The Osteology and Phylogenetic Position of Luperosuchus fractus (Archosauria: Loricata) from the Latest Middle Triassic or Earliest Late Triassic of Argentina

Argentina

2 authors:

Sterling Nesbitt
Virginia Tech
215 PUBLICATIONS **8,795** CITATIONS

SEE PROFILE

Julia B Desojo
National University of La Plata
158 PUBLICATIONS **3,124** CITATIONS

SEE PROFILE
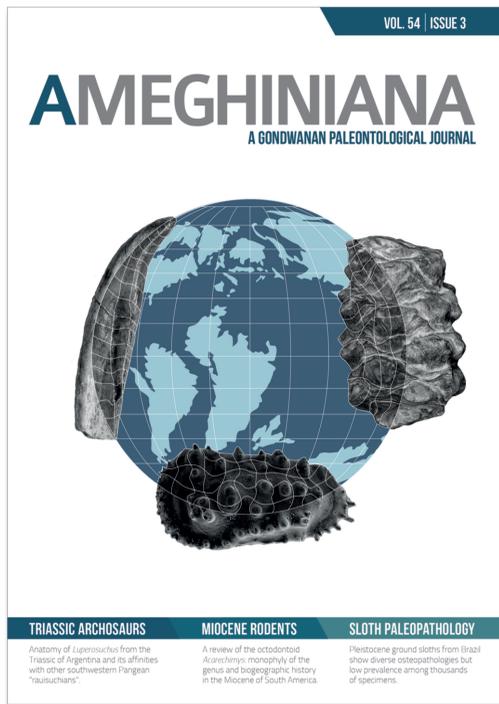
VOL. 54 | ISSUE 3

THE OSTEOLOGY AND PHYLOGENETIC POSITION OF *LUPEROSUCHUS FRACTUS* (ARCHOSAURIA: LORICATA) FROM THE LATEST MIDDLE TRIASSIC OR EARLIEST LATE TRIASSIC OF ARGENTINA

STERLING NESBITT[1]
JULIA BRENDA DESOJO[2,3]

[1]Department of Geosciences, Virginia Tech, Blacksburg, Virginia 24061, USA.
[2]CONICET, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina.
[3]División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina.

Also appearing in this issue:

TRIASSIC ARCHOSAURS

Anatomy of *Luperosuchus* from the Triassic of Argentina and its affinities with other southwestern Pangean "rauisuchians".

MIOCENE RODENTS

A review of the octodontoid *Acarechimys*: monophyly of the genus and biogeographic history in the Miocene of South America.

SLOTH PALEOPATHOLOGY

Pleistocene ground sloths from Brazil show diverse osteopathologies but low prevalence among thousands of specimens.

THE OSTEOLOGY AND PHYLOGENETIC POSITION OF *LUPEROSUCHUS FRACTUS* (ARCHOSAURIA: LORICATA) FROM THE LATEST MIDDLE TRIASSIC OR EARLIEST LATE TRIASSIC OF ARGENTINA

STERLING NESBITT[1], AND JULIA BRENDA DESOJO[2,3]

[1]Department of Geosciences, Virginia Tech, Blacksburg, Virginia 24061, USA. *sjn2104@vt.edu*

[2]CONICET, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina.

[3]División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina. *julideso@fcnym.unlp.edu.ar*

Abstract. Large archosaurs from the early part of the archosaur radiation are exceedingly rare and with few exceptions, most of these remains consist of fragmentary postcrania. We redescribe the fragmentary skull of *Luperosuchus fractus* from the early Middle−Late Triassic Chañares Formation of Argentina, assign newly discovered fragments from the original excavation to the same individual, and analyze its phylogenetic affinities. The dorsally convex and mediolaterally compressed anterior portion of the nasal (= 'Roman-nose'), convex and circular knob on the dorsolateral margin of the postorbital, and a long anterior process of the prefrontal that fails to extend to the anterior end of the frontal are considered autapomorphies of *Luperosuchus*. The elongated gap between the nasal and maxilla is likely an artifact of preservation and this prompted a critical reevaluation of the supposed openings in the anterior portion of the skull of other suchians. We confirm that *Luperosuchus* is a loricatan (composed mostly of the taxa classically termed as 'rauisuchians') using a well sampled phylogeny and find a close relationship with the other large southwestern Pangean forms, *Prestosuchus chiniquensis* and *Saurosuchus galilei*. We also show that the holotype of *Luperosuchus* is the only known specimen of the taxon and all other previously referred material cannot be assigned with confidence to it.

Key words. Anatomy. Archosaur diversification. Chañares Formation. Taxonomy.

Resumen. OSTEOLOGÍA Y RELACIONES FILOGENÉTICAS DE *LUPEROSUCHUS FRACTUS* (ARCHOSAURIA: LORICATA) DEL TRIÁSICO TARDÍO MEDIO O TEMPRANO TARDÍO DE ARGENTINA. Los grandes arcosaurios del comienzo de la radiación de este grupo son excesivamente raros salvo algunas excepciones, la mayoría de los restos consisten en fragmentos postcraneanos. Describimos el cráneo fragmentario de *Luperosuchus fractus* del Triásico temprano Medio−Tardío de la Formación Chañares de Argentina, asignamos nuevos fragmentos descubiertos de la excavación original del mismo individuo, y analizamos sus afinidades filogenéticas. La parte anterior dorsalmente convexa y mediolateralmente comprimida del nasal (= nariz romana), la protuberancia convexa y circular en el margen dorsolateral del postorbital, y un proceso anterior largo del prefrontal que no logra extenderse hasta el extremo anterior del frontal son considerados autapomorfías de *Luperosuchus*. El largo espacio entre el nasal y el maxilar es probablemente un artefacto preservacional y sugeriría una reevaluación crítica de las supuestas aberturas de la parte anterior del cráneo de otros suquios. Confirmamos que *Luperosuchus* es un loricata (compuesto mayormente por los clásicos nombrados "rauisuchians"), usamos un muestreo filogenético amplio y encontramos una relación más cercana con otras formas del sudoeste de Pangea, *Prestosuchus chiniquensis* y *Saurosuchus galilei*. También demostramos que el holotipo de *Luperosuchus* es el único espécimen conocido y todos los otros materiales referidos no pueden asignarse con certeza.

Palabras clave. Anatomía. Diversificación de arcosaurios. Formación Chañares. Taxonomía.

UNDERSTANDING of the evolution of Archosauria and its kin was transformed by the discovery of Romer's 'thecodonts' from the Triassic Chañares Formation of Argentina (Fig. 1) in the 1960s and subsequent publications in the 1970s. The collection of 'thecodonts' identified by Romer includes the proterochampsians *Gualosuchus reigi* and *Chanaresuchus bonapartei* (Romer, 1971a, 1972a), and the archosaurs *Gra-* *cilisuchus stipanicicorum* (Romer, 1972b), '*Lagosuchus talampayensis*' (Romer, 1971b, 1972c), *Lagerpeton chanarensis* (Romer, 1971b, 1972c), *Lewisuchus admixtus* (Romer, 1972d), and *Luperosuchus fractus* (Romer, 1971d). Recognized as a hodgepodge of a 'basic stock' that led to dinosaurs, pterosaurs and crocodylians, Romer (1972e) realized the importance of these forms to sort out the rela-

tionships of 'thecodonts' from more distantly related reptiles (*e.g.*, lepidosauromorphs and early diapsids). Moreover, over the following 40 years, the untangling of 'Thecodontia' has made it clear that Romer's Chañares 'thecodonts' represent some of the most important and earliest members of Archosauria and close relatives. The Chañares Formation 'thecodonts' are now identified as including a stem archosaur clade (Proterochampsia, Trotteyn *et al.*, 2013), an early suchian closer to crocodylians than birds (*G. stipanicicorum*, Nesbitt, 2011; Butler *et al.*, 2014; Ezcurra, 2016), and successive outgroups to Dinosauria (Sereno and Arcucci, 1994a, b; Novas, 1996; Arcucci, 1998; Nesbitt *et al.*, 2010; Bittencourt *et al.*, 2014).

Of all of Romer's original 'thecodonts', *Luperosuchus fractus* was the largest reptile discovered from the Chañares Formation, yet one of the more fragmentary. Over the last 40 years, the only mentions of *Luperosuchus fractus* have been in classification schemes. For example, *Luperosuchus*

fractus was listed as a rauisuchian (Krebs, 1976; Galton, 1977; Bonaparte, 1981; Chatterjee, 1985; Benton, 1986; Gower, 2000) based on general similarity to other rauisuchians (*e.g.*, *Saurosuchus*) without any explicit justification. The only known specimen (PULR 04) has likely been largely ignored for several reasons identified by us, such as 1) it consists of a poorly preserved partial skull, 2) it bears few identifying character states with other early archosaurs and 3) little was known about the relationships of potential close relatives until recently. A new, but substantially smaller specimen (PULR 057) from the Chañares Formation motivated a reevaluation of the holotype of *Luperosuchus fractus* and led to the attribution of this new specimen to the taxon (Desojo and Arcucci, 2009). Although this new specimen did not overlap much with the holotype, the authors provided new information on *L. fractus*; yet, the new information did not lead to a more precise phylogenetic position within Archosauria.
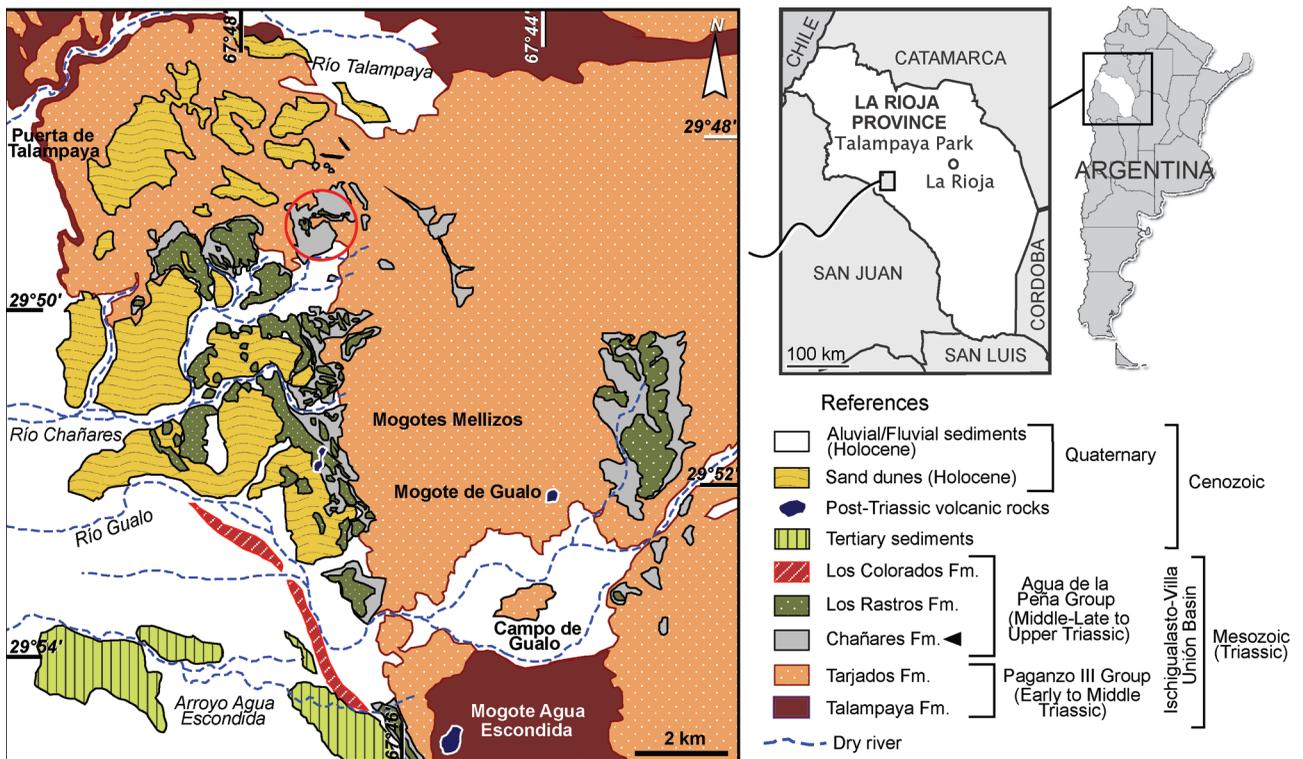

Figure 1. The type locality of **Luperosuchus fractus**. The exact locality of the holotype skull is not known, but through information in field notes from Romer specifying the general area and geology, we can deduce an approximate area where the specimen was collected. Modified from Fiorelli *et al.* (2013).

A surge of new discoveries, reinterpretation of previously discovered archosaurs, and analyses of the phylogenetic relationships of pseudosuchians (Brusatte *et al.*, 2010; Nesbitt, 2011; Nesbitt *et al.*, 2013a) has prompted a reevaluation of archosaurs known from more fragmentary fossils, particularly 'rauisuchians'. Here, we redescribe the holotype of *Luperosuchus fractus* and attribute fragments found with the holotype, but subsequently separated for 40 years, to the same individual. With a more complete picture of the anatomy of this taxon, we place it into a phylogeny sampling many of the more complete members of Archosauria that lived in the Triassic Period. *Luperosuchus fractus*, although known from a partial skull, is important because it is potentially one of the oldest suchians (beginning of the Late Triassic; Marsicano *et al.*, 2016) and therefore one of the first large (estimated skull length= ~60 cm or more) predators during the early radiation of Archosauria in the Triassic Period. We conclude that the holotype is the only specimen of *L. fractus* known at this time.

