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SHORT COMMUNICATION

NEW MATERIAL OF *LUPEROSUCHUS FRACTUS* (ARCHOSAURIA: CRUROTARSI) FROM THE MIDDLE TRIASSIC OF ARGENTINA: THE EARLIEST KNOWN SOUTH AMERICAN 'RAUISUCHIAN'

JULIA B. DESOJO[*,1] and ANDREA B. ARCUCCI[2]; [1]Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Angel Gallardo 470, C1405DRJ, Buenos Aires, Argentina, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), julideso@macn.gov.ar; [2]Área de Zoología, Universidad Nacional de San Luis, Argentina, arcucci@unsl.edu.ar

'Rauisuchian' archosaurs were some of the largest terrestrial carnivores during the Middle and Late Triassic in Europe, North Africa, Asia, India, and the Americas (Gower, 2000). Despite their worldwide distribution, 'rauisuchian' evolutionary history is poorly understood and their taxonomy remains problematic because many taxa were erected on fragmentary, undiagnostic remains, and some characters are convergent with other archosaurs (Nesbitt and Norell, 2006; Nesbitt, 2007). The earliest undoubted 'rauisuchians' are Anisian in age and include *Bromsgroveia* Galton, 1985 from England, *Arizonasaurus* Welles, 1947 from the U.S.A., and *Yarasuchus* Sen, 2005 from India. Several Lower Triassic possible 'rauisuchians' from Russia would represent the first record of the group if their affinities were confirmed (Gower and Sennikov, 2000). In the Ladinian, there is an increase in taxonomic diversity of 'rauisuchians,' which are then well represented in Europe, South America, and Africa (e.g., Krebs, 1965; Gower, 1999). The 'rauisuchian' record in South America is particularly diverse ranging from the Ladinian to the Norian, and includes well-preserved, complete specimens of *Prestosuchus* Huene, 1938 (Brazil), *Luperosuchus* Romer, 1971, *Saurosuchus* Reig, 1959, and *Fasolasuchus* Bonaparte, 1981 (Argentina).

Luperosuchus fractus from the Los Chañares Formation, in the Ischigualasto–Villa Unión Basin of northwestern Argentina, is the largest animal in the Chañares tetrapod assemblage (Bonaparte, 1997; Rogers et al., 2001), and the earliest 'rauisuchian' known from South America. The age of the Chañares Formation is constrained by a Ladinian–Carnian plant and pollen association from the overlying Los Rastros Formation (Stipanicic and Marsicano, 2002), and vertebrate biostratigraphic correlation using dicynodont and cynodont synapsids (e.g., Bonaparte, 1997; Schultz et al., 2000; Langer et al., 2007). Gonzalez and Toselli (1975) and Valencio et al. (1975) reported a K-Ar whole rock age of 224±5 Ma from the top of the Los Rastros Formation, but the quality and precision of these data is superseded by a Late Carnian $^{40}Ar/^{39}Ar$ age of 231.4±.3 Ma from low in the overlying Ischigualasto Formation (Rogers et al., 1993; re-calibrated by Furin et al., 2006). Taken together, these chrono- and biostratigraphic data indicate a Ladinian age for the Los Chañares Formation. This assemblage represents the best South American record of tetrapod evolution immediately prior to the Late Triassic diversification of dinosaurs, eucynodonts, and mammals (Rogers et al., 2001).

The type of *L. fractus* is an isolated find, and consists of a large incomplete skull of about 0.6 m in length. Romer (1971) doubtfully referred two osteoderms to *L. fractus* from the same locality; these specimens were not associated with the type material. These osteoderms were later assigned to *Tarjadia ruthae*, also known from the same locality (Arcucci and Marsicano, 1998). Here we describe new cranial material of *L. fractus*, collected by J. Bonaparte in the 1980s, which allows us to provide a new diagnosis of this taxon and to reevaluate some conflicting cranial characters of 'rauisuchian' archosaurs.

