ABSTRACT—Ornithosuchidae is a group of terrestrial quadrupedal pseudosuchian archosaurs from the Late Triassic of South America and Europe. *Riojasuchus tenuisceps* is arguably one of the best representative species of this clade because it comprises very well-preserved three-dimensional, almost complete skeletons. However, *R. tenuisceps* was originally described 50 years ago and compared then only with *Ornithosuchus woodwardi* and their affinities were discussed in detail. Here, we provide a detailed description of the postcranial skeleton of *R. tenuisceps*, which exhibits several remarkable features within pseudosuchians. When a wide spectrum of pseudosuchian archosaurs are considered, the alleged character that linked ornithosuchids with dinosaurs resulted in convergences and some were registered in other pseudosuchian groups as well. *Riojasuchus tenuisceps* also provided crucial information about the ‘crocodile-reversed’ tarsus, which is a unique feature of ornithosuchids, but it is not completely preserved in *O. woodwardi* and it is unknown in *Venaticosuchus rusconii*. In addition, the first histological analysis of cervical and dorsal osteoderms of *R. tenuisceps* was carried out as well, in order to test the utility of these structures as skeletochronological tools. Finally, the phylogenetic context of Ornithosuchidae is discussed based on the latest phylogenetic studies, which show a close affinity with Erpetosuchidae.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Ornithosuchids are an unusual and rather poorly known group of pseudosuchian archosaurs registered in Upper Triassic continental deposits of South America and Europe. Ornithosuchids are found alongside with erpetosuchids, aetosaurs, loricatans, gracilisuchids, and basal crocodylomorphs (Nesbitt, 2011; Butler et al., 2014; Ezcurra et al., 2017). They are terrestrial quadrupedal to facultatively bipedal animals, with medium body sizes of ca. 2 m in length and scavenger feeding habits (Benton, 1983; Baczko, 2018). This group is distinguished by a bizarre cranial morphology (downturned premaxilla, two-tooth diastema, palatine-pterigoid fenestra, mandible shorter than skull) and several controversial postcranial features (perforated acetabulum, rotated femoral head, crocodile-reversed ankle joint) that turned them into a phylogenetic riddle for decades (Sereno, 1991; Baczko and Ezcurra, 2013; Baczko and Desojo, 2016).

Ornithosuchidae is currently composed of three species from present-day Argentina and Scotland: *Riojasuchus tenuisceps* (Los Colorados Formation, middle Norian), *Venaticosuchus rusconii* (Ishigualasto Formation, late Carnian–early Norian), and *Ornithosuchus woodwardi* (Lossiomouth Sandstones Formation, late Carnian–early Norian). *Riojasuchus tenuisceps*, particularly, was discovered at the Quebrada de Los Jachalleros locality, La Rioja, northwestern Argentina, and formed part of the Coloradina fauna, a very rich and diverse assemblage of Late Triassic tetrapods, composed of ornithosuchids, basal loricatans, sphenosuchians, protosuchians, sauropodomorphs, theropods, quelonis, and cynodonts (Bonaparte, 1973; Arcucci et al., 2004). *Riojasuchus tenuisceps* includes four specimens of similar size, three of whom are very well preserved, and together represent almost the complete skeleton of this species, which provides crucial information about the anatomy of this peculiar archosaur. *Riojasuchus* was originally described by Bonaparte (1972) highlighting its similarities to *Ornithosuchus woodwardi* (= *Ornithosuchus ‘longidens’*; see Baczko and Ezcurra, 2016), the best-known ornithosuchid at that time, although its affinities were quite unclear by then.

Despite Ornithosuchidae being a small group with only three species known, some aspects of these species need to be studied in detail. As a continuation of the recently published description of the skull and cranial endocast of *Riojasuchus tenuisceps*, we provide here a detailed description of the postcranial skeleton, based on firsthand study of all known specimens. Additionally, a histological analysis of its cervical and dorsal osteoderms was carried out to document the microroanatomy of *Riojasuchus*. The phylogenetic position of Ornithosuchidae is also discussed.

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based on the latest analyses that revealed their close affinity with the clade Erpetosuchidae.

HORIZON AND LOCALITY

Upper beds of the Los Colorados Formation (Late Triassic), Quebrada de los Jachalleros, General Lavalle, La Rioja, northwestern Argentina (Fig. 1). This upper section of the Los Colorados Formation has yielded a particular fauna named the ‘Coloradian’ (‘Coloradense’), which is mainly composed of pseudosuchians (ornithosuchids, aetosaurians, rauisuchians, and crocodylomorphs), avemetatarsalians (sauropodomorphs and theropods), quelenids, and cynodonts. The latest radiometric and paleomagnetic studies dated the Coloradian strata at 227–213 Ma, corresponding to a late Norian age (Kent et al., 2014).

Institutional Abbreviations—SNSB-BSPG, Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany; CRILAR-PV, Paleontología de Vertebrados, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Anílaco, Argentina; GPIT, Institut für Geowissenschaften, Universität Tübingen, Tübingen, Germany; MACN-He, Colección Nacional de Herpetología, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; NHMUK, Natural History Museum, London, U.K.; PULR, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; SAM-PK, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, Texas, U.S.A.; TTU, Texas Tech University Museum, Lubbock, Texas, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UFRGS-PV, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

MATERIALS AND METHODS

Riojasuchus tenuisceps is currently represented by four specimens, PVL 3827 (holotype), PVL 3814, PVL 3826, and PVL 3828, three of which represent almost the complete skeleton (Fig. 2). All specimens were studied firsthand at the Instituto Miguel Lillo, where they are accessioned. No specimens were purchased or donated for the purpose of this study. Measurements were made with a digital caliper set with a maximum deviation of 0.02 mm, but measurements were rounded to the nearest 0.1 mm.

For the histological study, three transverse sections were made, one from a cervical osteoderm and two from a dorsal osteoderm of Riojasuchus tenuisceps (PVL 3814), and analyzed. Given the destructive nature of the procedure for obtaining thin sections, the sampled elements were photographed and measured before processing. Also, a cast of each osteoderm was made to avoid the loss of morphological information. The specimens were sectioned following the methodology of Chinsamy and Raath (1992). The histological sections were made in the Departamento de Geología de Universidad Nacional de San Luis, Argentina. The sections were analyzed under a petrographic microscope (Nikon E200 Pol and Zeiss Imager.A2m) under plane- and cross-polarized light. We use the term ‘external’ to refer to the portion of the osteoderm oriented toward the body surface and the term ‘basal’ for the portion that is oriented toward the interior of the organism (Scheyer and Sander, 2004). These terms are synonyms of ‘distal/proximal’ (Main et al., 2005) or ‘superficial/deep’ (Hill and Lucas, 2006; Hill, 2010). In addition, we use the term ‘marginal’ cortex to refer to the lateral and medial regions of the osteoderms. For the terminology of growth marks, we follow the nomenclature proposed by Francillon-Vieillot et al. (1990).

For the phylogenetic analyses, we augmented the data matrices of Ezcurra et al. (2017) and Lacerda et al. (2018), which are available as Supplemental Data 1 and 2, respectively. Changes made to the codings of characters in these matrices are summarized in Supplemental Data 3.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869, sensu Gauthier and Padian, 1985

PSEUDOSUCHIA Zittel, 1887–1890, sensu Gauthier and Padian, 1985

ORNITHOSUCHIDAE Huene, 1908, sensu Sereno, 1991

RIJOASUCHUS Bonaparte, 1967

RIJOASUCHUS TENUISCEPS Bonaparte, 1967 (Figs. 2–14)

Holotype—PVL 3827, a very well-preserved skull with postcranial elements. The skull has the right hemimandible articulated, but the left hemimandible was disarticulated during the original preparation. The skeleton comprises 26 partially articulated vertebrae (19 presacrals, three sacrals, and four caudals) with articulated paramedial osteoderms in some cervical and dorsal regions, incomplete scapulae and coracoids, incomplete humeri, a distal portion of left radius and ulna articulating with carpus, left ilium and pubis, left femur, left tibia and fibula articulating with complete pes, and partial right pes.

FIGURE 1. Geological map of the Los Colorados Formation, Ischigualasto–Villa Unión Basin, La Rioja, Argentina. Star indicates the location where the specimens were collected. Modified from Baczko and Desojo (2016).
Referred Material—PVL 3828, an almost complete skull with postcranial elements. The skull has some incomplete elements such as the premaxillae, nasals, left jugal and lacrimal, squamosals, left surangular, and right angular and articular. Both hemimandibles are articulated and occluded. The skeleton is constituted of several skeletal elements, including 32 partially articulated vertebrae (19 preasacrals, three sacrals, and 13 caudals); incomplete scapulae and coracoids, humeri, radii, and ulnae; left ilium and a fragmentary ischium; left femur; incomplete right femur; incomplete tibiae; fragmentary right fibula; isolated left 4th distal tarsal; left calcaneum; and several disarticulated phalanges.

PVL 3826, consisting of 28 partly articulated vertebrae (19 preasacrals and nine caudals), two fragmentary scapulae and coracoids, right humerus, fragmentary radius and ulna, incomplete right ilium, distal end of left femur, and fragmentary tibia.

PVL 3814, consisting of several isolated poorly preserved vertebrae, fragmentary left humerus, fragmentary tibia, and several isolated paramedial osteoderms.