Institutional abbreviations. **BSPG,** Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MCN PV,** Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil; **MCZ,** Museum of Comparative Zoology, Cambridge, USA; **PULR,** Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL,** Instituto Miguel Lillo, Tucumán, Argentina; **PVSJ,** División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; **SMNS,** Staatliches Museum für Naturkunde, Stuttgart, Germany; **TTU,** Texas Tech University Paleontology Collection, Lubbock, USA; **UFRGS,** Institute of Geosciences, Federal University of Rio Grande do Sul, Porte Alegre, Brazil; **ULBRA,** Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil; **ZPAL,** Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

MATERIAL AND METHODS
Phylogenetic analysis

We incorporated the holotype specimen of *Luperosuchus fractus* (PULR 04) and fragments hypothesized to belong to the holotype into the dataset of Nesbitt (2011) with modifications by Butler *et al.* (2014) for a total of 79 taxa and 415 characters (two new characters added, see below). We used *Prestosuchus* 'combined' and *Lewisuchus/Pseudolagosuchus* 'combined' following Nesbitt (2011), removed *Archosaurus rossicus* because it is scored for only a few characters and thus limits the support throughout the tree, and we removed *Parringtonia gracilis* and *Erpetosuchus granti* because of their highly unresolved relationships within Archosauria (following Nesbitt and Butler, 2013). Additionally, the scores for the ilium of *Rauisuchus tiradentes* were removed and character 52 was scored as ? following a recent description of the taxon by Lautenschlager and Rauhut (2015). *Decuriasuchus quartacolonia* was not added to this analysis because the phylogenetic relationships of this taxon is the subject of a separate study. The rhynchosaur *Mesosuchus browni* was used to root the most parsimonious trees (**MPTs**). The dataset was analyzed in PAUP*4.0b10 (Swofford, 2002) using a heuristic search subjected to 1000 random addition replicates with tree bisection and reconnection branch swapping. Characters 32, 52, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 399, and 413 were ordered following Nesbitt (2011) and additions of Butler *et al.* (2014). Zero length branches were collapsed if they lacked support under any of the most parsimonious reconstructions.

SYSTEMATIC PALAEONTOLOGY

Reptilia Laurenti, 1768
Archosauria Cope, 1869, *sensu* Gauthier and Padian, 1985
Loricata Merrem, 1820 *sensu* Nesbitt, 2011

Luperosuchus fractus Romer, 1971c
Figures 2–6

Holotype. PULR 04, partial, articulated skull including: frontals, nasals, anterior portions of the parietals, left postorbital, posterodorsal process of the premaxilla, anterior portion of the left maxilla, left prefrontal, partial left lacrimal, part of the left squamosal, part of the left jugal (Figs. 2–6). Fragments that pertain to the same individual, but found dislodged from the partially articulated portion of the skull include: lateral surface of the left maxilla and other fragments, dorsal portion of left quadrate, supraoccipital with partial prootics, other braincase fragments, basiptery-

goid articular facet of the left pterygoid and the atlas inter-centrum.

Horizon and locality. Chañares Formation, north of the north fork of the Chañares River, about 5 km northeast of the point where this river emerges into the Plano de Talampaya (Fig. 1; Romer, 1971c). The specimen was found by Ruth Romer on January 17, 1965 near a large dicynodont "about at the junction of darker gray below, and lighter-colored clays above" (Romer's notes within Jensen, 2001). The description of the locality from Romer (1971c) and his field notes indicates that the holotype was likely found at the top of lower member (*sensu* Fiorelli *et al.*, 2013) of the Chañares

Formation, below the concretion level that has produced much of the assemblage (Romer and Jensen, 1966; Rogers *et al.*, 2001). In support of this, the similarity of the preservation of the bone and the associated matrix (sandstone with various angled rock fragments) is consistent with other specimens (*e.g.*, dicynodonts, cynodonts, rhynchosaurs, and early pseudosuchians: Fiorelli *et al.*, 2013; Desojo *et al.*, 2015) from this interval and differs from the much finer sediments found in the concretions from higher in the stratigraphic section. This estimated stratigraphic position lies below the recently dated strata of the Chañares Formation (Marsicano *et al.*, 2016), thus giving a minimum age
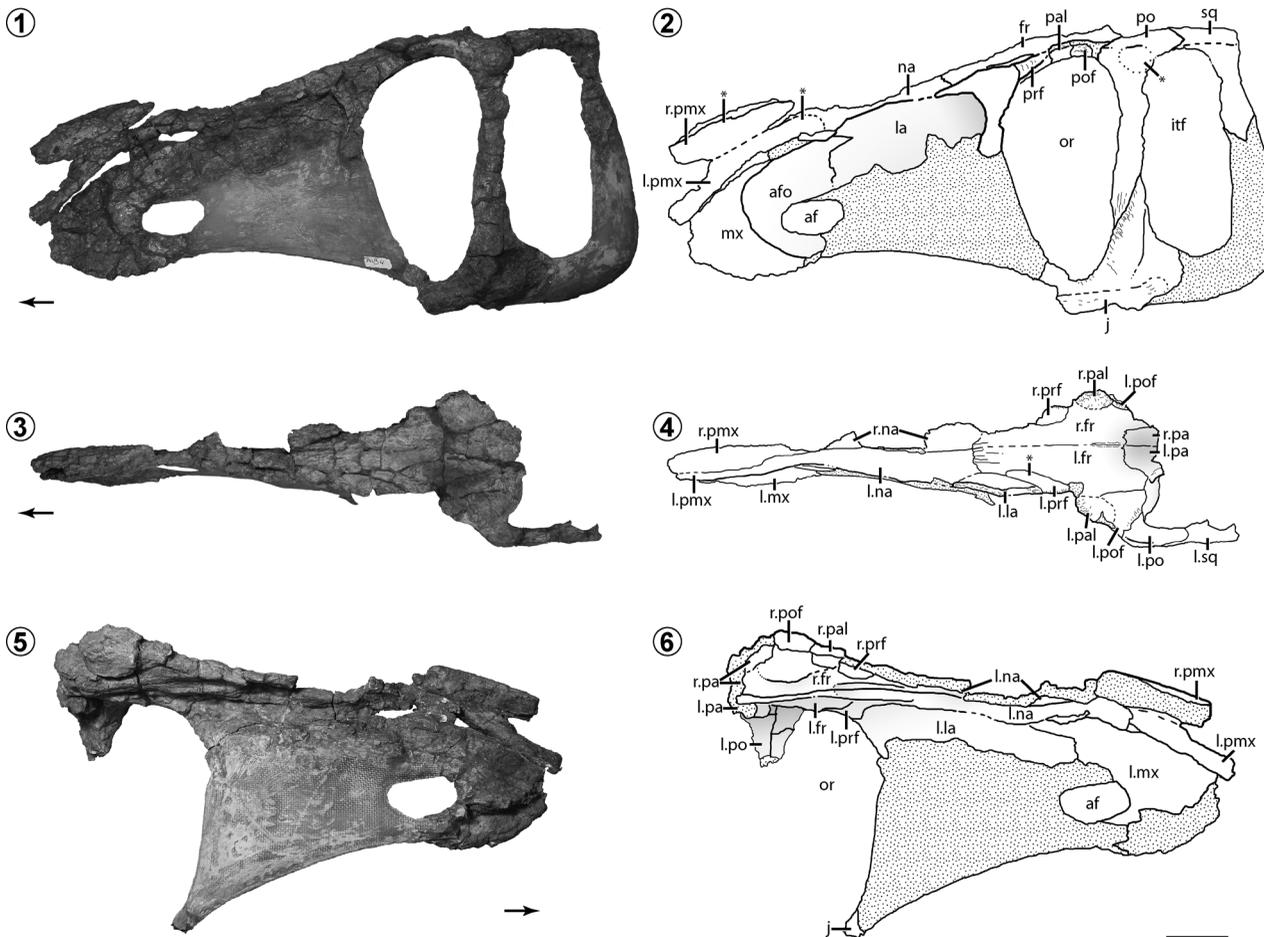

Figure 2. Partially articulated holotype skull of ***Luperosuchus fractus*** (**PULR** 4) from the Chañares Formation (latest Middle Triassic or earliest Carnian). **1,** Left lateral view; **2,** interpretive drawing of 1; **3,** dorsal view; **4,** interpretive drawing of 3; **5,** medial view; **6,** interpretive drawing of 5. Arrow indicates anterior direction. Abbreviations: *,** autapomorphy; **af,** antorbital fenestra; **afo,** antorbital fossa; **fr,** frontal; **itf,** infratemporal fenestra; **j,** jugal; **l.,** left; **la,** lacrimal; **mx,** maxilla; **na,** nasal; **or,** orbit; **pa,** parietal; **pal,** palpebral; **po,** postorbital; **pof,** postfrontal; **pmx,** premaxilla; **prf,** prefrontal; **r.,** right; **sq,** squamosal. Scale bar= 5 cm. Stippled area denotes broken surfaces, large cracks, or epoxy that was added during original preparation.

of 236.1 +/- 0.6 Ma. This indicates that the age of *L. fractus* is either the latest portion of the Middle Triassic or the earliest Late Triassic.

Revised diagnosis. Loricatan archosaur with an estimated skull length of 60 cm, with the following combination of character states (autapomorphies indicated by an asterisk; Fig. 2): rounded palpebral fused with the skull table; posterodorsal (= maxillary) premaxillary process greatly elongated as it extends posterior of the external naris, reaching nearly to the dorsal portion of the skull*; poorly developed rugosities on the lateral surface of the maxilla; ectopterygoid with one lateral articular head; long and gracile postorbital; dorsally convex and highly mediolaterally compressed anterior portion of the nasal* (= 'Roman-nose' of Romer, 1971c); rounded and circular knob on the dorsolateral margin of the postorbital*; long anterior process of the prefrontal that fails to extend to the anterior end of the frontal*; narrow postorbital bar (~8 times taller than wide at the jugal–postorbital contact).

Referred specimens. None, see discussion.

Comments. Romer (1971c) reported that "a considerable number of weathered scraps of bone" were collected from the type locality of *Luperosuchus fractus*, but noted that he was unsure if the fragments belonged to the holotype of *L. fractus* or the dicynodont collected from the same locality. These fragments (Fig. 6) are not currently with the holotype skull, but were instead located in the collection at the MCZ, USA. The identifiable fragments do not duplicate the portions present in the skull, are consistent in size with belonging to the same individual as the skull, and some of the larger fragments are consistent with loricatan archosaurs (see below). Identifiable fragments include the lateral surface of the left maxilla with three alveoli, a piece of the posterior part of the maxilla, the dorsal fifth portion of the left quadrate, the supraoccipital with portions of the opisthotics, other fragments of the braincase, the basipterygoid articular facet of the left pterygoid, and the atlas intercentrum (Figs. 5–6). The preservation of the fragments is generally good, but weathering has made differentiating the bone from the similarly textured matrix difficult. Furthermore, many of the edges of the fragments are rounded and the smoother surfaces are checkered with partially delaminated external surfaces.

Preservation. Since the original preparation (Romer, 1971c;

Fig. 1), epoxy and other consolidates were added to the surface of the specimen to preserve and add support to the thin portions of the specimen (see Figs. 2–6). These additives largely prevent observation of the surfaces of the skull, especially of sutures and details of articulation surfaces. During the course of this study, some of these materials were removed with acetone to expose the finer anatomical details of the skull.

Ontogenetic age. Little from the skull indicates the ontogenetic age of the specimen and more generally, it is very difficult to determine ontogenetic stage in any archosaur from a skull (Bailleul and Horner, 2016; Bailleul *et al*., 2016). Many of the sutures seem to be fused completely, and the skull bones are well ossified. Furthermore, the sculpturing of the skull elements is well developed where observable. None of these features indicate that the skull belongs to either a skeletally mature individual or a necessarily young individual either (see Bailleul and Horner, 2016; Bailleul *et al*., 2016). The age cannot be assessed independently because vertebrae and long bones are not available from the holotype (contra Ricqlés *et al*., 2008; see below).

DESCRIPTION
Skull openings

In the holotype of *Luperosuchus fractus*, the preserved portion of the external naris tapers posteriorly, as in *Saurosuchus galilei* (PVL 2062; PVSJ 32), a referred specimen of *Prestosuchus chiniquensis* (UFRGS-PV-156T) and *Postosuchus kirkpatricki* (TTU-P 9000; Weinbaum, 2011), but not to the same degree as the highly acute angle of the homologous area in *Decuriasuchus quartacolonia* (de França *et al*., 2013). The antorbital fenestra and fossa are completely posterior to the posterior edge of the external naris (Fig. 2). The anterior termination of the antorbital fenestra has an obtuse curvature in lateral view much like that of *Arizonasaurus babbitti* (Nesbitt, 2005) and *Batrachotomus kupferzellensis* (Gower, 1999) as opposed to the much more acute condition in *S. galilei* (Alcober, 2000; PVL 2062; PVSJ 32), *Decuriasuchus quartacolonia* (de França *et al*., 2013), and a referred specimen of *Pr. chiniquensis* (UFRGS-PV-156T). The complete shape of the antorbital fenestra is not clear because of incomplete preservation, but it was likely triangular like that of *S. galilei* (Sill, 1974; Alcober, 2000) and *Po. kirkpatricki* (Weinbaum, 2011) based on the depth of the pre-

served portion of the maxilla and the postorbital-jugal bar. The orbit is dorsoventrally tall without the 'key-hole' shape present in some loricatans (*e.g.*, *B. kupferzellensis*, *Po. kirk-patricki*) because there is no change in angle where the postorbital contacts the jugal. The infratemporal fenestra, although incomplete, is dorsoventrally taller than wide, similar to that of the dimensions of the orbit. Fragments of the posterior process of the jugal (see below) indicate that the posteroventral portion of the infratemporal fenestra would have been expanded relative to the posterodorsal portion as in *B. kupferzellensis* (Gower, 1999), *Qianosuchus mixtus* (Li *et al.*, 2006), and a referred specimen of *Pr. chiniquensis* (UFRGS-PV-156T). The incomplete suprathemporal fenestra is oval with a longer anteroposterior axis that mediolateral axis.

