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New information on the anatomy and histology of *Gracilisuchus stipanicicorum* (Archosauria: Pseudosuchia) from the Chañares Formation (early Carnian), Argentina

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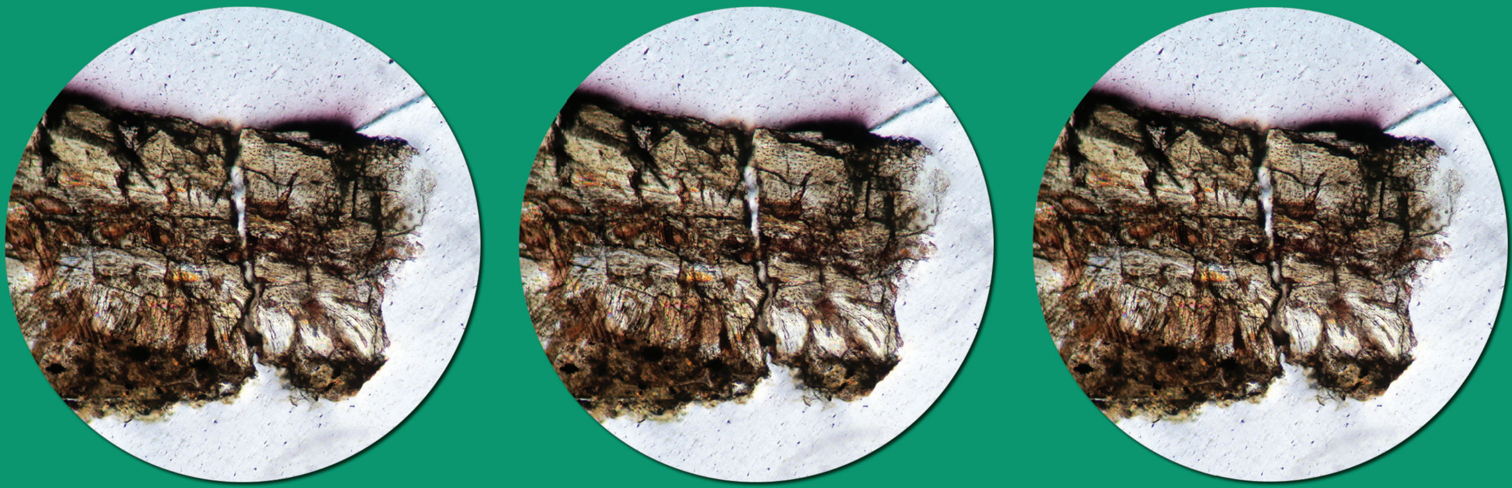

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New information on the anatomy and histology of *Gracilisuchus stipanicicorum* (Archosauria: Pseudosuchia) from the Chañares Formation (early Carnian), Argentina

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ABSTRACT

Gracilisuchus stipanicicorum Romer, 1972 is a basal suchian from the Late Triassic Chañares Formation (Argentina), nested in the recently erected Gracilisuchidae, along with *Turfanosuchus dabanensis* Young, 1973 and *Yonghesuchus sangbiensis* Wu *et al.,* 2001 from China. The six known specimens of *Gracilisuchus* Romer, 1972 preserve most of the skeleton, lacking only most of the shoulder girdle and forelimb. Our latest fieldwork has recovered two specimens that preserve previously unknown elements, including the humerus, radius, and ulna, as well as the femur, presacral vertebrae, and paramedian osteoderms. The femur and osteoderms were histologically sectioned, which has never been done for Gracilisuchidae. The anatomical analysis revealed characters in the new elements that improve our understanding of the anatomy of *Gracilisuchus*. Bone histology revealed that the specimen CRILAR PV 490 died before reaching somatic maturity and that growth was relatively slow compared to other pseudosuchians. This study increases the knowledge of the anatomy of *Gracilisuchus* and represents a new step towards a broader understanding of Gracilisuchidae and basal suchian clades.

KEY WORDS
Chañares Formation,
Triassic,
Pseudosuchia,
Gracilisuchidae,
Bone Histology,
Lamellar bone tissue.

RÉSUMÉ

Nouvelle information sur l'anatomie et l'histologie de Gracilisuchus stipanicicorum (Archosauria : Pseudosuchia) de la Formation Chañares (Carnian inférieur), Argentine.

Gracilisuchus stipanicicorum Romer, 1972 est un suchien souche de la Formation Chañares du Trias supérieur (Argentine), inclus dans les Gracilisuchidae, un groupe récemment créé avec *Turfanosuchus dabanensis* Young, 1973 et *Yonghesuchus sangbiensis* Wu *et al.,* 2001 de Chine. Les six spécimens connus de *Gracilisuchus* Romer, 1972 conservent la majorité du squelette, à l'exception de la plupart de la ceinture scapulaire et du membre antérieur. Nos derniers travaux sur le terrain, ont exhumé deux spécimens qui préservent des éléments non encore connus, tels que l'humérus, le radius et l'ulna, ainsi qu'un fémur, des vertèbres et ostéodermes. Le fémur et les ostéodermes paramédiaux ont été sectionnés en vue d'une histologie, encore jamais abordée chez les Gracilisuchidae. L'analyse anatomique a révélé, dans les nouveaux éléments, des caracréristiques qui améliorent notre compréhension de l'anatomie de *Gracilisuchus.* L'histologie osseuse, elle, a révélé que l'individu CRILAR PV 490 était mort avant atteindre sa taille adulte et que sa croissance était relativement lente comparée à celle d'autres pseudosuchiens. Cette étude approfondit la connaissance de *Gracilisuchus* et constitue un pas supplémentaire vers une meilleure compréhension de Gracilisuchidae et des clades de suchiens souches.

MOTS CLÉS
Formation Chañares,
Trias,
Pseudosuchiens,
Gracilisuchidae,
Histologie osseuse,
Tissu osseux lamellaire.

INTRODUCTION

Gracilisuchus stipanicicorum Romer, 1972 is a basal suchian archosaur from the Late Triassic of north-western Argentina (Chañares Formation, Ischigualasto–Villa Unión Basin, early Carnian; Desojo *et al.* 2011; Marsicano *et al.* 2016). This species, discovered more than four decades ago (Bonaparte 1975; Romer 1972), has been subject to various phylogenetic interpretations over the years but no detailed study has been made until recently (see Lecuona *et al.* 2017 for a summary). *Gracilisuchus* Romer, 1972 is a monospecific genus nested within the recently erected family Gracilisuchidae (Butler *et al.* 2014), along with the Chinese species *Turfanosuchus dabanensis* Young, 1973 and *Yonghesuchus sangbiensis* Wu *et al.,* 2001. Gracilisuchidae is resolved as a basal taxon within Pseudosuchia, the clade of crocodile-like archosaurs. Pseudosuchia has been traditionally divided into five main subclades, Phytosauria, Ornithosuchidae, Aetosauria, "Rauisuchia" and Crocodylomorpha (e.g. Benton & Clark 1988; Brusatte *et al.* 2010; Sereno 1991); but other analyses recovered different groupings within this clade (e.g. Irmis *et al.* 2013; Nesbitt 2011), including a recent analysis that also included a further monophyletic Erpetosuchidae (Ezcurra 2016; Ezcurra *et al.* 2017). Pseudosuchia presents a broad diversity of forms, displaying a wide range of sizes and anatomical specializations that indicate considerable disparity and ecomorphotypes (e.g. Foth *et al.* 2016; Sookias *et al.* 2012; Turner & Nesbitt 2013). They range from large to medium-sized quadrupedal predators with parasagittal limb posture (e.g. rauisuchids, prestosuchids), quadrupedal forms with sprawling or semi-erect posture (e.g. phytosaurs), quadrupedal omnivores (e.g. aetosaurs), facultatively or obligate bipedal poposaurids, ornithosuchids with enigmatic locomotor adaptations, the small-sized erpetosuchids, and possibly facultatively bipedal carnivorous basal crocodylomorphs (e.g. Bates & Schachner 2012; Irmis *et al.* 2013; Parrish 1986; Stubbs *et al.* 2013). All these pseudosuchian taxa are well represented in Upper Triassic deposits of Pangea, but they were gradually replaced by the bird-line clade of archosaurs (Avemetatarsalia), being today represented only by Crocodylia.

Gracilisuchus stipanicicorum was previously known from six specimens housed in Argentina (Instituto Miguel Lillo, Tucumán and Museo de Ciencias Antropológicas y Naturales, La Rioja) and the United States (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts), representing most of the skeleton but missing most of the pectoral girdle and forelimb elements. Some anatomical features including small size, open sutures in the skull and along the axial skeleton, suggest that some specimens are possibly juveniles (Lecuona *et al.* 2017). Recent fieldwork in the Chañares Formation (by Desojo & Lecuona in 2011 and 2013; Desojo *et al.* 2015) has yielded two new specimens of *Gracilisuchus* (CRILAR PV 480, CRILAR PV 490), which, although highly incomplete, preserve previously unknown elements (e.g. humerus, radius, ulna) along with other elements already known in other specimens (e.g. cervical vertebrae, femur).

Palaeohistological studies have increasingly played a central role in palaeobiology, and the number of such contributions has greatly increased in recent years. Since the origins of palaeohistology, back in the 19th century, with Owen's description of *Scelidosaurus harrisonii* (Owen 1861; Padian 2011), such studies have been undertaken and several major studies were published early in the last century (e.g. Seitz 1907; Gross 1934; Peabody 1961). A major contribution was provided by the studies of Enlow (Enlow & Brown 1956, 1957, 1958; Enlow 1969) and the dissertation research by de Ricqlès (1968-1977; see Padian 2011). It has increasingly been realized that many aspects of the biology of fossil organisms can be better understood through histological studies. The microanatomy and histology of bone tissues are influenced by several factors, including ontogenetic maturity and rate of bone deposition, physical influences on the bone due to the mode of life, and various environmental effects (Padian 2011). Thus, studying the microanatomical and palaeohistological characteristics of bone can provide a broad range of information regarding the palaeobiology of the organisms under

TABLE 1. — Measurements of long bones of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490). Measurements are given in millimetres (mm). Abbreviations: *****, incomplete element; **n/a**, not applicable to that element; **A-P**, anteroposteriorly measured; **D-V**, dorsoventrally measured; **L-M**, lateromedially measured.