Comment—Bonaparte (1972) indicated that the assignment of some elements to each of the four specimens of *Riojasuchus* is arguable because they were found close together and their sizes are even. For example, he affirmed that the two left ilia and the fragment from the right ilium known for *Riojasuchus* were not in articulation and therefore cannot be assigned to any of the four specimens with certainty. For that reason, we would like to point out that the original assignment of these elements was arbitrary. However, the left ilium assigned to the holotype is dorsoventrally deformed, and the same kind of deformation can be recognized in its left femur. In contrast, the left ilium assigned to PVL 3828 does not exhibit postmortem deformation, which is consistent with the left femur of the same specimen. Following this reasoning, the original arbitrary assignment of both left ilia by Bonaparte (1967) seems adequate and is not modified here. Concerning the incomplete right ilium of PVL 3826, this fragmentary element is not deformed and could correspond to either PVL 3828 or PVL 3826. Moreover, the sacral vertebrae of PVL 3828 do not preserve the sacral ribs; therefore, it is impossible to test whether it articulated with this ilium or not. And on the other hand, only the last sacral of PVL 3826 is poorly preserved, but the fragmentary ilium is represented by its anterior portion and does not articulate with the last sacral at all. Therefore, the assignment of the right ilium cannot be confirmed or rebutted, because there is no evidence against the original assignment, and we opt not to modify it.

Diagnosis—*Riojasuchus tenuisceps* is distinguished from all other archosaurs by the combination of the following characters (autapomorphies noted with asterisk): (1) strongly downturned premaxilla; (2) three premaxillary teeth; (3) seven maxillary teeth; (4) second and third teeth on dentary hypertrophied; (5) two-tooth diastema between premaxilla and maxilla; (6) deep antorbital fossa with the anterior and ventral edges almost coinciding with the same edges of the maxilla itself*; (7) nasal-prefrontal contact absent; (8) jugal with vertical process separating...
antorbital fenestra from infratemporal fenestra; (9) orbit with ventral point surrounded by ‘V’-shaped dorsal processes of the jugal; (10) suborbital fenestra equal in size to the palatine-pterigo-
goid fenestra*; (11) posterolateral process of the parietals ante-
riorly inclined greater than 45°; (12) reduced supratemporal 
fenestra; (13) ‘L’-shaped infratemporal fenestra; (14) presence of a palatine-pterigo-
goid fenestra; (15) lower jaws shorter than skull 
length; (16) presence of a first small tooth anterior to the two 
hypertrophied teeth; (17) anterior end of the dentary dorsi-
ally expanded; (18) ventral keel of cervical vertebrae extends 
ventral to the central rims; (19) pubis longer than 70% 
of femoral length; (20) anterior trochanter (+ M. iliofemoralis crane-
ialis insertion) forms a steep margin with the shaft but is completely 
connected to the shaft; (25) ventral astragaloalcaneal articular 
surface concavoconvex with concavity on astragalus; and (26) 
metatarsal V without ‘hooked’ proximal end.

RESULTS

Axial Skeleton

Proatlas—It is composed of two dorsoventrally compressed slits of bone slightly curved lateroventrally (Fig. 3A); they 
contact each other medially, constituting the roof of the neural 
caetal arches of the atlas contact medially (Fig. 3A, B, D), which, accord-
ing to Sereno (1991), is considered an autapomorphic character for 
Riojasuchus tenuisceps, but this feature is also present in 
modern crocodylians such as Crocodylus novaguineae (SMNS 
6664) and Osteolaemus tetraspis (SMNS 6665).

Axis—It is the longest element of the axial series, and its 
centrum is laterally compressed, being half its maximum width. 
It has a well-developed hypapophysis at the midline of its 
ventral surface, although it is partially broken in some regions 
in PVL 3827 and PVL 3828 (Fig. 3A, B). The axis is articulated 
within the vertebral series; therefore, its anterior and posterior 
articular facets cannot be seen in PVL 3827 and PVL 3828. The 
ventral margin of the anterior articular surface is wider than the 
posterior one, and it is markedly curved. The diapophyses and 
apophyses of the axis cannot be clearly recognized on any 
 specimen of R. tenuisceps (PVL 3827, PVL 3828), but the corre-
spanding cervical ribs are preserved in articulation with the axis of the holotype (Fig. 3A, B). The neural spine of the axis of 
R. tenuisceps is anteroanteroposteriorly expanded, reaching the anterior 
margin of the atlas anteriorly and the middle region of the third 
vertebral vertebra posteriorly. The external surface of the spine 
is striated at its base (PVL 3828), possibly for the insertion of the neck muscles (M. interarticularis and M. epistropheo-
capitis; Tsuihiji, 2005). The prezygapophyses of the axis are 
completely covered by the postzygapophyses of the atlas in both PVL 
3827 and PVL 3828. Their anterior extent and articular facets 
cannot be seen in any of these specimens. The postzygapophyses 
are elongated and posterolaterally projected, extending posterior 
to the posterior margin of the centrum (Fig. 3A). These were also 
preserved in articulation with the third cervical vertebra, and their articular facets cannot be observed.

Postaxial Cervical Vertebrae—These correspond to the region 
between the third and tenth vertebrae (C3–C10), although the 
posterior cervical vertebrae are difficult to differentiate from 
the anterior dorsal vertebrae. The centra of the postaxial cervical 
vertebrae of R. tenuisceps are as long as high in all the series, 
becoming slightly shorter toward the posterior ones. The anterior 
and posterior articular facets are round, approximately as high 
as long, and concave (amphicoelic). The middle region of the centra is 
compressed, granting the cervical vertebrae a spool shape, 
although these centra are less compressed than the axis 
centrum. There are no lateral fossae or accessory laminae 
between the apophyses, nor between the apophyses and the 
centrum. There is no evidence of the presence of a hypophy-
sis or a hypanthrum in any specimen of R. tenuisceps. The ventral 
surface of the cervical centra has a well-developed hypapophysis 
(ventral keel) that becomes anteroposteriorly longer and dorso-
ventrally higher toward the middle cervical vertebrae, reaching 
its largest development at the C5 (Fig. 3A, B). The hypapophysis of 
the posterior cervical vertebrae is much shorter, occupying 
only the anterior half of the centrum and becoming lower 
toward the last cervical vertebrae and being almost imperceptible 
at the C10 (PVL 3827) (Fig. 4A, B).

The diapophyses of the postaxial cervical vertebrae of R. tenuisceps can be recognized as a small ventrolateral projection on each side of the centrum located ventral to the neurocentral 
suture. These diapophyses are very short on the first postaxial cer-

vical vertebrae but are longer toward the posterior ones; their rela-
tive position changes toward the posterior cervical vertebrae (C7–
C10), being located on top of the neurocentral suture. The parap-
ophyses can be identified from C4 (PVL 3828) on the anterior 
margin of the centrum, below the dorsoventral midline (Figs. 3A, B, F, G, 4A–D). The parapophyses are short; they are laterally pro-
jected on the anterior cervical vertebrae (PVL 3828: C4–C6) and 
posterolaterally projected on the posterior cervical vertebrae 
(PVL 3827: C7–C10). On the last cervical vertebra (PVL 3827: 
C10), the parapophyses are located at the dorsoventral midline 
of the centrum and are dorsoventrally expanded, resembling the 
condition of the first dorsal vertebrae, but without contacting the 
neurocentral suture as in the latter (PVL 3827: D1).

The neural spines of the postaxial cervical vertebrae are 
located on the posterior margin of the centra; they are as 
high as the centra and anteroposteriorly short. They are dorsoventrally 
oriented and widen abruptly on their apical end, forming a well-
defined spine table (Fig. 3F). The spine tables of the postaxial cer-
vical vertebrae of R. tenuisceps are rectangular in dorsal view, 
being approximately three times wider than anteroposteriorly 
long and triple the width of its base (PVL 3827: C7–C8). The 
dorsal surface of the spine tables is flat, whereas that of eptosu-
chids is concave (Tarajadus ruthae: CRILAR-Pv 478).

The prezygapophyses of the postaxial cervical vertebrae are 
anterolaterally oriented, barely extending beyond to the anterior 
margin of the centrum (Fig. 3G), whereas the postzygapophyses 
are posterolaterally oriented and extending entirely posterior to 
the posterior margin of the centrum. The articular facets of the 
prezygapophyses can only be seen in a couple of vertebrae 
(PVL 3827: C8, PVL 3828: C6); these facets are oval and dor-
onsomediately oriented at 45° from the horizontal plane. The postzy-
agapophyses are either in articulation or severely damaged; 
therefore, their preservation does not allow the observation of any detail of their articular facets (Fig. 3F, C).

Dorsal Vertebrae—These are better preserved in the holotype 
(PVL 3827) than in the referred materials. In the holotype, they 
were preserved in two articulated sections plus two isolated pos-
terior dorsal vertebrae. These sections were here identified as the 
first three dorsal vertebrae articulated with the two last cervical 
vertebrae and their corresponding ribs, and the other section
FIGURE 3. Cervical vertebrae of *Riojasuchus tenuisiceps*. Articulated cervical vertebrae 1–7 of PVL 3827 in A, lateral and B, ventral views; atlas of PVL 3826 in C, anterior, D, posterior, and E, lateral views; cervical vertebra 8 of PVL 3827 in F, anterior and G, lateral views. Arrows indicate dorsal and anterior directions. Abbreviations: dia, diapophysis; hyp, hypapophysis; nac, neural arch contact; os, osteoderm; pa, proatlas; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis; rb, rib; st, spine table. Scale bars equal 20 mm (A–B) and 10 mm (C–G).
FIGURE 4. Posterior cervical vertebrae and dorsal vertebrae of *Riojasuchus tenuisceps*. Articulated presacral vertebrae 9–13 of PVL 3827 in A, lateral and B, ventral views; articulated mid-dorsal vertebrae of PVL 3827 in C, left lateral, D, right lateral, and E, posterior views; posterior dorsal vertebra of PVL 3828 in F, lateral and G, anterior views; last dorsal vertebra of PVL 3827 in H, anterior, I, lateral, and J, posterior views; isolated dorsal osteoderm of PVL 3814 in K, anterior and L, dorsal views. Arrows indicate dorsal and anterior directions. Abbreviations: cr, crest; dia, diapophysis; dlp, dorsolateral prominence; hyp, hypapophysis; ncs, neurocentral suture; ns, neural spine; os, osteoderm; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis; trp, transverse process. Scale bars equal 20 mm (A–D) and 10 mm (E–L).
was identified as four dorsal vertebrae of the middle to posterior region of the dorsal series (Fig. 4A–D). The referred specimen, PVL 3828, has 10 dorsal vertebrae preserved, but most of these are only represented by their centrum excepting one, a posterior dorsal vertebra, which has its left diapophysis and parapophysis well preserved.

