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Osteology of the Middle Triassic archosaur *Lewisuchus admixtus* Romer (Chañares Formation, Argentina), its inclusivity, and relationships amongst early dinosauromorphs

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Lewisuchus admixtus is an enigmatic early dinosauriform from the Chañares Formation, Ladinian of Argentina, which has been recently considered a member of Silesauridae. Yet, it differs markedly from Late Triassic silesaurids in dental and vertebral anatomy. Indeed, a detailed redescription of its holotype allowed the identification of several features of the skeleton previously unrecognized amongst silesaurids. These include pterygoid teeth, a dorsomedial posttemporal opening on the otoccipital, foramina associated with cranial nerves X–XII on the caudal region of the prootic–otoccipital, and postaxial neck/trunk vertebrae with craniocaudally expanded neural spines. The presence of a single row of presacral scutes was also confirmed. Some elements previously referred to, or found associated with, the holotype, including a lower jaw, pedal elements and an astragalus, more probably correspond to proterochampsid remains. The anatomical information available for the holotype of *L. admixtus* was rescored into a new phylogenetic dataset for dinosauromorphs, mostly based on previous works. *Lewisuchus admixtus* and *Pseudolagosuchus major* are treated as distinct OTUs because their preserved skeletons mostly lack overlapping parts. The parsimony analysis supports the basal position of *L. admixtus* within dinosauriforms, prior to the silesaurid–dinosaur split, rather than at the base of Silesauridae. This suggests that a higher number of early dinosauriform clades branched in the Middle and Late Triassic than previously suggested.

Keywords: *Lewisuchus*; *Pseudolagosuchus*; basal dinosauromorphs; Middle Triassic; silesaurids

Introduction

Archosaur remains discovered from the Middle to Late Triassic of Europe (Dzik 2003; Dzik & Sulej 2007), North America (Ezcurra 2006; Nesbitt *et al.* 2007; Nesbitt *et al.* 2010), Brazil (Ferigolo & Langer 2007) and Africa (Nesbitt *et al.* 2010; Kammerer *et al.* 2012; Peecook *et al.* 2013) have improved the record of lightly built dinosaur precursors (Bakker & Galton 1974; Bonaparte 1978; Sereno 1991a; Novas 1996), until recently known only from the Ladinian of the Chañares Formation, in Argentina (Romer 1971, 1972c; Bonaparte 1975; Arcucci 1987). Various studies positioned these taxa as successive outgroups to Dinosauria, including Lagerpetidae, *Marasuchus* and Silesauridae (see Nesbitt 2011, for review). Lagerpetids comprise three species (i.e. *Lagerpeton chanarensis*, *Dromomeron romeri* and *D. gregorii*), which are currently known from Ladinian and Norian deposits of Argentina and USA (Arcucci 1986; Sereno & Arcucci 1994a; Irmis *et al.* 2007a; Nesbitt *et al.* 2009a). *Marasuchus* is monoespecific (*M. lilloensis*), and restricted to the Chañares Formation (Sereno & Arcucci 1994b). Silesaurids are minimally known from Anisian to Norian strata in Poland, Brazil, Argentina, United States, Tanzania, Morocco and Zambia (Dzik 2003; Ferigolo & Langer 2007; Nesbitt *et al.* 2010; Kammerer *et al.* 2012; Peecook *et al.* 2013). Some authors support the position of silesaurids as basal ornithischians (Ferigolo & Langer 2007; Langer *et al.* 2007b; Langer & Ferigolo 2013), but this hypothesis has been disputed (Irmis *et al.* 2007b; Nesbitt *et al.* 2010). *Marasuchus*, silesaurids and dinosaurs comprise together the Dinosauriformes (Novas 1996; Langer & Benton 2006; Nesbitt *et al.* 2010), into which the poorly known *Saltopus* from the Late Triassic of Scotland has been recently included (Benton & Walker 2011).

An enigmatic specimen collected by the La Plata-Harvard expedition during 1964–1965 in the Chañares Formation (Romer 1966; Romer & Jensen 1966; Rogers *et al.*

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2001), La Rioja, Argentina, became the holotype of *Lewisuchus admixtus* Romer, 1972c. The specimen comprises a partial skull and post-cranial remains, including most of the pre-sacral column, pectoral and hind limb elements. As it was recovered from a concretion that also included remains of cynodonts and proterochampsids, the association of the non-articulated parts to the preserved skeleton is problematic (Arcucci 1998).

Although the taxonomic validity of *L. admixtus* has never been disputed, its phylogenetic position is controversial. Romer (1972c, p. 13) allied the taxon with the traditional 'pseudosuchians' (Cruickshank 1979), supporting a possible bearing on the origin of 'coelurosaurs'. Other authors have suggested affinities with gracilisuchids (Carroll 1988; Sues 1997), or basal crocodylomorphs (Sereno 1991a), more specifically with sphenosuchians (Bonaparte 1981; Olshevsky 1991). Parrish (1993) performed a phylogenetic study in which *L. admixtus* resulted as a basal suchian, but this pioneer analysis employed low sampling of characters and taxa. Alternatively, Paul (1988) and Arcucci (1997, 1998) suggested its placement closer to dinosaurs than to other archosaurs, a hypothesis that has gained support due to its positioning within Silesauridae (Brusatte *et al.* 2010; Nesbitt *et al.* 2010; Nesbitt 2011). Data gathered from the femoral anatomy of the coeval *Pseudolagosuchus major* Arcucci, 1987, often regarded as a junior synonym of *L. admixtus* (Arcucci 1997, 1998; Nesbitt *et al.* 2010), have added support to that relationship. However, the synonymization between these taxa is problematic due to the scarcity of overlapping elements in their preserved skeletons.

In order to improve the available information about *L. admixtus* to phylogenetic studies, we performed a detailed description of its holotype. Both the assignment of the preserved elements to the type specimen and the synonymy between *L. admixtus* and *P. major* are scrutinized via the phylogenetic signal of the preserved bones. The revised anatomical information on *L. admixtus* is rescored in a new character–taxon matrix for basal dinosauromorphs, in order to discuss its phylogenetic position within that clade.

Institutional abbreviations
AMNH: American Museum of Natural History, New York, USA; **NHMUK**: The Natural History Museum, London, UK; **GPIT**: Institut für Geologie und Paläontologie, Tübingen, Germany; **GR**: Ghost Ranch Ruth Hall Museum of Palaeontology, Abiquiu, NM, USA; **MACN**: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MCN**: Museu de Ciências Naturais/ Fundação Zoobotânica, Porto Alegre, Brazil; **MCP**: Museu de Ciências e Tecnologia/PUC, Porto Alegre, Brazil; **MNA**: Museum of Northern Arizona, Flagstaff, AZ, USA; **NMMNHS**: New Mexico Museum of Natural

History and Science, Albuquerque, NM, USA; **NMT**: National Museum of Tanzania, Dar es Salaam, Tanzania; **PULR**: Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**: Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; **PVSJ**: Universidad Nacional de San Juan, San Juan, Argentina; **SAM**: South African Museum, Cape Town, South Africa; **SMNS**: Staatliches Museum für Naturkunde, Stuttgart, Germany; **UCMP**: University of California Museum of Paleontology, Berkeley, CA, USA; **UFRGS**: Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **ULBRA**: Universidade Luterana do Brasil, Canoas, Brazil; **ZPAL**: Institute of Paleobiology of the Polish Academy of Science, Warsaw, Poland.

Systematic palaeontology

Archosauria Cope, 1869 *sensu* Nesbitt, 2011
Ornithodira Gauthier, 1986 *sensu* Sereno, 1991a
Dinosauromorpha Benton, 1985 *sensu* Nesbitt, 2011
Dinosauriformes Novas, 1992 *sensu* Nesbitt, 2011
Genus ***Lewisuchus*** Romer, 1972c

Revised diagnosis.   As for type and only species.

Type species.   *Lewisuchus admixtus* Romer, 1972c.

Lewisuchus admixtus Romer, 1972c
(Figs 1–11)

1972c *Lewisuchus admixtus* Romer: figs 1 (except mandible), 2–4, 6–7, 8a.
1978 *Lewisuchus admixtus* Romer; Bonaparte: fig. 134 (except mandible).
?2011 *Lewisuchus admixtus* Romer; Nesbitt: figs 24G, 28E, 30F.

Holotype.   PULR 01: incomplete left and right maxillae with teeth; caudal portion of the skull, including the left laterotemporal region: jugal, postorbital, quadratojugal, squamosal, and quadrate; braincase, comprising supraoccipital, basioccipital, otoccipital, laterosphenoid, parabasisphenoid and prootic; articulated left pterygoid and ectopterygoid; cervical vertebrae from atlas to the seventh vertebra, 11 dorsal vertebrae, nine proximal to mid-caudal vertebrae; both scapulocoracoids and humeri; incomplete tibiae. Bones previously referred to the holotype, including an isolated dentary and pedal elements (Romer 1972c) are now assigned to indeterminate proterochampsids.

Locality and horizon.   Los Chañares Locality, Talampaya National Park, La Roja Province, north-western Argentina, Chañares Formation (Romer & Jensen 1966; Rogers *et al.* 2001). Several authors assigned a Middle

Triassic age to the Chañares Formation (Bonaparte 1982; Arcucci 1990), including Anisian (Romer & Jensen 1966; Arcucci 1990; Bonaparte 1997), Anisian–Ladinian (Arcucci & Marsicano 1998) or Ladinian (Mancuso & Marsicano 2008; Desojo & Arcucci 2009). Desojo *et al.* (2011) suggested a possible earliest Carnian age for this stratigraphical unit. New data are required to corroborate this hypothesis.

Revised diagnosis. Dinosauromorph that can be distinguished from its kin by the following combination of features (asterisks indicate potential autapomorphies): extremely elongated skull, supraoccipital nearly horizontal, three foramina caudal to the metotic strut*, craniocaudally extending rugose ridge on the mid-height of the lateral surface of the axial neural spine*, postzygodiapophyseal lamina of the caudal cervical vertebrae projecting caudally to the tip of the postzygapophysis, and the presence of a single row of scutes associated to the distal tip of the cervical and dorsal neural spines.