	Humerus	Ulna	Radius	Femur
Total length	41.8	36.7*	34.1*	31*
Mid-diaphysis width	4.9	3.7 (D-V)	3.1 (L-M)	3.4
Proximal width	10	8.5 (D-V)	–	–
Distal width	9.7	–	6.2 (L-M)	6.8
Distal depth	–	–	5 (D-V)	–
Deltopectoral crest distal end	17.3	n/a	n/a	n/a
Trochlear recess proximal end	10.7	n/a	n/a	n/a
Lateral condyle	n/a	n/a	n/a	4.7 (A-P)
Medial condyle	n/a	n/a	n/a	5.1 (A-P)

consideration, including longevity (e.g. Chinsamy 1993; Curry 1999), growth rate (e.g. Erickson *et al.* 2001; de Ricqlès *et al.* 2003, 2008; Padian *et al.* 2004; Taborda *et al.* 2013), somatic maturity (e.g. Klein & Sander 2007; Lee & Werning 2008), adult body size (e.g. Klein & Sander 2007), and sexual maturity (e.g. Erickson *et al.* 2007; Lee & Werning 2008; Cerda *et al.* 2014).

Numerous studies have focused on elucidating the palaeobiology of a variety of extinct and extant vertebrate taxa, including anamniotic tetrapods (e.g. Enlow & Brown 1956; Hill 2005; Schoch 2009), turtles (e.g. Scheyer *et al.* 2007; Vlachos *et al.* 2015; Jannello *et al.* 2016), basal sauropsids (e.g. Enlow & Brown 1957; Enlow 1969; Scheyer 2007; Klein *et al.* 2015), mammals (e.g. Hill 2006), basal archosauromorphs (e.g. Botha-Brink & Smith 2011; Legendre *et al.* 2013), archosaurs (e.g. de Ricqlès *et al.* 2003, 2008; Hill 2010; de Buffrénil *et al.* 2015), and, within the latter, particularly in the avian line of archosaurs (e.g. Chinsamy 1994; Chinsamy *et al.* 1995, 2014; Horner *et al.* 2001; Klein & Sander 2008; Cubo *et al.* 2012; Klein *et al.* 2012; Farke *et al.* 2013; Cerda *et al.* 2014. The latter clade, Avemetatarsalia, has historically received more attention than the crocodilian clade of archosaurs, Pseudosuchia, in part due to the research focus on the origin and evolution of avian thermophysiology and flight, and the growth rate and longevity of sauropod dinosaurs (e.g. Cubo *et al.* 2012). However, in recent years, palaeohistological studies on pseudosuchian archosaurs and non-archosaurian archosauromorphs have increased interest among palaeontologists, and various studies have begun to be carried out revealing interesting findings regarding these highly diverse groups (e.g. Parker *et al.* 2008; Klein *et al.* 2009, 2017; Hill 2010; Botha-Brink & Smith 2011; Cerda & Desojo 2011; Filippi *et al.* 2013; Legendre *et al.* 2013; Ezcurra *et al.* 2014; Scheyer *et al.* 2014; Cerda *et al.* 2015; Werning & Nesbitt 2016; Company & Pereda-Suberbiloa 2017; Cubo *et al.* 2017; Ponce *et al.* 2017).

The most appropriate skeletal elements for histological studies are those with little remodelling, such as femur and tibia, that have faster growth rates than other long bones and ribs, which can be subjected to remodelling and other ontogenetic processes (Horner *et al.* 1999; Padian 2011). Other elements frequently used in these studies are osteoderms, which are bony structures embedded within the dermis, and widely found among extant tetrapods, such as squamates, turtles, some mammals (e.g. armadillos), and several extinct reptilian groups within archosauriforms. These elements provide protection for the organism (e.g. Scheyer & Sander 2004) and calcium storage in ovipositing females (e.g. Klein *et al.* 2009). They are also involved in pH regulation (e.g. Janis *et al.* 2012), in thermoregulation (e.g. Clarac & Quilhac 2019), and can stabilize the axial skeleton (e.g. Buchwitz *et al.* 2012). Additionally, they have been demonstrated to be useful for estimating the age of individuals (e.g. Erickson & Brochu 1999; Cerda & Desojo 2011) as well as providing other information, such as inferences concerning soft-tissue structures (e.g. Scheyer & Sander 2004; Hill 2006; Cerda & Powell 2010; Buchwitz *et al.* 2012), palaeoecology (Hua & Buffrénil 1996; Scheyer & Sander 2007; Witzmann 2009), and phylogenetic affinities (Scheyer & Sander 2004; Burns 2008; Nesbitt 2011; Wolf *et al.* 2012; Cerda *et al.* 2013).

Considering all of this, describing and comparing the osteology of the previously unknown elements of *Gracilisuchus stipanicicorum* as well as studying its palaeohistology, promises to provide important new information regarding this taxon in particular, and Pseudosuchia in general. Sectioning the bony elements of the specimen CRILAR PV 490 referred to this taxon, allows us to determine the minimum ontogenetic age of this specimen and compare it with the holotype and previously referred specimens in order to better estimate the ontogenetic ages of these specimens. Furthermore, this work will allow us to better understand different aspects of the palaeobiology of this species, including its growth rate, and allow us to compare it with other pseudosuchians, inferring probable phylogenetic trends on the lineage leading to extant crocodilians.

INSTITUTIONAL ABBREVIATIONS

CRILAR, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, La Rioja, Argentina; IVPP V, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; MCZVP, Department of Vertebrate Paleontology, Museum of Comparative Zoology, Harvard University, Cambridge, MA, United States; MNHN.F, Muséum national d'Histoire Naturelle de Paris, Paris, France; NCSM, North Carolina Museum of Natural Sciences, Raleigh, NC, United States; NHM UK, Natural History Museum, London, UK; PIMUZ T, Paläontologisches Institut und Museum der Universität, Zürich, Switzerland;

PULR, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja Province, Argentina; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán Province, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan Province, Argentina; SAM-PK, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UFRGS-PV, Laboratório de Paleovertebrados da Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil.

MATERIAL AND METHODS

The material assessed in this study consists of specimens CRILAR PV 480 and CRILAR PV 490, which are referred to *Gracilisuchus stipanicicorum*. An osteological description and comparisons are performed and measurements taken, focussing on previously unknown bones and unknown features of each specimen. Histological thin-sections were made from the paramedian osteoderms and the femur of CRILAR PV 490 in the Geology Department of the National University of San Luis, Argentina, using the methodology outlined by Padian & Lamm (2013). Two sections of a single fragment of femur and four sections of paramedian osteoderms were prepared. The femoral fragment was sectioned transversely at two points of the diaphysis close to each other, and no differences were noticed between the sections (see below). The paramedian osteoderms were sectioned transversely (samples G2a, G2d, and G3) and longitudinally along the midline (sample G4). The thin-sections were examined with a light microscope using both normal and polarized light.

The histological terminology used in the present study is based on Francillon-Vieillot *et al.* (1990). Throughout the description, the femoral region closer to the surface of the bone is referred to the “external” cortex, and the region toward the medulla is referred to the “middle” and “inner” cortex. Regarding description of the paramedian osteoderms, the term “superficial” is used to refer to the region closer to the outer surface of the animal body, and “deep” to the region toward the interior of the specimen (Hill 2006; 2010). These are equivalent to the “distal and proximal” of Main *et al.* (2005) and “external and basal” of Scheyer & Sander (2004). Additionally, as the osteoderms are organized in pairs, they are considered to have a lateral and a medial “wing” divided in the middle by a longitudinal dorsal crest.

SYSTEMATIC PALAEONTOLOGY

ARCHOSAURIA Cope, 1869 *sensu* Gauthier & Padian 1985
PSEUDOSUCHIA Zittel, 1887-1890 *sensu* Gauthier & Padian 1985
SUCHIA Krebs, 1974 *sensu* Benton & Clark 1988
Family GRACILISUCHIDAE Butler *et al.,* 2014

Genus *Gracilisuchus* Romer, 1972

DIAGNOSIS. — Same as the type species by monotypy.

Gracilisuchus stipanicicorum Romer, 1972
(Figs 2-7)

HOLOTYPE. — PULR 08, incomplete cranium, one disarticulated mandibular ramus; incomplete series of presacral vertebrae and incomplete first sacral vertebra, incomplete paramedian osteoderms, distal ends of the right scapula and humerus (see Lecuona *et al.* 2017 for full details).

REFERRED MATERIAL. — CRILAR PV 480, one and a half incomplete cervical centra articulated with each other and with two incomplete ribs, a series of three incomplete vertebrae articulated with one rib, dorsally in contact with the left row of the paramedian osteoderms, and posteriorly four ribs with no articulating vertebrae but in anatomical position (Fig. 2A, B), a series of six incomplete cervicodorsal vertebrae with some of their ribs preserved and half of a centrum attached posteriorly (Fig. 2C, D), and moulds of two short fragments of paramedian osteoderms. This specimen was found associated with a scapulocoracoid and an osteoderm series of a proterochampsid archosauriform and several indeterminate remains. CRILAR PV 490, two articulated cervical vertebra in contact with a short paramedian osteoderm series, one isolated dorsal vertebrae, left humerus, right ulna, right radius, left femur, and six histological sections of the femoral diaphysis and osteoderms (Figs 3-10). See Lecuona *et al.* (2017) for a complete list of the hypodigm of *Gracilisuchus stipanicicorum*.

HORIZON, LOCALITY AND AGE. — Chañares Formation, Ischigualasto–Villa Unión Basin, La Rioja Province, northwestern Argentina (Fig. 1). Specimens deposited in PVL, PULR, and MCZVP collections come from the type locality of the Chañares Formation (Fig. 1; Sereno & Arcucci 1994; Lecuona *et al.* 2017), whereas CRILAR PV 480 and CRILAR PV 490 come from two different localities. CRILAR-PV 480 was collected from Campo de Córdoba locality, and, stratigraphically, from the lower member of the Chañares Formation, at the concretionary level that characterizes this member and where most of the previously reported fossil tetrapods from the *Massetognathus-Chanaresuchus* assemblage zone (AZ) were found (Rogers *et al.* 2001; Fiorelli *et al.* 2013; Marsicano *et al.* 2016; Gouiric-Cavalli *et al.* 2017). CRILAR PV 490 was found at the El Torcido locality, in the lowermost levels of the *Massetognathus-Chanaresuchus* AZ of the Chañares Formation, approximately 4 km east of the “Chañares type” locality (= Far East Pocket locality of A. S. Romer). CRILAR PV 490 was found in a fine-grained grey sandstone, in levels lacking concretions, and was associated with a cynodont ilum and the skeleton of a rhadinosuchine proterochampsid CRILAR PV 488 (Ezcurra *et al.* 2019). The Chañares Formation has been traditionally interpreted as Ladinian in age (Middle Triassic; Stipanicic 1983; Rogers *et al.* 2001; Morel *et al.* 2003), but recent U-Pb zircon analyses of samples from the lower and middle levels of the Chañares Formation (Marsicano *et al.* 2016) constrained the age of the fossiliferous horizon to 236.1±*0.6* to 233.7±*0.4* Ma, 5-10 Mya younger than the Middle Triassic, representing an early Carnian (early Late Triassic) age. Additional new analyses from detrital zircons taken from two volcanoclastic deposits of the Chañares Formation (Ezcurra *et al.* 2017), recovered maximum depositional ages consistent with those previously determined (236.2±1.1 Ma and 233.1±1.1 Ma), confirming the earlier work (Desojo *et al.* 2011).