Premaxilla

Romer (1971c) identified small fragments of the pre-maxilla on the anterior portion of the maxilla, but we interpret this portion of the skull to all be maxilla with a broken anterior margin. We agree with Romer (1971c) in the identification of a long posterodorsal process (= maxillary process) of the premaxilla but with slight differences in interpretation (Fig. 2). We could not discern a suture between the nasal and posterodorsal process of the premaxilla either on the dorsal margin or the posterior extent of the process. The process is laterally convex in cross section and mediolaterally thick, which argues that it is a portion of the lateral part of the ventral process of the nasal. The exact posterior termination of the posterodorsal process of the premaxilla is not clear because of poor surface preservation, but the laterally convex surface of the element appears to terminate dorsal to the majority of the articulation between the maxilla and the lacrimal, where presumably the premaxilla meets the nasal or even the lacrimal. With this configuration, the premaxilla excludes the maxilla from participating in the external naris.

Romer (1971c) highlighted the long gap between the maxilla and the premaxilla, and referred to this opening as a "narrow slit". The length of this slit in *Luperosuchus fractus* (PULR 04) is longer than any other archosaur taxon in that it extends well posterior to the external naris. In *L. fractus* (PULR 04) and *Saurosuchus galilei* (PVL 2062; PVSJ 32) there is a clear gap between the maxilla and the posterodorsal

process of the premaxilla and the tapering termination of the premaxillary process occurs between the maxilla and the nasal at a tight contact. The ventral surface of the posterodorsal process of the premaxilla is convex whereas the dorsolateral surface of the maxilla is concave with a developed lip that extends laterally. In both *L. fractus* (PULR 04) and *S. galilei* (PVL 2062; PVSJ 32) the ventral margin of the posterodorsal process of the premaxilla curves posterodorsally and this curvature is closely matched with the anterodorsal surface of the maxilla. The well preserved and articulated skulls of *Decuriasuchus quartacolonia* (de França *et al.*, 2013) have this same morphology.

Maxilla

The maxilla of the holotype of *Luperosuchus fractus* is represented by the dorsal (= ascending) process and anterodorsal portion of the maxilla preserving the antorbital fenestra and fossa in articulation with the surrounding elements (Fig. 2), a large fragment of the lateral surface of the maxilla from the anterior portion (Fig. 5), and various other fragments from the ventral, tooth-bearing margin. The depth of the jugal suggests that the body of the maxilla was much deeper than the portion preserved in articulation with the other portions of the skull roof. In articulation, the dorsal process of the maxilla overlaps the anterior portion of the lacrimal laterally for approximately 15 mm of contact. The dorsal margin of the dorsal process of the maxilla tapers posteriorly where it meets the lacrimal. The height of the dorsal process remains constant for its length, resulting in a rectangular lateral profile as in *Saurosuchus galilei* (PVL 2062; PVSJ 32), *Decuriasuchus quartacolonia* (de França *et al.*, 2013), and a referred specimen of *Prestosuchus chiniquensis* (UFRGS-PV-156T). The entire lateral surface of the dorsal process of the maxilla of *L. fractus* forms the antorbital fossa. We estimate that the dorsal process is directed at an angle of ~45° relative to the anteroposterior plane as occurs in *D. quartacolonia* (de França *et al.*, 2013). A ridge defines the anterior edge of the laterally facing antorbital fossa in *L. fractus*. The entire preserved antorbital fossa is exposed in lateral view as occurs in *S. galilei* (PVL 2062; PVSJ 32), *D. quartacolonia* (de França *et al.*, 2013), and a referred specimen of *Pr. chiniquensis* (UFRGS-PV-156T) and this is in contrast to those of poposauroids (Nesbitt, 2011, *e.g.*, *Arizonasaurus babbitti*) where some of the antorbital fossa
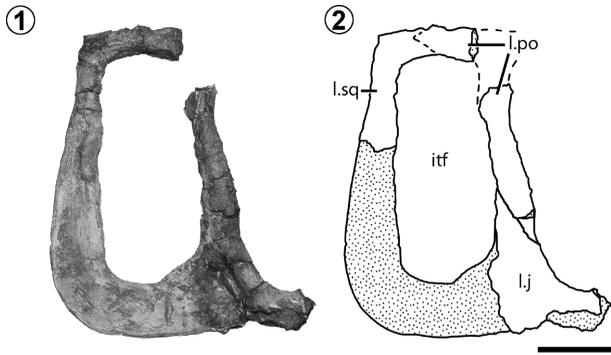
Figure 3. Broken posterior portion of the holotype skull of ***Luperosuchus fractus*** (PULR 4). **1,** Medial view photo; **2,** interpretive drawing of 1. Abbreviations: **itf,** infratemporal fenestra; **j,** jugal; **l.,** left; **po,** postorbital; **sq,** squamosal. Scale bar= 5 cm. Stippled area denotes broken surfaces, large cracks, or epoxy that was added during original preparation.

the holotype maxilla of *L. fractus* near the dental margin. Larger nutrient foramina open ventrally and lie about 1 cm dorsal to the dental margin. Medially, little can be discerned, but it is clear there is a distinct anteroposteriorly oriented groove at least 15 mm from the ventral margin. It is not clear if the interdental plates are completely fused into a sheet as in rauisuchids and *Fasolasuchus tenax* (Nesbitt, 2011; Lessner *et al.*, 2016), but it appears they are at least
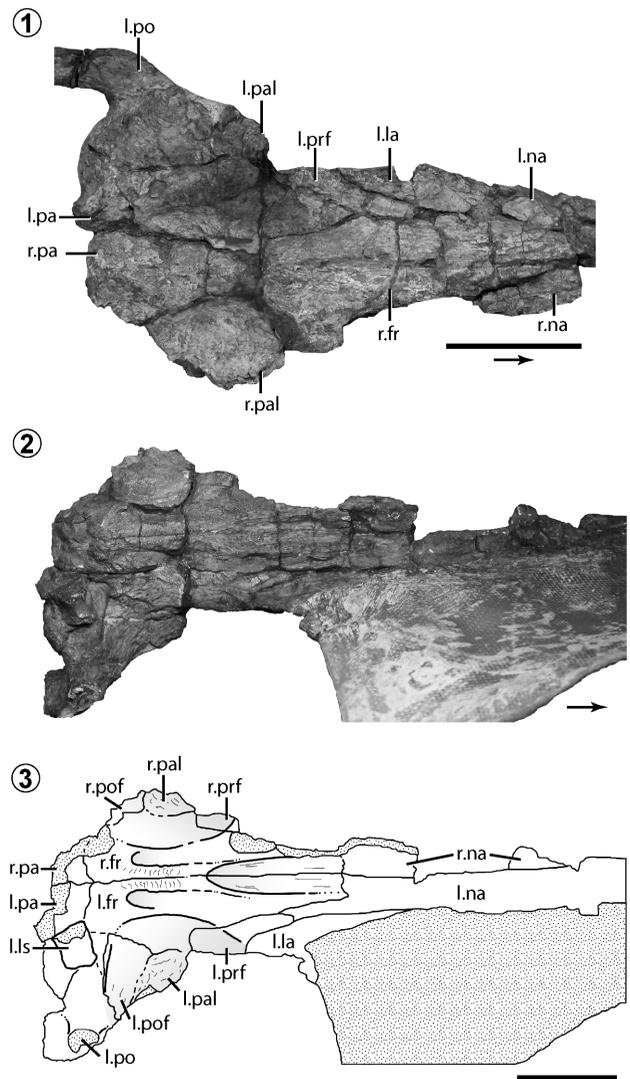
is hidden in lateral view (Parker and Nesbitt, 2013). The lateral surface of the antorbital fossa is smooth without any smaller fossae within the structure. The height of the antorbital fenestra is about one third that of the lateral exposure of the height of the antorbital fossa.

Most of the medial surface of the maxilla is smooth. There is a clear depression anterior to the antorbital fenestra and ventral to the posterior margin of the external naris as occurs in *D. quartacolonia* and *Polonosuchus silesiacus* (de França *et al.*, 2013). No part of the palatal process of the maxilla is preserved. The anterodorsal edge of the maxilla is mediolaterally broad and nearly flat.

A thin sheet of the lateral surface of the left maxilla is preserved as well as a number of fragments that represent the medial surface of the maxilla (Fig. 5), all of which were found as fragments and reassembled at MCZ. The width of the largest alveolus measures ~31 mm at its widest point. The lateral surface of the maxilla is distinctly rugose and the surface texture consists of short rounded ridges with no obvious orientation. A similar pattern of rugosity is present on the lateral surface of the maxilla of *S. galilei* (Alcober, 2000; PVSJ 32) and the depth of the rugosities is even more exaggerated in the holotype of that taxon (Sill, 1974); these rugosities have been suggested to be diagnostic for *S. galilei*, but are also present in *L. fractus*. In comparison, the lateral surface of the maxilla of a referred specimen of *Pr. chiniquensis* (UFRGS-PV-156T) and *D. quartacolonia* appear to be nearly smooth. Tiny foramina dot the lateral surface of

Figure 4. Close ups of the skull roof of the partially articulated holotype skull of ***Luperosuchus fractus*** (PULR 4) as a **1,** photo in dorsal view and in ventral view as a **2,** photo and **3,** interpretive drawing. Abbreviations: **fr,** frontal; **l.,** left; **la,** lacrimal; **ls,** laterosphenoid; **na,** nasal; **pa,** parietal; **pal,** palpebral; **po,** postorbital; **pof,** postfrontal; **prf,** prefrontal; **r.,** right. Arrow indicates anterior direction. Scale bars= 5 cm. Stippled area denotes broken surfaces, large cracks, or epoxy that was added during original preparation.

partially separated based on the fragments found with the skull. Impressions in the form of a natural mold of tooth serrations on the posterior (= distal) edge of one tooth (exact position unknown) indicates that there are 10 serrations per 5 mm in the maxillary teeth (Fig. 5).

Frontal

Both frontals are preserved nearly in their entirety and have well-preserved surfaces (Figs. 2, 4). Overall, the frontals are the thickest portion of the skull roof (at the pos-

terior margin of the elements at the midline they are about 20 mm thick) and the frontals taper a little in thickness anteriorly (about 15 mm thick at the anterior margin). In dorsal view, the midline suture is completely fused and absent but the midline is marked by a thin anteroposteriorly oriented and slightly rugose ridge posteriorly. Anteriorly, this low ridge disappears at the level medial to the articulation with the prefrontal. This ridge is not as pronounced as the condition in some crocodylomorphs, *Batrachotomus kupferzellensis* (Gower, 1999) and some other suchians (*e.g.*,
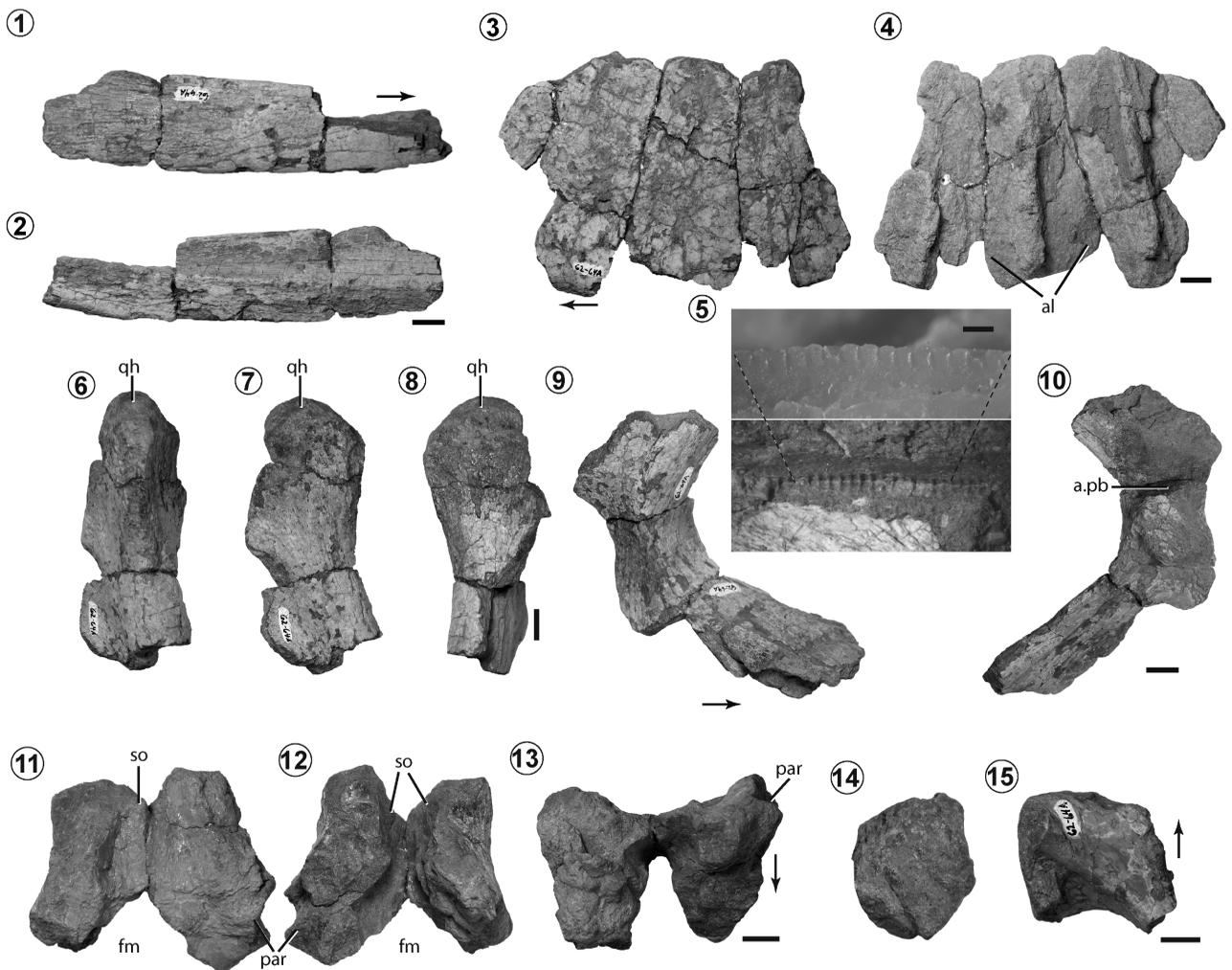

Figure 5. Fragments of the holotype skull of ***Luperosuchus fractus*** found at MCZ that were separated from the holotype. Photograph of the posterior process of the right jugal in **1,** lateral and **2,** medial views. Photograph of the left maxilla in **3,** lateral and **4,** medial views. Photograph of tooth serrations cast in silicon **5,** and the impression within a fragment of maxilla (bottom). Photograph of the proximal half of the left quadrate in **6,** posterior, **7,** lateral, and **8,** medial views. Photograph of a partial left pterygoid in **9,** lateral and **10,** medial views. Photograph of the dorsal portion of the braincase in **11,** posterior, **12,** anterior, and **13,** ventral views. Photograph of a partial left ectopterygoid in **14,** lateral and **15,** dorsal views. Abbreviations: **a.,** articulates with; **al,** alveolus; **fm,** foramen magnum; **par,** paroccipital process of the braincase; **pb,** parabasisphenoid; **qh,** quadrate head; **so,** supraoccipital. Scale bars=1 cm in **1–4, 6–15** and 1 mm in **5**. Arrows indicate anterior direction.