Description and comparisons

We conducted a comparative description of the holotype of *Lewisuchus admixtus* based on the first-hand analysis of several archosaur specimens and on the literature (Supplemental Table 1). Because *L. admixtus* has been variously related to coeval archosauriforms such as proterochampsids, *Gracilisuchus* and Sphenosuchia, comparisons with those taxa were also performed, albeit no evidence supports a close relationship of this species with any of them.

Maxilla. The isolated right maxilla referred to *Lewisuchus admixtus* is elongated, low and transversely compressed (Fig. 1A–F). Its dimensions suggest that the skull was low and elongated, similar to that of basal crocodylomorphs (Walker 1990; Clark *et al.* 2000), and longer than that of any known basal dinosauriform. It differs from the lower and medially inclined maxillae of the proterochampsids, and from the dorsoventrally enlarged maxillary body of the robust pseudosuchians (Sill 1974; Barberena 1978). There is no definitive evidence that the maxilla belongs to the holotype, because the rostral portion of the jugal is damaged, and they cannot be unambiguously articulated. However, they match in anatomy and size, so we tentatively associate the maxilla to the holotype until further evidence is available.

The rostrally rounded rostral ramus (measured from the rostral edge of the external antorbital fenestra) encompasses approximately one-fifth of the total length of the preserved maxilla (Fig. 1A, B). The ascending ramus tapers dorsocaudally as in most archosauriforms (Gower 1999; Nesbitt 2011), and its rostral margin forms an angle of 30° with the alveolar margin of the bone. The base of the ascending ramus bears a shallow notch, which sets it apart from the rostral ramus of the maxilla.

On its rostrolateral surface, between the antorbital fenestra and the alveolar margin, the maxilla is pierced by a small foramen. Other Late Triassic dinosauriforms, such as *Silesaurus* (ZPAL AbIII/361/26), *Sacisaurus* (MCN PV10050), *Pampadromaeus* (ULBRA-PVT016) and *Coelophysis* (e.g. MNA V3315), possess multiple foramina on the lateral maxilla. The external antorbital fenestra is craniocaudally elongated, and is marked by a faint rim bordering the caudolateral margin of the ascending ramus, and the dorsolateral surface of the maxillary caudal process. An enlarged version of this rim is seen in saurischians, including *Eoraptor* (PVSJ 512), and theropods (Rowe 1989; Rauhut 2003). Ventral to the rim, the lateral surface of the maxilla bears a shallow and rostrocaudally elongated sulcus, which ends rostral to the caudal tip of the caudal ramus, similar to that seen in *Sacisaurus* (MCN PV10050).

The antorbital fossa is shallower than the lateral surface of the caudal maxillary ramus. This morphology is comparable to that of *Sacisaurus* (MCN PV10050), and early dinosaurs (Langer & Benton 2006). The area of the medial wall of the antorbital fossa compares to that of early dinosauriforms, such as *Sacisaurus* (MCN PV10050), *Agnosphitys* (Fraser *et al.* 2002), and most basal dinosaurs (Langer & Benton 2006), because it is transversely wider than the maxillary ascending ramus. Due to poor preservation, the existence of an excavation or aperture on the lateral surface of the antorbital fossa, as widely recognized in dinosauriforms (Sereno 1999; Rauhut 2003; Langer & Benton 2006) cannot be evaluated.

As in most archosaurs (Brusatte *et al.* 2010; Nesbitt 2011), the caudal maxillary ramus is elongated (77% of the total preserved length), tapers caudally, and bears dental alveoli along its entire preserved ventral margin.

Medially, the maxilla is convex along its whole extension. A faint crest extends along the dorsal portion of the caudal ramus, internally to the medial wall of the antorbital fossa. An enlarged version of this crest is present in one maxilla of *Silesaurus* (ZPAL AbIII/361/26). Rostrally, two additional crests extend on the medial surface of the maxilla. The upper one is a rostrocaudally bulged area restricted to the base of the ascending ramus, which bears a peculiar foramen that probably connects the antorbital fossa with the palatal portion of the maxilla. The lower crest is the palatal process, which forms a steep margin above the three rostralmost dental alveoli. The palatal process, like that of *Agnosphitys* (Fraser *et al.* 2002), is short and rod-like, but it is unclear if it contacted its antimere. The dorsal surface of the palatal process forms a horizontal shelf that probably contacted the caudal portion of the premaxilla.

An additional fragment of a left maxilla with seven *in situ* teeth plus two empty alveoli (Fig. 1G) was referred to *L. admixtus* by Romer (1972c). The maxillary rim on the lateral margin of the external antorbital fenestra is similar
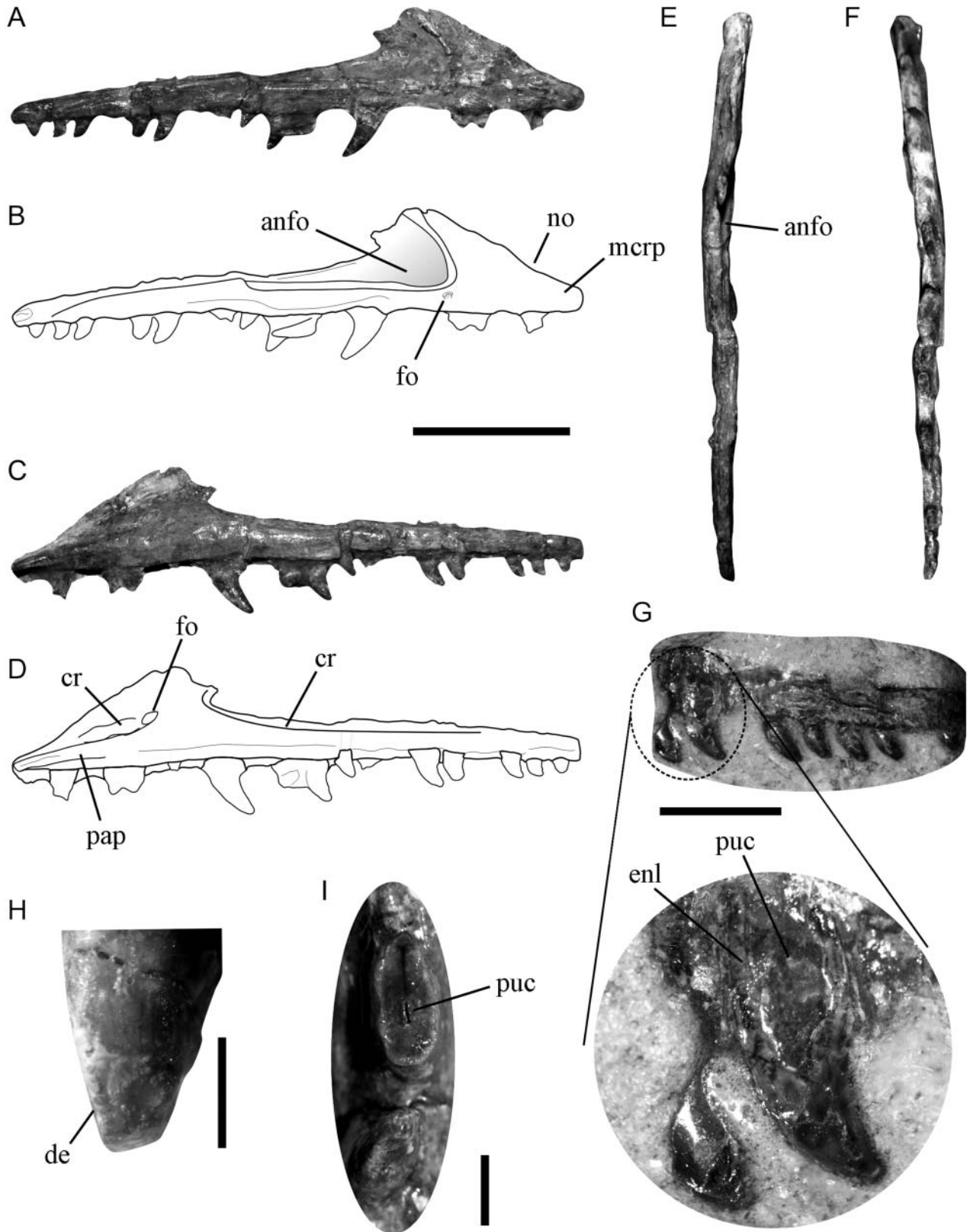
Figure 1. *Lewisuchus admixtus,* PULR 01. Right maxilla in **A, B,** lateral, **C, D,** medial, **E,** dorsal and **F,** ventral views. **G,** left maxilla in lateral view, with a detail of the tooth attachment. **H,** Sixth and **I,** seventh preserved maxillary teeth, respectively, in lingual view and in cross section. Abbreviations: anfo, antorbital fossa; cr, crest; enl, enamel layer; de, denticles; fo, foramen; mcrp, maxillary cranial process; no, notch; pap, palatal process; puc, pulp channel. Scale bars: A–F = 20 mm; G–I = 10 mm.

to that described above for the right maxilla, supporting a tentative assignment of this bone to PULR 01.

Dentition. The right maxilla possesses 20 preserved tooth positions with remains of at least 13 teeth in various states of preservation (Fig. 1A–D). Although the maxilla is not complete, there is no evidence of additional alveoli caudal to the last preserved one, thus the maxilla of *Lewisuchus admixtus* bears 20 teeth. Overall, the teeth display the anatomical pattern of the carnivorous archosauriforms, being similar to those described for *Tropidosuchus* (PVL 4601) and *Marasuchus* (PVL 3870). The crowns are mostly elongated, labiolingually compressed, caudally curved, with convex mesial margin and concave distal margin (Fig. 1A–I). They do not expand from the base (i.e. basal constriction absent), nor possess a basal cingulum or wear facets, as in herbivorous/omnivorous dinosauriforms (Yates 2003; Butler *et al.* 2008; Nesbitt *et al.* 2010). The tooth crowns are elliptical in cross section due to their labiolingual compression.