DIAGNOSIS. — Lightly built pseudosuchian with a total skull length that slightly exceeded 90 mm (in the largest specimen, PVL 4612, with incomplete anterior end of the snout) and the length of the

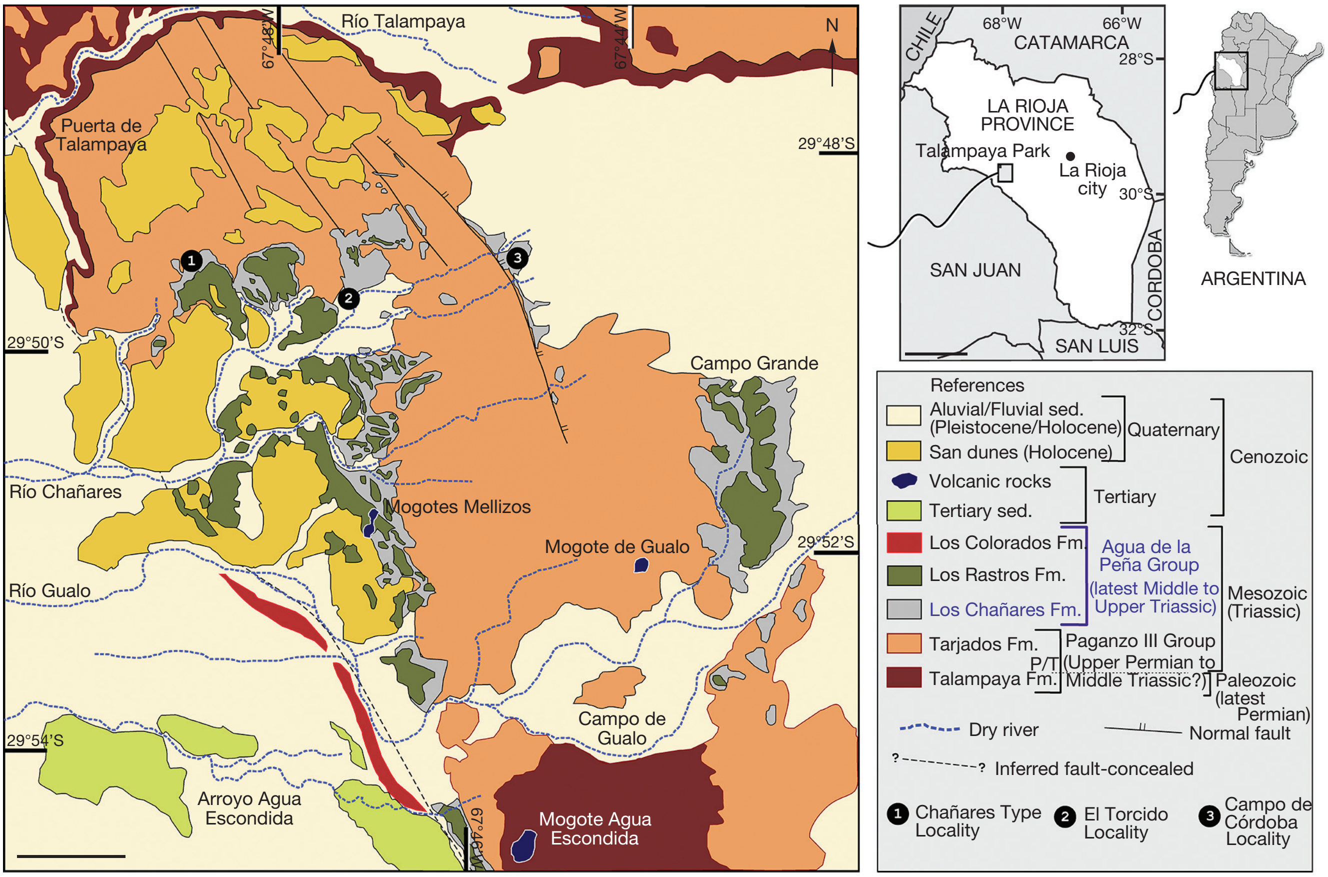

Fig. 1. — Geographical map showing the location of Ischigualasto-Villa Unión Basin, La Rioja and San Juan provinces, NW Argentina, and localities where the specimens were found. Modified from Fiorelli *et al.* 2018.

largest preserved femur being 80 mm (PVL 4597, one of the largest specimens), diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): relatively large cranial openings: antorbital fenestra occupying between 30% and 36%, antorbital fossa between 36% and 40%, and orbit between 35% and 42% of the anteroposterior length of skull roof (measured back to the posterior end of the parietals); supratemporal fenestra wider than long*; sclerotic ring with ossicles that not overlap in lateral contact; straight posterior edge of postorbital process of jugal*; presence of postfrontal, with a long lateral process that projects over the postorbital bar*; presence of a small triangular postparietal; large postemportal foramen in proportion to the width of the occipital region; laterally extending anterior process of squamosal; premaxillary teeth with no mesial carina, faint distal carina, and lacking mesial or distal denticles; postzygapophyseal facet of the axis in horizontal plane and with the longitudinal axis posteriorly directed*; high, vertical anterior border of the axial neural spine*; longitudinal median ventral keel on the axial centrum; poorly developed ventral keels on cervical vertebrae; mid-dorsal region of cervical vertebral neural arch with a circular anterolateral depression; spine tables on posterior cervical vertebrae (at least on cervicals 4 of PVL 4597, and 6 and 7 of MCZVP 4118); distal (lateral) end of first sacral rib slightly expanded relative to the proximal (medial) portion*; lack of a well-defined acetabular surface on the pubis; thin L-shaped lamina on proximal pubic apron; lateroventral corner of pubic peduncle with short bony tongue; ischiadic symphysis proximally located*; proximodistally elongated and poorly developed iliofibular trochanter on fibula; staggered paramedian osteoderms; longitudinal keels on dorsal surfaces of laterally bent osteoderms slightly medially located with respect to the centre of the element and (Lecuona *et al.* 2017).

OSTEOLOGY

Vertebrae and ribs

The specimen CRILAR PV 480 presents a series of three incomplete cervical vertebrae, the last of which articulates with one rib, and posteriorly four cervico-dorsal ribs in natural position but missing their corresponding vertebrae (Fig. 2A, B), a series of six fragmentary vertebrae spanning the cervicodorsal transition with several articulated ribs (Fig. 2C, D), two incomplete articulated cervical centra with two incomplete cervical ribs, two isolated probable vertebrae (not figured), and one isolated dorsal rib. CRILAR PV 490 preserves two articulated mid cervical vertebrae (Fig. 3) and one isolated posterior cervical vertebra; no ribs are preserved in this specimen. As the axial skeleton of *Gracilisuchus* has been described recently (Lecuona *et al.* 2017), the present description will focus on differences from the previously known specimens and from other taxa.

The vertebrae of the series of three cervicals (CRILAR PV 480, Fig. 2A, B) are incomplete and poorly preserved, with the last two preserving only the neural arch and spine and probably from the left side. The morphology of the five ribs preserved in this series suggests a transitional cervicodorsal position. They contrast with the ribs of this region in other specimens of *Gracilisuchus* (e.g. PVL 4597, see below), but the poor preservation as a thin layer of bone in some regions in CRILAR PV 480, suggests they may be incomplete. The first rib has a short shaft and a strongly expanded, triangular distal end, almost equal in size anteriorly and posteriorly. The second rib has a thicker shaft and is distally triangular, but narrower anteroposteriorly than the first. The remaining ribs have lost their proximal articular ends. The third rib is distally expanded and triangular, being more expanded posteriorly than anteriorly. The fourth and fifth ribs are more like dorsal ribs, where the posterior surface is straight and the anterior is convex. The fourth rib has the anterior projection that extends more anteriorly and is more distally located than in the fifth. The ribs of this series (Fig. 2A, B) differ from those of other *Gracilisuchus* specimens (e.g. PULR 08, PVL 4597) in being distally less expanded anteroposteriorly and thus not contacting with each other as occurs in PULR 08 and PVL 4597. This difference could be interpreted as intraspecific variation but may also be due simply to the poor preservation of the ribs of CRILAR PV 480, as only a thin layer of bone in some regions suggests they may be incomplete. The series of six cervico-dorsal vertebrae (Fig. 2C, D) and the fragmentary series with one and a half vertebral (not figured) of CRILAR PV 480, and the three cervicals of CRILAR PV 490 (Fig. 3) are quite similar to those in other specimens of *Gracilisuchus*. The vertebrae of specimen CRILAR PV 490 have a neural spine inclined anteriorly to the same degree as PVL 4597 (Lecuona *et al.* 2017), an anterolateral depression anterior to the neural spine in the neural arch, as well as an infrapostzygapophyseal depression below the postzygapophysis (Fig. 3A, B; Lecuona *et al.* 2017: fig. 7). They have long longitudinal lateral fossae on the vertebral centra, and the parapophysis continues posteriorly as a longitudinal crest (Fig. 3B, D). Anterior cervical ribs are only present in CRILAR PV 480 (Fig. 2C, D); they are posteriorly elongated and contact the immediately posterior rib dorsally through a dorsal groove. The dorsal ribs each have a short capitulum and tuberculum and expand anteriorly at the proximal end of the shaft (Fig. 2C, D).