Turfanosuchus dabanensis; Wu and Russell, 2001; Nesbitt, 2011; Butler *et al.*, 2014). The dorsal surface of the frontal is ornamented by anteroposteriorly oriented ridges and grooves. At their anteriormost portions and contact with the nasals, the frontals are distinctly convex at the midline. Here, the frontals meet the nasals at interdigitated sutures. The posterior half of the frontals is depressed relative to the lateral portion of the skull roof, similar to the depressed parietals. The lateral portions of the frontals rise antero-laterally, but are excluded from the lateral margin of the orbit by palpebral elements (see below) that are fused to the frontal.

In ventral view, the anterior half of the frontals has a well-developed depression at the midline framed by an-teroposteriorly oriented ridges. This depression records the dorsal margin of the olfactory bulbs as suggested for *B. kupferzellensis* (Gower, 1999) and *Postosuchus kirkpatricki* (Weinbaum, 2011). Lateral to the ridges, there are fossae defined laterally by the prefrontal and the lacrimal. Poste-riorly, the ridges converge medially at the posterior extent of the prefrontals. The well-defined midline suture is clearly present adjacent to the orbital fossa. Here, the suture sits in a valley surrounded by rugose ridges. Lateral to these ridges, there are deep anteroposteriorly oriented fossae laterally demarcated by the medial extent of the orbital fossa. These depressions may articulate with the anterior-most portion of the laterosphenoids given the similar posi-tion to that of *B. kupferzellensis* (Gower, 1999) and *Po. kirkpatricki* (Weinbaum, 2011). Posteriorly, the frontals taper where they meet the parietals. The lateral surface of the frontal forms the middle third of the orbital fossa.

Palpebral

We interpret small extra bones at the dorsolateral mar-gin of the orbits as palpebral elements, as in *Saurosuchus galilei*, *Postosuchus kirkpatricki*, *Polonosuchus silesiacus*, and possibly *Batrachotomus kupferzellensis* (Nesbitt *et al.*, 2013). We interpret these as palpebral elements in *Luperosuchus fractus* (Figs. 2, 4) for several reasons following the identifi-cation criteria previously proposed for non-crocodylomorph pseudosuchians (Nesbitt *et al.*, 2013). First, the external surface of each element is distinct from the surrounding skull roof bones in that the palpebrals have more striations and pits. These external patterns are consistent with those

of other loricatans with palpebrals including *S. galilei* and rauisuchids (Nesbitt *et al.*, 2013). Second, the palpebral elements of *L. fractus* lie completely lateral to the orbital fossa of the frontal, and thus exclude the frontal from the lateral edge of the orbit as in other loricatans. Third, the elements of *L. fractus* arc dorsally at their anteroposterior midpoint and arc dorsal relative to the rest of the skull roof and as in *S. galilei* (PVSJ 32) and other closely related taxa (*e.g.*, *Po. kirkpatricki*). It appears that there was a single palpebral element dorsal to each orbit as in *S. galilei* (PVSJ 32). The palpebral element in *L. fractus* is longer than wide and is completely fused to the frontal and the postfrontal, making the demarcation of the element difficult (Fig. 2.3–4). The palpebrals of *L. fractus* are proportionally smaller (~50%) compared to those of *S. galilei* (PVSJ 32) and *Po. kirk-patricki*. Using the size and characteristics of the palpebral of *L. fractus*, we hypothesize that a similarly shaped, small palpebral is also present in a referred specimen of *Presto-suchus chiniquensis* (UFRGS-PV-156T). If this is the case, the presence of a palpebral would be a character state shared possibly by all loricatans (*sensu* Nesbitt, 2011; see below).

Prefrontal

The prefrontal is complete on the left side and only the posterior portion is preserved on the right side (Figs. 2, 4). The sutures are clear around the entire element and can be traced on the dorsal and ventral surfaces. The prefrontal forms only a small portion of the dorsal margin of the orbit and in lateral view, this margin is rugose with vertical stria-tions. The prefrontal does not contact the palpebral ele-ment. In ventral view, the prefrontal has a short ventral process and this forms the anterior portion of the orbital fossa similar to that process of *Postosuchus kirkpatricki* (Weinbaum, 2011). However, unlike in *Po. kirkpatricki* the prefrontal and the lacrimal remain unfused in *Luperosuchus fractus*. Medially, the prefrontal forms the lateral wall of a distinct fossa shared with the frontal. The anterior process is finger like in dorsal view fitting between the lacrimal and the frontal. This anteromedially projected process fails to reach the level of the anterior extent of the frontal (Fig. 2), similar to the short prefrontal of *Po. kirkpatricki* (Weinbaum, 2011). In *Decuriasuchus quartacolonia* (de França *et al.*, 2013), *Batrachotomus kupferzellensis* (Gower, 1999), *Saurosuchus galilei* (PVSJ 32), and a referred specimen of *Prestosuchus*

chiniquensis (UFRGS-PV-156T) the anterior process reaches the anterior extent of the frontal. Therefore, the long anterior process combined with the lack of extension to anterior end of the frontal of *L. fractus* appears to be autapomorphic.

Postfrontal

The left postfrontal is complete whereas the right element is represented by only a few fragments still in articulation with the rest of the skull roof (Figs. 2, 4). The postfrontal is distinctly convex in dorsal view and is excluded from the orbital margin by the palpebral. The postfrontal and the palpebral are fused with no visible suture. Overall, the postfrontal is much larger than the prefrontal in dorsal view, and the postfrontal is as dorsoventrally thick as the frontal. Relative to other skull roof elements, the size of the postfrontal of *Luperosuchus fractus* is similar to that of *Decuriasuchus quartacolonia* (de França *et al.*, 2013) and much larger than those in *Batrachotomus kupferzellensis* (Gower, 1999) and *Postosuchus kirkpatricki* (Weinbaum, 2011). In *L. fractus*, the postfrontal meets the postorbital in a well-defined interdigitating suture on the posterolateral margin and it meets the parietal posteriorly. The postfrontal contacts the frontal medially. This suture is poorly defined dorsally but visible ventrally. Posteriorly, the postfrontal is excluded from the supratemporal fenestra by the postorbital and the parietal (Fig. 2). A rim defines the supratemporal fossa posteriorly within the supratemporal fenestra in dorsal view, but the supratemporal fossa does not extend onto the dorsal surface as in *Po. kirkpatricki* and crocodylomorphs (Nesbitt, 2011). In ventral view, the postfrontal forms the posterior and posterolateral portion of the orbital fossa.

Nasal

The nasal is represented by much of the left element and the posterior and anterior portions of the right one (Figs. 2, 4). The suture between the nasals and the frontals is difficult to discern in dorsal view; it appears that the suture is nearly fused but the surface of the nasal is not completely preserved. The anterior portion of the nasals form a 'Roman nose' as previously described (Romer, 1971c; Desojo and Arcucci, 2009) and this morphology consists of dorsally arching nasals that lie dorsal to the anterior portion of the antorbital fossa and then curve anteroventrally dor-

sal to the posterior portion of the external naris. The left and right nasals meet as mediolaterally compressed elements as in *Batrachotomus kupferzellensis* (SMNS 80260; Gower, 1999), *Decuriasuchus quartacolonia* (de França *et al.*, 2013), *Qianosuchus mixtus* (IVPP V14300), and *Prestosuchus chiniquensis* (UFRGS-PV-156T) (see below). However, the left nasal is mediolaterally thinner than the more mediolaterally expanded right element, and this incongruence between the left and right sides is probably the result of poor preservation. Additionally, the right portion of the nasal is slightly twisted laterally from its natural position.

The suture between the ventral portion of the nasal and the premaxilla is not observable, but likely present in a lateral depression between the elements (Fig. 2; dotted line). A similar depression is present in *Saurosuchus galilei* (PVL 2062; PVSJ 32) where the nasal contacts the posterior portion of the posterodorsal process of the premaxilla. A depression is also present in a similar position in *Pr. chiniquensis* (UFRGS-PV-156T), but here the nasal directly contacts the ascending process of the maxilla. In this region in *B. kupferzellensis* a postnarial fossa is present (Gower, 1999), but this is not very similar to the features in *L. fractus*, *S. galilei*, and *Pr. chiniquensis*.

The posterior portion of the nasal of *L. fractus* articulates with the frontal at a partially interdigitating, partially fused suture that is generally mediolaterally oriented. This suture is more clearly pronounced on the ventral surface. The suture lies between the anterior portions of the dorsal exposure of the lacrimals instead of the prefrontal as illustrated in Romer (1971c). Here, the articulation is convex across the midline. More anteriorly, the nasal appears to be depressed at the midline relative to the lateral margin. The ventral surface of the nasals is convex but poorly preserved and covered in glue and some matrix.

Postorbital

The entire left postorbital is preserved in *Luperosuchus fractus*. Anteriorly it meets the postfrontal in an interdigitating suture at the posterodorsal margin of the orbit. The suture wraps laterally around the ventral surface posterior to the orbital fossa of the postfrontal. Anteromedially, the lateral process of the parietal overlaps the postorbital. Consequently, the anterolateral margin of the supratemporal fenestra forms part of a posterolaterally concave

supratemporal fossa. The dorsomedial surface of the proximal portion of the postorbital has a slight depression for the articulation with the laterosphenoid. A rounded knob is present on the lateral portion of the main body of the postorbital just posterior from the posterodorsal edge of the orbit. This rounded knob extends onto the lateral surface of the ventral process. A rounded lateral margin of the postorbital is present in *Saurosuchus galilei* (PVL 2062; PVSJ 32), *Prestosuchus chiniquensis* (UFRGS-PV-156T), *Batrachotomus kupferzellensis* (SMNS 52970), *Postosuchus kirkpatricki* (Weinbaum, 2011), and *Decuriasuchus quartacolonia* (de França *et al.*, 2013), but in these taxa, the rounded region is dorsoventrally compressed, restricted to the dorsal portion of the postorbital and is not as robust as that of *L. fractus*. Therefore, we consider the condition in *L. fractus* an autapomorphy of the taxon (Fig. 2.2). Dorsal to the rounded knob, there is a small depression present in dorsal view. Additionally, there is a small fossa ventral to the knob where the ventral process originates. Posteriorly, the postorbital meets the squamosal (Fig.2) and the articulation is poorly preserved, but it appears that the tapering posterior process of the postorbital lies dorsal to the anterior process of the squamosal as in the condition in *B. kupferzellensis* (Gower, 1999).

The ventral process is triangular in cross section where the anterior edge of the postorbital is mediolaterally expanded and the posterior edge thins; the lateral surface of the ventral process is nearly flat. Ventrally, the process becomes more robust in medial view and consequently, has a rounded cross section. The anterior edge of the postorbital is S-shaped where the dorsal half is concave and the ventral portion is slightly convex in lateral view. This is also present in *S. galilei* (PVL 2062; PVSJ 32), *Pr. chiniquensis* (UFRGS-PV-156T), and *D. quartacolonia* (de França *et al.*, 2013), but in contrast to the ventral processes of *B. kupferzellensis* (SMNS 52970) and *Po. kirkpatricki* (Weinbaum, 2011) that expand into the orbit creating a key-hole shaped orbit. The postorbital meets the dorsal (= ascending) process of the jugal at an anteroventrally oriented suture measuring about 80° to the horizontal. In lateral view, the postorbital tapers on the orbital margin whereas the articulation is observable in medial view because of breakage. The ventral process extends for three quarters the length of the orbit.

Lacrimal

Much of the left lacrimal (138 mm long and max height preserved 59 mm) is preserved, except for the ventral process and portions of the ventral margin of the anterior process (Fig. 2). The posterior portion of the lacrimal forms the anterodorsal margin of the orbit and contacts the prefrontal posteriorly and medially. The anterolateral margin of the orbit is poorly preserved but is slightly rugose and mediolaterally thin, in contrast with the mediolaterally thicker ventral portion of the prefrontal. No lacrimal foramen can be seen. Anterior to this orbital margin, a vertically oriented, rugose ridge with transversely oriented ridges on the lateral surface demarcates the posterior and posterodorsal portion of the antorbital fossa. Dorsal to the vertical ridge, the rugose surface continues and is raised dorsal to the other portions of the skull table in the immediate area. Consequently, the posterior third of the bone is exposed in dorsal view. Anteriorly of this vertical ridge, an anteriorly opening pocket hides the posterodorsal extent of the antorbital fossa. This is the same condition as in *Saurosuchus galilei* (PVL 2062; PVSJ 32), *Prestosuchus chiniquensis* (UFRGS-PV-156T), *Decuriasuchus quartacolonia* (de França *et al.*, 2013), and the crocodylomorph *Carnufex carolinensis* (Zanno *et al.*, 2015). In contrast, the posterodorsal portion of the antorbital fossa is not laterally covered in *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III 563; Sulej, 2005), and *Batrachotomus kupferzellensis* (SMNS 80260). Medially, the lacrimal contacts the nasal in a poorly defined contact.