Although the rostralmost teeth are not complete, the evidence available from the alveoli and the preserved base of some crowns suggests that the largest maxillary teeth are located within the rostral third of the bone. Those elements are both apicobasally higher and mesiodistally wider than more caudal teeth. In fact, the overall dimensions of the maxillary teeth gradually diminish towards the caudal end of the bone. Based on the preserved basal portion of the fourth tooth, this is probably the largest maxillary tooth, suggesting the presence of an enlarged fang-like element close to the rostral portion of the maxilla. Because the maxilla/premaxilla contact is not preserved, the existence of a rostral diastema cannot be evaluated. Likewise, because the caudal portion of the maxilla is missing and the contact with the jugal and/or lacrimal is elusive, the extension of the maxillary tooth row below the orbit cannot be determined.

The 11th maxillary tooth bears conspicuous evidence of serration (Fig. 1H). Its crown is shorter than those of more caudal teeth, suggesting that it was not completely erupted. It bears five serrations along 0.60 mm in the apical portion of the mesial carina. The serrations are small knob-like protuberances, distally rounded (i.e. spatulate in lateral view), expanding with an angle of 90° to the tooth margin, similar to that observed in carnivorous archosaurs. Shallow grooves separate each serration, but these do not mark the tooth crown beyond the base of the serration. This differs from the typical chisel-like structure of the herrerasaurids (Bittencourt & Kellner 2009) and neotheropods (Abler 1997). They also differ from the coarser serration of silesaurids and ornithischians (Dzik 2003; Norman *et al.* 2004a; Ferigolo & Langer 2007), and the sharply pointed denticles of 'prosauropods' (Barrett 2000; Galton & Upchurch 2004).

The serrations observed in the basal portion of the distal carina of the tooth occupying the 15th maxillary tooth are somewhat distinct. They are not distally rounded as the mesial serrations of the 11th tooth, but bear a somewhat pointed edge in their 'apical' portion. This difference may reflect either a preservation artefact or an individual polymorphism given the relative state of development of the tooth. The tenth maxillary tooth has only faint evidence of serration, which may result from poor preservation or wearing. The differences in the serration morphology between the 11th and 15th maxillary teeth are not due to wearing.

The incomplete isolated left maxilla bears seven teeth (Fig. 1G), the two rostralmost of which are the largest ones (basally longer and apicobasally deeper). Compared to the more complete right maxilla, the dimensions of the preserved teeth suggest that they belong to the caudal third of the bone. Yet, the mode of preservation of the bone and teeth is rather distinct. The colour of the teeth varies from red-brown in the more complete maxilla, to strong carmine in the less complete one. The preserved teeth are bulged on the labial surface. Differently from the right maxilla, the more distal teeth are less caudally curved and apparently not as pointed at the crown tip. However, these differences may be related to preservation.

The internal structure of the second preserved tooth of the left maxilla is exposed (Fig. 1G, detail). The root is slightly longer than the crown, and is formed by a broad hollow pulp cavity, encased by a two-layered wall. The external cementum layer is very thin and covers the thick dentine layer, which is composed of a palisade of incremental lines. It does not show evidence of ankylosis, as has been assumed for some silesaurids (Nesbitt *et al.* 2010; Nesbitt 2011). From the proximal third of the tooth, a thin layer of enamel fulfils the space between the dentine and the cementum. The thickness of the enamel layer increases towards the tip of the tooth, but never achieves more than twice the width of the dentine stratum. The serrations in the distal carina are spatulate, with a density of nine serrations per mm.

Postorbital. The low postorbital body expands medially (Fig. 2A, B), and its dorsal border is marked by a rostrocaudally oriented crest, similar to those of *Tropidosuchus* (PVL 4601) and *Gracilisuchus* (Romer 1972b; Brinkman 1981). The participation of the postorbital in the dorsotemporal (= supratemporal) fenestra cannot be assured in *Lewisuchus admixtus* due to poor preservation. The basal portion of the incomplete rostral ramus is dorsoventrally wider than that of the caudal ramus. Despite this incompleteness, the postorbital body was probably closer to the dorsal edge of the orbit than that of *Gracilisuchus* (Brinkman 1981). The dorsal crest roofs a broad lateral excavation that extends caudally along the preserved

rostral portion of the caudal process. The excavation spans ventrally as an elongated sulcus halfway the length of the ventral ramus, as also seen in other archosauriforms, such as *Chanaresuchus* (PULR 07), *Gracilisuchus* (Brinkman 1981) and *Pampadromaeus* (ULBRA-PVT016).

The elongated ventral ramus is slender, and tapers smoothly ventrally. By contrast, the ventral ramus of the postorbital of *Silesaurus* (Dzik & Sulej 2007) possesses a caudal kink. In this respect, the postorbital of *L. admixtus* is comparable to that of *Gracilisuchus* (Brinkman 1981) and some early dinosaurs (e.g. *Pampadromaeus*, ULBRA-PVT016). The dorsal ramus of the jugal is mostly overlapped by the ventral ramus of the postorbital, along an extensive suture between both bones. As seen in most archosauriforms (Nesbitt 2011), the ventral ramus curves rostrally, and the rostral border has a concave outline. Its distal third also bends medially, reaching the floor of the orbit.

Ventrally, the postorbital contacts both the lateral margin of the ectopterygoid and a medial portion of the jugal. The medial surface of the postorbital is mostly concave and bears a faint ridge extending along the proximal third of the caudomedial border. The transverse width of the postorbital at its broadest preserved portion (the dorsal region) encompasses approximately one-fifth of its height.

Jugal. The preserved jugal is interpreted as aligned sub-horizontally (Fig. 2A, B). Contrasting with *Sphenosuchus* (SAM-PK-3014), its rostral ramus is transversely wider than dorsoventrally high, the medial part of which articulates with the pterygoid–ectopterygoid complex, forming the floor of the orbit. In this portion, the rostral ramus is laterally bordered by a low sharp crest, which extends caudally, disappearing rostral to the caudal ramus of the bone. A sharp crest on the jugal is recorded amongst archosauriforms, including proterochampsids and dinosaurs (Nesbitt 2011).

The dorsal ramus of the jugal is similar to that of most archosaurs (Brusatte *et al.* 2010), its caudal margin forming an angle of 70° to the rostrocaudal axis of the bone. The caudal ramus is bifurcated and forms a slot that receives the quadratojugal. The ventral tine of the caudal ramus is caudally pointed, bears a faint ridge along its dorsal surface, and expands farther caudally than the dorsal tine, as also seen in basal theropods (Rauhut 2003). The dorsal tine is laterally bulged, with a rounded caudoventral border and pointed dorsocaudal edge.

We were not able to identify the mandibular bones associated with the jugal and quadratojugal as figured by Romer (1972c, fig. 1).
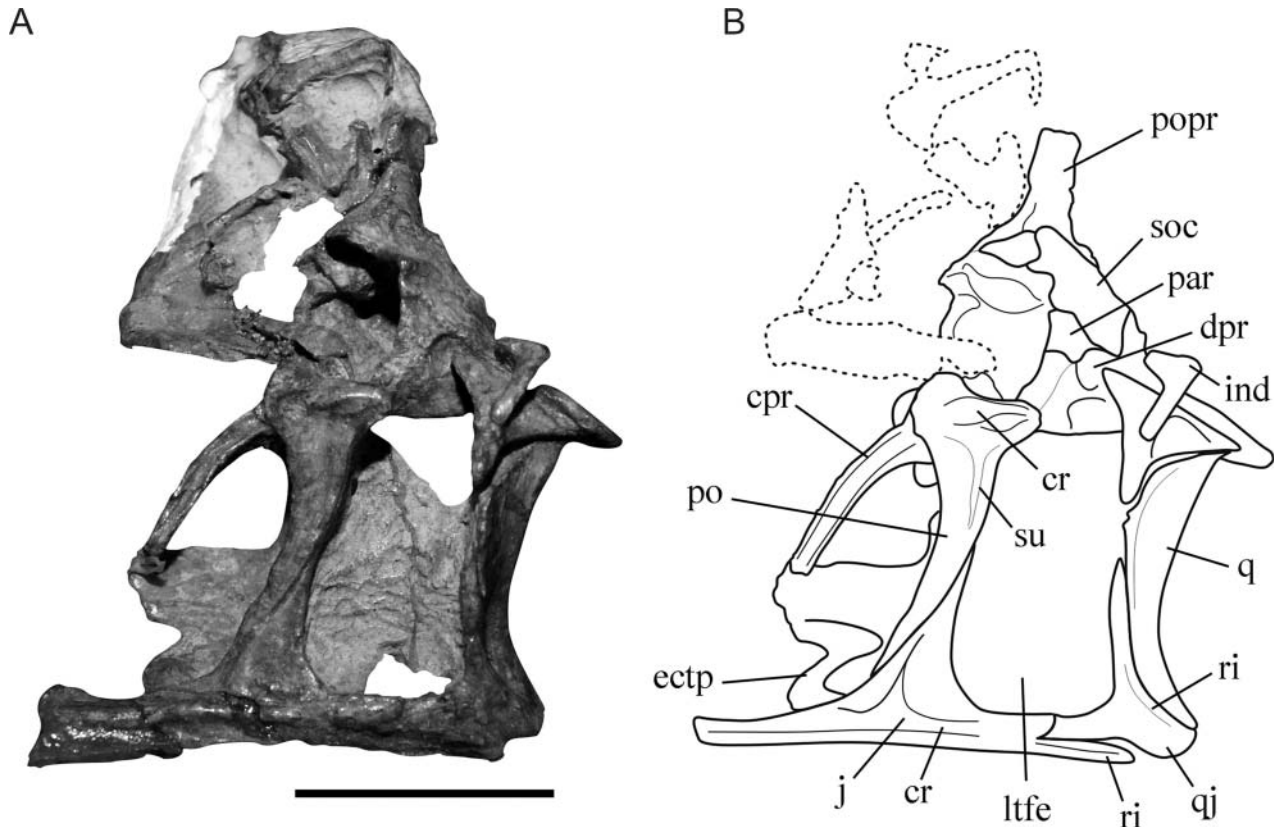
Figure 2. *Lewisuchus admixtus*, PULR 01. **A, B,** caudal portion of the skull in lateral view. Abbreviations: cr, crest; dpr, dorsal prootic recess; cpr, cultriform process; ectp, ectopterygoid; ind, indeterminate bone; j, jugal; ltfe, laterotemporal fenestra; par, parietal; po, postorbital; popr, paraoccipital process (otoccipital); q, quadrate; qj, quadratojugal; ri, ridge; soc, supraoccipital; su, sulcus. Scale bar = 20 mm.