The anterior dorsal vertebrae of *Riojasuchus tenuisceps* (PVL 3827) resemble the general shape of the preceding cervical vertebrae and has the parapophyses located above the dorsalventral midline of the centrum as well. However, the anterior dorsal vertebrae differ from the cervical vertebrae because the base of the parapophyses of the first dorsal vertebra (D1) expands dorsally, contacting the neurocentral suture (Fig. 4A). Moreover, D1 lacks a hypapophysis and the ventral surface of its centrum is flat, unlike the anteroposteriorly concave centrum of the succeeding dorsal vertebrae (Fig. 4B).

In general terms, the anterior dorsal vertebrae (PVL 3827: D1–D3; Bonaparte, 1972: ‘dorsals 11–13’) are slightly shorter than tall and they are barely laterally compressed (Fig. 4A, B). The anterior and posterior articular facets are almost circular and slightly concave. The lateral surfaces of the centrum are markedly anteroposteriorly concave and lack lateral fossae. No accessory laminae could be recognized between the apophyses or between the centrum and the apophyses. The ventral surface of the centrum is gently concave and does not have a hypapophysis as in the cervical vertebrae. The diapophyses are located dorsal to the neurocentral suture; they are long and posteroanterolaterally projected (Fig. 4A, B). The posterolateral direction of the diapophyses is not as posteriorly inclined as that observed in middle dorsal vertebrae. The parapophyses of the first anterior dorsal vertebrae (D1) are located in the middle region of the anterior margin of the centrum, although toward the third dorsal vertebra (D3) the parapophyses are located on the anterodorsal margin of the centrum (Fig. 4A). The parapophyses of the anterior dorsal vertebrae contact the neurocentral suture and are located ventral to the diapophyses; they are short and laterally projected. The neural spines of the anterior dorsal vertebrae are anteroposteriorly short and dorsolaterally oriented. They are taller than the centra, but their total height could not be determined because all the preserved spines are missing their apical region; therefore, it is also unknown whether they expanded into a spine table as seen in the cervical vertebrae or not (Fig. 4A). Pre- and postzygapophyses are too damaged to allow the observation of any detail in both specimens PVL 3827 and PVL 3828. The ribs corresponding to the anterior dorsal vertebrae were preserved near their natural position (Fig. 4B). The two bicipital ribs are partially articulated and still covered by sediment; they are posterolaterally curved, and the capitulum is disarticulated and exposes an oval-shaped articular surface. The tuberculum of these ribs is not exposed.

The middle region of the dorsal series is represented by an articulated series of four centra plus a fifth neural spine of PVL 3827 and several disarticulated centra of PVL 3828. The centrum of the middle dorsal vertebrae is approximately as long as high and laterally compressed. The anterior and posterior articular facets are oval, being higher than wide and gently concave. The lateral and ventral surfaces of the centrum are anteroposteriorly concave and lack of lateral fossae and hypapophysis (PVL 3827, PVL 3828). The diapophyses are located at the level of the postzygapophyses; they are elongated and project posterolaterally with a marked dorsal orientation as well. They are located immediately posteroanal to the parapophyses and at the anteroposterior midline of the centrum (Fig. 4C–E). The parapophyses are located on the lateral margin of the anterior articular facet of the centrum; its base is fused to the base of the diapophyses, and it projects laterally just anterolateral to the latter. The parapophyses are therefore located dorsal to the neurocentral suture and elevated at a height equivalent to the height of the centrum. The neural spines of the middle dorsal vertebrae are high, being 1.5 times higher than the centrum (Fig. 4C, D); they are anteroposteriorly longer than the neural spines of the anterior dorsal vertebrae and do not expand toward their apex, differing from the spine tables of the cervical region. The neural spines of these dorsal vertebrae are posterodorsally oriented at ca. 10° from the vertical plane. The prezygapophyses and postzygapophyses were preserved in articulation, and their articular facet cannot be observed. The prezygapophyses extend slightly anterior to the anterior margin of the centrum, whereas the postzygapophyses are almost entirely projected posterior to the posterior margin of the centrum.

The posterior dorsal vertebrae of *R. tenuisceps* are represented by a fairly complete vertebra, previously identified by Bonaparte (1972) as adjacent to the middle dorsal section of the holotype (PVL 3827: ‘dorsal 24’), and by several disarticulated/isolated centra of the specimen PVL 3828, from which only one has preserved the complete left apophyses (Fig. 4F–J). These vertebrae are almost equally high as wide, with anterior and posterior articular facets concave and circular. The parapophyses and diapophyses are fused together on their bases, but their articular surfaces are still differentiated (Fig. 4F, G) and they fuse completely into transverse processes toward the last dorsal vertebrae (Fig. 4H–J). The parapophyses are located at the level of the anterior margin of the centrum; they are short, circular in section, and dorsolaterally directed with a slight anterior orientation. The diapophyses are located at the anteroposterior midline of the centrum; they are almost three times longer than the parapophyses, oval in section, and project dorsolaterally. On the posterior-most vertebrae, the transverse processes are anteroposteriorly wide and project laterally. The prezygapophyses, postzygapophyses, and neural spines were not preserved on the isolated vertebra of PVL 3827 (Fig. 4H–I). The prezygapophyses have oval articular facets that are oriented at 40° from the horizontal plane, and the postzygapophyses have more rounded facets and are oriented at 30° from the horizontal plane. Only the base of a neural spine was preserved; it is anteroposteriorly longer than that of the middle dorsal vertebrae, but its orientation cannot be determined. No accessory fossae, laminae, or hypapophysis could be identified on these posterior dorsal vertebrae.

**Sacral Vertebrae**—There are three sacral vertebrae in *R. tenuisceps*; these were preserved in articulation in the holotype (PVL 3827) and partially disarticulated in the referred specimen PVL 3828. The centrum of the sacral vertebrae is more robust than that of the cervical and dorsal vertebrae, being wider than high and equally wide as long. The centrum has no hypapophysis on its ventral surface, as the previous dorsal vertebrae, and no fossae or accessory laminae on its lateral surface. The anterior and posterior articular surfaces are almost flat and suboval in shape. The base of the laterally projecting transverse processes is almost circular in section (Fig. 5A, B), which contrasts with the dorsolaterally flat base of the transverse processes of the posterior dorsal vertebrae. The transverse processes of the sacral vertebrae are short and robust and would articulate with the medial surface of the ilium. The transverse processes of the second sacral are twice as wide as those of the first sacral. The neural spines of the first and second sacral vertebrae of the holotype (PVL 3827) were preserved but seem to be fused to each other (Fig. 5A). These spines are 1.5 times higher than the centrum; they do not expand on its distal tips, neither laterally nor anteroposteriorly (Fig. 5A). The fusion of the sacral spines, as well as that of the corresponding centra, appears to be a pathology in PVL 3827 because the centro of all the sacral vertebrae of the referred specimen of the same-size PVL 3828 are disarticulated, which implies that in a normal condition the sacral vertebrae of PVL 3827 should not have been fused to each other.

**Caudal Vertebrae**—The caudal vertebrae of *R. tenuisceps* are shorter than the sacral vertebrae, and their centra are spool-
shaped. The anterior caudal vertebrae are almost as high as wide, with the middle to posterior ones laterally compressed and more elongated (PVL 3827, PVL 3828; Fig. 5F, G, I, J). The anterior articular facet of the caudal vertebrae is slightly concave, whereas the posterior one is flat (PVL 3828). On the posterior margin of the ventral surface of the centrum, two articular facets for the hemal arches can be recognized. These facets are oval, anteroposteriorly elongated, on the anterior caudal vertebrae and more rounded toward the posterior ones (PVL 3828; Fig. 5D, E). The first two caudal vertebrae had no hemal

FIGURE 5. Sacral and caudal vertebrae of Riojasuchus tenuisceps. Articulated sacral vertebrae of PVL 3827 in A, lateral and B, ventral views; first three caudal vertebrae of PVL 3827 in C, lateral and D, ventral views; E, nine caudal vertebrae of PVL3828 in ventrolateral view; isolated caudal vertebra of PVL 3827 in F, lateral and G, posterior view; H, isolated caudal neural arch of PVL 3826 in lateral view. Arrows indicate dorsal and anterior directions. Abbreviations: a.ha, articulation for the hemal arches; ns, neurocentral suture; ns, neural spine; ost?, possible ossified tendons; poz, postzygapophysis; prz, prezygapophysis; trp, transverse process. Scale bars equal 10 mm.
arches because they do not have the corresponding articular facets (PVL 3827, PVL 3828; Fig. 5D). The lateral surfaces of the caudal centra lack both lateral fossae and accessory laminae between the centrum and the apophyses (Fig. 5E–H). The transverse processes are elongated, posterolaterally directed, and located dorsal to the neurocentral suture (Fig. 5E–G). The prezygapophyses barely extend beyond the anterior margin of the centrum; their articular facets are oval, concave, and dorsomedially oriented at 40° from the horizontal. The postzygapophyses are more elevated and extend almost entirely posterior to the posterior margin of the centrum; the articular facets are flat to slightly concave, ventromedially directed at 45° from the horizontal, a more pronounced angle than that of the posterior dorsal vertebrae (Fig. 5F–H). Neural spines are anteroposteriorly short and posterodorsally directed at 25° from the vertical axis. Even though their surface has been damaged during their original preparation, it is evident that the caudal neural spines keep the same width along their entire length and that they do not expand laterally on their distal ends, as described in the previous dorsal and sacral series (PVL 3826, PVL 3828) (Fig. 5E–H).