The anterior process of the lacrimal is much longer than tall and forms most of the preserved portion of the antorbital fossa. The process is smooth and flat laterally and mediolaterally thin (~5–7 mm). The antorbital fossa is dorsally capped by the lateral process of the nasal, but not to the same extent suggested to be autapomorphic for *D. quartacolonia* (de França *et al.*, 2013). The anterior process lies medial to the dorsal process of the maxilla.

Jugal

The main body of the left jugal is present but missing the anterior process, much of the posterior projections (see below) and the ventral margin. The main body of the jugal is convex laterally and concave medially. In the anteroposterior center of the main body, a rounded projection about

the same size as the postorbital knob is present. This projection of the jugal extends anteriorly as a low rounded ridge as in *Decuriasuchus quartacolonia* (MCN-PV10.105a), *Saurosuchus galilei* (PVL 2062; PVSJ 32), and *Prestosuchus chiniquensis* (UFRGS-PV-156T). On the lateral side of the jugal of *Luperosuchus fractus*, a small groove dorsal to the horizontally oriented rounded ridge marks the dorsal margin. The jugal forms the ventral margin of the orbit and its radius of curvature is smaller than that of the ventral portion of the orbits of *Postosuchus kirkpatricki* (Weinbaum, 2011) and *S. galilei* (PVSJ 32). The dorsal process of the jugal tapers posterodorsally where it meets the postorbital and the lateral surface of the process has a similar rugosity on the lateral surface as the ventral process of the postorbital. The postorbital bar is much narrower than other loricatan taxa. For instance, the ratio of the length (from the dorsal to ventral portion of the margin) versus the width at the articulation between the jugal and the postorbital is ~8 in *L. fractus* whereas the same ratio is ~3.6 in *S. galilei* (PVSJ 32), ~4 in *Pr. chiniquensis* (UFRGS-PV-156T), and ~3.5 in *D. quartacolonia* (MCN-PV10.105a). Medially, the orbital margin of the jugal of *L. fractus* is much thicker and rounded relative to the other portions of the jugal. The articulation with the ectopterygoid is not preserved.

A long, mediolaterally compressed element recently found among the fragment collected from the surface by Romer likely represent the posterior process of the jugal (Fig. 5). This fragment suggests that ventral border of the infratemporal was similar to those of *D. quartacolonia* (de França *et al.*, 2013) and *Pr. chiniquensis* (UFRGS-PV-156T) in that the length of the posterior process is elongated.

Squamosal

Part of the main body and the ventral process of the left squamosal is preserved; the posterior portion and the articulations with quadrate, braincase, and parietal are not preserved (Figs. 2–4). The dorsal margin is rounded without any clearly defined supratemporal fossa on the dorsal surface. This rounded surface continues laterally to form a rounded ridge. This rugose ridge is oriented anteroposteriorly and is also present in *Saurosuchus galilei* (PVSJ 32), *Decuriasuchus quartacolonia* (de França *et al.*, 2013), *Arizonasaurus babbitti* (Nesbitt, 2005), and a referred specimen of *Prestosuchus chiniquensis* (UFRGS-PV-156T). Ventral to

this ridge, there is a depression that frames the posterodorsal margin of the infratemporal fenestra in *Luperosuchus fractus*. The depression arcs ventrally at the posterior margin of the preserved portion of the squamosal. The ventral process of the squamosal is mediolaterally thin and slightly expands anteroposteriorly at its ventrally preserved portion (covered in plastic). There does not appear to be a lateral ridge or an anterior projection into the infratemporal fenestra as in a referred specimen of *Pr. chiniquensis* (UFRGS-PV-156T) or *S. galilei* (PVSJ 32). In medial view, the dorsal expansion continues onto the medial surface and is underlined by an anteroposteriorly oriented groove. Ventral to this, the medial surface is flat.

Parietal

The anteriormost portions of the left and right parietals are present, but broken at the anterior margin of the supratemporal fenestra (Figs. 2, 4). The parietals meet the frontals anteriorly in an interdigitating suture at the posterior margin of the orbit. This suture continues posterolaterally where the frontal forms the anterolateral margin of the skull roof. Further posterolaterally, the parietal meets the posterior portion of the postfrontal in a poorly defined suture that appears to be partially fused. Laterally, the parietal contacts the postorbital within the supratemporal fenestra. It appears that the supratemporal fossa on the posterior portion of the postorbital continues medially onto the parietal. At the midline, the parietal is not as dorsoventrally thick as the frontal because there is a large depression on the dorsal surface of the parietal framed by components of the frontals and postfrontals; this is also present in referred specimens of *Prestosuchus chiniquensis* (UFRGS-PV-156T) and *Saurosuchus galilei* (PVSJ 32). A slightly raised midline suture between the parietals is nearly obliterated in dorsal view whereas the midline crest in *Pr. chiniquensis* (UFRGS-PV-156T) is more dorsally expanded. The lateral edge of the parietal preserves a tall ridge representing the medial wall of the supratemporal fenestra (Fig. 2) as is the condition in *Pr. chiniquensis* (UFRGS-PV-156T) and *S. galilei* (PVSJ 32). This anterolaterally oriented ridge in *Luperosuchus fractus* is more dorsally expanded than any other part of the skull table.

Quadrate

Approximately the top fifth of the left quadrate is preserved (Fig. 5). The dorsal head of the quadrate is mediolaterally narrow and the dorsal surface is highly convex. The concave posterior edge (in lateral view) is robust and the anterior portion splits into a pterygoid ramus medially and a squamosal ramus laterally.

Pterygoid

The central and most mediolaterally thickened part of the left pterygoid is preserved, but highly weathered (Fig. 5). The articulation with the pterygoid process of the parabasisphenoid is concave but nearly all of the surrounding rim is missing. In lateral view, the quadrate process bears a triangular depression that divides the dorsal and ventral processes as in *Batrachotomus kupferzellensis* (Gower, 1999). The robust lateral process is largely broken, but it is clear that there were no palatal teeth on the ventral surface of the pterygoid.

Ectopterygoid

The lateral portion of the left ectopterygoid is preserved (Fig. 5). The flat lateral surface likely articulated with the jugal as in other archosauromorphs. This surface consists of only one single head as in *Saurosuchus galilei* (PVSJ 32) whereas a groove divides this surface into two distinct heads in rauisuchids (*e.g.*, *Postosuchus kirkpatricki* TTU-P 9000, 9002; Nesbitt, 2011) and some other loricatans (*e.g.*, *Batrachotomus kupferzellensis*; Gower, 1999). The dorsal surface has a small projection at the articulation with the jugal and this projection continues posteriorly as a ridge. The anterior portion thins, but is broken.

Braincase

Much of the braincase must have been originally preserved in the holotype, but unfortunately the entire braincase fractured and weathered (Fig. 5). Much of the supraoccipital, left and right prootics, opisthotics, and exoccipitals and basitubera were preserved. No sutures are apparent between any of the elements, similar to the obliteration of sutures in several other bones of the skull. The anteroposteriorly thick supraoccipital has a thin ridge at the midline dorsal to the foramen magnum which is laterally bounded by shallow depressions. This ridge or crest is also present in other lori-

catans such as *Saurosuchus galilei*, *Batrachotomus kupferzellensis,* and *Prestosuchus chiniquensis* (Mastrantonio *et al.*, 2013) and the poposauroid *Arizonasaurus babbitti* (Gower and Nesbitt, 2006). The dorsal articulation with the laterosphenoids and parietals is eroded. The medial wall of the inner ear appears to be incompletely ossified as in *B. kupferzellensis* (see Gower, 2002). The lateral opening for the facial nerve (VII) is small, opens posterolaterally and does not open into a distinct groove as in other loricatans (*e.g.*, *B. kupferzellensis*, Gower, 2002). The right exoccipital is complete, but disarticulated from the occipital condyle. It is not clear if the exoccipitals would meet at the midline. One clear exit of cranial nerve XII is present through the exoccipital and the lateral exit of CN XII is located anterior to a distinct vertical ridge on the lateral side. This ridge in *Luperosuchus fractus* trends anteroventrally and a similar ridge is also present in *Postosuchus kirkpatricki*, *B. kupferzellensis*, *S. galilei*, and *A. babbitti*, and *Pr. chiniquensis* (Gower, 2002; Gower and Nesbitt, 2006; Mastrantonio *et al.*, 2013). A smaller, more ventrally and anteriorly located foramen likely represents a second exit of CN XII. A lateral portion of the preserved left basituber of the parabasisphenoid indicates that there was a large unossified gap present medial to this rounded structure as in *S. galilei* and *B. kupferzellensis* (Gower, 2002).

Atlas intercentrum

A nearly complete atlas intercentrum represents the only known postcranial element of *Luperosuchus fractus* (Fig. 6). The large intercentrum indicates that the element was not preserved in direct contact with the occipital condyle because there is matrix in the articulation surface between the two elements and the occipital condyle had an estimated diameter of 27 mm. The length versus width ratio of the atlas intercentrum, measured from the ventral surface, is 0.6 for *Luperosuchus fractus* compared to that of 0.43 for *Saurosuchus galilei* (PVSJ 32; Trotteyn *et al.*, 2011); thus it is clear that *S. galilei* has a proportionally much wider atlas intercentrum. The height versus length, measured from the ventral surface and anterior surface, is ~1 for both *L. fractus* and *S. galilei* (PVSJ 32). Ventrally, the surface of the atlas intercentrum of *L. fractus* is convex and it lacks the anteroposteriorly oriented ridge present in *S. galilei* (PVSJ 32). The atlas intercentrum of *L. fractus* seems to lack a rib facet, but this cannot be confirmed based on the present material. The
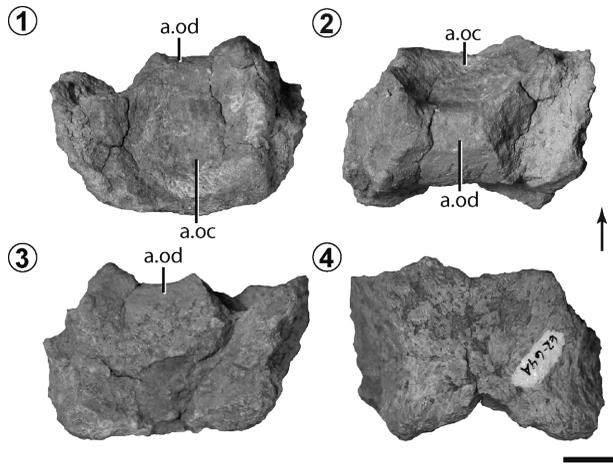
Figure 6. Atlas intercentrum of ***Luperosuchus fractus*** recently found at MCZ in **1,** anterior, **2,** dorsal, **3,** posterior, and **4,** ventral views. Abbreviations: **a.,** articulates with; **oc,** occipital condyle; **od,** odontoid. Scale bar=1 cm. Arrow indicates anterior direction.

posterior surface has a partially convex articulation surface for the axis intercentrum and the odontoid process. Anteriorly, the surface is concave for articulation with the occipital condyle and a small notch is located at the midline dorsal to the concave depression.

DISCUSSION

Relationships of **Luperosuchus fractus**

We recovered *Luperosuchus fractus* as a loricatan archosaur in our strict consensus (Fig. 7.1) of 180 most parsimonious trees (= MPTs), with a tree length of 1332 steps, a consistency index of 0.364, and retention index of 0.768. The large antorbital fossa on the dorsolateral portion of the preserved section of the maxilla (Nesbitt, 2011 character 137-state 2 abbreviated to *e.g.* '137-2' hereafter) and the absence of teeth on the pterygoid (175-1; 176-1) indicates that *L. fractus* is an archosaur. At the base of Loricata, *L. fractus* was found within a clade that also includes *Prestosuchus chiniquensis* and *Saurosuchus galilei* and that is the sister taxon of all other loricatans. Within this clade, *L. fractus* occupied two alternative positions: 1) the sister taxon of a *Prestosuchus chiniquensis + S. galilei* (Fig. 7.2); 2) as the sister taxon of *S. galilei*, with *Pr. chiniquensis* as the sister of *S. galilei + L. fractus* (Fig. 7.3). In all MPTs, *L. fractus* is supported as a shallowly nested loricatan, excluded from a clade comprising most other loricatans by the following unambiguous

character states: a posterodorsal process of the premaxilla greater than the anteroposterior length of the premaxilla (2-1); four premaxillary teeth (6-1); a tall and narrow orbit (maximum width is less than half the maximum height) (142-1); and the presence of palpebral(s) in the orbit (147-1) (Fig. 2).

In the following description of the character support for the two hypotheses about the least inclusive position of *L. fractus*, we only cite the unambiguous character states and states that could be scored for the taxon.

Hypothesis 1 (Fig. 7.2). *Luperosuchus fractus* as the sister taxon of *S. galilei + Pr. chiniquensis* is supported by a dorsal (= ascending) process of the maxilla that remains the same width posteriorly (29-1) and palpebral(s) extensively sutured to each other and to the lateral margin of the frontals (149-1). Both supporting character states appear within Rauisuchidae (Nesbitt, 2011). The sister taxon relationship between *S. galilei* and *Pr. chiniquensis* is supported by a squamosal with ridge on the lateral side of the ventral process (51-1). This character state is homoplastic in this analysis because it also is present in *Batrachotomus kupferzellensis* (Gower, 1999).