Quadratojugal. The quadratojugal has the common L-shape morphology seen in several archosauriforms (Nesbitt 2011), and forms the caudoventral margin of the laterotemporal (= infratemporal) fenestra (Fig. 2A, B). The rostral ramus is aligned with the caudal ramus of the jugal, and its visible portion ends before the mid-length of the laterotemporal fenestra, as is common amongst dinosauriforms (Nesbitt 2011).

The dorsal ramus of the quadratojugal is straight, rostrocaudally slender, and forms a near right angle to the rostral ramus. As in *Gracilisuchus* (Brinkman 1981) and some Late Triassic saurischians (e.g. *Herrerasaurus*, PVSJ 407), the dorsal ramus is considerably longer than the rostral one. Romer (1972c) inferred that the dorsal ramus probably contacted the ventral tip of the squamosal, but this cannot be ascertained. Along most of its extension, the dorsal ramus is appressed to the rostroventral half of the lateral ala of the quadrate, but there is no evidence of co-ossification to each other. The base of the caudal margin of the dorsal ramus, i.e. the region that merges with the caudal ramus, overlaps part of the craniolateral edge of the ventral portion of the quadrate. Both the rostral and the dorsal rami converge into a plate-like body that continues caudally in a subtriangular process. Unlike some basal dinosaurs (Yates 2003), the caudal ramus does not form a waisted process or a distinct heel, although it is somewhat elongated and slightly projected medially. Caudally, the quadratojugal bears a faint ridge extending onto the ventral end of its dorsal ramus. The latter condition differs from that of *Chanaresuchus* (PVL 4575; PULR 07), in which the lateral surface of the quadratojugal shows a conspicuous ridge, bordering the caudoventral margin of the laterotemporal fenestra (Nesbitt 2011).

Squamosal. The left squamosal is preserved as an incomplete, slightly displaced subtriangular bone, articulating with both the quadrate and the paraoccipital process of the opisthotic (Fig. 2A, B). Both the rostral and ventral rami are incomplete, so comparisons are hampered. The squamosal of *Lewisuchus admixtus* contrasts with the plate-like, rostrally and caudally rounded squamosal body of *Gracilisuchus* (Brinkman 1981).

The preserved portion of the ventral ramus of the squamosal of *L. admixtus* is short, and contacts the rostrodorsal half of the lateral ala of the quadrate. The reconstruction of Romer (1972c) suggests that it formed half the height of the laterotemporal fenestra. However, the squamosal is displaced, and its contact with the quadratojugal is elusive. Accordingly, its participation in the laterotemporal fenestra can only be estimated as equivalent to the quadratojugal contribution. The ventral ramus of the squamosal is connected to the caudal ramus of the same bone by a thin and caudally projected lamina, rendering a concave outline to the caudal portion of the squamosal. The caudal process is short, sharply pointed, and caps part of the

dorsal portion of the quadrate, a feature already noticed in basal archosauriforms and ctenosauriscids (Nesbitt 2011). A small piece of an elongated bone, which is expanded at one extremity, is attached to the lateral body of the squamosal, but does not fit the size and shape of its missing parts. As pointed out by Romer (1972c), this is probably a skull element, but we also consider it as indeterminate.

Laterotemporal fenestra. The laterotemporal fenestra is subrectangular, and its ventral margin is slightly longer than the dorsal one (Figs 2A, B). The cranial margin of the fenestra is bordered by the ventral ramus of the postorbital and the dorsal ramus of the jugal. The relative participation of each of these bones in the cranial margin of the fenestra is equivalent. The ventral margin possesses concave cranial and caudal corners. The dorsal tine of the caudal portion of the jugal contributes with 60% of the floor of the fenestra, the remainder of which is formed by the cranial ramus of the quadratojugal. Considering that the ventral ramus of the squamosal is longer than preserved, this ramus and the dorsal ramus of the quadratojugal probably had subequal participation in the caudal rim of the laterotemporal fenestra. The dorsal margin of the fenestra is not preserved. Nevertheless, there is no evidence of a strong narrowing of the laterotemporal fenestra either at the mid-height or at the dorsal portion of the external opening.

Parietal. The caudomedial portion of the parietal is preserved in contact with the rostrolateral margin of the otoccipital (Figs 2A, B, 3A–C). It displays a small rostral excavation, and is laterally bordered by a sharp crest, which probably composed the medial margin of the dorsotemporal fenestra. The parietal extends cranially, roofing the laterodorsal sinus of the endocranial cavity.

Supraoccipital. The supraoccipital is nearly horizontal to the presumed rostrocaudal axis of the skull (Figs. 2A, B, 3A–C). It is a flattened bone, except for its small sagittal nuchal crest. The convex dorsal portion of this crest corresponds ventrally to a canal in the roof of the endocranial cavity (Fig. 6A, B). The laterodorsal contact of the supraoccipital with the preserved caudal portion of the parietals is formed by a notch on each side of the bone, rendering a rectangular appearance to the rostral portion of the supraoccipital. This configuration is similar to that observed in *Chanaresuchus* (PULR 07). Some dinosaurs (e.g. *Massospondylus*, SAM-PK-K1314) have a foramen associated with the supraoccipital notch. In *Silesaurus* (ZPAL AbIII/361), the notches are elliptical and deeply incised in the supraoccipital body, for which they are presumed to be homologous to the posttemporal opening of dinosaurs (Langer & Benton 2006; Nesbitt 2011). However, the posttemporal aperture in basal saurischians (Sereno & Novas 1994), sauropodomorphs (contra Sues *et al.* 2004), neotheropods (Sampson & Witmer 2007), and some

ornithischians (e.g. *Scelidosaurus*, NHMUK R1111), is located dorsally on the paraoccipital process, and *L. admixtus* has an equivalent opening on the same position (see below). In this sense, we do not consider the supraoccipital notch as an equivalent to the posttemporal opening. The notches are caudally bordered by a shallow excavated area lateral to the sagittal crest.

The concave caudal margin of the supraoccipital roofs half of the lateromedial extension of the foramen magnum, similar to the condition of early dinosauriforms (Smith *et al.* 2007). The bulk of the nuchal crest is located on the rostral portion of the supraoccipital, but it expands caudally as a slightly elevated surface and terminates as a median small knob on the caudal edge of the bone. The contact between the supraoccipital and the otoccipital is visible in dorsal view. The supraoccipital possesses an elevated rugose contact with the otoccipital (Nesbitt *et al.* 2010), resembling the condition of *Euparkeria* (SAM-PK-5687), and some dinosauriforms, such as *Silesaurus* (ZPAL AbIII/361) and *Herrerasaurus* (PVSJ 407) (Fig. 3D, E). The condition of *Marasuchus* is unknown due to poor preservation.

Basioccipital. The basioccipital participates in the floor of the foramen magnum and forms the central portion of the occipital condyle, which is wider than high in caudal view (Fig. 3A, B).

In ventral view, the condyle is transversely wider at the caudal end, and is bordered by a transversely narrow condylar neck (Fig. 5A, B). The basioccipital portion (= caudal) of the basal tubera expands ventrocranially as divergent processes, with an almost right angle between them. A narrow crevice extends cranially onto the basisphenoid recess, and separates the right and left processes. The basioccipital processes that forms the basal tubera are transversely broad due to a possible lateral contribution of the ventral projections of the otoccipital (exoccipital portion), resembling the condition seen in *Chanaresuchus* (PULR 07).

Otoccipital (= opisthotic–exoccipital). The opisthotic and the exoccipital are partially fused in the holotype of *Lewisuchus admixtus* (Figs 2A, B, 3A–C, 4A, B), forming the otoccipital (*sensu* Sampson & Witmer 2007). The contacts of this bone are complex. It articulates rostrally with the prootic; rostromedially with the parietal; rostrolaterally with the squamosal and quadrate; medially with the supraoccipital; caudoventrally with the basioccipital; and rostroventrally with parabasisphenoid.

The paraoccipital process is elongated and expands caudolaterally and ventrally from the area of contact with the supraoccipital (Fig. 3A, B). In dorsal view (Fig. 3C), it forms an angle of 120° to its pair. The process has concave dorsal and ventral margins in caudal view, and bulges ventrolaterally at its distal portion. This condition is similar to that of *Herrerasaurus* (PVSJ 407) and

Plateosaurus (GPIT skeleton), but contrasts with that of *Tropidosuchus* (PVL 4601), in which the paraoccipital processes are rather straight and dorsally expanded at the distal portion.

Caudally, the medial region of the otoccipital forms the laterodorsal and lateroventral border of the foramen magnum. The region immediately lateral to this border is concave, but the remainder of the paraoccipital process is nearly flat on its caudal surface. In the right process, at the contact of the otoccipital and the dorsocaudal portion of the prootic, there is a medial foramen followed laterally by a shallow lateromedially extended sulcus (Fig. 3A–C, pto). This sulcus opens dorsocaudally on the paraoccipital process and is laterally bounded by the squamosal and probably roofed by the parietal. This is the posttemporal opening (*sensu* Sampson & Witmer 2007) noted in several dinosaurs (Sereno & Novas 1994), such as *Herrerasaurus* (PVSJ 407), *Coloradisaurus* (PVL 3967), *Massospondylus* (SAM-PK K1314), *Carnotaurus* (Carabajal 2011), *Majungasaurus* (Sampson & Witmer 2007) and *Alioramus* (Bever *et al.* 2011). A foramen totally enclosed within the paraoccipital process of *Coelophysis rhodesiensis* (Raath 1969, 1977) and *Lesothosaurus* (Sereno 1991b), which is absent in *L. admixtus*, may be reminiscent of the posttemporal opening. The condition of *Scelidosaurus* (NHMUK R1111) is intermediate, with a partially enclosed foramen on the dorsal portion of the paraoccipital process. Norman *et al.* (2011) found a corresponding foramen on the paraoccipital process of *Heterodontosaurus*, but contrary to what is assumed herein, they interpreted the ventrally located supraoccipital notch as the posttemporal opening.