The first caudal vertebrae of PVL 3827 have some anteroposteriorly oriented rod-like ossifications on the left side of the centra. These are slightly laterally compressed, are located ventral to the transverse processes, and could possibly be interpreted as ossified tendons (Fig. 5F). This condition seen in Riojasuchus is quite uncommon because the ossified tendons preserved in other archosauriforms are located in the epaxial region, dorsal to the transverse processes and lateral to the neural spines (e.g., sauropods, hadrosaurs, ankylosaurs) (Forster, 1990; Coombs, 1995; Organ, 2006; Cerda et al., 2015b).

The scapula is tightly sutured to the coracoid (Fig. 7A). The scapular girdle is formed by the articulated scapula and coracoid and has been preserved, partially at least, in three specimens of Riojasuchus tenuisceps (PVL 3826, PVL 3827, PVL 3828).

**Appendicular Skeleton**

The scapular girdle is formed by the articulated scapula and coracoid and has been preserved, partially at least, in three specimens of Riojasuchus tenuisceps (PVL 3826, PVL 3827, PVL 3828).

**Scapula**—The scapula is tightly sutured to the coracoid (Fig. 7A–C) and has a wide ventral end that narrows abruptly toward the base of the scapular blade (PVL 3827, PVL 3828). The scapular blade is oval in cross-section, being twice wider anteroposteriorly than thick lateromedially. The dorsal margin of the scapular blade is slightly convex; its anterior margin is straight, and its posterior margin is markedly convex (Fig. 7E). Toward the dorsal end, the anterior margin is gradually expanded anteriorly whereas the posterior margin expands abruptly. Because of this expansion, the dorsal end of the scapula is almost twice as wide as the scapular neck, which can also be seen in several archosauriforms (e.g., Erythrosuchus africanus: Gower, 2003; Nicrosaurus kapfi: SMNS 6328; Euoparkeria capensis: cast SAM-PK 5867; Parringtonia gracilis: NHMUK PV R8646; Ticinosuchus ferox: Lautenschlager and Desojo, 2011; Cuiman vacare: MACN-He 48841; Lewisuchus admixtus: PULR 01). The acromial process can be recognized in the ventral region of the scapula; it is well developed, projecting toward the lateral surface (Fig. 7A, D). The scapula forms the dorsal third of the glenoid fossa, which is delimited by a well-developed...
FIGURE 6. *Riojasuchus tenuisiceps*, histology of osteoderms of PVL 3814. External view of A, dorsal osteoderm and its transverse sections (R 2d, R 2a) and B, cervical osteoderms and its transverse section (R 2b); C, D, detail of the basal cortex; E, basal cortex showing three LAGs; F, G, detail of cancellous bone of internal region; H, close up to internal region; I–J, detail of external cortex (ridge of ornamentation); K, detail of external cortex of R 2b section. C, E–F, H–I, K, under normal light; D, J, under cross-polarized light; G, under cross-polarized light with lambda compensator. Abbreviations: cc, circumferential canal; cl, cementing line; its, intertetrabecular space; LB, lamellar bone; PFB, parallel-fibered bone. Scale bars equal 50 mm (A, B).
supraglenoid rim that is shorter than the subglenoid lip of the coracoid (Fig. 7A–D). The dorsolateral surface of the ventral end of the scapula has an oval tuberosity that could be associated with the insertion of the M. triceps (Fig. 7A), resembling that seen in the loricatans *Batrachotomus kupferzellensis* (SMNS 80271) and *Prestosuchus chiniquensis* (SNSB-BSPG AS XXV 12), but...
differing from this element of most archosauriforms, in which this tuberosity is much smaller (Nessbit, 2011:char. 219).

**Coracoid**—The coracoid of *R. tenuisceps* is semicircular, being rounded on its anterior margin. It forms the lower two-thirds of the glenoid fossa, which is posteroventrally oriented and has a marked subglenoid rim projecting posteriorly further than the supraglenoid rim of the scapula (Fig. 7A–C). The subglenoid rim is separated from the postglenoid process by a deep furrow. The postglenoid process is short but extends slightly posterior to the subglenoid rim (Fig. 7D), as also happens in *Ornithosuchus woodwardi* (NHHUK PV R3916), rauschianus (e.g., *Batrachotomus kupferzellersis*; SMNS 80271; Postosuchus kirkpatricki; TTU-P90002; *Postosuchus chiniquensis*; BSPG AS XXV 12), and dinosauriforms (e.g., *Lewisiuchus admixtus*; PULR 01). The posteroventral margin of the coracoid is smooth in PVL 3828, and no furrow or notch could be recognized for the articulation of the clavicle as those seen in crocodiliforms or the loricatan *Postosuchus kirkpatricki* (Weinbaum, 2013; TTU-P90002). The coracoid foramen for the passage of the supracoracoid nerve is located anterior to the glenoid fossa; it is circular and surrounded by a well-delimited oval fossa on the lateral surface of the coracoid (PVL 3827, PVL 3828) (Fig. 7A, D). This fossa is absent on most archosauriforms and was only recognized on the loricatan *Batrachotomus kupferzellersis* (SMNS 80271) and *Postosuchus chiniquensis* (SNSB-BSPG AS XXV 2).

**Humerus**—The humerus of *Riojasuchus tenuisceps* is slender and slightly sigmoid in medial view. The proximal end is remarkably expanded in a fan shape, being four times wider than the shaft and twice wider than its distal end (Fig. 7F–I). The head of the humerus is globose and has a medially projected internal tuberosity (PVL 3827, PVL 3826) (Fig. 7F–J). The head is restricted to the anterior half of the proximal surface of the humerus in *Riojasuchus tenuisceps* (PVL 3827, PVL 3826) as in most archosaurs. The deltopectoral crest extends along the proximal third of the humerus of *Riojasuchus tenuisceps* and projects anteriorly from the lateral margin; it is moderately developed and forms a 90° angle with the sagittal plane (PVL 3827) (Fig. 7F–J). The shaft of the humerus is slightly twisted, and as a result the main axis of the proximal end is rotated 25° from that of the distal end. The cross-section of the shaft is elliptic, being twice lateromedially wider than anteroposteriorly thick. The distal end of the humerus is ca. 2.5 times wider than the shaft and has well-developed ent- and ectepicondyles (Fig. 7K). The ectepicondyle is posteriorly expanded, almost duplicating the anteroposterior thickness of the entepicondyle, and it is slightly lateromedially thinner than the latter, from which it is separated by a shallow trochlear groove (Fig. 7F, H, K). The humerus has no ectepicondyar groove on its lateral surface. The entepicondyle of *R. tenuisceps* (PVL 3826, PVL 3827, PVL 3828) also lacks an entepicondylar foramen as that seen in aetosaurs (e.g., *Neoaeotosauroides ingens*; PVL 3525; *Desmatosuchus smallii*; Parker, 2005) or a lateral supinator process as that of loricatan *Postosuchus kirkpatricki* (TTU-P90000; *Batrachotomus kupferzellersis*; SMNS 80276).

**Radius**—The radius of *R. tenuisceps* is known by the proximal end and the distal half of PVL 3828, and the distal half preserved in articulation with the carpus in PVL 3827 (Fig. 8A–G). The radius is an elongate element with an expanded proximal end that abruptly triplicates the width of the shaft. The proximal surface is concave and triangular, with a slight globous projection on its medial margin for its articulation with the humerus (Fig. 8D, E). The distal end of the radius becomes anteroposteriorly expanded and mediolaterally flattened, resulting in an oval cross-section with its main axis anteroposteriorly oriented (PVL 3827, PVL 3828) (Fig. 8A–C). The medial surface of the distal end of the radius is flat, whereas the lateral surface is slightly concave. The complete distal surface of the radius articulates with the radiale but does not contact the intermediate (PVL 3827) (Fig. 8F, G).

**Ulna**—The ulna of *R. tenuisceps* is a gracile, slightly sigmoid element that is barely 10% shorter than the humerus. The proximal end of the ulna is triangular in cross-section and has a well-developed olecranon with a well-defined articular surface for the humerus (PVL 3828) (Fig. 8A–C). This articular surface is concave and is anteriorly delimited by a crest that separates it from the contact surface for the radius (Fig. 8A–C). The lateral surface of the proximal half of the ulna is convex, whereas the medial surface is concave. The shaft is 2.5 times narrower than the proximal end; it curves anteriorly and is subcircular in cross-section. The distal end of the ulna is laterally compressed, and its main axis is perpendicular to that of the proximal end. Two articular facets can be recognized on the distal margin of the ulna, the lateral one for the ulnare and the medial one for the intermedium (PVL 3827) (Fig. 8A–C).

**Carpus**—It has been exceptionally well preserved in full articulation in the holotype of *R. tenuisceps* (PVL 3827). The proximal carpals are proximodistally short as in most archosauriforms. The radiale is an almost cubic element, more robust than the ulnare, with a concave proximal surface for the articulation of the radius, a slightly concave lateral surface for the articulation of the intermedium, and a convex distal surface that contacts the metacarpal I (Fig. 8F–J). The dorsal surface of the radiale has a deep concavity on its proximolateral corner, restricted by a thick oblique crest that extends proximomedially. The medial surface of the radiale is slightly concave, and the distal surface has a marked thickening on its proximal half. The intermedium is a dorsoventrally flattened element that articulates medially with the radiale, laterally with the ulnare and the ulna, and distally with the metacarpals II and probably III. The intermedium is pentagonal in dorsal view and slightly longer than the radiale (Fig. 8F, G). Its dorsal surface is flat, whereas its ventral surface is concave. The ulnare is quadrangular in dorsal view, slightly laterally thinner than proximodistally long, and it is dorsoventrally depressed (Fig. 8F, G). It is slightly narrower than the radiale and the intermedium, and its dorsal and ventral surfaces are concave. The proximal carpals configuration of *Riojasuchus tenuisceps* differs from that of basal crocodylomorphs, which have a pisiform carpal located lateral to the ulnare and lack an intermedium carpal (e.g., *Protosuchus richardsoni*; Colbert and Mook, 1951; *Hesperosuchus agilis*; Colbert, 1952).