Hypothesis 2 (Fig. 7.3). The sister taxon relationship between *L. fractus* and *S. galilei* is supported by a long posterodorsal (= maxillary, = subnarial) process of the premaxilla that terminates posterior of the posterior extension of the external naris (415-1; see description below). *Prestosuchus chiniquensis* as the sister taxon of *S. galilei + L. fractus* is supported by a dorsal (= ascending) process of the maxilla that remains the same width posteriorly (29-1) and palpebral(s) extensively sutured to each other and to the lateral margin of the frontals (149-1).

Additionally, *L. fractus* shares a few character states with other taxa that were not used in this phylogenetic analysis, but which were described above. For example, *Luperosuchus fractus* has a distinct, rugose ridge on the dorsolateral portion of the lacrimal as in a referred specimen *Pr. chiniquensis* (UFRGS 0156-T), *S. galilei* (PVSJ 32), *B. kupferzellensis* (Gower, 1999), and *Postosuchus kirkpatricki* (TTU-P 9000). The prefrontal and lacrimal appear to be partially fused in *L. fractus* as in *Rauisuchus tiradentes* (BSP AS XXV-60-121), *Po. kirkpatricki* (TTU-P 9000), and *S. galilei* (PVSJ 32), but this is not clear and, therefore, scored as unknown. *Luperosuchus fractus* appears to have a triangular-shaped antorbital fenes-

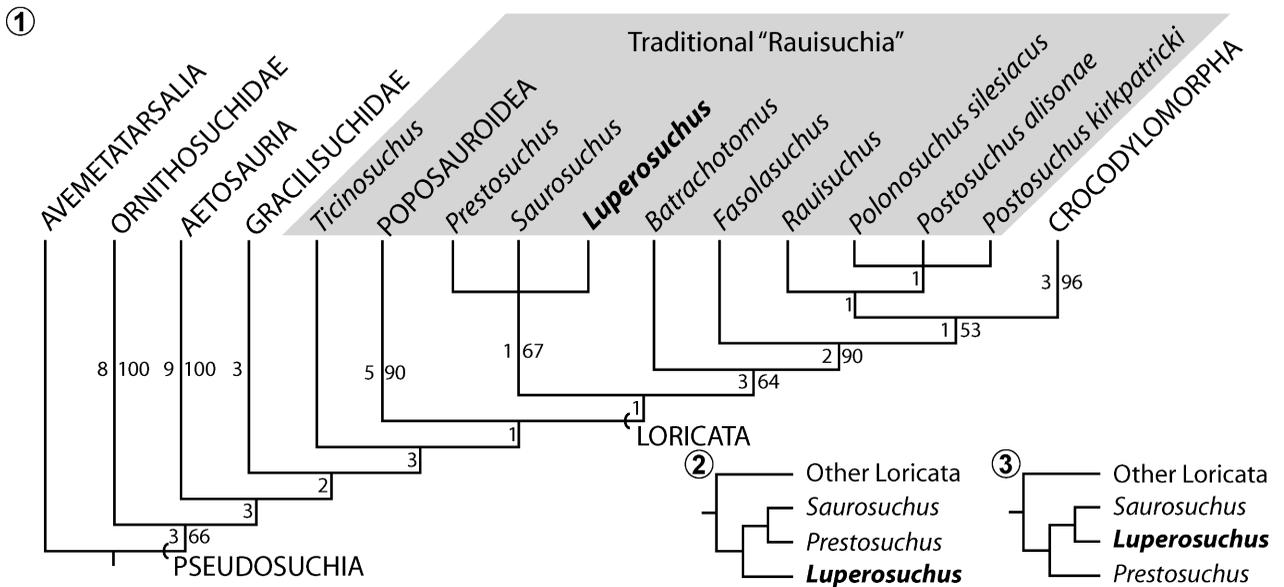**Figure 7.** Inferred phylogenetic relationships of ***Luperosuchus fractus*** among Archosauria. **1,** strict consensus of 180 MPTs (tree length= 1332, Consistency Index= 0.364, Retention Index= 0.768) and (**2–3**) two possible positions of ***Luperosuchus fractus*** among early loricatans. Major clades of archosaurs collapsed, but relationships within those clades identical to Nesbitt (2011).

tra as in *Pr. chiniquensis* (UFRGS 0156-T), *S. galilei* (PVSJ 32), and *Po. kirkpatricki* (TTU-P9000).

Referred specimens

A number of specimens have previously been referred to *Luperosuchus fractus* (Romer, 1971c; Desojo and Arcucci, 2009). A much smaller partial skull (PULR 057) with overlapping bones with the holotype (premaxilla, maxilla, nasal, frontals, and postorbital) represents the most complete non-type specimen assigned to *L. fractus* and the differences in morphology between this specimen and the holotype were considered ontogenetic variation (Desojo and Arcucci, 2009). Here, based on the additional material identified for the holotype and a thorough comparative description with modified interpretations, we suggest that the differences between PULR 057 and the holotype of *L. fractus* are taxonomic instead of ontogenetic variation. For example, following Romer (1971c), we find that the posterodorsal process of the premaxilla in the holotype is autapomorphically long and terminates well posterior of the external naris whereas the same process in PULR 57 is short and terminates well anterior to the external naris. Moreover, the posterodorsal process of the premaxilla seems to be loosely articulated

with the maxilla (see discussion below) in the holotype whereas the same process in PULR 57 is securely attached to the maxilla through a much tighter fitting articulation surface. The new fragment of the facial portion of the maxilla of the holotype bears rugosity on the lateral surface whereas the homologous region in PULR 57 is flat and smooth. Additionally, this new fragment of the lateral surface of the maxilla indicates that the maxilla was relatively much more expanded dorsoventrally compared to PULR 57 (Fig.5; proportionally three times higher). Also, concerning the comparative morphology of the maxilla, the anterior extent of the antorbital fenestra (anterodorsal margin versus the ventral margin) has a more acute angle in the holotype compared to that of the PULR 57. Finally, the dorsolateral portion of the postorbital of the holotype bears a robust knob that is absent in PULR 57. A redescription and interpretation of PULR 57 will be carried out by one of the authors and collaborators (JBD).

Postcranial elements have also been referred to *L. fractus*. Desojo and Arcucci (2009) correctly pointed out that the osteoderms (MCZ 4076) tentatively assigned to *L. fractus* were referred to *Tarjadia ruthae* by Arcucci and Marsicano (1998). Therefore, it is not known if *L. fractus* possessed os-

teoderms. Lastly, Ricqlès *et al.* (2008) described histological sections of a limb bone of *L. fractus* recorded as MCZ 4077. Unfortunately, the holotype is known only from the skull and now and a portion of the atlas, so it is unclear what Ricqlès *et al.* (2008) sectioned and interpreted (Scheyer and Desojo, 2011; Nesbitt *et al.*, 2013a). Thus, the growth pattern of *L. fractus* is currently unknown.

Extra slit-like openings in loricatans

The cranial openings between the nasals, maxillae, and premaxillae of loricatans (formerly 'rauisuchians') have garnered much attention following the descriptions of *Luperosuchus fractus* and *Saurosuchus galilei* (Benton and Clark, 1988; Parrish, 1993; Juul, 1994; Gower, 2000; Desojo and Arcucci, 2009; Brusatte *et al.*, 2010; Nesbitt, 2011; de França *et al.*, 2013; Roberto da Silva *et al.*, 2016). These openings occur as a "narrow slit" (*sensu* Romer, 1971c) between the premaxilla and the maxilla as in *L. fractus* and *S. galilei* or as a subnarial fenestra or foramen as in *Batrachotomus kupferzellensis* or *Postosuchus kirkpatricki* (Gower, 2000). Questions on the homology of these openings among these taxa remain largely unanswered (Gower, 2000; Nesbitt, 2011), but a new study examining the distribution of these features within pseudosuchians hypothesizes that they may be homologous across paracrocodylomorphs (Roberto da Silva *et al.*, 2016). Even more frustrating is that these openings have been named differently across the literature (slit-like opening of Romer, 1971c compared to "accessory antorbital fenestra" (*sensu* Sill, 1974); subnarial foramen versus subnarial fenestra and some of these terms such as "accessory antorbital fenestra" are used to describe openings far outside of Archosauria (see Ezcurra, 2016). However, progress is being made by the description of these features more carefully (Roberto da Silva *et al.*, 2016) and with new phylogenetic analyses (Brusatte *et al.*,

2010; Nesbitt, 2011; Butler *et al.*, 2014). Beyond the questions of homology of the openings in for example *Saurosuchus galilei* (slit-like, extensive, more dorsal) and *Batrachotomus kupferzellensis* (subcircular, small, more ventral), which is beyond the scope of this paper, we carefully examined the taxa with slit-like openings of early loricatans centered on the new observations based on *L. fractus*. The presence of a slit-like gap between the posterodorsal process of the premaxilla and the maxilla in *S. galilei*, *L. fractus*, and *Decuriasuchus quartacolonia* (Fig. 8) has been discussed in the literature as either a real feature or an artifact of preservation without any clear conclusion being reached (Romer, 1971c; Gower, 2000; Nesbitt, 2011; de França *et al.*, 2013). Although all of the specimens of these taxa have some kind of slit-like gap between the maxilla and the premaxilla, we are not convinced this is a structure that was present in life and we suggest that it could be the result of deformation during taphonomic processes. We present our argument below based on the morphology and articulation of the elements using and documenting the variable articulation configuration of paracrocodylomorphs known from more than one specimen in comparison with that of *L. fractus*.

The long gap between the posterodorsal process of the premaxilla and the maxilla of *Luperosuchus fractus* appears also to be the result of slight disarticulation (see above) and this appears to be the case in *Saurosuchus galilei* given that there are two well preserved examples (PVL 2062 and PVSJ 32). The specimens of *S. galilei* preserve differences in the length and shape of the opening between when compared to each other and even when right and left sides of a single specimen are compared (Fig. 8.2, 5–6). In the holotype of *S. galilei* (PVL 2062), the slit on the left and right sides extends to the posterior extent of the external naris whereas the slit fails to reach the posterior extent of the external naris in the referred skull (PVSJ 32). In comparison

Figure 8. The anterior portion of the skull of loricatan archosaurs highlighting the contacts among the premaxilla, maxilla, and nasal. Photograph of *Luperosuchus fractus* (**PULR** 4) in **1,** left lateral view. Photographs of the holotype of *Saurosuchus galilei* (**PVL** 2062) in **2,** right lateral view. Photograph of a referred specimen of *Prestosuchus chiniquensis* (**UFRGS-PV**-156T) in **3,** left lateral and **4,** right lateral views. Photographs of a referred specimen of *Saurosuchus galilei* (**PVSJ** 32) in **5,** left lateral and **6,** right lateral views. Photographs of the holotype of *Decuriasuchus quartacolonia* (**MCN-PV**10.105a) in **7,** left lateral view and a referred specimen (**MCN-PV**10.105d) in **8,** right lateral view. Abbreviations: **af,** antorbital fenestra; **en,** endonarina; **l.,** left; **mx,** maxilla; **na,** nasal; **pmx,** premaxilla; **r.,** right. Scale bars= 5 cm. Photographs **7–8** modified from de França *et al.* (2013).
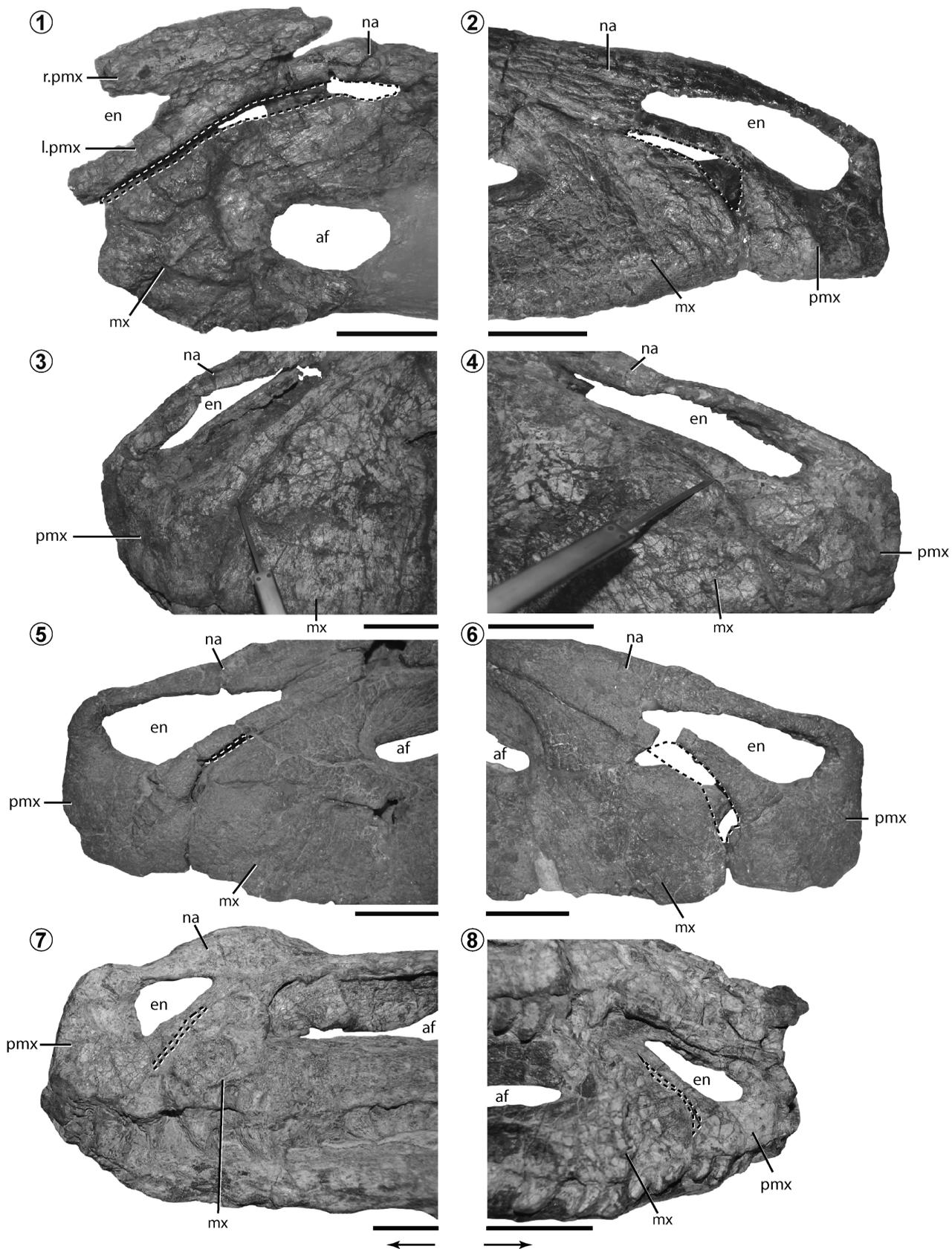
across the left and right sides, the left side of PVSJ 32 has a gap between the premaxilla and maxilla, whereas there is little or no gap at all on the right side (Fig. 8.5–6). There is a clear break on the posterodorsal process of the premaxilla on the right side; the articulated posterior portion fits precisely with the dorsal border of the maxilla. The left side of PVSJ 32 is better preserved and does have a clear slit between the elements. However, the morphology of the ventral margin of the posterodorsal process of the maxilla and the anterodorsal margin of the maxilla are complementary as they are on the right side, indicating that the left side elements were disjointed after death.