From the mid-length of the rostral surface of the paraoccipital process, a stout otosphenoidal crest projects rostrally onto the laterodorsal portion of the prootic (Fig. 3C). Ventromedially, three laminae are seen on the caudal portion of the otoccipital (Fig. 4A, B). The rostralmost of them (crista interfenestralis; Fig. 4A, B, cri) is a medial extension of the ventral margin of the opisthotic (at this portion, its separation from the exoccipital is clear), which forms part of the caudodorsal wall of the stapedial groove into the columellar recess (*sensu* Gower & Weber 1998). As in *Batrachotomus* (Gower & Sennikov 1997; Gower 2002), this lamina separates the fenestra ovalis (Fig. 4A, B, fov) from the metotic fissure, although in *L. admixtus* this separation is not complete.

The intermediary lamina is entirely derived from the exoccipital (Fig. 4A, B, mes), and it has been referred to as the metotic strut (= 'posterior strut' of Romer 1972c; crista tuberalis of Sampson & Witmer 2007). Similar to other archosaurs (Witmer 1990), the metotic strut projects ventrally and connects the otoccipital to the basal tubera. The metotic fissure (Fig. 4A, B, mef) is regarded herein as homologous to the fenestra cochleae and fenestra 'pseudorotunda' (Gower & Weber 1998; Sampson & Witmer 2007). It is a rostrocaudally narrow, transversely
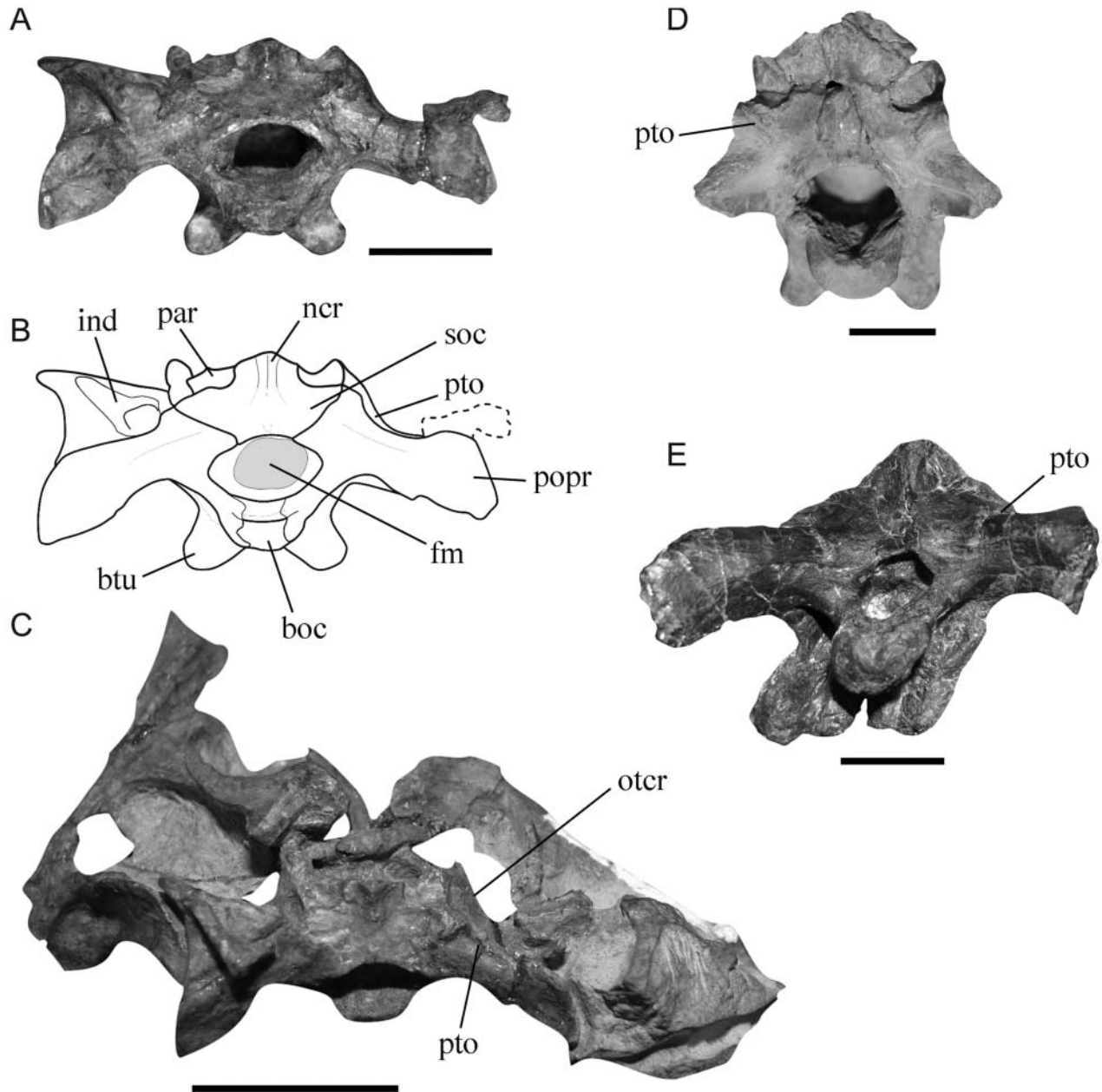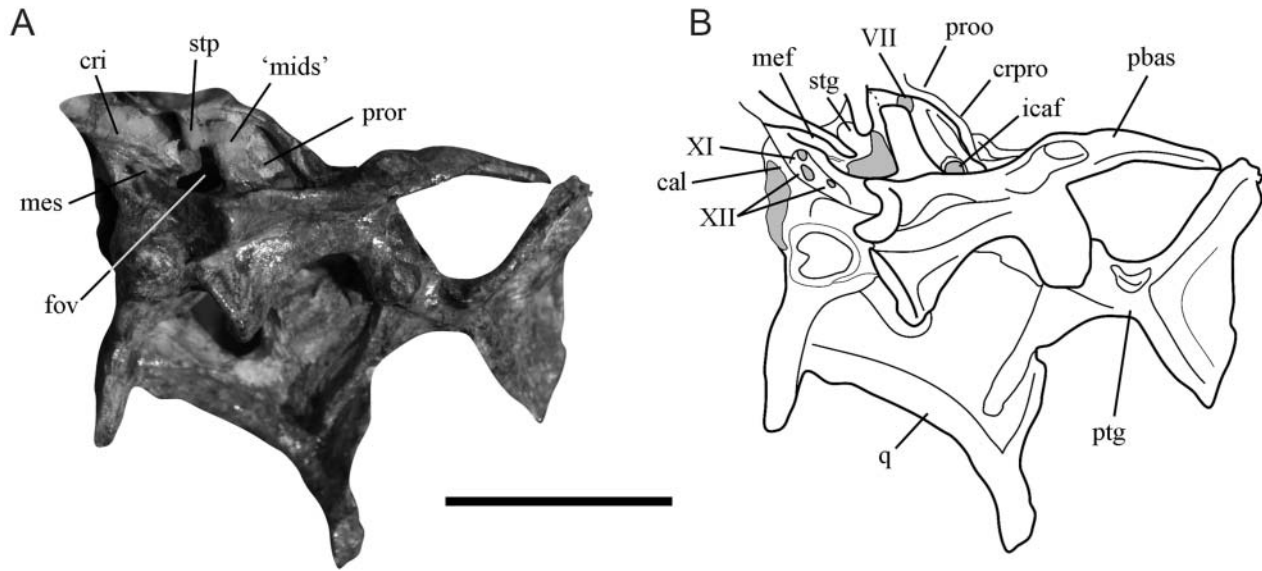
Figure 3. *Lewisuchus admixtus*, PULR 01. Caudal portion of the skull in **A, B,** caudal and **C,** dorsal views. **D,** *Silesaurus*. **E,** *Herrerasaurus*. Abbreviations: boc, basioccipital condyle; btu, basal tubera; fm, foramen magnum; ind, indeterminate bone; ncr, nuchal crest; otcr, otosphenoidal crest; par, parietal; popr, paraoccipital process (otoccipital); pto, posttemporal opening; soc, supraoccipital. Scale bars: A–D = 10 mm; E = 30 mm.

wide, and laterally opened chamber, which is also inserted into the columellar recess. A narrower furrow (Fig. 4B) diverges from this groove and leads to a foramen caudally opened just caudal to the metotic strut, and possibly serves as passage for the cranial nerves X and/or XI. This suggests a diversion of the vagal canal, as described for theropod dinosaurs (Rauhut 2003; Sampson & Witmer 2007), and this condition contrasts with the undivided metotic fissure of basal archosauriforms (Gower & Sennikov

1996) and rauisuchians (e.g. *Batrachotomus*, Gower 2002).

The caudal lamina (Fig. 4A, B, cal), which is limited by a short and transverse crest at the mid-height of the occipital condyle, is also restricted to the exoccipital. It forms the laterodorsal knobs of the basioccipital condyle, differing from the bulged condylar surface of basal archosauriforms (Desojo *et al.* 2011; Trotteyn & Haro 2011). The space between the caudal lamina and the metotic

Figure 4. *Lewisuchus admixtus*, PULR 01. **A, B,** caudal portion of the skull in lateroventral view. Abbreviations: cal, caudal lamina; cri, crista interfenestralis; crpro, crista prootica; fov, fenestra ovalis; icaf, internal carotid artery foramen; mef, metotic fissure; mes, metotic strut; 'mids', middle strut; pbas, parabasisphenoid; proo, prootic; pror, prootic–parabasisphenoid recess; ptg, pterygoid; q, quadrate; stg, stapedial groove; stp, stapes; VII, foramen for the facial nerve; XI, foramen for vagal nerve; XII, foramen for hypoglossal nerve. Scale bar = 20 mm.

strut harbours three subvertically aligned conspicuous foramina. The upper two were regarded by Romer (1972c, figs 3, 4) as the openings for the cranial nerve XII, giving that in several reptiles (Romer 1956; Gower & Sennikov 1997; Gower & Weber 1998) the hypoglossal nerve has a dichotomous exit in the braincase. However, as mentioned above, the dorsal foramen is interpreted herein as the passage for the vagal and/or accessory nerves. The intermediary and the ventral foramina are the exit for the hypoglossal nerve (XII), which is congruent with its position in some early dinosaurs (Sereno 1991b; Rauhut 2003). The position of the hypoglossal nerve foramina caudal to the metotic strut is not exclusive of *L. admixtus* and silesaurids (Nesbitt *et al.* 2010; Nesbitt 2011). A partial braincase attributed to *Marasuchus* (PVL 3872) shows a similar configuration (Sereno & Arcucci 1994b), suggesting that the exit of the cranial nerve XII occupied a similar position amongst non-dinosaur dinosauriforms.