Humerus

A complete humerus was found in specimen CRILAR PV 490 (Fig. 4). It is a slender bone, 41.3 mm long, 4.9 mm wide at the midshaft, and 10 and 9.7 mm wide at its proximal and distal ends, respectively. This general gracile morphology resembles that of *Erpetosuchus granti* Newton, 1894 (Benton & Walker 2002) or the crocodylomorphs CM 29894 (Clark *et al.* 2000) and *Dromicosuchus grallator* Simmons, 1965 (Sues *et al.* 2003), but contrasts with the robust element of *Nundasuchus songeaensis* Nesbitt *et al.,* 2014, *Batrachotomus kupferzellensis* Gower, 1999 (SMNS 80275), aetosaurs (e.g. *Aetosauroides scagliai* Casamiquela, 1960, PVL 2073), phytosaurs (e.g. *Smilosuchus gregorii* Camp, 1930 *sensu* Long & Murry 1995, USNM 18313), and basal loricatans. In anterior and/or posterior view, the proximal end has a triangular outline, with the proximal surface rather flat and obliquely inclined, with its lateral corner being proximally projected with respect to the medial corner. The humeral head is poorly defined on the proximal end. It is nearly flat and forms an angle with the proximal surface of the humerus. This morphology is similar to *Euparkeria capensis* Ewer, 1965 (SAM PK 5867), but contrast with some other pseudosuchians (e.g. *Erpetosuchus granti* [Benton & Walker 2002]; *Batrachotomus kupferzellensis*, SMNS 92042, SMNS 80276 [Gower & Schoch 2009]; *Nundasuchus songeaensis* [Nesbitt *et al.* 2014]; *Terrestrisuchus gracilis* Crush, 1984, NHM UK P 47/22ii), which have a rounded, clearly defined protuberance located at some distance from the medial margin, and the proximal surface between the head and the medial margin is distally inclined. The lateral and medial margins of the shaft are gently curved, contrasting with the highly concave medial margin of *Nundasuchus* or both margins of *Erythrosuchus africanus* Broom, 1905 (Gower 2003). The long axes of the proximal and distal ends in transverse view are nearly parallel to one another (Fig. 4C, F), differing from the offset condition in *Erythrosuchus africanus* (Gower 2003), *Euparkeria capensis* (Ewer 1965), *Nundasuchus songeaensis* (Nesbitt *et al.* 2014), *Postosuchus kirkpatricki* Chatterjee, 1985 (Weinbaum 2013), *Aetobarbakinoides brasiliensis* Desojo *et al.,* 2012, or *Batrachotomus kupferzellensis* (SMNS 80275), for example. The deltopectoral crest is slightly raised from the diaphysis, merging with the centre of the shaft at 40% from the proximal end. The medial surface of the crest has a shallow fossa (Fig. 4D: f).

The midshaft of the humerus is nearly circular in section and becomes flattened anteroposteriorly toward the distal end. The distal end has a poorly defined entepicondyle and ectepicondyle, forming simple corners at the medial and lateral sides (Fig. 4), instead of rounded articular condyles, as in some other taxa (e.g. *Turfanosuchus dabanensis*, IVPP V3237; *Postosuchus kirkpatricki* [Weinbaum 2013]; *P. alisonae* Peyer *et al.*, 2008, NCSM 13731; *Batrachotomus kupferzellensis*, SMNS 80275, SMNS 80276, SMNS 92042; *Terrestrisuchus gracilis*, NHM UK P 47/22).

The distal half of the humerus of CRILAR PV 490 can be compared with the only known humerus of *Gracilisuchus* (PULR 08), which is very similar in size, with the mid-diaphysis width of the former being 1.11 times larger than PULR 08. The humerus of PULR 08 preserves the distal end partially as a mould, where a trochlear recess can be seen to be similar in width to that of CRILAR PV 490, whereas the morphology of the distal condyles differs, as these are barely rounded and separated distally in PULR 08. Additionally, the medial condyle of PULR 08 is more narrow than the lateral, whereas in CRILAR PV 490 the lateral one is narrower (Fig. 4D). The medial distal condyle of CRILAR PV 490 is slightly more distally projected than the lateral one. On the anterior distal surface, there is a shallow trochlear recess that fades proximally and disappears at 25% from the distal end (Fig. 4D: tr). The lateral margin has a low bump at 7.6 mm (almost 20%) from the ectepicondyle (Fig. 4B), which might be homologous to the ectepicondylar flange of *Nundasuchus* (Nesbitt *et al.* 2014) and the supinator process of *Batrachotomus* (SMNS 80275, Gower & Schoch 2009). However, the latter two taxa differ in that they show elongated ridges, whereas CRILAR PV 490 merely has a bump (Fig. 4B: lb). Lateral to this structure, CRILAR PV 490 presents a small and shallow circular depression (Fig. 4B: cd), that may be homologous to the ectepicondylar

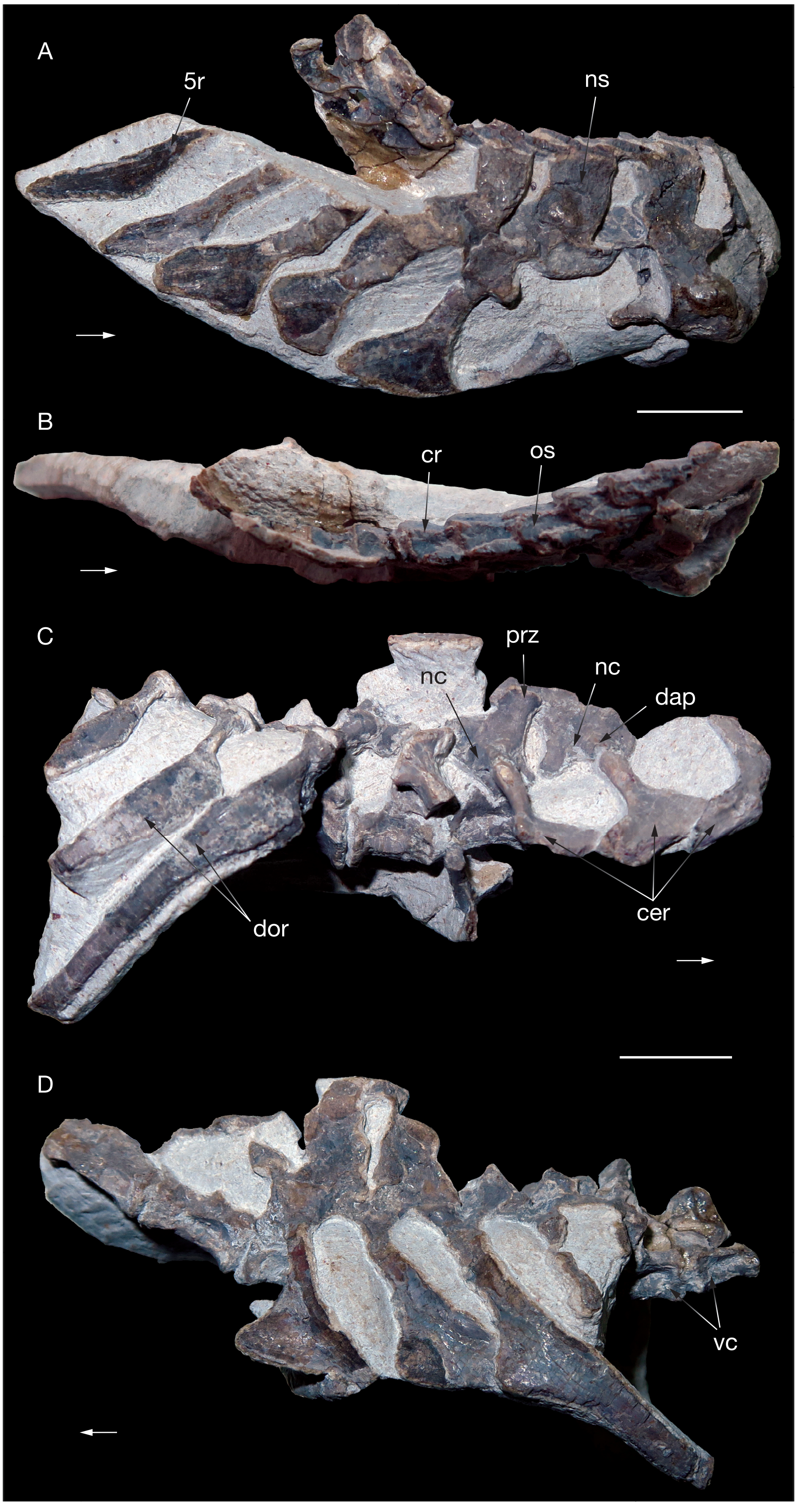

Fig. 2. — Vertebrae of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 480), mid cervical vertebrae and 1st to 5th preserved ribs in **A**, right lateral view; **B**, dorsal view. Fragmentary cervico-dorsal vertebrae in **C**, right lateral view; **D**, left lateral view. Abbreviations: **5r**: fifth preserved rib; cer: cervical ribs; **cr**: dorsal osteoderm crest; **dap**: diapophysis; **dor**: dorsal ribs; **nc**: inverted V-shaped notch in vertebral centra; **ns**: neural spine; **os**: osteoderm; **prz**: prezygapophysis; **vc**: vertebral centra. Arrows indicate anterior direction. Scale bars: 10 mm.

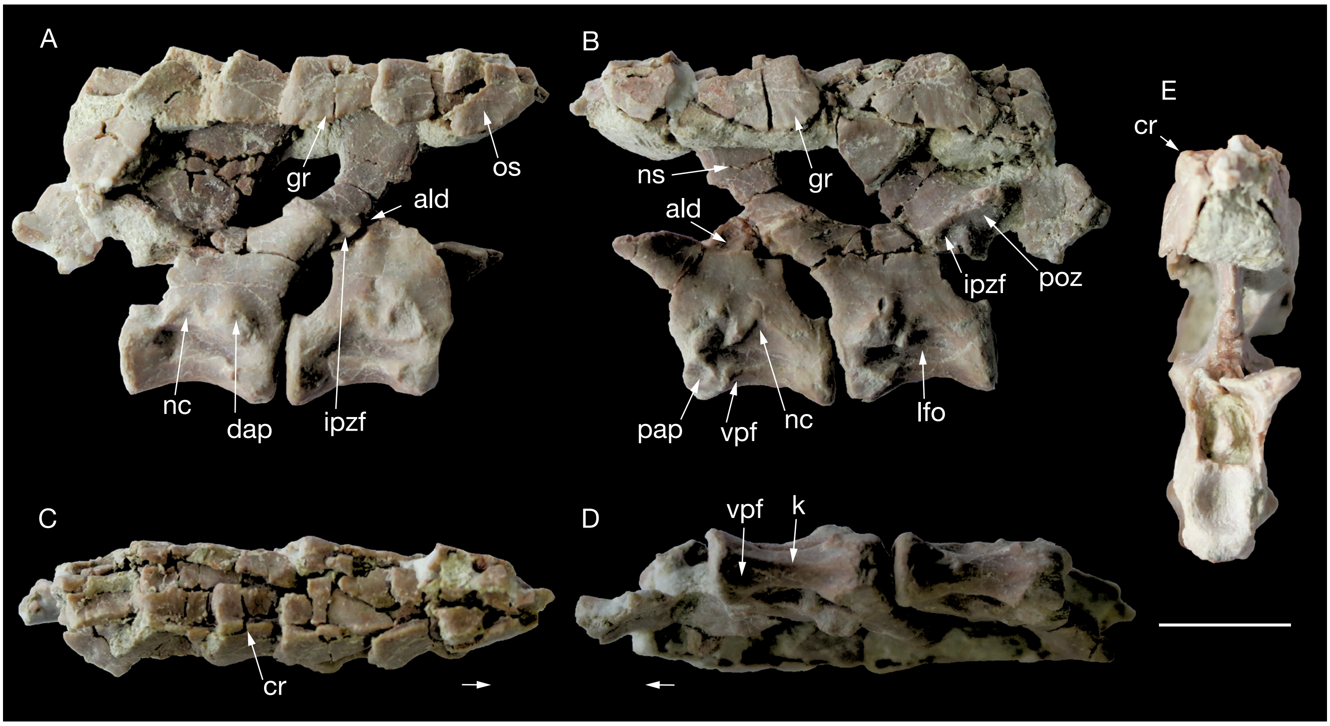

Fig. 3. — Mid cervical vertebrae of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, right lateral view; **B**, left lateral view; **C,** dorsal view; **D**, ventral view; **E**, anterior view. Abbreviations: **ald**: anterolateral depression; **cr**: dorsal osteoderm crest; **dap**: diapophysis; **gr**: groove in osteoderms; **ipzf**: infrapostzygapophyseal depression; **k**: keel; **lfo**: longitudinal lateral fossa on vertebral centrum; **nc**: inverted V-shaped notch in vertebral centra; **ns**: neural spine; **os**: osteoderm; **pap**: parapophysis; **poz**: postzygapophysis; **vpf**: ventral parapophyseal fossa. Arrows indicate anterior direction. Scale bar: 10 mm.

groove for the passage of the radial nerve; however, this depression is very different in shape from the groove morphology (being longer than wide) of the ectepicondylar groove in taxa such as *Postosuchus kirkpatricki* (Weinbaum 2013), *Nundasuchus songeaensis* (Nesbitt *et al.* 2014), and *Batrachotomus kupferzellensis* (SMNS 80275, SMNS 80276, SMNS 92042).