**Metacarpals**—The metacarpals of *R. tenuisceps* were partially preserved in the holotype, in articulation with each other specimen, and they are slightly offset from the carpus. The metacarpal I is the only element completely preserved, whereas the metacarpals II to V lost their distal ends (Fig. 8F, G). The proximal end of the metacarpal I is markedly dorsoventrally expanded, triplicating the thickness of the shaft, but the distal end is barely expanded compared with the shaft. On the other hand, the lateromedial expansion of both ends of the metacarpal I is very slight. The condyles of the proximal end are offset from the horizontal plane, with the lateral condyle being more dorsally located than the medial one. The condyles of the distal end of the metacarpal I are asymmetric, with the lateral one being more expanded than the medial one. It is not possible to identify with certainty whether the distal end has an articular ginglymus because it is partially covered by sediment. Both lateral surfaces of the distal end of the metacarpal have a fossa (Fig. 8F). The preserved region of the metacarpals II to V corresponds to the proximal end and shaft. Their proximal ends are lateromedially expanded but do not duplicate the width of the shaft, and the medial corners of the metacarpals dorsally overlap the lateral corner of the adjacent one. The proximal articular surfaces are covered by sediment excepting that of metacarpal IV, which is barely concave.

**Manual Phalanges**—Only two manual phalanges of *Riojasuchus tenuisceps* were preserved (PVL 3827): the first phalanx from digit I and a disarticulated one that is misplaced between
FIGURE 8. Radius, ulna, and manus of *Riojasuchus tenuisceps*. Articulated left ulna and partial radius of PVL 3828 in A, lateral, B, anterior, and C, medial views; isolated proximal end of radius of PVL 3828 in D, lateral and E, proximal views; incomplete articulated radius, ulna, and manus of PVL 3827 in F, anterior and G, posterior views; isolated right radiale in H, dorsal, I, ventral, and J, proximal views. Arrows indicate anterior direction. **Abbreviations:** a.hu, articulation for the humerus; a.in, articulation for the intermedium; a.mc, articulation for the metacarpals; a.ra, articulation for the radius; a.rl, articulation for the radiale; a.ur, articulation for the ulnare; fo, fossa; iph, isolated phalanx; ol, olecranon; ph I, phalanx 1-1; ra, radius; rl, radiale; ul, ulna; ur, ulnare. Scale bars equal 20 mm (A–C, F, G) and 10 mm (D, E, H–J).
the metacarpal IV and the ulnare. This last one could be the element that Bonaparte (1972) erroneously identified as a possible distal element of the carpus (Fig. 8F–G). Phalanx I-1 is short, wide, and dorsoventrally depressed. The proximal end is more laterally expanded than the distal one, being 1.5 times wider than the latter. Moreover, the proximal end of the phalanx is ventrally expanded, duplicating the height of the shaft. This phalanx also has a lateral pit that is ventrolaterally oriented because of the deformation of the element. Neither extensor nor depressor fossae could be recognized on the dorsal and ventral surfaces of the phalanx (Fig. 8F). The disarticulated phalanx is smaller than phalanx I-1, and only its ventrolateral surface is exposed (Fig. 8G). The anterior end is partially covered and therefore its articular ginglymus cannot be clearly distinguished, although in lateral view it is possible to see that it is anteriorly convex, keeping the same height of the shaft, and it has a small lateral pit (Fig. 8G).

**Ilium**—This element is better preserved in the referred specimen PVL 3828 of *R. tenuisceps* because the ilium of PVL 3827 suffered some degree of dorsoventral deformation and the iliac blade is incomplete, and that of PVL 3826 only preserved its anterior half. The preacetabular process of the ilium is remarkably short; it curves anterolaterally and thickenis anteriorly (Fig. 9A–D). This process does not extend beyond the pubic peduncle but only reaches the level of the anterior margin of the acetabulum (Fig. 9A–B). The postacetabular process is elongated, duplicating the anteroposterior length of the acetabulum and tapering posteriorly (PVL 3828). It has a well-developed crest on its medial surface that extends anteroventrally to posteriorly near its ventral margin (Fig. 9B), but no brevis crest or fossa on its lateroventral margin. The iliac blade represents one-third of the height of the ilium and is tilted at 45° from the vertical plane of the iliac body (Fig. 9A, B). The lateral surface of the iliac blade is flat, the medial surface is concave, and the dorsal margin is slightly concave (PVL 3828). There is no vertical ridge or rugosity on the lateral side of the iliac blade of *R. tenuisceps*, unlike in several basal loricatans (e.g., *Batrachotomus kupferzellensis*: SMNS 52970; *Postosuchus kirkpatricki*: TTU-P09002; *Papasaurus gracilis*: UCMP 25962; *Shuvosaurus inexpectatus*: TTU-P09003; *Arizonasaurus babbitti*: Nesbitt, 2005; *Effigia okeeffeae*: Nesbitt, 2007). The pubic process is larger than the ischiadic process and is anteroventrally projected, forming the anterior wall of the acetabulum. Its articular surface is 'comma'-shaped, being anteriorly convex and posteriorly concave and tapering abruptly into a lamina toward its posteromedial end (Fig. 9A–D). The ischiadic process is dorsoventrally shorter than the public one and is ventrally projected, forming the posterior margin of the acetabulum. Its articular surface is ‘teardrop’-shaped and ventrally convex (Fig. 9A–D). The acetabular wall is incipiently perforated, as seen in poposaurid and some crocodylomorph pseudosuchians and in avemetatarsalians, differing form the closed acetabular wall seen in...
most pseudosuchians (aetosaurs, gracilisuchids, erpetosuchids, basal loricatans). The supraacetabular crest of the ilium of *Riojasuchus tenuisceps* is well developed and laterally projecting (Fig. 9A, D) as in most archosauriforms and archosaurus, excepting the poposauroids *Effigia okeeffeae*, *Shuvosaurus inexpectatus*, *Poposaurus gracilis*, and *Sillosuchus longicervix*, in which the distal margin of this crest is ventrally projected. The articular surfaces for the sacral ribs are not clearly defined on the medial surface of the ilium, although the crest on the postacetabular process probably defines the ventral margin of the articular surface for the last sacral rib (PVL 3828).

**Pubis**—The pubis of *R. tenuisceps* is an elongated element that forms a well-expanded pubic apron probably reaching its distal end; however, it cannot be confirmed with certainty whether it contacts its counterpart entirely. The proximal end of the pubis is subtriangular in lateral view, and its proximal margin has two distinguishable articular surfaces: an anterior one for the ilium and a posterior one for the ischium. The articular surfaces for the sacral ribs are not clearly defined on the medial surface of the ilium, although the crest on the postacetabular process probably defines the ventral margin of the articular surface for the last sacral rib (PVL 3828).

**Ischium**—The ischium of *R. tenuisceps* is only known for a small fragment of the posterior region of the proximal end (PVL 3828) (Fig. 10D–F). The anteroventral margin is broken, and its contact with the pubis is unclear. The small portion preserved of the anteroventral margin is smooth and concave as in most pseudosuchians, differing from the loricatans *Prestosuchus chiniquensis* (SNSB-BSPG AS XXV, UFRGS-PV-0629T), *Postosuchus kirkpatricki* (TTU-P09002), and *Stagonosuchus nyassicus* (GPIT/RE/3832), which have a notch in the proximal region. The posterior margin of the ischium is complete; it is markedly concave and does not have any tuberel as that seen in *S. nyassicus* (GPIT/RE/3832). The proximal surface of the ischium has a thin articular surface for the ilium on its medial border and a concavity on its lateral side that contributes to the acetabulum (Fig. 10D–F). This region of the acetabulum is...
FIGURE 11. Femur and tibia of *Riojasuchus tenuisceps* PVL 3827. A, anterior; B, medial; C, posterior; D, lateral; E, proximal; and F, distal views of left femur; G, proximal; H, distal; I, anterior; J, medial; K, posterior; and L, lateral views of left tibia. Arrows indicate anterior direction. Abbreviations: 4tr, fourth trochanter; a.as, articulation for the astragalus; a.fe, articulation for the femur; a.fi, articulation for the fibula; alt, anterolateral tuber; amt, anteromedial tuber; atr, anterior trochanter; cnc, cnemial crest; feh, femoral head; fic, fibular condyle; gtr, greater trochanter; itf, intertrochanteric fossa; lc, lateral condyle; mc, medial condyle; pfo, popliteal fossa; pmt, posteromedial tuber; tfc, tibiofibular crest; tic, tibial condyle. Scale bars equal 50 mm (A–D, I–L) and 10 mm (E–H).
delimited by a well-developed laterally projected subacetabular crest (Fig. 10D, F). The lateral surface on the proximal end of the ischium of *R. tenuisceps* is concave, whereas the medial surface is completely flat. The distal end of the preserved fragment of the ischium is posterolaterally rotated; therefore, its anteromedial margin would probably reach and contact its counterpart and the posterior margin would diverge from the other.