Prootic. The prootic forms most of the lateral portion of the braincase (Fig. 4A, B). It is tightly attached to the dorsal surface of the parabasisphenoid and their separation is elusive. Indeed, several prootic structures described in this section are probably also composed by parts of the parabasisphenoid. The prootic is largely exposed in lateral view, and is also seen in dorsolateral (the otosphenoidal crest, Fig. 3C) and ventral view (the recesses on the lateral surface, Fig. 4A, B). It contacts the otoccipital caudally, the parietal dorsally, and probably the laterosphenoid

cranially. The dorsolateral portion of the prootic is marked by a dorsal recess close to the supraoccipital-parietal contact, which receives the rostral ramus of the squamosal (Fig. 2A, B).

The otosphenoidal crest extends from the caudal margin of the otoccipital, spanning rostrally onto the lateral surface of the prootic, similar to *Marasuchus* (PVL 3872) and *Silesaurus* (ZPAL AbIII/361). The rostral margin of this crest folds down and forms part of the 'middle strut' of Romer (1972c), which is also composed by the ascending ramus of the parabasisphenoid (Fig. 4A, B, 'mids'). The dorsocaudal portion of the prootic forms the rostral border of the columellar recess, which houses the stapedial groove dorsally (Fig. 4A, B, stg), the fenestra ovalis (= fenestra vestibuli, Sampson & Witmer 2007) cranially (fov), and the metotic fissure caudally (mef). The latter two structures are opened into the endocranial space. A fragmentary right stapes (Fig. 4A, B, stp) is associated to the corresponding stapedial groove.

A thin lamina projects rostroventrally from the region of the 'middle strut', forming the roof of a cavity here referred to as the prootic–parabasisphenoid recess. In rauisuchians (Wu & Russell 2001; Gower 2002), the thin lamina has been referred to as the crista prootica (Fig. 4A, B, crpro), homologous to that described in dinosaurs (Galton & Upchurch 2004, fig. 12.2). The 'anterior strut' of Romer (1972c, pp. 5–6) is formed by both the crista prootica and the caudal wall of the clinoid process of the parabasisphenoid. The prootic–parabasisphenoid recess, which is topologically equivalent to the 'anterior tympanic recess' of

theropods (Rauhut 2003), harbours at least two internal openings. Contrary to the interpretation of Romer (1972c), the dorsal opening is the foramen for the facial nerve (cranial nerve VII), which occupies an equivalent position in several archosauriforms (Gower & Sennikov 1997; Gower & Weber 1998; Sampson & Witmer 2007). The rostroventral opening is larger and is floored by the parabasisphenoid. We tentatively interpret it as the passage for the internal carotid artery and/or the palatine branch of the facial nerve (Fig. 4A, B, icaf), because a similar configuration is described for *Euparkeria* (Gower & Weber 1998), *Batrachotomus* (Gower 2002) and *Marasuchus* (PVL 3872).

The prootic–parabasisphenoid recess also houses two pneumatic spaces: a small excavation below the foramen for the facial nerve that does not pierce into the endocranial cavity, and a dorsoventral wedge-like concavity that leads into the internal opening of the carotid artery. Both the foramen for the facial nerve and the rostral concavity are at least partially covered by the lateral flange of the 'anterior strut'. The rostral lamina that roofs the prootic–parabasisphenoid recess is rostrally covered by a bony shield (Fig. 6A, B), which can be interpreted as an ossification of the laterosphenoid (Romer 1972c). Dorsomedially to the prootic–parabasisphenoid recess and dorsocaudally to the shield of the 'anterior strut', there is an oval opening of the endocranial cavity (the "? fenestra epiotica" of Romer 1972c, p. 6). This is better interpreted as the trigeminal foramen, or the exit for the cranial nerve V, which is in a similar position to the corresponding foramen of several archosauriforms (Gower & Weber 1998), including dinosaurs (Rauhut 2003).

The caudal portion of the endocranial cavity is exposed. Its wall above the columellar recess expands laterally forming the cavity for the auricular lobe (flocculus) of the cerebellum (Larsell 1932; ten Donkelaar 1998), which is also well developed in *Marasuchus* (PVL 3872), *Silesaurus* (ZPAL AbIII/361) and dinosaurs (Franzosa & Rowe 2005). At the entrance of the sinus, the dorsal border of the internal crest bears a blind excavation associated with a small cranial concavity (not shown), which may be the passage for the vena cerebralis media (Galton 2001; Galton & Upchurch 2004).

Laterosphenoid. A partial laterosphenoid is preserved rostrally to the trigeminal foramen (Fig. 6), but its contacts with other cranial bones are not clear. Apparently, it lies rostrally to the prootic and caudodorsally to the clinoid process of the parabasisphenoid. This position is consistent with that observed in other archosaurs (Gower & Sennikov 1996), in which the laterosphenoid lies rostral to the prootic, and caudal to the sphenethmoid. The position of the latter bone can be inferred by the dorsal sulcus of the cultriform process (parabasisphenoid), which

probably received the "cartilaginous sphenethmoidal braincase" (Romer 1972c, p. 6).

Parabasisphenoid. As commonly observed in archosauriforms (Ewer 1965; Walker 1990; Parrish 1994; Yates 2003), both parasphenoid and basisphenoid are co-ossified, thus they are referred to here as the parabasisphenoid. This is tightly attached to the ventral margin of the prootic, and forms most of the floor of the braincase (Figs 4A, B, 5). The basisphenoid component of the basal tubera is closely attached rostral to its basioccipital portion (Fig. 5). From the rostral margin of each ramus of the basal tubera, a shallow flange expands dorsomedially and rostrally, forming the body of the parabasisphenoid.

The basisphenoid recess is shallow if compared to that of early theropods (Rauhut 2003; Nesbitt *et al.* 2009b), and extends from the basal tubera to the proximal portion of the cultriform process. The foramina for the internal carotid artery pass through the lateroventral portion of the prootic–parabasisphenoid, as also described for *Marasuchus* (Sereno & Arcucci 1994b). By contrast, in *Chanaresuchus* (PULR 07) and *Silesaurus* (ZPAL AbIII/361), these foramina are located on the ventral surface of the parabasisphenoid.

The lateral borders of the parabasisphenoid are rather thickened. In ventral view, this bone is constricted at the base of the basipterygoid process, achieving half of the width of the basal tubera. Each basipterygoid process projects ventrolaterally, forming an angle of 45° to the transverse axis of the skull, and a right angle to its pair. As in various dinosauriforms (Dzik 2003; Yates 2007), the basipterygoid process is as long as the basal tuber, distally rounded, and there is no web of bone spanning towards its pair. The distal end of the basipterygoid process contacts the medioventral surface of the pterygoid, forming a loose articulation. The parabasisphenoid is excavated dorsolaterally to the base of the basipterygoid process, where the well-developed clinoid process projects laterocaudally (Fig. 6). The sella turcica is deep and excavates the rostrodorsal body of the parabasisphenoid, caudal to the cultriform process. This excavation is caudally delimited by the prootic and rostrolaterally by the medial margin of the clinoid process.