This discrepancy between shape and length of the slit from the left and right side is also present in other paracrocodylomorphs. The skulls of *Decuriasuchus quartacolonia* also show variability in the length and width of the slit-like opening. For example, the holotype skull (MCN-PV10.105a; Fig. 8.7–8) has a very narrow slit (de França *et al.*, 2013: fig. 4a, b, d), the slit is much wider and oval at a similar horizontal plane as the external naris in MCN-PV10.105c (de França *et al.*, 2013: fig. 3), whereas the opening of MCN-PV10.105d (de França *et al.*, 2013: fig. 4e–g) is widest ventral to the external naris and more slit-like dorsally. A referred skull of *Prestosuchus chiniquensis* (UFRGS-PV-156T) possesses a similar configuration between the maxilla and the premaxilla as *Luperosuchus fractus*, *D. quartacolonia* and *Saurosuchus galilei*. The specimen has a small slit on the right side (apparent because of the presence of matrix), but not on the left side (Fig. 8.3–4). In support of this feature being an artifact of taphonomy, a biomechanical model of the skull of a partially published specimen referred to *Pr. chiniquensis* (UFRGS-PV-0629-T; Liparini and Schultz, 2013), indicates that there was likely movement between the premaxilla and the maxilla along the area that forms the slit (Liparini, 2008). Furthermore, a gap opens with little movement in sagittal and coronal planes between the premaxilla relative to maxilla (Liparini, 2008). Additionally, a newly referred and exceptionally preserved specimen of *Pr. chiniquensis* (ULBRA-PVT-281) lacks a slit between premaxilla and maxilla altogether, but has a clearly defined foramen that opens anteriorly into a groove (Roberto da Silva *et al.*, 2016). Thus this further demonstrates high variability in the preserved morphology of this region of the skulls of paracrocodylomorphs.

The asymmetry of these taphonomy-influenced features is difficult to explain but could be related to the anatomy of the premaxilla and maxilla and the geometry of their articulation with each other. In *Saurosuchus galilei*, *Luperosuchus fractus,* and *Decuriasuchus quartacolonia*, the morphology of the posterior process of the premaxilla and the corresponding anterodorsal edge of the maxilla is very similar in having a complementary convex-concave relationship between the two surfaces. This joint is loose and does not have any interdigitation between the articulation surfaces in any of the taxa. Moreover, the long length and weak joint of the posterodorsal process of the premaxilla also could have resulted in the process been easily disarticulated during any pressures from the fossilization process.

In our view, these slit-like openings in *Decuriasuchus quartacolonia*, *Prestosuchus chiniquensis*, *Luperosuchus fractus*, and *Saurosuchus galilei*, are not anatomical features in themselves, but are the result of post-mortem taphonomic processes, and the repeated, but variable, shapes of these openings are the result of a weak connection between the maxilla and premaxilla. This weak connection could be a possible synapomorphy of these taxa. Regardless whether future authors accept this hypothesis or not, the slit-like openings of the aforementioned taxa should not be homologized with the subnarial foramina of rauisuchids or other closely related taxa without careful consideration.

ACKNOWLEDGEMENTS

REFERENCES

Alcober, O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). *Journal of Vertebrate Paleontology* 20: 302–316.

Arcucci, A.B. 1998. New information about dinosaur precursors from the Triassic Los Chanares fauna, La Rioja, Argentina. *Journal of African Earth Sciences* 27: 9–10.

Arcucci, A.B., and Marsicano, C.A. 1998. A distinctive new archosaur from the Middle Triassic (Los Chañares Formation) of Argentina. *Journal of Vertebrate Paleontology* 18: 228–232.

von Baczko, M.B., and Desojo, J.B. 2016. Cranial anatomy and palaeoneurology of the archosaur *Riojasuchus tenuisceps* from the Los Colorados Formation, La Rioja, Argentina. *PLoS ONE* 11: e0148575.

Bailleul, A.M., and Horner, J.R. 2016. Comparative histology of some craniofacial sutures and skull-base synchondroses in non-avian dinosaurs and their extant phylogenetic bracket. *Journal of Anatomy* doi:10.1111/joa.12471.

Bailleul, A.M., Sconnella, J.B., Horner, J.R., and Evans, D.C. 2016. Fusion patterns in the skulls of modern archosaurs reveal that sutures are ambiguous maturity indicators for the Dinosauria. *PLoS ONE* 11: e0147687.

Benton, M.J. 1986. The Late Triassic reptile *Teratosaurus* a Rauisuchian not a dinosaur. *Palaeontology* 29: 293–301.

Benton, M.J., and Clark, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: M.J. Benton (Ed.), *The Phylogeny and Classification of the Tetrapods. Vol 1: Amphibians and Reptiles*. Oxford, Clarendon Press, p. 295–338.

Benton, M.J., and Walker, A.D. 2002. *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Zoological Journal of the Linnean Society* 136: 25–47.

Bittencourt, J.S., Arcucci, A.B., Marsicano, C.A., and Langer, M.C. 2014. Osteology of the Middle Triassic archosaur *Lewisuchus admixtus* Romer (Chañares Formation, Argentina), its inclusivity, and relationships amongst early dinosauromorphs. *Journal of Systematic Palaeontology* 13: 189–219.

Bonaparte, J.F. 1972. Los tetrapodos del sector superior de la Formacion Los Colorados, La Rioja, Argentina. (Triásico Superior) I parte. *Opera Lilloana* 22: 1–183.

Bonaparte, J.F. 1981. Descripción de *Fasolasuchus tenax* y su significado en la sistemática y evolución de los Thecodontia. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'* 3: 55–101.

Brusatte, S.L., Benton, M.J., Desojo, J.B., and Langer, M.C. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* 8: 3–47.

Butler, R.B., Sullivan, C., Ezcurra, M.D., Liu, J., Lecuona, A., and Sookias, R.B. 2014. New clade of enigmatic early archosaurs yields insights into early pseudosuchian phylogeny and the biogeography of the archosaur radiation. *BMC Evolutionary Biology* 14: 1–16.

Chatterjee, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. *Philosophical Transactions of the Royal Society of London B* 309: 395–460.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society (New Series)* 14: 1–252.

De França, M.a.G., Langer, M.C., and Ferigolo, J. 2013. The skull anatomy of *Decuriasuchus quartacolonia* (Pseudosuchia: Suchia: Loricata) from the middle Triassic of Brazil. In: S.J. Nesbitt, J.B. Desojo, and R.B. Irmis (Eds.), *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin.* London, Geological Society, London, Special Publications, p. 469–501.

Desojo, J.B., and Arcucci, A.B. 2009. New material of *Luperosuchus fractus* (Archosauria: Crurotarsi) from the Middle Triassic of Argentina: the earliest known South American rauisuchian. *Journal of Vertebrate Paleontology* 29: 1311–1315.

Desojo, J.B., Ezcurra, M.D., Fiorelli, L.E., Martinelli, A., Taborda, J.R.A., von Bazcko, M.B., Hechenleitner, M., Ezpeleta, M., Trotteyn, M.J., and Gouric-Cavalli, S. 2015. New insights into vertebrate

assemblages from the lower Chañares Formation (Ladinian– earliest Carnian, Ischigualasto–Villa Unión Basin), northwest Argentina. *13th Annual Meeting of the European Association of Vertebrate Palaeontologists* (Opole), *Abstract book*: 108.

Ezcurra, M.D. 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* 4: e1778.

Fiorelli, L.F., Ezcurra, M.D., Hechenleitner, E.M., Argañaraz, E., Taborda, J.R.A., Trotteyn, M.J., von Baczko, M.B., and Desojo, J.B. 2013. The oldest known communal latrines provide evidence of gregarism in Triassic megaherbivores. *Scientific reports* 3: 1–7.

Galton, P.M. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. *Paläontologische Zeitschrift* 51: 234–245.

Gauthier, J., and Padian, K. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: M.K. Hecht, J.H. Ostrom, G. Viohl, and P. Wellnhofer (Eds.), *The Beginning of Birds.* Freunde des Jura Museums, Eichstatt, p. 185–197.

Gower, D.J. 1999. The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttgarter Beitraege zur Naturkunde Serie B (Geologie und Palaeontologie)* 280: 1–49.

Gower, D.J. 2000. Rauisuchian archosaurs (Reptilia, Diapsida): An overview. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 218: 447–488.

Gower, D.J. 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): Evidence from the rauisuchian *Batrachotomus kupferzellensis. Zoological Journal of the Linnean Society* 136: 49–76.

Gower, D.J. 2003. Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. *Annals of the South African Museum* 110: 1–84.

Gower, D.J., and Nesbitt, S.J. 2006. The braincase of *Arizonasaurus babbitti*- further evidence of the non-monophyly of Rauisuchia. *Journal of Vertebrate Paleontology* 26: 79–87.

Jensen, J.A. 2001. *The Road to Chilecito*. Launceston, Tasmania: Queen Victoria Museum and Art Gallery.184 p.

Juul, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana* 31: 1–38.

Krebs, B. 1976. Pseudosuchia. In: O. Kuhn (Ed.), *Handbuch Palaoherpetology.* Stuttgart, Gustav Fischer Verlag, p. 40–98.

Laurenti, J.N. 1768. *Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum.* J.T.N. de Trattnern, Vienna, 214 p.

Lautenschlager, S., and Rauhut, O.W.M. 2015. Osteology of *Rauisuchus tiradentes* from the Late Triassic (Carnian) Santa Maria Formation of Brazil, and its implications for rauisuchid anatomy and phylogeny. *Zoological Journal of the Linnean Society* 173: 55–91.

Lessner, E.J., Stocker, M.R., Smith, N.D., Turner, A.H., Irmis, R.B., and Nesbitt, S.J. 2016. A new taxon of rauisuchid (Archosauria, Pseudosuchia) from the Upper Triassic of New Mexico increases the diversity and temporal range of the clade. *PeerJ* 4: e2336.

Li, C., Wu, X.-C., Cheng, Y.-N., Sato, T., and Wang, L. 2006. An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften* 93: 200–206.

Li, C., Wu, X.-C., Zhao, L.-J., Sato, T., and Wang, L.-T. 2012. A new archosaur (Diapsida, Archosauriformes) from the marine Triassic of China. *Journal of Vertebrate Paleontology* 35: 1064–1081.

Liparini, A. 2008. [*Estudo da biomecânica craniana de um rauissuquídeo a partir de tomografias computadorizadas e técnicas de ima-*

gens digitais em 3 dimensões. Universidade Federal do Rio Grande do Sul, Tese de maestrado, Instituto de Geociências, Universidade Federal do Rio Grande do Sul. 124 p. Unpublished.].

Liparini, A., and Schultz, C.L. 2013. A reconstruction of the thigh musculature of the extinct pseudosuchian Prestosuchus chiniquensis from the Dinodontosaurus Assemblage Zone (Middle Triassic Epoch), Santa Maria 1 Sequence, southern Brazil. In: S.J. Nesbitt, J.B. Desojo, and R.B. Irmis (Eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. London Geological Society, London, Special Publications, p. 441–468.

Marsicano, C.A., Irmis, R.B., Mancuso, A.C., Mundil, R., and Chemale, F. 2016. The precise temporal calibration of dinosaur origins. Proceedings of the National Academy of Sciences 113: 509–513.

Mastrantonio, B.M., Schultz, C.L., Desojo, J.B., and Garcia, J.B. 2013. The braincase of Prestosuchus chiniquensis (Archosauria: Suchia). In: S.J. Nesbitt, J.B. Desojo, and R.B. Irmis (Eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. London Geological Society, London, Special Publications, p. 425–440.

Merrem, B. 1820. Versuch eines Systems der Amphibien. Tentamen systematis amphibiorum. Iohann Christian Krieger, Marburg, 412 p.

Nesbitt, S.J. 2005. The osteology of the Middle Triassic pseudosuchian archosaur Arizonasaurus babbitti. Historical Biology 17: 19–47.

Nesbitt, S.J. 2007. The anatomy of Effigia okeeffeae (Archosauria, Suchia), theropod convergence, and the distribution of related taxa. Bulletin of the American Museum of Natural History 302: 1–84.

Nesbitt, S.J. 2011. The early evolution of Archosauria: relationships and the origin of major clades. Bulletin of the American Museum of Natural History 352: 1–292.

Nesbitt, S.J., and Norell, M.A. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). Proceedings of the Royal Society of London B 273: 1045–1048.

Nesbitt, S.J., Irmis, R.B., Lucas, S.G., and Hunt, A.P. 2005. A giant crocodylomorph from the upper Triassic of New Mexico. Palaeontologische Zeitschrift 79: 471–478.

