-gatherer groups (Bonomo *et al.*, 2011; Politis *et al.*, 2011; Ottalagano *et al.*, 2015). Secondly, due to biases in the collection and disposal of sediments without clearly visible faunal remains of vertebrates. Also, it is

important to mention that there is a great temporal difference between radiocarbon dates of the archaeological sites, less than 3,000  $^{14}\text{C}$  years BP (Late Holocene; Bonomo, 2012) and the analyzed Holocene section at the Molino Doll locality, which is close to 10,000  $^{14}\text{C}$  years BP (Early Holocene). Also, to this day, there has been no evidence of aboriginal presence during the Early Holocene in the area.

#### Paleoenvironmental and paleoclimatological remarks

The fossiliferous assemblage recovered from the stratigraphic Holocene section in the Molino Doll locality presents taxa characteristic of lotic or semi-lentic environments, such as lagoons or sporadic streams (*Synbranchus* sp., *Physalaemus* sp., *Gallinula galeata*, Cichlidae indet.), others with clear grasslands and savannah affinities (*Amphisbaena* sp., *Nothura* cf. *maculosa*, *Ctenomys* sp., *Calomys* sp., and *Necromys* sp.) and others with abundant precipitation preferences (*Dasypus hybridus*). In view of this diversity and its ecological requirements (see Comments in Systematic Paleontology), it can be inferred that the climatic conditions in the studied area during the beginning of the Early Holocene were similar to the present ones, with a temperate-warm and humid climate with abundant rainfall, and the presence of lotic or semi-lentic environments with grassland developments. This scenario is consistent with previous inferences, taking into account several proxies, such as gastropods, ostracods, and diatoms, which have provided useful paleoclimatic and paleoenvironmental data (Pérez Pincheira *et al.*, 2018; Zilli *et al.*, 2019). These studies, combined with our paleofaunistic results and the composition of the matrix of the unit, mainly composed of silt and clay (see Behrensmeyer, 1988), would indicate that the analyzed Holocene stratigraphic section displays characteristics of slow currents of water and abundant floating and submerged vegetation.

In consonance with the preceding fossil data and considering the stratigraphic position and thickness of the analyzed section, we assume a relatively short time of deposition period at the beginning of the Holocene, around 10,000–9,000  $^{14}\text{C}$  years BP, based on the radiocarbon ( $^{14}\text{C}$ ) data obtained. This timeframe is consistent with water availability and a rise in the base level in an old Paraná Delta (Stieffel Jr., 2019).

## CONCLUSIONS

This work presents an unprecedented paleofaunal assemblage comprising the five major groups of vertebrates (fishes, anurans, reptiles, birds, and mammals) corresponding to the Early Holocene, located in Entre Ríos Province, southern Mesopotamian Region, Argentina.

The faunistic richness reported and the preliminary taphonomical analysis provide evidence of a combination of environments, including savannahs, grasslands, and fluvial-lacustrine environments with vegetation cover, such as lagoons and semipermanent watercourses. These characteristics resemble the current conditions in the area, as suggested by previous studies.

The Doll creek paleochannel constitutes a new Early Holocene fossiliferous locality in Argentina with new and novel records of vertebrates in the area, showing a promising potential of fossil preservation and improving our paleontological knowledge. Also, it is an important site to understand the changes in the recent past in transitional periods to current climatological conditions.

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