The cultriform process is relatively deep, stripe-shaped, and at least as long as the remainder of the parabasisphenoid (Fig. 5). Its ventral and dorsal surfaces are respectively marked by a sharp edge and a shallow longitudinal sulcus. The latter is bordered in both sides by the crests that project rostroventrally from the medial margin of the clinoid processes. Unlike some early archosauriforms (Gower & Sennikov 1996, 1997), the basal tubera and basipterygoid processes of *Lewisuchus admixtus* are horizontally aligned to each other, whereas the cultriform process and the occipital condyle are placed more dorsally,
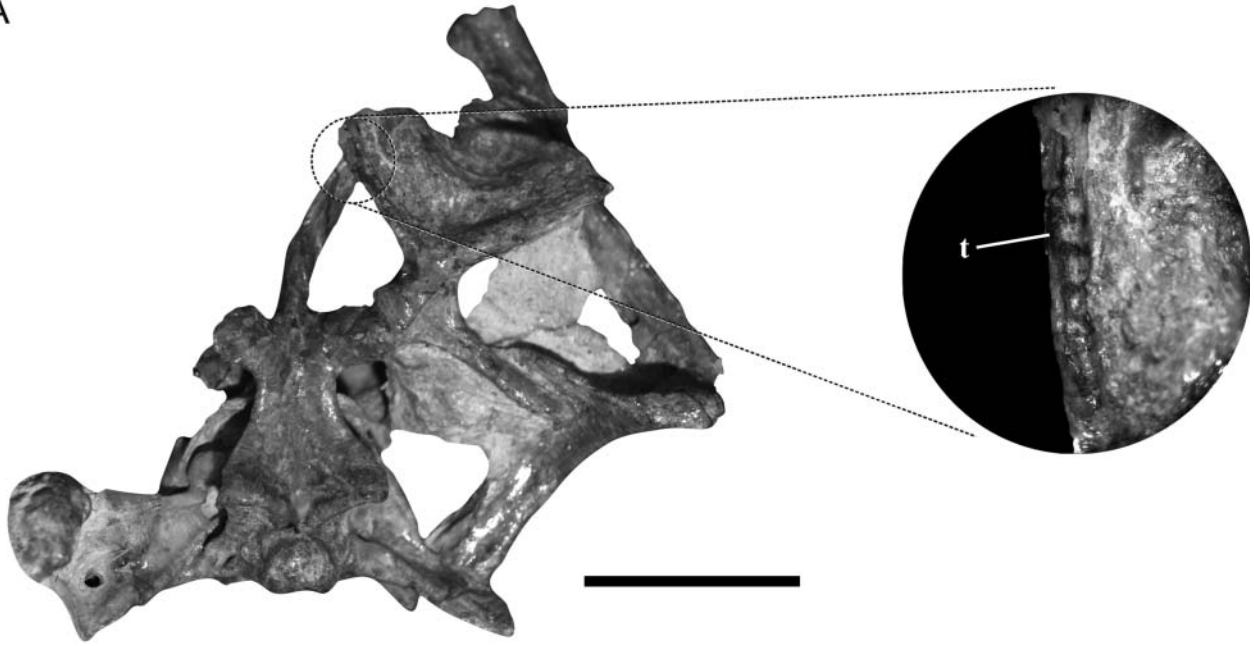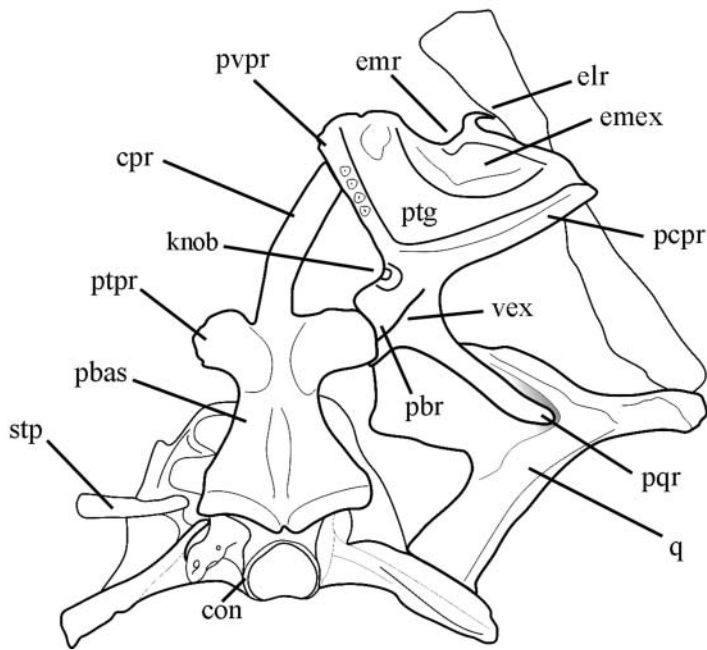
Figure 5. *Lewisuchus admixtus*, PULR 01. **A, B,** caudal portion of the skull in ventral view with a detail of the pterygoid teeth. Abbreviations: con, condylar neck; cpr, cultriform process; elr, ectopterygoid lateral ramus; emex, ectopterygoid medial excavation; emr, ectopterygoid medial ramus; knob, knob-like ventral projection; pbas, parabasisphenoid; pbr, pterygoid basisphenoid ramus; pcpr, pterygoid ectopterygoid ramus; pqr, pterygoid quadrate ramus; ptg, pterygoid; ptpr, pterygoid process (parabasisphenoid); pvpr, pterygoid vomeropalatine ramus; q, quadrate; stp, stapes; vex, ventral excavation on the pterygoid. Scale bar = 20 mm.

although also aligned to one another. This configuration is also described for basal saurischians (Yates 2003), but differs from the condition of *Silesaurus* (ZPAL AbIII/361), in which the basipterygoid processes are ventrally offset relative to the basal tubera.

As also seen in *Silesaurus* (Dzik 2003), the dorsocaudal portion of the parabasisphenoid is occupied by an ascending process (= the "middle strut" of Romer 1972c, p. 5), which fuses dorsally with the lateral surface of the prootic, and possesses a shallow sulcus on its caudoventral portion.

Quadrate. The left quadrate is partially preserved, missing portions of which include the dorsocranial region of the medial (= pterygoid) ala (Figs 2A, B, 5A, B). Similarly to most archosauriforms (Nesbitt 2011), the bone is subvertical, and the caudal edge of the head is roughly aligned with the cranio-mandibular articulation. As in *Gracilisuchus* (Brinkman 1981), the quadrate head is capped by the caudal ramus of the squamosal and the rostroventral surface of the lateral tip of the paraoccipital process. The caudal margin of the quadrate shaft is dorsoventrally concave.

The lateral (= quadratojugal) and the medial alae are set in right angles to each other. The lateral ala is broad and bends rostrolaterally, forming a dorsoventral concave area facing caudolaterally. The quadrate foramen is located in this region. It is associated with a rounded fossa that expands onto the medial margin of the quadratojugal.

Most of the ventral portion of the quadrate is concealed by the quadratojugal, and the point of maximal lateral expansion of the bone is the region of the possible squamosal/quadratojugal contact (Romer 1972c). The condyles for cranio-mandibular articulation flush ventrally, but the medial condyle is craniocaudally narrower than the lateral one.

The subtriangular medial ala of the quadrate projects further rostrally than the lateral ala. The ventral margin of the lateral ala possesses a horizontal shelf, in which the dorsal portion receives the caudal ramus of the pterygoid (Fig. 5A, B). Although slightly displaced from its original position, the rostrodorsal margin of the medial ala did not contact the lateral surface of the braincase.

Pterygoid. The preserved right pterygoid has a transversely waisted body, with a caudally opened excavation and a cranial knob-like process on its ventral surface (Fig. 5A, B). Four rami project from the pterygoid body across the caudal portion of the palate. Similarly to *Chanaresuchus* (PULR 07) and basal rauisuchians (Sereno 1991a), the basisphenoid ramus is short, caudomedially projected, and contacts the basipterygoid process of the parabasisphenoid and the medial ala of the quadrate. The latter contact occurs via a caudally directed spur-like process of this ramus.

Similarly to most archosaurs (Walker 1964; Sereno 1991a), the quadrate ramus is more slender than the basisphenoid ramus, and extends caudolaterally. By contrast, the quadrate ramus of *Chanaresuchus* (PULR 07) is dorsoventrally expanded, forming a plate-like structure. The quadrate ramus fits into the medial excavation of the quadrate medial ala (Fig. 5A, B).

The vomeropalatine and the ectopterygoid rami (Fig. 5A, B) are connected by a thin lamina projecting mediolaterally from the thickened medial rim of the former, and rostrally from the caudal border of the latter. This lamina bears an L-shape excavated area on the rostroventral portion of the pterygoid. The concave craniolateral margin of the fan-shaped lamina is tightly appressed to the medial margin of the ectopterygoid.

The vomeropalatine ramus projects rostromedially from the pterygoid body and forms a right angle to the ectopterygoid ramus. Its ventral rim bears small alveoli encased by cortical bone, elliptical in cross section, with a hint of a central canal. These are interpreted as palatal teeth (Fig. 5A). They are not as conspicuous as those of basal archosauriforms (Sereno 1991a; Welman 1998; Wu & Russell 2001) or dinosaurs (e.g. *Eoraptor*, PVSJ 512; *Eodromaeus*, PVSJ 562; *Pampadromaeus*, ULBRA-PVT016), but this may be result of poor preservation.

Ectopterygoid. The preserved left ectopterygoid is composed of a rostrocaudally elongate shaft and a dichotomous rostral portion (Fig. 5A, B). The shaft is dorsoventrally deep, slightly curved laterally, and with a thickened ventral crest extending along its rostrocaudal extension. At the rostral tip, it splits in a lateral process, which bends caudodorsally, forming a hook-like jugal ramus; and a medial process, which arcs rostromedially and contacts the craniolateral portion of the vomeropalatine ramus of the pterygoid. The bone is positioned dorsal to the pterygoid, as in other dinosauriforms (Sereno 1999; Nesbitt 2011).

The jugal ramus is short and sharply pointed at its caudodorsally bowed tip (Fig. 4). It also possesses a transverse crest on its dorsal surface, which forms part of the orbital floor. The lateral surface of the hook-like process articulates with the medial surface of the jugal, and also contacts the ventral tip of the jugal ramus of the postorbital.