Nesbitt, S.J., Sidor, C.A., Irmis, R.B., Angielczyk, K.D., Smith, R.M.H., and Tsuji, L.A. 2010. Ecologically distinct dinosaurian sister-group shows early diversification of Ornithodira. Nature 464: 95–98.

Nesbitt, S.J., Brusatte, S.L., Desojo, J.B., Liparini, A., Gower, D.J., França, M.a.G.D., and Weinbaum, J.C. 2013a. "Rauisuchia". In: S.J. Nesbitt, J.B. Desojo, and R.B. Irmis (Eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. London Geological Society, London, Special Publications, p. 241–274.

Nesbitt, S.J., Turner, A.H., and Weinbaum, J.C. 2013b. A survey of skeletal elements in the orbit of Pseudosuchia and the origin of the crocodylian palpebral. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103: 365–381.

Novas, F.E. 1996. Dinosaur monophyly. Journal of Vertebrate Paleontology 16: 723–741.

Parrish, J.M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. Journal of Vertebrate Paleontology 13: 287–308.

Parker, W.G., and Nesbitt, S.J. 2013. Cranial remains of Poposaurus gracilis (Pseudosuchia: Poposauroidea) from the Upper Triassic, the distribution of the taxon and its implications for poposauroid evolution. In: S.J. Nesbitt, J.B. Desojo, and R.B. Irmis (Eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. London Geological Society, London, Special Publications, p. 503–523.

Ricqlés, A., Padian, K., Knoll, F., and Horner, J.R. 2008. On the origin of high growth rates in archosaurs and their ancient relatives: Complementary histological studies on Triassic archosauriforms and the problem of a "phylogenetic signal" in bone histology. Annales de Paléontologie 94: 57–76.

Roberto Da Silva, L., França, M.A., Cabreira, S.F., Müller, R.T., and Dias Da Silva, S. 2016. On the presence of the subnarial foramen in Prestosuchus chiniquensis (Pseudosuchia: Loricata) with remarks on its phylogenetic distribution. Anais da Academia Brasileira de Ciências 88: 1309–1323.

Rogers, R.R., Arcucci, A.B., Abdala, F., Sereno, P.C., Forster, C.A., and May, C.L. 2001. Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), Northwestern Argentina: spectacular preservation in volcanogenic concretions. Palaios 16: 461–481.

Romer, A.S. 1971a. The Chañares (Argentina) Triassic reptile fauna. XI. Two new long snouted thecodonts, Chanaresuchus and Gualosuchus. Breviora 379: 1–22.

Romer, A.S. 1971b. The Chañares (Argentina) Triassic reptile fauna. X. Two new but incompletely known long-limbed pseudosuchians. Breviora 378: 1–10.

Romer, A.S. 1971c. The Chañares (Argentina) Triassic reptile fauna. VIII. A fragmentary skull of a large thecodont, Luperosuchus fractus. Breviora 373: 1–8.

Romer, A.S. 1972a. The Chañares (Argentina) Triassic reptile fauna. XII. The postcranial skeleton of the thecodont Chanaresuchus. Breviora 385: 1–21.

Romer, A.S. 1972b. The Chañares (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, Gracilisuchus stipanicicorum, gen. et sp. nov. Breviora 389: 1–24.

Romer, A.S. 1972c. The Chañares (Argentina) Triassic reptile fauna. XV. Further remains of the thecodonts Lagerpeton and Lagosuchus. Breviora 394: 1–7.

Romer, A.S. 1972d. The Chañares (Argentina) Triassic reptile fauna. XIV. Lewisuchus admixtus, gen. et sp. nov., a further thecodont from the Chañares beds. Breviora 390: 1–13.

Romer, A.S. 1972e. The Chañares (Argentina) Triassic reptile fauna. XVI. Thecodont classification. Breviora 395: 1–24.

Romer, A.S., and Jensen, J.A. 1966. The Chañares (Argentina) Triassic reptile fauna. II. Sketch of the geology of the Rio Chañares-Rio Gualo region. Breviora 252: 1–20.

Scheyer, T.M., and Desojo, J.B. 2011. Palaeohistology and external microanatomy of rauisuchian osteoderms (Archosauria: Pseudosuchia). Palaeontology 54: 1289–1302.

Sereno, P.C., and Arcucci, A.B. 1994a. Dinosaurian precursors from the Middle Triassic of Argentina: Lagerpeton chanarensis. Journal of Vertebrate Paleontology 13: 385–399.

Sereno, P.C., and Arcucci, A.B. 1994b. Dinosaurian precursors from the Middle Triassic of Argentina: Marasuchus lilloensis, gen. nov. Journal of Vertebrate Paleontology 14: 53–73.

Sill, W.D. 1974. The anatomy of Saurosuchus galilei and the relationships of the rauisuchid thecodonts. Bulletin of the Museum of Comparative Zoology 146: 317–362.

Sulej, T. 2005. A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. Journal of Vertebrate Paleontology 25: 78–86.

Swofford, D.L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony. Sinauer Associates, Inc., Sunderland, Massachusetts.

Trotteyn, M.J., Arcucci, A.B., and Raugust, T. 2013. Proterochampsia: an endemic archosauriform clade from South America. In: S.J. Nesbitt, J.B. Desojo, and R.B. Irmis (Eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. London Geological Society, London, Special Publications, p. 59–90.

Trotteyn, M.J., Desojo, J.B., and Alcober, O. 2011. Nuevo material postcraneano de *Saurosuchus galilei* Reig (Archosauria: Cruro-tarsi) del Triasico Superior del centro-oeste de Argentina. *Ameghiniana* 48: 605–620.

Walker, A.D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus*, and their allies. *Philosophical Transactions of the Royal Society of London* 244: 103–204.

Weinbaum, J.C. 2011. The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. *PaleoBios* 30: 18–44.

Wu, X.-C., and Russell, A.P. 2001. Redescription of *Turfanosuchus dabanensis* (Archosauriformes) and new information on its phylogenetic relationships. *Journal of Vertebrate Paleontology* 21: 40–50.

Zanno, L.E., Drymala, S., Nesbitt, S.J., and Schneider, V.P. 2015. Early crocodylomorph increases top tier predator diversity during rise of dinosaurs. *Scientific reports* 5: 1–6.

Phylogenetic scores and modification of the Butler *et al.* (2014) dataset

Luperosuchus fractus: (character state) 2-1, 3-0, 4-0, 5-0, 14-0, 25-0, 26-0, 28-0, 29-1, 30-0, 33-1, 34-0, 35-0, 36-0, 37-1, 38-0, 40-0, 41-0, 42-1, 43-1, 44-0, 49-0, 51-0, 53-0, 56-0, 58-0, 65-0, 66-0, 67-0, 73-0, 75-2, 136-1, 137-2, 139-0, 140-0, 142-1, 143-0, 144-0, 147-1, 148-1, 149-1, 168-1, 174-1, 175-1, 414-1, 415-1

Saurosuchus galilei: 29-1

Prestosuchus chiniquensis: 147-1, 149-1

Additional characters

414. Nasal, position of anterior portion in lateral view: below or at same level as skull roof (0); elevated above skull roof, giving the skull a 'Roman nose' appearance (1). Brusatte *et al.* (2010): character 25.

This character focuses on the anterior portion of the nasal dorsal to the external naris. In most early archosaurs the nasal anteroventrally slopes in this region and this character is clearly present in *Diandongosuchus fuyuanensis* (Li *et al.*, 2012), aetosaurs (*e.g.*, *Stagonolepis robertsoni*, Walker, 1961), *Erpetosuchus granti* (Benton and Walker, 2002), *Effigia okeeffeae* (Nesbitt and Norell, 2006; Nesbitt, 2007), *Postosuchus kirkpatricki* (Weinbaum, 2011), *Saurosuchus galilei* (PVL 2062; PVSJ 32) and *Fasolasuchus tenax* (PVL 3850). The nasals of *Batrachotomus kupferzellensis* (SMNS 80260; Gower, 1999), *Decuriasuchus quartacolonia* (de França *et al.*, 2013), *Qianosuchus mixtus* (IVPP V14300), and *Prestosuchus*

chiniquensis (UFRGS-PV-156T) also have a 'Roman nose' characterized by a convex dorsal arching dorsal to the anterior margin of the antorbital fossa and this character state was used to support a close relationship between *Batrachotomus kupferzellensis* and *Prestosuchus chiniquensis* (Brusatte *et al.*, 2010: character 25). This area of the nasal is easily distorted as evidenced by deformation in a referred specimen of *Prestosuchus chiniquensis* (UFRGS-PV-156T), but it is clear that the nasals are convex and raided above the posterior half of the nasals in *Prestosuchus chiniquensis* (UFRGS-PV-156T), *Batrachotomus kupferzellensis* (SMNS 80260), *Luperosuchus fractus* (PULR 04), and the ornithosuchid *Riojasuchus tenuisceps* and, thus these taxa are scored as 1. However, we note that the nasal of *Batrachotomus kupferzellensis* (SMNS 80260) is more laterally convex than the mediolaterally compressed 'Roman nose' of *Luperosuchus fractus* and *Prestosuchus chiniquensis*. Additionally, the two skull of the ornithosuchid *Riojasuchus tenuisceps* (PVL 3027, 3028; Bonaparte, 1972; Baczko and Desojo, 2016) have a 'Roman nose' in the homologous position, but this structure is much wider and bulbous than in *Luperosuchus fractus*.

Scored as (0): *Mesosuchus browni, Prolacerta broomi, Proterosuchus, Erythrosuchus africanus, Vancleavea campi, Chanaresuchus bonapartei, Tropidosuchus romeri, Euparkeria capensis, Gracilisuchus stipanicicorum, Turfanosuchus dabanensis, Ornithosuchus longidens, Revueltosaurus callenderi, Stagonolepis robertsoni, Aetosaurusferratus, Longosuchusmeadei, Xilousuchussapingensis, Lotosaurusadentus, Effigia okeeffeae, Fasolasuchus tenax, Rauisuchus tiradentes, Polonosuchus silesiacus, Postosuchus kirkpatricki, Dromicosuchus grallator, Hesperosuchus agilis, Dibothrosuchus elaphros, Litargosuchus leptorhynchus, Orthosuchus stormbergi, Alligator mississippiensis, Protosuchus haughtoni, Protosuchus richardsoni, Eudimorphodon ranzii, Dimorphodon macronyx, Heterodontosaurus tucki, Lesothosaurus diagnosticus, Herrerasaurus ischigualastensis, Tawahallae, Coelophysisbauri, Allosaurus fragilis, Velociraptor mongoliensis*.

Scored as (1): *Riojasuchus tenuisceps, Qianosuchus mixtus*, UFRGS 0156 T, Combined *Prestosuchus, Luperosuchus fractus, Saurosuchus galilei, Batrachotomus kuperferzellensis, Eoraptor lunensis, Plateosaurus engelhardti*.

All other taxa scored as ?

415. Premaxilla, posterodorsal (= maxillary, = subnarial)

process, termination: anterior to or at the posterior end of the external naris (0); posterior of the posterior extension of the external naris (1).New.

In most early archosaurs, the posterodorsal process of the premaxilla fails to extend posterior of the posterior end of the external naris (state 0), no matter the length of the process relative to the anteroposterior length of the pre-maxilla. In pseudosuchians, state (0) appears common and this state is present in a referred specimen of *Prestosuchus chiniquensis* (UFRGS–PV–156T), *Postosuchus kirkpatricki* (Chatterjee, 1985; Weinbaum, 2011), and *Batrachotomus kupferzellensis* (Gower, 1999), aetosaurs and other pseudo-suchians (*e.g., Riojasuchus tenuiceps,* PVL 3827). The process just reaches the posterior extent of the external naris in some taxa, but fails to extend posterior to the open-ing in *Decuriasuchus quartacolonia* (de França *et al.*, 2013) and *Fasolasuchus* (PVL 3850; Bonaparte, 1981) so these taxa are scored as (0). In contrast the posterodorsal process of the premaxilla of *Luperosuchus fractus* (PULR 04) and *Saurosuchus galilei* (PVL 2062; PVSJ 32) is very long, and ex-tends posterior to the external naris. Furthermore, the process in *Luperosuchus fractus* is the longest of all other early loricatans. Among early crocodylomorphs, *Redondave-nator quayi* (Nesbitt *et al.*, 2005) also possesses a long pos-terodorsal process of the premaxilla (state 1).

Scored as (0): *Mesosuchus browni, Prolacerta broomi, Pro-terosuchus, Erythrosuchus africanus, Vancleavea campi, Chanaresuchus bonapartei, Tropidosuchus romeri, Gracilisuchus stipanicicorum, Turfanosuchus dabanensis, Ornithosuchus longidens, Riojasuchus tenuiceps, Stagonolepis robertsoni, Ae-tosaurus ferratus, Longosuchus meadei, Qianosuchus mixtus, Xilousuchus sapingensis, Lotosaurus adentus, Effigia okeeffeae, Shuvosaurus inexpectatus,* UFRGS 0156 T, Combined *Presto-suchus, Batrachotomus kuperferzellensis, Fasolasuchus tenax, Rauisuchus tiradentes, Polonosuchus silesiacus, Postosuchus kirkpatricki, Eudimorphodon ranzii, Dimorphodon macronyx, Plateosaurus engelhardti, Coelophysis bauri, Dilophosaurus wetherilli, Allosaurus fragilis, Velociraptor mongoliensis*

Scored as (1): *Euparkeria capensis, Revueltosaurus callen-deri, Luperosuchus fractus, Saurosuchus galilei, Dromicosuchus grallator, Hesperosuchus agilis, Dibothrosuchus elaphros, Sphenosuchus acutus, Kayentasuchus walkeri, Orthosuchus stormbergi, Alligator mississippiensis, Protosuchus haughtoni, Protosuchus richardsoni, Heterodontosaurus tucki, Lesothosaurus diagnosticus, Herrerasaurus ischigualastensis, Eoraptor lunensis.*

All other taxa scored as ?