Institutional Abbreviations—**PULR**, Museo de Ciencias Naturales Universidad Nacional de La Rioja, La Rioja, Argentina; **PVSJ**, División Paleontología Vertebrados Museo de Ciencias Naturales de la Universidad Nacional de San Juan, San Juan, Argentina; **PVL**, Instituto Miguel Lillo, Tucumán, Argentina; **PVUFRGS**, Instituto de Geociências de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Anatomical Abbreviations—**aj**, articulation for jugal; **antc**, antorbital cavity; **arspmx**, articular surface for the premaxilla; **a.ptf**, postfrontal articulation; **de**, deep excavation; **dr**, dorsal ridge; **dvr**, dorsoventral ridge; **en**, external naris; **f**, frontal; **in**, internal naris; **j**, jugal; **l**, lacrimal; **m**, matrix; **mx**, maxilla; **mxintpl**, maxillary interdental plates; **n**, nasal; **nf**, nutritive foramina; **p**, parietal; **pld**, palatal depression; **plpmx**, palatal process of maxilla; **plppmx**, palatal process of premaxilla; **pmx**, premaxilla; **pmxintpl**, premaxillary interdental plates; **prf**, prefrontal; **ptf**, postfrontal; **po**, postorbital; **rn**, roman nose**; sf**, subnarial fenestra; **sq,** squamosal.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA sensu Gauthier, 1986
CRUROTARSI Sereno and Arcucci, 1990
RAUISUCHIA Huene, 1942
LUPEROSUCHUS FRACTUS Romer, 1971
(Figs. 1–4)

Hypodigm—PULR 04 (holotype), an incomplete skull roof; PULR 057 (referred material), a partial skull roof and palate (Figs. 2–4).

Horizon and Age—Los Chañares locality, Ischigualasto-Villa Unión Basin, La Rioja province, Argentina. Los Chañares Formation, Middle Triassic (Ladinian).

Revised Diagnosis—*Luperosuchus* differs from all crurotarsans in having an elongated subnarial fenestra between nasal and maxilla, a 'roman nose' formed by conjoined nasals that makes a sharp crest over the dorsal margin of the external nares, a deep excavation formed by the posterior margin of premaxilla and anterior of maxilla, and lower temporal fenestra with vertical anterior margin.

DESCRIPTION

The left maxilla, both premaxillae, and nasals of PULR 057 are articulated, as are the left frontal and postorbital, but the left lacrimal, and vomers are not articulated. However, the size, state of preservation, and close association suggest that all of the elements belong to the same individual. The new material allows us to present a reconstruction of the skull in lateral and dorsal views (Fig. 1).

*Corresponding author.

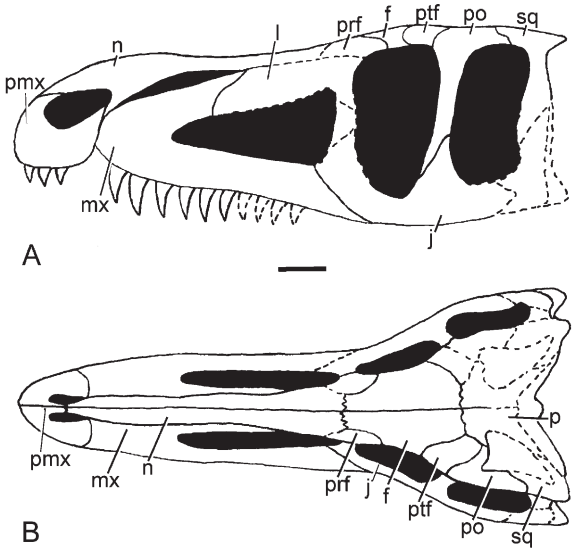


FIGURE 1. *Luperosuchus fractus* Romer, 1971. Reconstruction of skull based on PULR 04 (holotype) and PULR 057 (referred specimen). **A**, left lateral and **B**, dorsal views. Scale bar equals 5 cm.