**Femur**—The femur of *R. tenuisceps* is sigmoid in posterior view, with it head slightly rotated and anteromedially directed (Fig. 11A–D), but it is not differentiated by any neck, constriction, or flange (PVL 3827, PVL 3828). The proximal surface of the femoral head is convex and does not have a longitudinal furrow as that seen in Ornithosuchus woodwardi (NHMUK PV R3561), Poposaurus gracilis (TTU-P10419, TMM 31100-408), or Shuvosaurus inexpectatus (TTU-P18307, TTU-P18308, TTU-P18309). The main axis of the proximal surface of the femur of *R. tenuisceps* is anteromedially to posterolaterally oriented and is almost twice as long as its perpendicular axis. The anterolateral tuber (sensu Nesbitt, 2011) is rounded and prominent (Fig. 11E). This differs from most pseudosuchians, but in dinosauromorphs the anterolateral tuber is sharp and forms a crest (Nesbitt, 2011). The cnemial crest is slightly laterally compressed but with a round apex slightly posteromedially oriented (Fig. 11F). The tibiofibular condyle is rounded and globe and extends distally further than the tibial condyle (Fig. 11C). The distal surface of the femur is smooth and lacks any furrow between the tibiofibular crest and the tibial condyle, as also happens in phytosaurs, Revueltosaurus callenderi, aetosaurs, and Gracilisuchus stipanicorum.

**Tibia**—The tibia of *R. tenuisceps* is slightly more robust than the fibula; its proximal end is anteroposteriorly expanded, being three times the thickness of the shaft. Its proximal surface is convex, as happens in most archosauromorphs. The tibia has a large lateral condyle that, in proximal view, occupies the anterior half of the lateral surface of the tibia (Fig. 11G). The lateral condyle is rounded and has a marked concavity on its proximolateral edge where it articulates proximally with the fibular condyle and the tibiofibular crest of the femur and laterally with the fibula (Fig. 11G, I, K, L). This condition is also present in most pseudosuchians (e.g., Batrachotomus kuyperzellensis, Saurosuchus galilei, Effigia okeeffeae, Hesperosuchus agilis) but differs from the lateral condyle of the tibia of avemetatarsalians, which does not have said concavity (Nesbitt, 2011). The posterior margin of the proximal end of the tibia of *R. tenuisceps* (PVL 3827, PVL 3828) has a fibro-medial condyle that is lateromedially half as wide as the proximal end of the tibia (Fig. 11G, I–K). Unlike most archosauromorphs and pseudosuchians, the tibia of *R. tenuisceps* has a well-developed cnemial crest on the anteromedial edge of the proximal end of the tibia, which is anteriorly projected (Fig. 11G, I–J, L). It resembles the condition in non-dinosaurian dinosauromorphs and proterochampsids in which the cnemial crest is straight; moreover, it differs from dinosaurs because in these the cnemial crest is anterolaterally projected and curved (Nesbitt, 2011). There is no fibular crest on the lateral surface of the tibia as that present in some basal dinosaurs (e.g., Silesaurus opolensis: Dzik, 2003; Saurosuchus aguadoensis: Ferigolo and Langer, 2007; Saturnalia tupiniquim: Langer, 2003; Hetrodontosaurus tucki: Santa Luca, 1980). The shaft of the tibia of *R. tenuisceps* is oval in cross-section, with its main axis anteroposteriorly oriented. The distal end of the tibia is slightly anteroposteriorly expanded and has a thin edge delimiting the articular facet for the astragalus. The lateral surface of the distal end of the tibia is concave, whereas the medial surface is convex (Fig. 11H). The articular facet for the astragalus is concave, and its posterior half is more distally projected than the anterior one (PVL 3827) (Fig. 11H, L).

**Fibula**—The fibula of *R. tenuisceps* (PVL 3827) is a gracile element, slightly thinner than the tibia. Its proximal end is posteromedially projected, barely laterally expanded, and its articular surface for the femur is flat (Fig. 12A–D). The shape is anteriorly arched and has a subcircular cross-section. On its anterolateral surface, there is a distinct tubercle for the insertion of the musculus iliofibularis located slightly proximal to the mid-length of the fibula (Fig. 12A–C). This tubercle is elongated, symmetric, laterally compressed, and has a rounded apex, which resembles the condition in phytosaurs and aetosaurs. The distal end of the fibula is slightly anteroposteriorly expanded; its articular surface is gently concave and articulates distally with the calcaneum and medially with the astragalus (Fig. 12A–C, E).

The astragalus and the calcaneum of *R. tenuisceps* form a ‘crocodile-reversed’ eurortarsan articulation in which the calcaneum has the concavity that holds the condyle of the astragalus (Fig. 13), a condition that is currently only recognized in ornithosuchids.
of *R. tenuisceps* (PVL 3827) extends from the apex of the astragalus to its lateral edge; it is concave and complements the convex articular surface in the calcaneum (Fig. 13E, F).

**Calcaneum**—The calcaneum of *R. tenuisceps* (PVL 3827, PVL 3828) has a subtriangular body, in dorsal view, that articulates proximomedially with the astragalus and distally with the distal tarsal 4 (Fig. 13G–I). The lateral third of the proximal surface of the calcaneum forms the articolar facet for the fibula; it is convex and anteroposteriorly elongated (Fig. 13G) and is complemented by the articular surface for the fibula on the astragalus (Fig. 13E, F). This condition of the calcaneum resembles that in *Euparkeria capensis* and differs from that in phytosaurs and suchians, in which the articular surface for the fibula is hemicylindrical. The medial two-thirds of the calcaneum of *R. tenuisceps* (PVL 3827, PVL 3828) tapers abruptly to form a medially projected articular condyle. This surface is dorsally and ventrally convex; its dorsal and medial regions articulate with the astragalus, whereas the ventral region articulates with the distal tarsal 4 (Fig. 13G–I). Because of this peculiar tarsal configuration, the articular facet for the astragalus and the one for the fibula form a continuous surface, not separated by any change in slope or ridge (Fig. 13G). This condition differs from that in most pseudosuchians and also differs from the crocodile-reversed tarsus of *Ornithosuchus woodwardi* (NMUK PV R2410), in which these facets are apparently separated by a strong change of slope.

The lateral surface of the calcaneum has a deep concavity (Fig. 13B). The calcaneal tuber is well developed, as long as the body of the calcaneum, and posterodorsally directed (Fig. 13G–I), differing from *Proterosuchus fergusi*, phytosaurs, and non-crocodylian crocodylomorphs in which the tibia is more posteriorly expanded. Its posterior surface is convex, differing from some aetosaurs (e.g., *Stagonolepis robertsoni*: Walker, 1961) and loricatans (e.g., *Fasolasuchus tenax*: PVL 3850; *Prestosuchus chimiquensis*: SNSB-BSPG AS XXV; *Poposaurus gracilis*: TTM 19886, TMM 31100-378) in which the posterior surface of the calcaneal tibia has a deep dorsoventrally directed furrow. The tuber of *R. tenuisceps* is anteriorly constricted, forming a neck that is lateromedially wider than dorsoventrally high (Fig. 13G–I), similar to that of *Euparkeria capensis*, *Ornithosuchus woodwardi*, and other pseudosuchians. Moreover, the posterior margin of the tibia is expanded on its dorsal, medial, and ventral margins, as also seen in other pseudosuchians (including phytosaurs).

On its ventral surface, the calcaneum of *R. tenuisqueps* has a depressed area that separates the articular facet for the distal tarsal 4 from the calcaneal tuber, as also happens in phytosaurs and suchians. *Postosuchus kirkpatricki* and *Prestosuchus chimiquensis* and the crocodylomorphs *Hesperosuchus agilis*, *Dromicosuchus grallator*, *Terrestrisuchus gracilis*, and *Protopsasuchus richardsoni* in which this depressed area is much deeper, forming a fossa (Nesbitt, 2011).

**Distal Tarsals**—These are represented by distal tarsals 3 and 4 only; distal tarsals 1 and 2 are either not present or unossified, as suggested for proterochampsids and most archosauromorphs. Distal tarsals 3 and 4 were preserved in articulation with the astragalus, calcaneum, and metatarsals of the holotype (Figs. 13A, B, 14A, B), and one distal tarsal 4 of PVL 3828 was preserved isolated. Distal tarsal 3 is rectangular, lateromedially compressed, and elongated on its dorsoventral axis. It articulates medially with the metatarsal II, proximally with the metatarsal III, laterally with the distal tarsal 4, and distally with the astragalus (Fig. 14B). Distal tarsal 5 is approximately three times narrower than the distal tarsal 4. This last one is trapezoidal in distal view, and, as happens in archosauriforms and other pseudosuchians, it is lateromedially wider than the distal tarsal 3. Distal tarsal 4 articulates medially with the distal tarsal 3, proximally with the metatarsals III and IV, lateroventrally with the metatarsal V, and dorsodistally with the calcaneum (Figs. 13A, B, 14A, B). In ventral view, the proximal margin of its dorsolateral half. This posterior depression is located between the articular facet for the tibia and that for the fibula and has been identified by Sereno (1991) as homologous to the posterior groove of the astragalus. The posterior groove separates the dorsal from the ventral articular facet of the astragalus, and when articulating with the calcaneum, it forms the astragalo-calcaneal canal. This posterior groove and astragalo-calcaneal canal can be seen in other pseudosuchians such as phytosaurs, crocodylians, *Gracilisuchus stianicicorum*, and *Fasolasuchus tenax*. However, the posterior depression of the astragalus of *R. tenuisceps* (Fig. 13F) does not seem to correspond to the same structure as the posterior groove of other pseudosuchians because it is not located between the same articular facets and does not participate in forming the same anatomical structure: an astragalo-calcaneal canal. The dorsal process is well developed and anterodorsally directed (Fig. 13E, F). The postero-medial surface of the dorsal process is represented by the articular surface for the tibia, which is concave, medially delimited by a crest, and dorsally restricted by a thick astragalar ridge that projects anterodorsally (Fig. 13E, F). The articular facet for the fibula...
Distal tarsal 4 is rounded and the mediodistal corner is more distally projected than the laterodistal one. The proximodorsal surface is convex, whereas the ventrodorsal surface is concave; the articular surfaces for the calcaneum and the metatarsals are slightly concave.