Ulna

Most part of the diaphysis including the proximal end of a right ulna is preserved in CRILAR PV 490 (Fig. 5). The preserved element is 36.7 mm long, 3.7 mm wide dorsoventrally at the diaphysis, and 8.5 mm wide dorsoventrally at the incomplete proximal end. The ulna is estimated to have lost around 3.5 mm, based on comparison with the gracilisuchid *Turfanosuchus dabanensis* (IVPP V3237), the ulna of which is around 0.97 times the length of the humerus.

The incomplete proximal end is flared in medial or lateral view, exhibiting only part of the olecranon processes and a slightly raised bump on the lateral proximal surface. In proximal view, it has a teardrop-shaped outline, tapering dorsally (Fig. 5C). The proximal lateral bump probably represents a lateral tuber (=radius tuber, Nesbitt 2011; Fig. 5D). This tuber is present in most paracrocodylomorphs (e.g. *Batrachotomus*, SMNS 80275; *Fasolasuchus tenax* Bonaparte, 1978, PVL 3850; *Postosuchus alisonae* [Peyer *et al.* 2008]), aetosaurs, and basal dinosauriforms, and absent in most archosaurian outgroups (Nesbitt 2011), although it may be poorly developed in the euparkeriid *Halazhaisuchus qiaoensis* Wu, 1982 (Sookias *et al.* 2014). In the proximal region, the medial surface has a wide and long depression, and the dorsal surface has a narrower and shorter depression for contact with the radius (Fig. 5D: ra). The dorsal surface of the shaft has a medially faint ridge (Fig. 5D: r) starting near the proximal end and extending all the way down the preserved portion of the shaft, probably for the insertion of the *flexor ulnaris* muscle on the dorsal surface (Meers 2003; Otero 2018). This ridge is also present in other taxa, such as the euparkeriid *Halazhaisuchus qiaoensis* (Sookias *et al.* 2014), and the loricatans *Batrachotomus kupferzellensis* (SMNS 80275), *Postosuchus kirkpatricki* (Weinbaum 2013), and *P. alisonae* (NCSM 13731), among others.

Radius

CRILAR PV 490 also preserves the distal portion of the right radius, probably representing less than the half of the distal region (Fig. 6). The total preserved length is 34.1 mm, the mid-diaphysis is 3.1 mm wide lateromedially, and the distal end is 6.2 mm wide lateromedially. The distal articular surface is almost flat and faces posterodistally. It has a shallow, lateromedially elongated depression in the middle of the facet when observed in posterior view (Fig. 6E). A subcircular outline is observed in distal view (Fig. 6E). This distal end is somewhat similar to the bevelled surface present in *Halazhaisuchus qiaoensis* (Sookias *et al.* 2014: fig. 7R) and differs from the directly distally facing surface of some paracrocodylomorphs (e.g. *Batrachotomus kuferzellensis*, SMNS 80275; *Fasolasuchus tenax*, PVL 3850; *Postosuchus kirkpatricki*, Weinbaum 2013). Additionally, paracrocodylomorph taxa also contrast with CRILAR PV 490 in having elongated distal outlines,

Fig. 4. — Left humerus of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, medial view; **B**, lateral view; **C,** proximal view; **D**, anterior view; **E**, posterior view; **F,** distal view. Abbreviations: **cd**: circular depression; **dp**: deltopectoral crest; **ec**: ectepicondyle; **en**: entepicondyle; **f**: fossa; **lb**: low bump; **tr**: trochlear recess. Arrow indicates anterior direction. Scale bar: 10 mm.

whereas CRILAR PV 490 has a subcircular one. The dorsomedial surface of the shaft shows an elongate scar near the distal end, which is nearly twice as long as wide (Fig. 6D: sc) and probably represents the origin of the *extensor digitorum superficialis* muscle (Otero 2018). This scar was not observed in other taxa used for comparison. The lateral surface of the shaft shows a very faint ridge (Fig. 6D: r) that slightly twists posteriorly near the distal end.

Femur

The approximate distal half of a left femur is preserved in CRILAR PV 490 (Fig. 7). The femur is described with its longitudinal axis oriented dorsoventrally, and the axis through its distal condyles perpendicular to the axial plane of the animal. This fragment is 31 mm long, 6.8 mm wide at its distal end, and has a very narrow diaphysis (3.4 mm wide) that is almost circular in cross-section. It is slightly posteriorly bowed in lateral view but straight in anterior view (Fig. 7A-D). The posterolateral surface shows a well developed ridge that extends nearly one third of the preserved length of the shaft from the distal end (Fig. 7A: lip). This ridge might represent the adductor ridge (ar, *sensu* Hutchinson 2001), the linea intermuscularis caudalis (lip), or the merging of both structures, because sometimes they join together (Hutchinson 2001). This ridge is particularly sharp in CRILAR PV 490, contrasting with the low ridge in taxa such as *Erythrosuchus africanus* (Gower 2003), *Pseudochampsa ischigualastensis* Trotteyn *et al.*, 2012 (Trotteyn & Ezcurra 2014), *Turfanosuchus dabanensis* (IVPP V3237), *Arganasuchus dutuiti* Jalil & Peyer, 2007 (AMNH.F AZA 900), and *Effigia okeeffeae* Nesbitt & Norell,

Fig. 5. — Right ulna of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, dorsal view; **B**, ventral view; **C**, proximal view; **D**, lateral view; **E**, medial view. Abbreviations: **lt**: lateral tuber; **op**: olecranon process; **r**: ridge; **ra**: articulation with the radius. Arrow indicates dorsal direction. Scale bar: 10 mm.

2006 (Nesbitt 2007: fig. 44, r). At the distal end, the lateral and medial condyles are separated anteriorly by a shallow intercondylar groove (Fig. 7C, E). The medial condyle is more distally projected and is lateromedially narrower than the lateral one; it has a posteriorly tapering distal end and is slightly inclined medially. The lateral condyle is damaged on its posterior surface and a distally incomplete ridge arise from the proximal end of this condyle, which is interpreted as the crista tibiofibularis (Fig. 7D: ctf). This crista is present in other early archosaurian and archosauriform taxa including *Vancleavea campi* Long & Murry, 1995 (Nesbitt *et al.* 2009: fig. 16), probably *Aetosauroides scagliai* (PVL 2073), *Batrachotomus kupferzellensis* (SMNS 80278), *Arganasuchus dutuiti* (AMNH.F AZA 900), and *Nundasuchus songeaensis* (Nesbitt *et al.* 2014), and is probably homologous with the lateral condyle of the crocodylomorph *Dromicosuchus grallator* (NCSM 13733). The morphology of this bone is very similar to the single previously known femur of *Gracilisuchus stipanicicorum* (PVL 4597), sharing a sigmoid curvature, a narrow diaphysis compared to the width of the distal end, and the presence of a medially inclined medial condyle. However, CRILAR PV 490 differs from PVL 4597 in the stronger development of the adductor ridge and crista tibiofibularis ("lateral condyle"; Lecuona & Desojo 2011).

Fig. 6. — Right radius of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, medial view; **B**, lateral view; **C**, ventral view; **D**, dorsal view; **E**, distal view. Abbreviations: **bev**: beveled area; **r**: ridge; **sc**: scar. Arrow indicates dorsal direction. Scale bar: 10 mm.

FIG. 7. — Left femur of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, lateral view; **B**, medial view; **C**, anterior view; **D**, posterior view; **E**, distal view. Abbreviations: **ctf**: crista tibiofibularis; **icg**: intercondylar groove; **lc**: lateral condyle; **lip**: linea intermuscularis caudalis (*sensu* Hutchinson, 2001 = linea intermuscularis posterior); **mc**: medial condyle; **pf**: popliteal fossa. Arrow indicates anterior direction. Scale bar: 10 mm.

Osteoderms

Paramedian osteoderms have been recovered in both specimens, CRILAR PV 480 and 490. They are somewhat damaged and incomplete but exhibit the known morphological characters of *Gracilisuchus* (i.e., PULR 08, PVL 4597; Lecuona *et al.* 2017). CRILAR PV 480 preserves a sequence of nine osteoderms of the left paramedian row (Fig. 2B), and CRILAR PV 490 preserves a sequence of five fragmentary paramedian osteoderms (Fig. 3). The osteoderms are asymmetrical with a well developed dorsal crest located closer to the medial than to the lateral margin (Fig. 3C, E: cr); thus, the lateral surface ("wing") is larger than the medial one. The dorsal surface medial to the crest is slightly deeper right next to the crest than the surface lateral to the crest. The paired osteoderms are arranged in a staggered fashion and are longer than wide. In CRILAR PV 490, the osteoderms are somewhat larger than those in CRILAR PV 480 and their edges are faintly crenulated; the edges of CRILAR PV 480 are too poorly preserved to show any ornamentation.