Skull Roof—The premaxilla forms the anterior and ventral margins of the external naris and is rounded anteriorly and has a convex ventral margin. The ventral margin bears three small teeth that are separated medially by interdental plates. The sutures with the nasal are dorsally oriented; the posterior suture is longer than the anterior one. Posteriorly, the premaxilla has a short contact with the maxilla and does not form part the margin of the subnarial fenestra. The main body of the premaxilla is strongly compressed laterally, but, in lateral view, it is slightly oval to quadrangular, being a little taller than long. In medial view, the palatal process of each element is completely preserved behind the third tooth. The palatal process of the left premaxilla has a flat surface that articulates with the maxillary palatal process. The triradiate maxilla consists of an anterior portion, a posterior process, and a dorsal process (Figs. 2, 3). The main body of the maxilla is low, laterally compressed, and the ventral margin is laterally concave. The upper half of the anterolateral margin of the maxilla contacts the posterior side of the posterior process of the premaxilla and the nasal. The anterodorsal margin of the dorsal (ascending) process is thicker than the posteroventral side. The posterior margin of the dorsal process forms the anterior margin of the antorbital cavity, and the anterior margin, together with the posterior margin of the nasal, forms a subnarial fenestra. The subnarial fenestra is very long, being longer than the external naris. Its anterior tip is located at the level of the posterior end of the external naris, and the fenestra extends posteriorly beyond the level of the anterior margin of the antorbital fenestra. The posterior process of the maxilla forms the ventral border of the antorbital fossa, contacts the jugal at its posterior end, and sutures to the palatine medially. In lateral view, the anteroventral portion of the maxilla does not contact the premaxilla because of a deep excavation between the two elements. The two bones articulate only up to the level of the ventral margin of the external naris and diverge ventrally. This condition is similar to that in *Saurosuchus* and *Batrachotomus*, though in the latter taxon the separation between these bones is less developed. In *Prestosuchus* (PVUFRGS 0156) and *Fasolasuchus*, the bones do not diverge and the maxilla contacts the premaxilla up to the ventral border. In medial view, the narrow palatal process projects anteriorly, reaching the posterior portion of the premaxilla (Figs. 2C, 3B). The medial surface of this process has a groove anteriorly and a ridge posteriorly. On the medial surface of the anterior portion of the maxilla, posterodorsal to the palatal process, there is a large, triangular concavity, known as the palatal depression, which is interpreted to accommodate the Jacobson's organ (Jalil and Peyer, 2007). Each nasal is long and slender, with anterior and posterior descending processes that articulate with the premaxilla and the maxilla, respectively (Fig. 2). The anterior process is mediolaterally compressed, triangular in cross-section, and longer than the posterior process. Both processes form the dorsal margin of the large external naris. The posterior rim of the posterior descending process participates in the anteroventral margin of the subnarial fenestra. A thickened ridge extends along most of the anterodorsal margin at both sides of the medial edge of the nasals. In lateral view, each longitudinal ridge has a rounded dorsal margin and a slight groove, forming the so-called 'roman-nose' profile (Romer, 1971). Posterolaterally, the nasal has a broad and long facet for the anterodorsal part of the lacrimal, which is confluent with the posterior part of the facet for the maxillary ascending process and the posterior end of the subnarial fenestra. The thick and short frontal is known from the left side of PULR 057 (Fig. 4A). A deep dorsal ridge extends along the full length of the medial margin of the frontal. As in other 'rauisuchians', the dorsal surface of the frontal exhibits three distinctive main depressions. A medial depression extends posteriorly from the nasals, and the lateral margin of this depression is formed by a thickened area that is confluent with the posteromedial ridge on the dorsolateral surface of the prefrontal. A second lateral depression, along the dorsal border of the orbit, probably receives the anterior portion of the postfrontal. As indicated by a third posterolateral depression at the frontopostorbital suture, the postfrontal extended posteromedially to overlap the frontal posterolaterally and the postorbital anterodorsally. Such a configuration is preserved in the holotype (personal obs.), which was reconstructed erroneously by Romer (1971). The ventrolateral extension of the frontal is evident in both specimens, where it forms part of the roof of the orbit. The ventral surface of the frontal forms a long and narrow depression close to the medial margin. This structure extends from the posterior edge of the frontal up to the level of the anterior end of the frontal contribution to the orbit. The left postorbital is incompletely preserved and sutured to the frontal (Fig. 4A). The element consists of a flat, horizontal dorsal region, from which a slender subvertical process descends. Anteriorly, the postorbital articulates with the posterior edge of the frontal dorsally, and has an oblique facet at its posteromedial corner. The thickened dorsolateral edge of the orbit overhangs the descending process of the postorbital and a cavity at the dorsal end of the lower temporal fenestra. The lacrimal is known from the incomplete left element (Fig. 4B), which consists of an extensive, transversely compressed plate with a dorsoventrally smooth ridge. The lacrimal has a strongly curved anterior surface that forms the posterior margin of the antorbital fenestra. The lacrimal forms the anterior margin of the orbit posteriorly, has a slight groove medially, and is striated dorsally.