**Pes**—Both pedes of *R. tenuisceps* were preserved in PVL 3827 and some isolated phalanges in PVL 3828. The right pes of PVL 3827 has five metatarsals articulated with the complete tarsus and most of the phalanges (Fig. 14A, B), whereas the left pes is only represented by metatarsals I to IV with most of the articulated phalanges. The metatarsals of *R. tenuisceps* become longer from I to IV, whereas metatarsal V is almost as short as metatarsal I. Metatarsal I is the shortest of the series, and, unlike the other metatarsals, its proximal end is not laterally expanded but instead is dorsoventrally expanded, duplicating the height of the shaft. Metatarsals II to IV are lateromedially expanded on their proximal ends, partially overlapping their medial third over the lateral side of the next one (Fig. 14A, B). This condition can be seen in most basal pseudosuchians, differing from avemetatarsalians and crocodylomorphs (e.g., *Terrestrisuchus gracilis*, *Protosuchus haughtoni*) in which the metatarsus is compact, with metatarsals II to IV overlapping half of their proximal ends (Sereno, 1991; Nesbitt, 2011). Metatarsals I to IV of

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**FIGURE 13.** *Riojasuchus tenuisceps*, tarsal elements of PVL 3827. A, right tibia, fibula, tarsus, and pes preserved in articulation; B, detail of tarsus in lateral view; C, anterior and D, posterior views of left astragalus and calcaneum in 'crocodile-reversed' articulation; E, anterior and F, posterior views of left astragalus; G, dorsal, H, ventral, and I, medial views of left calcaneum. **Abbreviations:** a.as, articulation for the astragalus; a.ca, articulation for the calcaneum; a.dt, articulation of the distal tarsals; a.fi, articulation for the fibula; a.mt, articulation for the metatarsals; a.ti, articulation for the tibia; asr, astragalar ridge; ca, calcaneum; ctn, calcaneal tuber neck; dpr, dorsal process; fi, fibula; mt, metatarsal; mt IV, metatarsal IV; mt V, metatarsal V; pd, posterior depression; ti, tibia; t4, distal tarsal 4. Scale bars equal 20 mm (A) and 10 mm (B–I).
**Riojasuchus tenuisceps** (PVL 3827) have almost the same diameter. In *R. tenuisceps*, metatarsal IV is the longest of the series but it does not exceed half the length of the tibia. Lastly, metatarsal V is the most robust of the series; its proximal end is medially expanded, giving it a ‘hook’ shape. The proximal surface of this medial projection forms an acute angle of 65° with the main axis of the metatarsal (Fig. 14A, B). Metatarsal V is subparallel to the other metatarsals in *R. tenuisceps*, as also seen in some pseudosuchians such as *Parasuchus hislopi*, *Neoaeotosauroides engaeus*, *Stagonolepis robertsoni*, and *Gracilisuchus stipanicorum*, but differing from the divergent metatarsal V of *Euparkeria capensis*, *Ticinosuchus ferox*, and *Saurosuchus galilei* (Lecuona and Desojo, 2011).

The pedal phalanges of *Riojasuchus tenuisceps* are partially preserved, and although Bonaparte (1972) proposed a phalangeal formula of 2-3-4-4?-2?, this cannot be determined with certainty beyond a 2-3-2+-1+-1 formula. Digits I, II, and V were preserved complete in PVL 3827; the ungual of the first digit is larger than that of the second digit, and the phalanx corresponding to the fifth digit is reduced (Fig. 14A, B). On the preserved digits with more than one phalanx, it can be observed that the more distal phalanges are remarkably longer than the...
proximal ones; the longest one known is on digit IV, which is as long as half its corresponding metatarsus. The non-ulnar phalanges of R. teniusceps have both the proximal and distal ends dorsoventrally expanded, and the shafts are circular in cross-section. The proximal articular surface of the phalanges is concave and articulates with the corresponding metatarsal or proximal phalanx. The distal articular surface is a convex gin-glymus articulation that is slightly dorsoventrally higher than the proximal end and articulates with the following phalanx (Fig. 14C–E). The ventral surface of the distal end of the phalanges has an anteroposteriorly oriented furrow that separates it into two small elliptic condyles (Fig. 14C–E). The lateral surfaces, on the other hand, have a very slight lateral depression on each side that probably corresponds to the lateral pits, but the lateral surfaces were overprepared and the nature of the depression is difficult to determine. The phalanx of the fifth digit is remarkably different in morphology from the rest of the phalanges. It is reduced to an almost conical structure, and its proximal surface is smaller than that of the other pedal phalaxes. The preserved ungual phalanges of R. teniusceps correspond to the digits I and II of PVL 3827 and some isolated ones of PVL 3828 (Fig. 14A–E). These are anteroventrally curved, laterally compressed, dorsoventrally high, even duplicating the height of their previous phalans (Fig. 14C–E), and also longer than said phalans. Their lateral surfaces are smooth, and the dorsal and ventral margins taper, forming edges.

**Discussion**

**Osteology**

Numerous features recognized on the postcrania of *Rocioasuchus tenuisceps* were quite remarkable when compared with other pseudosuchians and are discussed below.

Concerning the axial skeleton of *R. tenuisceps*, the development of ventral keels and spine tables is noteworthy, as well as the absence of laminae and fossae in all regions of the axial skeleton and the presence of three sacral vertebrae. Cervical vertebrae have a ventral keel that extends ventral to the centrum rim. This condition is quite common among archosauromorphs such as erythrosuchids (*Erythrosuchus africanus* and *Garjainia prima*) and proterochampsids (*Protrochampsa barriotuernovii*, *Tropidosuchus romeri*, *Gialosuchus reigi*), but somewhat rare within pseudosuchians in which it can only be recognized in erpetosuchids (*Erpetosuchus granti* and *Tartajada rathae*), the aetosaur *Stagonolepis robertsoni*, and the loricatan *Batrachotomus kupferzellensis*.

On the other hand, spine tables are only present on the cervical vertebrae of *R. tenuisceps* and the rest of the axial skeleton has laterally compressed neural spines. These cervical spine tables are laterally expanded in their middle region, conferring them a suboval or subrectangular shape in dorsal view, as occurs in *Ornithosuchus woodwardi* (NHMUK PV R3916), *Euparkeria capensis* (Ewer, 1965), *Tartajada rathae* (CRILAR-Pv 478), *Parringtonia gracilis* (NHMUK PV R5846), *Erpetosuchus granti* (Benton and Walker, 2002), and some phytosaurs. These cervical vertebrae differ from those of several loricatans (*Postosuchus kirkpatricki*: TTU-P09235; *Saurosuchus galilei*: PVL 2198; *Batrachotomus kupferzellensis*: SMNS 80285-92) and *Nundasuchus songaeensis*, in which the neural spines are laterally expanded only on their anterior end, giving it a subtriangular shape in dorsal view. In the phylogenetic analyses of Lacerda et al. (2018) and Ezcurra et al. (2017), *R. tenuisceps* (PVL 3827), *Ornithosuchus woodwardi* (NHMUK PV R3916), and *Gracilisuchus stipanicicorum* (Lecuona et al., 2017) were scored as having spine tables on the dorsal vertebrae, but they only have spine tables on their cervical vertebrae, so it is here recommended to score them as ‘spine tables absent’ in future matrices (see Appendices 1, 2 in Supplemental Data 1). This was corrected in the phylogenetic revision of the latest matrices of Ezcurra et al. (2017) and Lacerda et al. (2018), which were discussed in the present contribution, but did not affect the relationships of said taxa.

The presence of three sacral vertebrae in *Rocioasuchus tenuisceps* differs from basal archosauromorphs and most pseudosuchians, which keep the plesiomorphic condition of having two sacral vertebrae. Only the rauisuchian *Batrachotomus kupferzellensis* (SMNS 80298), *poposauroid* (*Arizosaurus babbitt*: Nesbitt, 2005; *Poposaurus gracilis*: TMM 43683-1, UCMP 78719; *Shuvosaurus inexpectatus*: TTU-P09001), and the ornithosuchids *Ornithosuchus woodwardi* (Walker, 1964) and *Rocioasuchus tenuisceps* have three sacral vertebrae, which is here interpreted as independently acquired features in these three groups.

The perforated acetabulum and the anteromedially rotated proximal end of the femur are characters that have been typically regarded as diagnostic for dinosaurs (Gauthier, 1986; Novas, 1996; Ezcurra, 2006; Langer et al., 2010). Because of the presence of these same features in the ornithosuchids *R. tenuisceps* and *O. woodwardi*, a close affinity has been proposed between ornithosuchids and dinosaurs, supporting the group ‘Ornithosuchia’ (Gauthier, 1986; Benton and Clark, 1988; Bennett, 1996, 2012). However, the perforated acetabulum, defined by the concave ventral margin of the ilium (Nesbitt, 2011:char. 273; Ezcurra et al., 2017:char. 455), has also been registered in other pseudosuchians (poposauroids and crocodylomorphs); thus, it cannot be considered exclusively to be a dinosaurian feature. On the other hand, the anteromedially rotated head of the femur, evaluated as the orientation of the femoral head relative to the shaft (Nesbitt, 2011:char. 305; Ezcurra et al., 2017:char. 493), is in fact a widespread condition that can be registered in numerous archosauromorphs, including proterochampsids, pseudosuchians, pterosaurs, and dinosauromorphs. The majority of recent phylogenetic analyses (Benton and Walker, 2002; Brusatte et al., 2010; Nesbitt, 2011; Butler et al., 2014; Ezcurra et al., 2017) strongly support the inclusion of ornithosuchids within Pseudosuchia; therefore, those characters would be considered to be convergences between ornithosuchids and dinosaurs. Following the topology presented by Ezcurra et al. (2017), the perforated acetabulum was independently acquired at least four times within Archosaurus, and the rotated head of the femur would be a plesiomorphic condition for Archosauriformes.