HISTOLOGY

Femur

The femoral diaphysis of CRILAR PV 490 was sectioned for histological analysis at two points approximately at the mid-diaphysis, lacking the fourth trochanter or other superficial features. Both sections are almost identical. The medullary

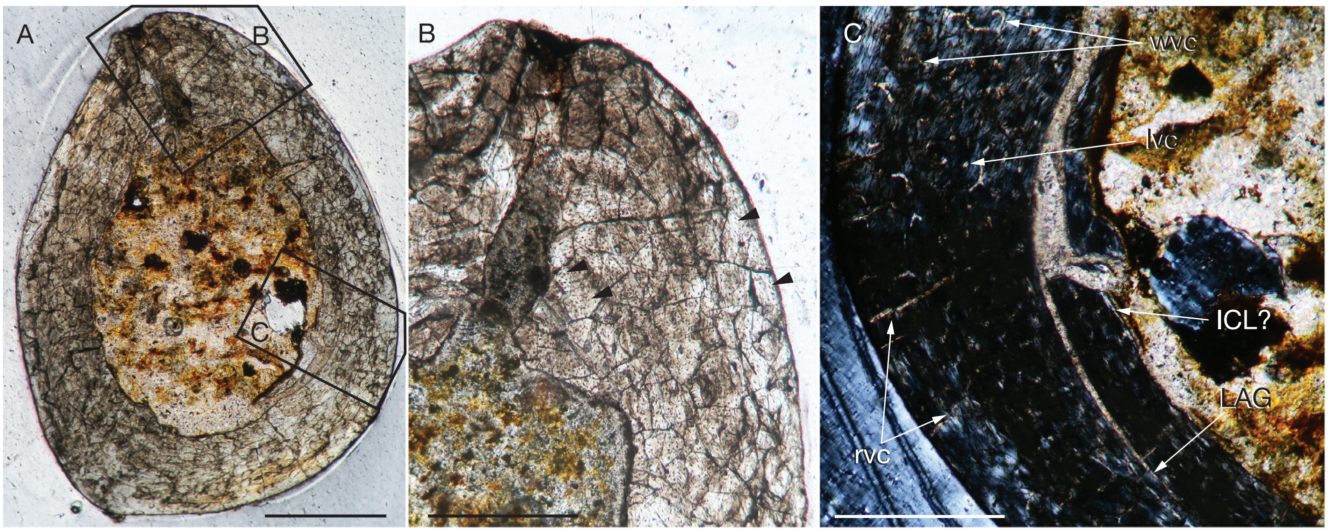

FIG. 8. — Bone histology of the femur of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, general view of the mid diaphysis cross section under normal light; **B**, close up of the femoral cortex under normal light; **C**, close up of the femoral cortex under polarized light. Abbreviations: **ICL?**: inner circumferential layer?; **LAG?**: line of arrested growth?; **lvc**: longitudinal vascular canals; **rvc**: radial vascular canals; **wvc**: vermiform vascular canals. Arrowheads indicate osteocyte lacunae. Scale bars: A,10 mm; B, C, 5 mm.

cavity is large and empty, occupying approximately 63% of the total diameter measured through the longest dimension, and 37.5% of the total surface area (Fig. 8A). The cortex is composed of primary tissue of parallel-fibered bone (PFB), which is more organized near the outer border and decreases in organization toward the inner cortex. In the external cortex, the osteocyte lacunae are oblong in shape, ordered, and parallel to the surface (Fig. 8B). Toward the inner cortex, the cell lacunae tend to be circular but still with the longest axis parallel to the surface and somewhat disorganized with respect to the outer cortex. The primary vascular canals are simple, and one single primary osteon is observed. The vascular organization is mostly longitudinal, but a few radial and several irregular vermiform canals are present (Fig. 8C). The inner cortex presents more vascular canals than the mid- and external cortex, which is consistent with the better organization of the external cortex mentioned above.

A thin layer of secondarily formed lamellar tissue is observed in a short portion of the perimedullar border, interpreted as a probable fragment of the inner circumferential layer (ICL) (Fig. 8C). There are no clear growth marks in the studied samples (e.g. lines of arrested growth [LAGs], zones and annuli), and thus the minimal age of the specimen cannot be estimated. However, close to the medulla, a fragment of inner cortex is separated from the remaining cortex by a clear and sharp border, suggesting that this fracture might have occurred along a line of weakness, such as a LAG (Fig. 8A, C). However, this interpretation is speculative and therefore discarded because the line of fracture does not continue through all or most part of the circumference.

Osteoderms

The histological and microanatomical characters of each section of the osteoderms are similar to each other and thus described together. The osteoderm samples consist of two isolated elements and an incomplete series of two continuous rows, probably corresponding to the left series of contiguous osteoderm rows (*sensu* Ross & Mayer 1983). The paramedian osteoderms of *Gracilisuchus stipanicicorum* have a dorsal longitudinal crest located slightly medial to the midline of the element; they present an inverted-V shape in transverse section and the lateral part (or "wing") is somewhat laterally bent. The outer surface is slightly rugose, with some radial and very shallow grooves (Fig. 3A, B: gr).

The osteoderms are relatively thin, with an inner cancellous core, or spongy bone, surrounded by two layers of compact bone, the superficial cortex and the deep cortex (Fig. 9A). The inner core is thick, occupying most of the central region of the osteoderm, or most of the superficial half of the osteoderm in different samples, leaving a low superficial cortex. The resorption cavities are large and separated by thin trabeculae in the centre of the osteoderm lateral "wing" (sample G2a, Fig. 9A) and in the dorsal longitudinal crest (samples G2d and G3, Fig. 9D). Here the trabeculae are almost completely formed by thick layers of lamellar bone of secondary origin, and some of them show small remains of the primary parallel-fibered bone in the centre. The resorption cavities decrease in size toward the margins of the osteoderm, where they are separated by thick trabeculae bordered by small layers of lamellar bone. These trabeculae are also formed by abundant remains of primary bone, formed by parallel-fibered tissue. The birefringent layers of secondary lamellar bone have elongate osteocyte lacunae in line with the fibres. These layers were deposited due to remodelling of the bone that had already begun when the animal died.

The deep cortex is thicker than the superficial one, presenting a primary matrix of parallel-fibered bone. The birefringence of this tissue reveals fibre bundles oriented diagonal and parallel to the cortical surface (Fig. 9A). Each bundle has intrinsic fibres extending parallel to each other and fusiform bone cell lacunae aligned with the intrinsic fibre orientation. The fibre

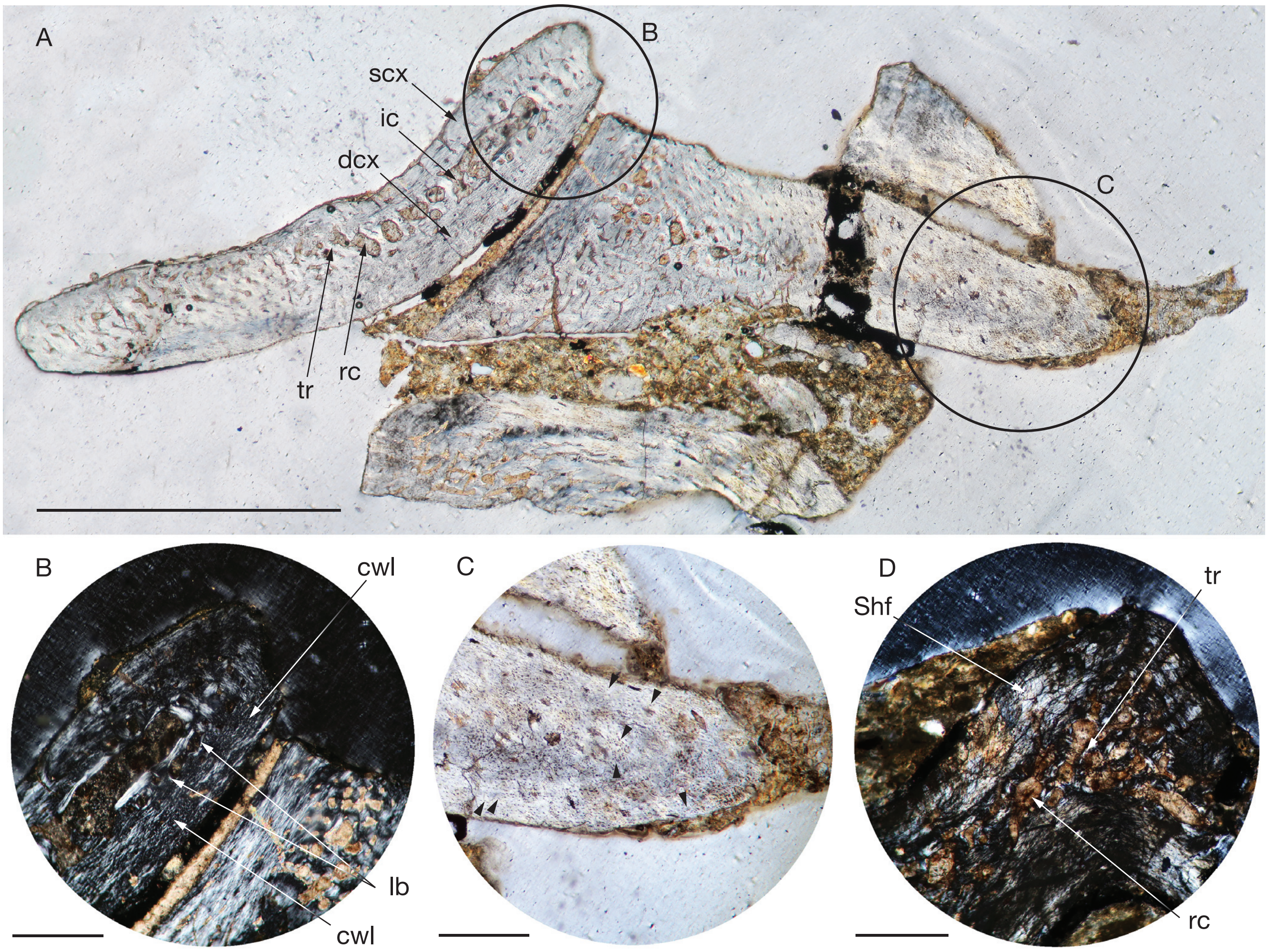

FIG. 9. — Bone histology of the osteoderms of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in **A**, general view in transversal section of sample G2a under normal light; **B**, close up of lateral end of the osteoderm marked in **A**, under polarized light; **C**, close up of lateral end of the osteoderm marked in **A**, under normal light; **D**, close up of the dorsal crest of the sample G2d under polarized light. Abbreviations: **dcx**: deep cortex; **cwl**: chicken wire-like structures; **ic**: inner cancellous core; **lb**: lamellar bone; **rc**: resorption cavities; **scx**: superficial cortex; **Shf**: Sharpey's fibres; **tr**: trabecula. Arrowheads indicate osteocyte lacunae. Scale bars: A, 25 mm; B, D, 5 mm and C, 10 mm.

bundles extend into the trabeculae of the inner core in various directions, but the osteocyte lacunae are less elongate in this region. This difference is more evident in some samples where the cell lacunae are small and elongate near the surface, but larger, less elongate, and more abundant in the inner core (Fig. 9C). Near the lateral and medial margins of the osteoderms, the fibre bundles follow the same curvature as the osteoderm surface, having been sectioned longitudinally. Some fibre bundles are perpendicular to all the surfaces of the osteoderm and others perpendicular to the section plane. Those perpendicular to the plane of section appear as minute (*ca.* 20 μm) circular monorefringent "dots" circled by a thin birefringent "line", creating an overall structure resembling "chicken wire" (Fig. 9B: cwl). These transverse bundles are present in different regions in the samples, such as in a long single layer next to the ventral surface around the midpoint of the lateral "wing" (Fig. 9B), in the ventralmost part of the inner core, as well as in the superficial cortex. In contrast, they are absent in the deep cortex.