Palate—Both vomers are well preserved except for an eroded region at the midsection. They form the anterior borders of the internal nares (Fig. 4C). Each vomer is thin and elongated medially, where it would overlap the palatine. At the midline, the vomers form a U-shaped structure surrounding the anterior pterygoid process.

Dentition—As described above, there are three premaxillary and ten maxillary teeth. The teeth have recurved tips, are labiolingually compressed, and are serrated along both mesial and distal edges. The premaxillary teeth are slender, whereas the teeth in the anterior part of the maxilla are more robust, and have convex mesial edges and straight distal edges. Teeth

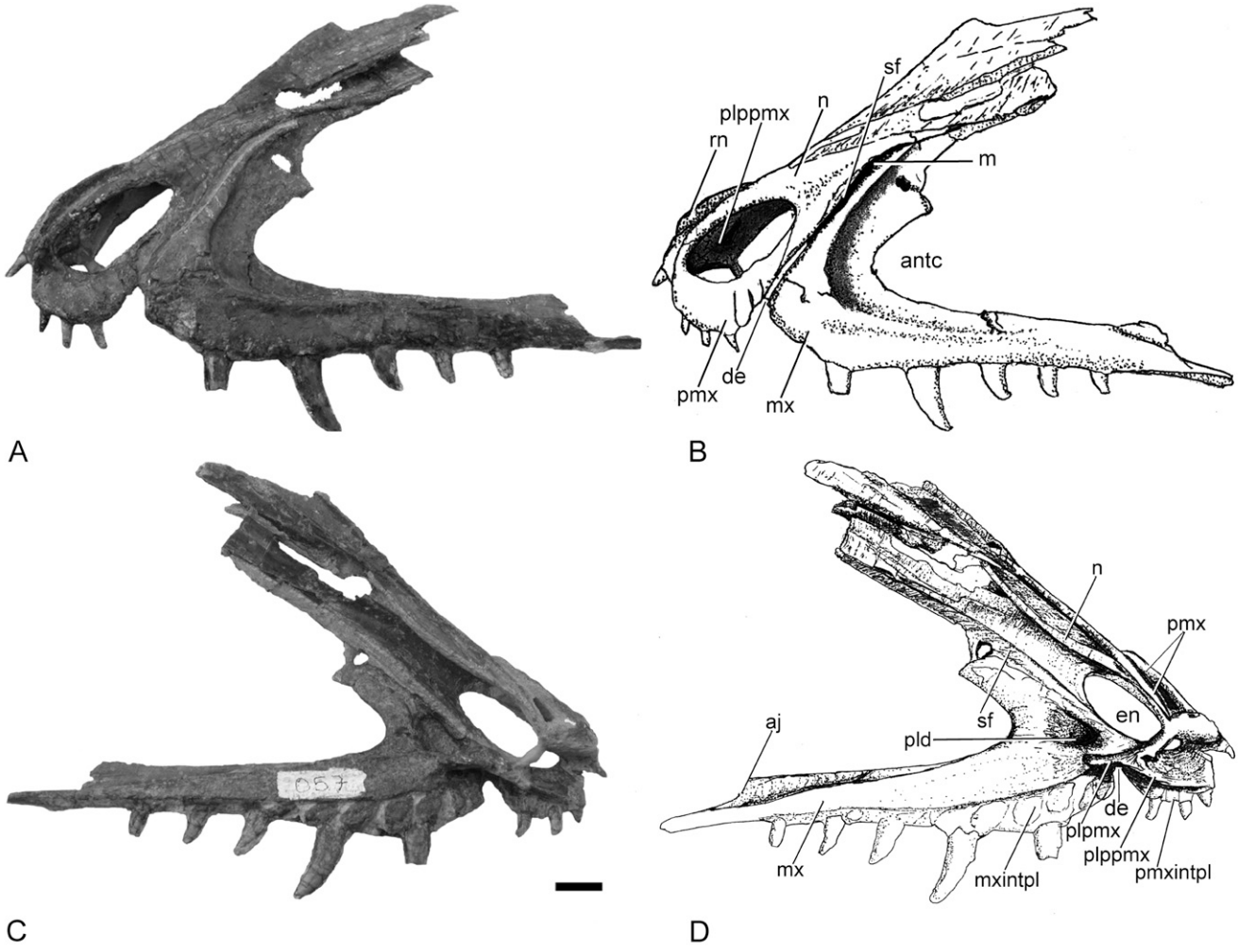


FIGURE 2. *Luperosuchus fractus* Romer, 1971. Articulated rostrum of PULR 057. **A**, photograph and **B**, line drawing of left lateral aspect; **C**, photograph and **D**, line drawing of medial aspect. Scale bar equals 1 cm.

in the posterior part of the maxilla are similarly shaped, but have shorter crowns and more convex mesial margins.

COMPARISON AND DISCUSSION

The new material described herein (PULR 057) represents a 'rauisuchian' referable to *Luperosuchus fractus* Romer, 1971 on the basis of the following cranial features: presence of an elongated extra opening associated with a movable joint between the nasal and the maxilla, a characteristic 'roman nose' formed by the anterodorsal portion of the nasals, and a deep excavation formed by the posterior margin of the premaxilla and an anterior projection of the maxilla. Although *L. fractus* is known only from cranial material (the holotype PULR 04 and PULR 057), the presence of several characters, such as large and narrow skull with tall keyhole-shaped orbit, the slit-like subnarial fenestra, a movable joint between the maxilla