Probably the most controversial feature present in ornithosuchids is their tarsal morphology. As previously described, this clade has a crocodile-reversed ankle joint, which is a unique condition among archosaurs. This particular condition has stimulated different evolutionary hypotheses in the past decades. Sereno and Arcucci (1990) discussed in detail the relationships among ‘crocodile-reversed’ (ornithosuchids), ‘crocodile-normal’ (other pseudosuchians), and ‘mesotarsal’ (avemetatarsalsians) archosaurs. They rebutted the monophyly of the clade ‘Ornithosuchia,’ which grouped ornithosuchids with avemetatarsalsians, because the synapomorphies proposed for the latter group were found to be ambiguous. Subsequently, numerous studies agreed with that rebuttal and presented ornithosuchids within the clade Pseudosuchia (Sereno, 1991; Benton and Walker, 2002; Brusatte et al., 2010; Nesbitt, 2011; Ezcurra, 2016). In this context, the similarities between the tarsus of ornithosuchids and that of the rest of the pseudosuchians became clearer. Both ‘crocodile-reversed’ and ‘crocodile-normal’ tarsi have unfused proximal tarsals (astragalus and calcaneum) that articulate freely with each other (Nesbitt, 2011:char. 370; Ezcurra et al., 2017:char. 532). Moreover, another similarity of the calcaneum of ornithosuchids to that of the rest of pseudosuchians (including phytosaurs) is the presence of a well-developed posterior tuber (Nesbitt, 2011:chars. 373, 374) and a convex articular surface for the fibula.
Phylogenetic Position

The latest phylogenetic analysis carried out by Lacerda et al. (2018) incorporated subsequent modifications applied to the data matrix of Nesbitt (2011) (Butler et al., 2011, 2014; Nesbitt and Butler, 2012; Baczo et al., 2014). In this study, Ornithosuchidae was recovered in a clade together with Erpetosuchidae in some (but not all) of the most parsimonious trees. In the remaining trees, Erpetosuchidae was recovered as sister group of Gracilisuchidae + Paracrocodylomorpha (Fig. 15A). In this analysis, Erpetosuchidae was represented only by three species, Pagocephalosaurus candelariensis, Erpetosuchus grantii, and Parringtonia gracilis, which are known from incomplete specimens and, despite grouping together, did not provide stability in the resulting topologies. Therefore, the results of the phylogenetic analysis of Lacerda et al. (2018) suggested a possible close affinity between Ornithosuchidae and Erpetosuchidae, but further studies are required for clarification. On the other hand, the phylogenetic analysis presented by Ezcurra et al. (2017) based on a modification of the data matrix of Ezcurra (2016) helped support the hypothesis of a monophyletic clade that nested Ornithosuchidae and Erpetosuchidae together (Fig. 15B). In the study of Ezcurra et al. (2017), the position of Erpetosuchidae was more stable than in the analysis of Lacerda et al. (2018) owing to the addition of Tarjadia ruthae, Dyoplosaurus araripes, and Archeopelta arborensis. These taxa, particularly Tarjadia ruthae, provided crucial information about the complete anatomy of erpetosuchids, and consequently their phylogenetic position as sister group of ornithosuchids. Furthermore, the phylogenetic relationships of Ornithosuchidae are currently under revision, with the incorporation of a new key specimen from Brazil (M.B.v.B., pers. observ.). This revision will focus on the internal relationships of this clade and among pseudosuchians; therefore, these are not discussed here.

Histogenesis

Several ossification mechanisms for osteoderms of extinct and extant reptiles have been proposed. The most common mechanism among these taxa is metaplastic ossification (Haines and Mohudin, 1968). In this process, the ossification occurs on a different tissue (e.g., tendinous tissue), which transforms into bone tissue. Metaplastic ossification in osteoderms can be identified by the presence of bundles of mineralized collagen, which represents the primary (unmineralized) tissue and interweave in different orientations (i.e., structural fibers; Scheyer and Sander, 2004, 2007; Main et al., 2005; Witzmann and Soler-Gijón, 2008; Cerda and Powell, 2010). Intramembranous ossification is another type of ossification mechanism. This process includes a periosteal layer replacing existing non-cartilage connective tissue. This mechanism is recognized by the absence of structural fibers. A third process of ossification is present only in placodont osteoderms and consists of the formation of osseous tissue from a fibrocartilaginous precursor tissue (Scheyer, 2007). Finally, bone histology reveals that osteoderms of some taxa are formed by a combination of more than one kind of ossification process. For example, although the main ossification process in aetosaurs and Vancleavea campi appears to be intramembranous, in some cases structural fibers from the dermis are incorporated to the element later during the ontogeny (Ponce et al., 2017; Cerda et al., 2018).

Following this line of reasoning, intramembranous ossification is proposed to be the main mechanism of osteoderm formation in Riojasuchus tenuisceps, because of the absence of structural fibers. However, an early metaplastic process cannot be discarded entirely. This is because abundant primary tissue has been remodeled, and it is possible that structural fibers could have been resorbed during the first stages of osteoderm formation. In a phylogenetic context, for pseudosuchians, the intramembranous ossification seen in R. tenuisceps appears to be a plesiomorphic condition. Also, this mechanism is commonly observed in early stages of ontogeny in pseudosuchian osteoderms, including aetosaurs (Cerda and Desojo, 2011; Scheyer et al., 2014; Cerda et al., 2018), Revueltosaurus callenderi (Scheyer et al., 2014), and erpetosuchids and proterochampsids (Scheyer et al., 2014; Cerda et al., 2015a; Ponce et al., 2017). The metaplastic ossification has a scarce and patchy distribution among pseudosuchians, including crocodylians, some phytosaurs, and loricatans (e.g.,
Vickaryous and Hall, 2008; Scheyer and Desejo, 2011; Scheyer et al., 2014).

**Skeletalchronology**

Growth marks (i.e., annuli and LAGs) within the osteodermal tissues indicate a slowdown or a complete interruption of bone deposition during the growth of the individual. Because the formation of these growth marks correspond with annual cycles, they have been used to estimate relative or absolute age in extinct and extant tetrapod osteoderms (e.g., Erickson and Brochu, 1999; Ricqlès et al., 2003; Hill and Lucas, 2006; Parker et al., 2008; Witzmann and Soler-Gijón, 2008; Hill, 2010; Scheyer and Sander, 2009; Witzmann, 2009, 2010; Cerda and Desejo, 2011; Scheyer and Desejo, 2011; Taborda et al., 2013; Scheyer et al., 2014; Cerda et al., 2015b; Ponce et al., 2017).

Considering our sample, the estimated minimum age at death for *Riojasuchus tenuisceps* (PVL 3814) is three years of age. Nevertheless, because of the prevalence of secondarily formed cancellous bone, it is more likely that most growth lines have been eroded due to the remodeling process. Thus, the number of growth lines, and therefore the age of specimen at death, is possible highly underestimated (Ponce et al., 2019). When compared with other pseudosuchians, such as eosaurs (e.g., *Aetosauroidea incognita*), and erpetosuchids (e.g., *Archeopelta arboresis*, *Tarajia ruthae*), osteoderms appear not to be useful for skeletochronological studies in *Riojasuchus tenuisceps* due to its high grade of bone remodeling. In eosaurs and erpetosuchids, the growth lines are conserved mainly in the basal cortex, which is formed by primary bone (Cerda and Desejo, 2011; Taborda et al., 2013; Cerda et al., 2015a; Ponce et al., 2017). On the other hand, and opposed to what is observed in most pseudosuchians, from a qualitative point of view, the osteoderms of *Riojasuchus tenuisceps* show less compact bone and the internal region of cancellous bone is more extensive. Osteoderms of pseudosuchians and basal archosauriforms (e.g., eosaurs, erpetosuchids, proterochampsids) are, in general, highly compacted (e.g., Ponce et al., 2017; Cerda et al., 2018).

**CONCLUSIONS**

We provide a detailed osteological description of the postcranial skeleton ornithosuchid *Riojasuchus tenuisceps*. This species is represented by almost complete specimens with excellent three-dimensional preservation and could be considered to be the best representative of Ornithosuchidae according to the knowledge of its morphology to date. Its osteological revision evidenced some remarkable features on its skeleton, such as the cervical vertebrae morphology (well-developed table spines and ventral keels), the number of sacral vertebrae, the morphology of the pelvic girdle (perforated acetabulum, elongated pubis), femur (anteromedially rotated head, well-developed anterior trochanter), and astragalus (only known in *Riojasuchus* within Ornithosuchidae), and the ‘crocodile-reversed’ ankle joint. The latter being a synapomorphic condition of ornithosuchids that is still key for understanding the early evolution of pseudosuchians. The histological analysis performed on its osteoderms provided novel information about its microstructure showing the typical pseudosuchian trilaminar structure with a very extensive internal region of cancellous bone. Intramembranous ossification is proposed to be the main mechanism of osteoderm formation, which seems to be a plesiomorphic condition for pseudosuchians, also known in phytosaurs, some loricatans, and crocodylians. A minimum age of three years can be inferred for the specimen PVL 3814; however, osteoderms of *Riojasuchus tenuisceps* proved to be not useful for skeletochronological studies due to the high degree of bone remodeling.

This detailed revision of the postcranial skeleton of *Riojasuchus tenuisceps* will provide essential information for further studies and will hopefully be useful as a database on ornithosuchid anatomy for comparative purposes and future phylogenetic studies. Moreover, the information provided here will be fundamental to testing hypotheses on the paleobiology of this group, namely, to test whether the postcranial information supports the hypothesis based on cranial biomechanics that implied ornithosuchids occupied scavenger niches in the Triassic continental communities of Pangea.

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