The superficial cortex is thin compared with the inner core and the deep cortex. Near the surface it shows numerous birefringent fibre bundles extending parallel to the surface, and, toward the inner core, the bundles start to take different directions and to be smaller in size. The vascularization of the osteoderms is poor, showing small simple canals of longitudinal orientation. They are more abundant in the deep cortex than in the superficial one, which are distinguished under normal light (Fig. 9A, C). Sharpey's fibres are observed in some samples. In two of them, these extrinsic fibres are present in the deep cortex next to the surface, being oriented in several directions. Another sample shows several Sharpey's fibres in the longitudinal dorsal crest, which orientation near the surface is perpendicular to the surface and further from it they take a diagonal direction (Fig. 9D). Growth marks are not evident in the osteoderm samples, with the possible exception of a very faint and short line near the ventral surface of the deep cortex of the G3 sample. This could be interpreted as a LAG;

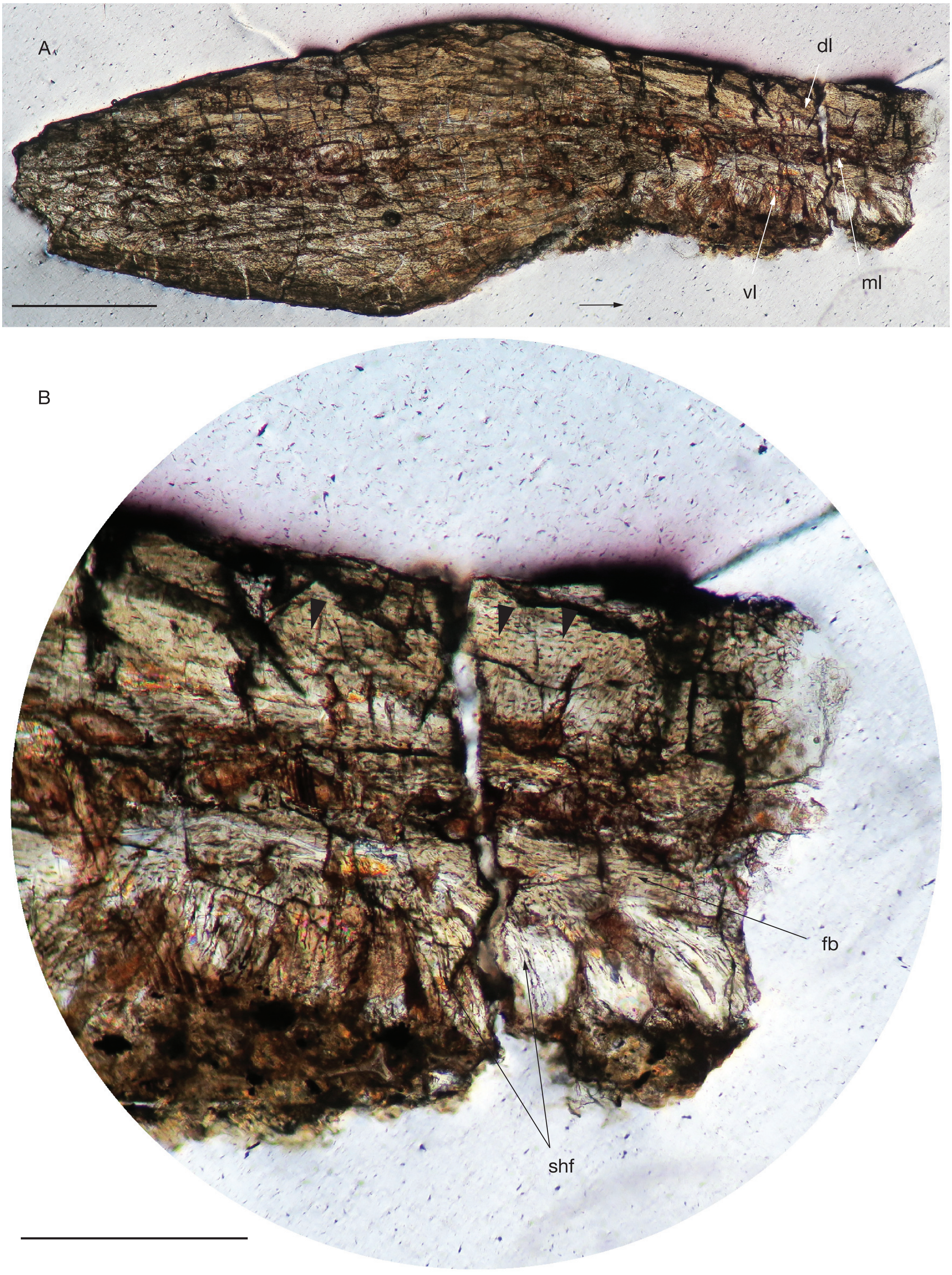

Fig. 10. — Bone histology of an osteoderm of *Gracilisuchus stipanicicorum* Romer, 1972 (CRILAR PV 490) in longitudinal section, sample G4. **A**, General view under normal light; **B**, close up of anterior region of the osteoderm in **A**. Abbreviations: **dl**: dorsal layer; **fb**: fibres; **ml**: middle layer; **Shf**: Sharpey's fibres; **vl**: ventral layer. Arrowheads indicate osteocyte lacunae, arrow indicates anterior direction. Scale bars: 10 mm (**A**) and 5 mm (**B**).

however, due to its short and faint condition, this is a dubious interpretation and therefore discarded.

In longitudinal section, there is an anterior region with three layers (Fig. 10), the correspondence of which to the cortices and the inner core cannot be ruled out because of the partially obscured microanatomy. These layers are recognized based on the general orientation of the fibres. The osseous matrix of the superficial layer is formed by fibres oriented parallel to the surface and several elongated osteocyte lacunae oriented almost parallel to the surface. Fibre orientation in the inner layer is difficult to assess, but some longitudinal fibres are recognized next to the deep layer. Finally, the deep layer contains abundant Sharpey's fibres oriented nearly perpendicular to the surface, which become more diagonal toward the middle region of the osteoderm and then horizontal at its posterior end.

DISCUSSION

Osteology

The new specimens of *Gracilisuchus stipanicicorum* (CRILAR PV 480 and CRILAR PV 490) recovered from the outcrops of the Chañares Formation preserve elements that are absent in the previously known specimens, including a complete humerus and fragmentary ulna and radius, allowing us to better understand the anatomy of this species.

The overlapping elements found in the new specimens are morphologically similar to those previously known (PULR 08, PVL 4597), sharing a diagnostic combination of characters. The cervical vertebrae show a circular anterolateral depression on the neural arch, an infrapostzygapophyseal depression under the postzygapophyses, and a ventral parapophyseal fossa. The paramedian osteoderms are staggered, with a dorsal crest slightly medially offset from the centre of the osteoderm. The femur shares some general characters including a sigmoid curvature and narrow diaphysis, but it differs in the presence of a better developed adductor ridge and *crista tibiofibularis* in CRILAR PV 490. The differences in the morphology of the femur may well be the result of better preservation of CRILAR PV 490 than in PVL 4597, which shows some cracks and deformations. Intraspecific variation may also be responsible for some of these differences but an ontogenetic hypothesis is less likely. The latter hypothesis is based on the interpretation that PVL 4597 might be older than CRILAR PV 490 (see ontogenetic section) but PVL 4597 shows anatomical structures less developed than CRILAR PV 490, what is usually associated with younger ontogenetic stages.

The overlapping distal region of the humeri of CRILAR PV 490 and PULR 08 are consistent, being nearly the same size (CRILAR PV 490 is 1.11 times larger than PULR 08), with similar trochlear recesses but somewhat contrast in the morphology of the distal condyles. These differences can be interpreted as intraspecific variation, a slight difference in maturity, or an artefact of preservation due to the preservation of this region in PULR 08 as a mould.

Skeletal elements previously unknown for *Gracilisuchus* are present in CRILAR PV 490, permitting a better characterization of the anatomy of the taxon. The ulna presents a probable broken lateral tuber at its proximal end and a probably muscular longitudinal ridge on its diaphysis. The distal region of the radius has a noticeable muscular scar in the dorsomedial surface and a bevelled distal articular facet.

Histology

The predominance of poorly vascularized parallel-fibered bone in the femur and osteoderms of CRILAR PV 490 suggests a low growth rate in this individual, which can possibly be extrapolated to the species. Some microanatomical differences exist between the inner, middle, and outer cortices of the femur, where the organization of the bone matrix increases centrifugally, concurrently with a decrease in the vascularization density, indicating a slowing down of growth through ontogeny.

No external fundamental system (EFS) is observed in the periphery of the femur of CRILAR PV 490, suggesting that this specimen had not reached an asymptotic size, or somatic maturity when it died. The absence of an EFS has usually been associated with an indeterminate growth strategy in tetrapods, but this assumption was demonstrated to be inaccurate on the basis of long-bone histology in *Alligator mississippiensis* (Daudin), 1802 (Woodward *et al.* 2011). The presence of an EFS in several specimens of *A. mississippiensis* indicates a determinate growth history with cessation in growth when an asymptotic size is attained (the average age at which skeletal maturity is achieved; Woodward *et al.* 2011). The absence of such a structure in *A. mississippiensis* suggests that this average asymptotic size was not reached (Woodward *et al.* 2011). Thus the absence of such a layer in tetrapods does not necessarily indicate an indeterminate growth but potentially still unreached skeletal maturity.