and the premaxilla, an antorbital fenestra that is triangular in lateral view with a narrow anterior corner, and a lacrimal that forms a heavy ridge dorsal to the orbit, allow us to identify it as a 'rauisuchian' (Benton and Clark, 1988; Chatterjee and Majumdar, 1987; Alcober, 2000). Recently, two phylogenetic analyses were carried by Weinbaum and Hungerbühler (2007) and Nesbitt (2007), but only the latter gives a detailed diagnosis of some of these groups in a strict phylogenetic context. Moreover, there is no evidence that the "Rauisuchidae" sensu lato is a monophyletic group, although it is quite clear that *Postosuchus* and *Teratosaurus* are close relatives. Therefore, pending a phylogenetic analysis of *Luperosuchus* relationships, *L. fractus* still cannot be refer a particular rauisuchian group.

The subnarial fenestra or accessory antorbital fenestra (opening in the skull roof between the naris and the antorbital fenestra) of some authors (e.g., Parrish, 1993) was described by Romer (1971:2) in *Luperosuchus* as "apparently present posterior to the nares between the premaxilla and maxilla." In *L. fractus*, however, this 'accessory' subnarial fenestra is only enclosed by the nasal and the maxilla, excluding the premaxilla. All the rostral bones are preserved and articulated in PULR 057, clearly showing the condition described above (Fig. 2). In the holotype the premaxilla is not preserved, although there is an excavation in the anterior process of the nasal, which would have received the posterior process of the premaxilla, separating the premaxilla from the antorbital fenestra. In both specimens, this fenestra is as long as the dorsal process of the maxilla and is located posterior (PULR 057) or posteroventral (holotype) to the external naris. Moreover, this is the longest accessory opening known (being