The capacity to form the fast-growing FLB tissue was already present in basal Archosauriformes (Botha-Brink & Smith 2011; Legendre *et al.* 2013; Klein *et al.* 2017; Cubo & Jalil 2019), and retained within both Pseudosuchia and Avemetatarsalia (Legendre *et al.* 2013; Klein *et al.* 2017). The deposition of fibrolamellar bone tissue (FLB) was retained in Avemetatarsalia, including dinosaurs and pterosaurs, and in most pseudosuchian groups, such as aetosaurs and basal paracrocodylomorphs, but reverted to a slow-growing lamellar zonal bone (LZB) in derived Crocodyliformes, including living representatives (e.g. de Ricqlès *et al.* 2003; Woodward *et al.* 2011; Company & Pereda-Suberbiola 2017; Klein *et al.* 2017). In this scenario, the presence of a slow-growing PFB in the relatively deeply nested suchian *Gracilisuchus stipanicicorum* may indicate a reversion to a low growth rate, but it also differs from the slow-growing LZB present in lepidosaurs and in the non-archosauriform archosauromorphs *Trilophosaurus* Case, 1928 and rhynchosaurs (Legendre *et al.* 2013). The presence of this low growth rate in *Gracilisuchus* could be related to particular environmental conditions of the Chañares Formation (Pérez Loinaze *et al.* 2018) and/or differences in the growth strategies with the aforementioned taxa.

On the basis of measurements of basal metabolic rates and growth rates in living species, where larger species of a group usually present larger parameters than smaller species of the same group (e.g. Case 1978; Sander *et al.* 2011), it is believed that the small size of the *Gracilisuchus* specimens reflects the low growth rate inferred from its histology. If CRILAR PV 490 and PULR 08 are considered juveniles (see below) and both of them present already low growth rates, it appears likely that the fully grown adult would have not reached very large size. This is also consistent with the consideration that the growth rate decreases though ontogeny as a strategy to shorten the period of vulnerability (Erickson 2005; Klein *et al.* 2017; Sander *et al.* 2011), a slowing down already inferred from the femur section (see above).

The largest known skull of *Gracilisuchus* (PVL 4612) is 90 mm long but it lacks the tip of the snout and thus probably reached a length of 95 mm; and the largest femur of *Gracilisuchus* is 80 mm long (PVL 4597). These specimens are considered at least subadults based on their somewhat larger size and the presence of fused neurocentral sutures in the vertebrae. These measurements are much smaller than those of the closely related gracilisuchids *Turfanosuchus dabanensis* (Wu & Russell 2001; IVPP V3237) and *Yonghesuchus sangbiensis* (Wu *et al.* 2001; IVPP V12378), which have skull lengths of 164 and 150 mm, respectively, and a femur with a length of 136 mm in *Turfanosuchus* (not preserved in *Yonghesuchus*). Other basal suchians show larger body sizes, such as *Ticinosuchus ferox* Krebs, 1965 (PIMUZ T2817, Krebs 1965; femoral length 250 mm), and the basal loricatans *Prestosuchus chiniquensis* von Huene, 1938 (UFRGS-PV 0152; femoral length approximately 480 mm), *Fasolasuchus tenax* (PVL 3850; femoral length 690 mm), and *Batrachotomus kupferzellensis* (SMNS 52970, SMNS 80278; femoral length 496 mm). *Gracilisuchus* is the smallest known gracilisuchid and shows a much smaller body size than other basal loricatans based on the length of the femur. Thus, we interpret that its small size is directly related with a low growth rate, contrasting with higher ones present in basal loricatans (Klein *et al.* 2017). There is no information available for the other gracilisuchids to date and thus no further comparisons can be made. We must note that a positive relationship between body size and growth rate is not always observed in all vertebrates. For example, Cubo *et al.* (2012) showed that a small bird (*Turdus merula*) has a bone growth rate (102 μm/day) higher than that measured in a large ratite (*Dromaius novaehollandine*, 91 μm/day). Nevertheless, the same authors considered that this rather exceptional result is due to the altricial strategy of *Turdus*. Given that such strong variation in developmental strategies has not been proposed for pseudosuchians, we argue that the slow growth rate of *Gracilisuchus* is likely to be related to its small body size. Finally, the data at hand does not allow determination of the direction of causality between these two parameters; it is not possible to infer if natural selection promoted small body sizes or if growth rates were actually more affected by selective pressures.

No definite growth marks are seen in the femur and the osteoderms of *Gracilisuchus*. The femur shows a very clean and short crack probably produced in a region of weakness, like a line of arrested growth. However, this crack does not continue as a LAG or another structure, and thus the interpretation as a LAG cannot be substantiated. One of the osteoderm samples shows a very faint line near the surface, but this one does not appears to be a LAG because of its short and faint condition. Growth marks in other parts of the osteoderms cannot be identified, or may be obscured by the profusion of Sharpey's fibres. In extant crocodilians the osteoderms begin to ossify a year after hatching (Chiappe *et al.* 1998; Vickaryous & Hall 2008). If this also occurred in extinct pseudosuchians, it would mean that the *Gracilisuchus* specimen sampled was younger than two years old. An alternative scenario is that it was older but had a relatively constant growth rate with no considerable decrease in growth that may have produced LAGs or zones and annuli. Such a histological pattern, however, has not been reported in suchians to our knowledge.

The virtual absence of a thick, well-developed inner circumferential layer (ICL) bordering the medullary cavity of the femur of *Gracilisuchus* is also the most widespread condition among basal archosauriforms and basal pseudosuchians. Nevertheless, the presence of a thin fragment of secondary lamellar bone tissue around the medullary cavity indicates that such a structure was actually present but poorly developed in CRILAR PV 490. This finding increases reports of ICL among archosauriforms, which are scattered to date, having been reported previously only in the non-archosaurian archosauriform *Euparkeria capenis* (Botha-Brink & Smith 2011), probably in the basal crocodylomorph *Terrestrisuchus gracilis* (de Ricqlès *et al.* 2003), and one eusuchian (Company & Pereda-Suberbiola 2017).

Some osteoderms show Sharpey's fibres in the deep cortex, interpreted to be located at the points of attachment of the ligaments that maintained the contact with the neural spines of the vertebrae below, as reported in extant crocodilians (Salisbury & Frey 2001). The presence of fibres in several directions suggests that several ligaments with different directions were maintaining this contact because the Sharpey's fibres are aligned in the same direction as the line of force. These extrinsic fibres are also observed in the dorsal crest of an osteoderm, where they are curved, only becoming perpendicular when they reach the surface. This change in orientation suggests that the soft tissues attached to the superficial surface (possibly related to the presence of keratinous scales) may have been changing with the direction of force as the osteoderm grew.

The anterior region of the osteoderm shows a trilaminar structure, probably corresponding to the superficial cortex, inner core, and deep cortex, although this cannot be ascertained with full certainty. The deeper layer is rich in nearly perpendicular Sharpey's fibres in the anteriormost region. In the middle region of the deeper layer, the fibres become diagonal and posteriorly inclined, and, in the posterior region of the osteoderm, they extend almost horizontal. The orientation of the fibres suggests an attachment with the soft tissues of the neural spines in the anterior region, where the force of the soft tissues was perpendicular to the surface and parallel to the fibres. Posteriorly, we interpret that the Sharpey's fibres took a diagonal direction from the point of attachment in order to resist the force of the tissues. The superficial and inner layers show intrinsic fibres and some faint osteocyte lacunae in some regions, and no other structure (e.g. resorption cavities) is evident.

ONTOGENETIC STAGES OF THE SPECIMENS OF *GRACILISUCHUS*

Based on the absence of growth marks in the histological sections of CRILAR PV 490 and information from extant crocodilians (Chiappe *et al.* 1998; Vickaryous & Hall 2008), we infer that this specimen was younger than two years. Based on osteological characters, PULR 08 was interpreted to be a juvenile specimen of *Gracilisuchus* (Lecuona *et al.* 2017). Comparing the overlapping elements of these two specimens, namely humeri and vertebrae, CRILAR PV 490 is slightly larger than the holotype (PULR 08). The width of the mid diaphysis of the humerus is 1.11 times larger in CRILAR PV 490, as is the length of the cervical (1.14) and the dorsal (1.13) vertebrae. On the other hand, the cervical and dorsal vertebrae of the specimen PVL 4597 are almost the same length as those of CRILAR PV 490, the latter being 1.08 (cervicals) and 1.01 (dorsals) times larger than PVL 4597. However, the femur of PVL 4597 is larger than that of CRILAR PV 490, being 2.8 times larger at the mid-diaphysis and 1.7 times wider at the distal end, but, PVL 4597 has suffered some postmortem distortion and thus these measurements and proportions may be overestimated. Campione & Evans (2012) investigated several parameters in extant mammals and reptiles, observing that the circumference of the stylopodia (humerus and femur) and the body mass (correlated to body size) maintain a highly conserved relationship. On this basis, it would be more accurate to compare the femora of PVL 4597 and CRILAR PV 490 instead of their vertebrae, which would lead us to conclude that PVL 4597 is larger and thus probably ontogenetically more mature than CRILAR PV 490.

The aforementioned interpretation of the histological sections indicate an estimated ontogenetic age of less than two years for CRILAR PV 490, based on the absence of growth marks and EFS. The same age is estimated for PULR 08 as both specimens are comparable in size. As PVL 4597 is larger than both of them, an older ontogenetic age is inferred, although it is not possible to determine this more accurately until new histological data becomes available.

CONCLUSIONS

The discovery of new material of *Gracilisuchus stipanicicorum*, preserving some well-preserved anatomical elements unknown in other specimens (e.g. humerus, radius, ulna), allows us to better characterize the anatomy of this basal suchian and can help in the identification of new material to this species. Some unique characters, not yet observed in the taxa compared, were identified on the radius, such as a muscular scar on the dorsomedial surface of the shaft and a bevelled distal articulation (the latter probably also seen in *Halazhaisuchus qiaoensis*; Sookias *et al.* 2014). Some differences have been found among the specimens, which have been interpreted as intraspecific variation or artefacts of preservation, but none of them appears to be associated to differences in maturity.

Histological sections of the femur and paramedian osteoderms of CRILAR PV 490 were made. This study allowed us to address an aspect of the anatomy and biology of *Gracilisuchus* never studied before. The absence of growth marks and EFS in the specimen sampled for histology suggest it was younger than two years. This conclusion and its small overall size help to confirm the previous interpretation of the holotype specimen (PULR 08) as a juvenile based on its morphology (Lecuona *et al.* 2017). A low growth rate was inferred from its poorly vascularized parallel-fibred bone tissue, which is consistent with the small size attained in the more mature specimens. *Gracilisuchus* is approximately one third smaller than the closely related species *Turfanosuchus dabanensis* and *Yonghesuchus sangbiensis* (0.58 and 0.63 respectively), which supports the idea that the largest specimen of *Gracilisuchus* may still not be a fully grown adult. This and other hypotheses regarding the ontogeny of *Gracilisuchus* may be able to be clarified when new specimens become available for histological analysis. Further conclusions about the palaeobiology of Gracilisuchidae are still precluded by the lack of information on other taxa. Thus, it will be highly relevant to study the bone histology in *Turfanosuchus* and recover new, more complete specimens of *Yonghesuchus* to perform the same studies in order to compare these taxa and clarify our understanding of the biology of this enigmatic basal pseudosuchian clade.

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