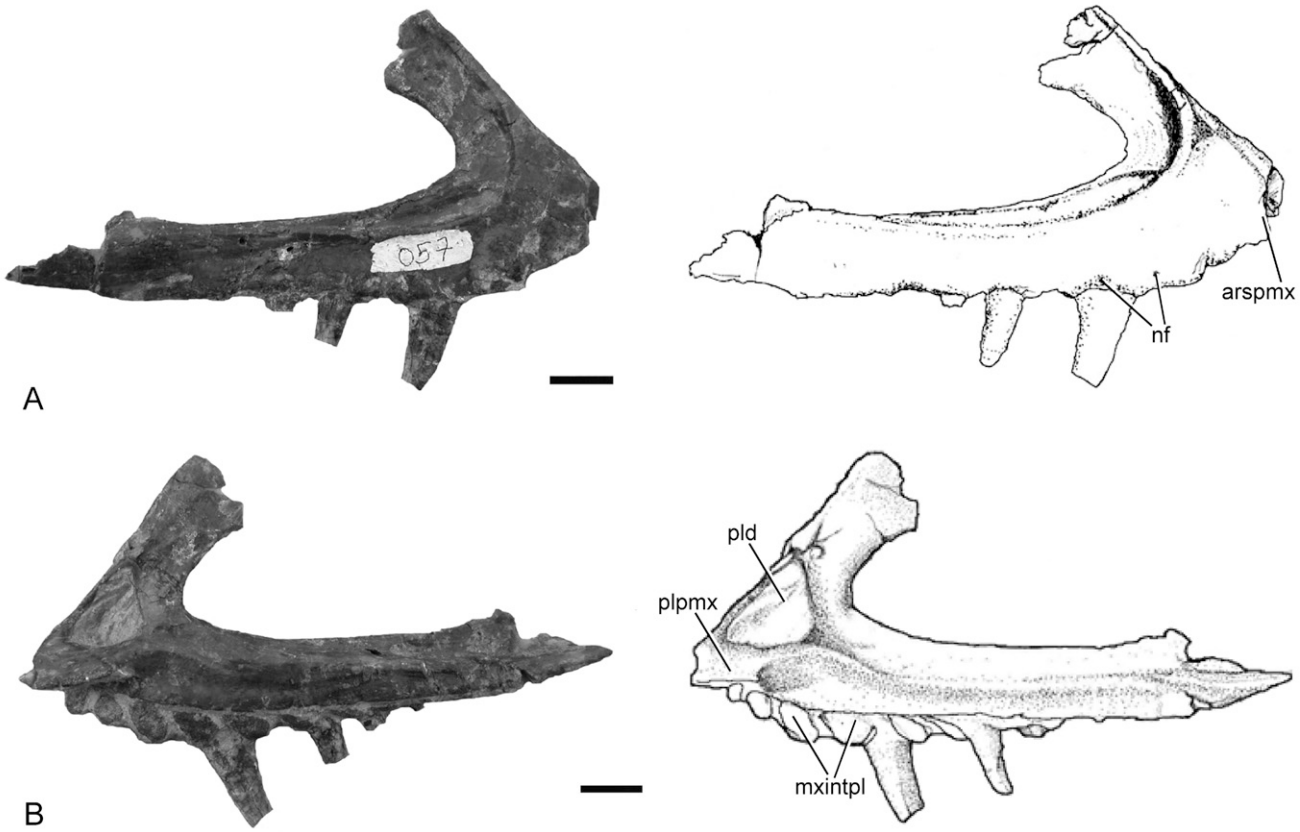


FIGURE 3. *Luperosuchus fractus* Romer, 1971. Photographs and line drawings of the right maxilla of PULR 057. **A**, lateral and **B**, medial views. Scale bar equals 1 cm.

longer than the external naris) among 'rauisuchian' archosaurs. The 'roman nose' is present in both specimens, but it is more anteroventrally placed in PULR 057 than in the holotype. These differences are most probably due to ontogenetic variation: the generally less ornamented aspect, the loose sutures, and the size of the skull of PULR 057 (one-third of the length of the type) indicate a juvenile stage. Also, the excavation between the maxilla and the premaxilla is more pronounced in the PULR 057 than in the type.

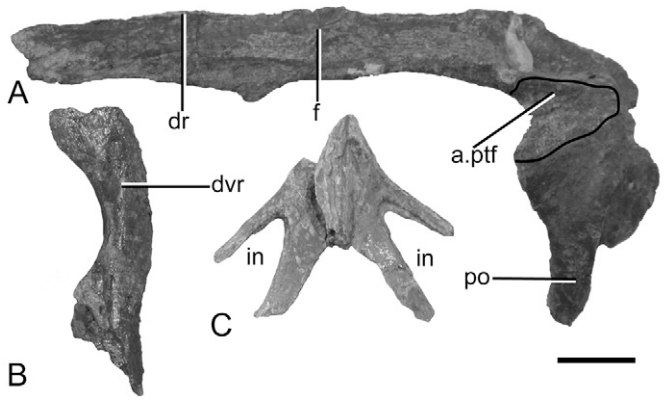


FIGURE 4. *Luperosuchus fractus* Romer, 1971. Photograph of disarticulated elements of PULR 057. **A**, left frontal and postorbital in lateral view; **B**, left lacrimal in lateral view; **C**, vomers in ventral view. Scale bar equals 1 cm.

In PULR 057, the posterior process of the premaxilla is shorter than that of *Fasolasuchus* (PVL 3850), *Saurosuchus galilei* (PVL 2062) (Sill, 1974; Alcober, 2000), and *Prestosuchus chiniquensis* (PVUFRGS 0156) (Barberena, 1978), and longer than in *Batrachotomus kupferzellensis* (Gower, 1999). Moreover, the cross-sectional oval shape of the premaxilla is different than the subquadrangular shape present in *Batrachotomus*, *S. galilei*, *Fasolasuchus*, and the quadrangular shape in *P. chiniquensis* and *T. silesiacus.* The maxilla of *L. fractus* is excluded from the naris, as in most 'rauisuchian' taxa; in *Batrachotomus* and *Arizonasaurus* the maxilla, however, forms the posterior margin of this opening. In both specimens of *L. fractus,* the ventral border of the maxilla is slightly convex, as in *Batrachotomus*, *Fasolasuchus*, *Yarasuchus*, *P. chiniquensis*, *S.galilei* (PVSJ 32), and *T. silesiacus*. The palatal process of the maxilla in *L. fractus* is anteroposteriorly long, projects anteromedially, and reaches the posterior margin of the premaxilla to contact the palatal process of this bone, as in *Batrachotomus*, *Fasolasuchus*, and *Arizonasaurus* but it is shorter than that in *Arganasuchus* (Jalil and Peyer, 2007). The palatal depression in *L. fractus* is deep, triangular, and large as in *S. galilei* and *T. silesiacus*, in contrast to the reduced depression present in *Arganasuchus.* The 'roman nose' formed by the nasals was recently described in *P. chiniquensis* and *Batrachotomus* (Gower, 1999), but in those forms it consists of low, dorsally arching anterior portions of the nasals, whereas

L. fractus has an extra growth not comparable with the other two taxa. Although 'rauisuchian' systematics are in a state of confusion (e.g., Gower, 2000; Gower and Nesbitt, 2006; Nesbitt, 2007; Weinbaum and Hungerbühler, 2007), it is important to describe and to establish rigorous diagnoses for all valid taxa before carrying on a phylogenetic analysis of this group of crurotarsan archosaurs. The new information provided herein on the cranial anatomy of *L. fractus*, South America's oldest 'rauisuchian' archosaur, will certainly contribute to our understanding of character evolution within this group when included in a phylogenetic analysis, which is beyond the scope of the present paper.

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