The medial flange of the ectopterygoid is rostrally concave, and bordered by a distinct medial rim connected to the vomeropalatine ramus of the pterygoid. Similarly to theropods (Gauthier 1986; Sereno 1999), an excavated area (Fig. 5A, B) is formed by the ventral concavity of the medial flange, achieving its maximal depth in the confluence of the rostral rim of the flange and the ventral margin of the ectopterygoid shaft. No foramen pierces the rostroventral surface of the ectopterygoid.
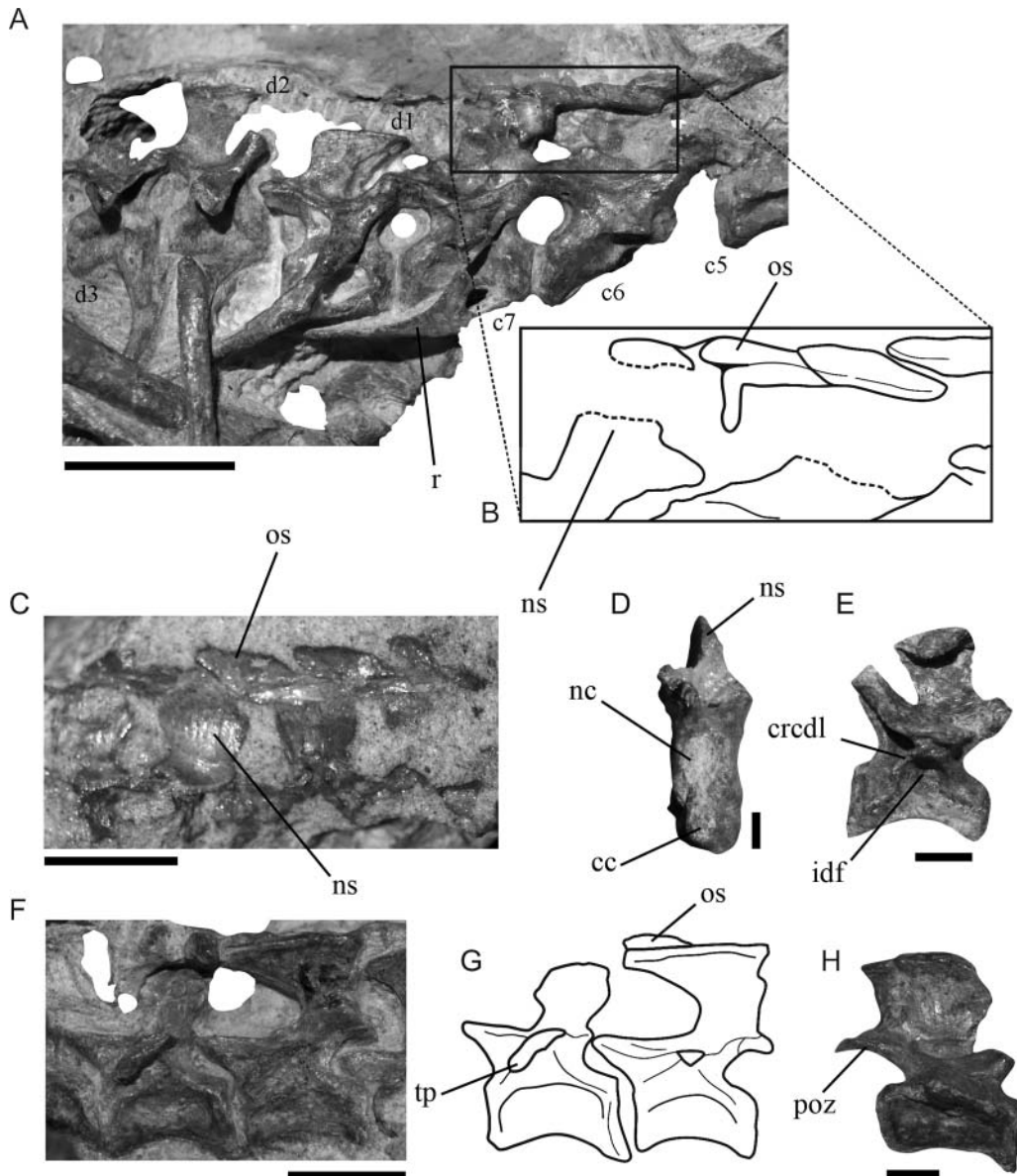
Vertebral column. The holotype of *Lewisuchus admixtus* has 16 presacral vertebrae preserved in articulation, including the atlantal intercentrum and neural arch, the axis complex (axial intercentrum, centrum and neural arch, plus the odontoid), and 14 postaxial vertebrae (Figs 7, 8). Similarly to *Marasuchus* (PVL 3870) and *Silesaurus* (Piechowsky & Dzik 2010), there is a conspicuous morphological transition between the seventh and eighth preserved vertebrae (Fig. 8A), which includes a reduction in the centrum length (approximately 20%), and a lesser ventral projection of the caudal articular facet. Although the preserved ribs articulate with both the neural arch and the ventrocranial margin of the centrum up to the 10th presacral vertebra, the ribs attached to the eighth to
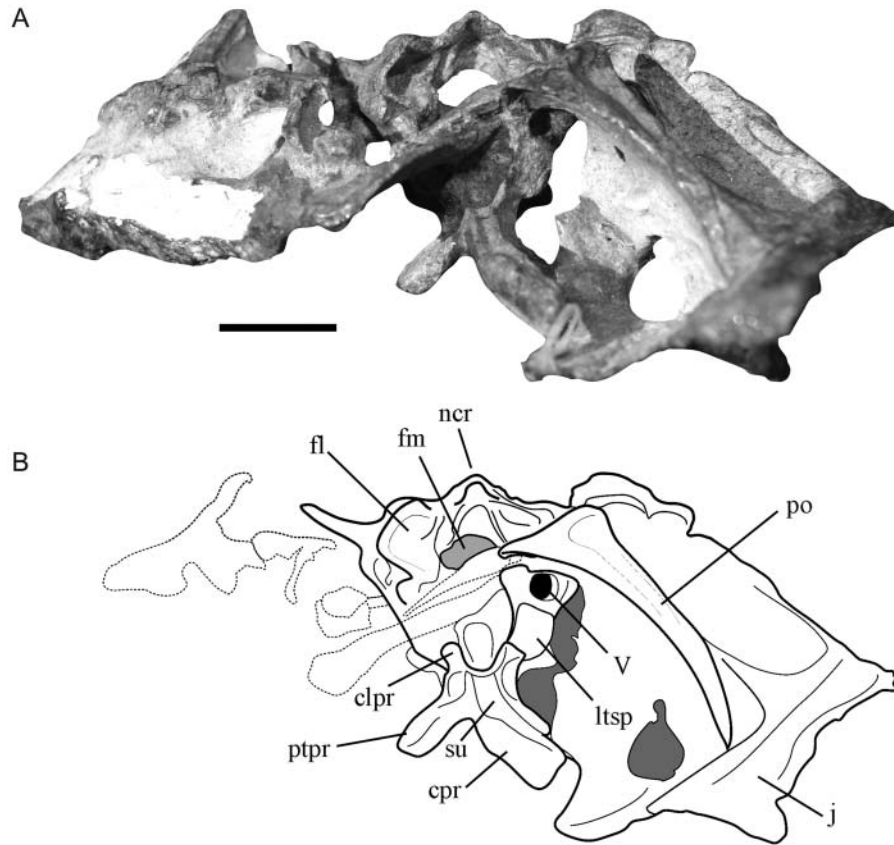
Figure 6. *Lewisuchus admixtus*, PULR 01. **A, B,** caudal portion of the skull in frontal view. Abbreviations: fl, floccular lobe; fm, foramen magnum; clpr, clinoid process; cpr, cultriform process; j, jugal; ncr, nuchal crest; ltsp, laterosphenoid; ptpr, pterygoid process (parabasisphenoid); po, postorbital; su, sulcus; V, foramen for the trigeminal nerve. Scale bar = 20 mm.
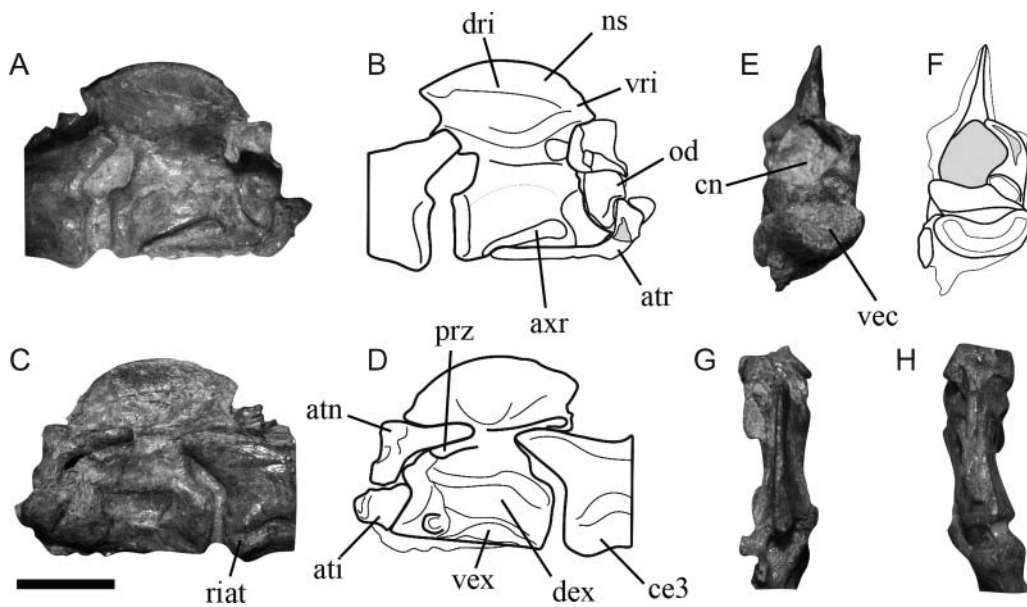
Figure 7. *Lewisuchus admixtus*, PULR 01. Atlas–axis complex in **A, B,** right and **C, D,** left lateral, **E, F,** cranial, **G,** dorsal and **H,** ventral views. Abbreviations: ati, atlantal intercentrum; atn, atlantal neural arch; atr, atlantal rib; axr, axial rib; ce3, cervical 3; cn, neural canal; dex, dorsal excavation; dri, dorsal ridge; ns, neural spine; od, odontoid; prz, prezygapophysis; riat, rib attachment area; vec, vertebral centrum; vex, ventral excavation; vri, ventral ridge. Scale bar = 10 mm.

Figure 8. *Lewisuchus admixtus*, PULR 01. Cervical and dorsal vertebrae in **A,** right lateral view, with **B,** a detail of the osteoderms. **C,** trunk vertebrae in right lateral view found with the holotype of the proterochampsid *Tropidosuchus* (PVL 4601). **D,** third cervical in cross section. **E,** second dorsal in left lateral view. **F, G,** seventh and eighth dorsal vertebrae in left lateral view. **H,** isolated caudal dorsal vertebra in right lateral view. Abbreviations: c5–7, cervical vertebrae; cc, cervical centrum; crcdl, cranial centrodiapophyseal lamina; d1–3, dorsal vertebrae; idf, infradiapophyseal fossa; ns, neural spine; os, osteoderm; poz, postzygapophysis; r, rib; tp, transverse process. Scale bars: A, E = 20 mm; C = 5 mm; D = 3 mm; F, G = 10 mm; H = 2 mm.

10th presacral vertebrae are more robust, thus the presacral vertebrae from eighth to 16th are considered as belonging to the dorsal series (Piechowsky & Dzik 2010). An isolated vertebra embedded in the slab close to the last articulated dorsal may correspond to a more caudal element within the dorsal series (Fig. 8H).

Three semi-articulated vertebrae plus the fragment of a fourth element lie close to the left scapula, on the left side of the slab (Fig. 9A). These are probably proximal caudal vertebrae. Another set of five semi-articulated vertebrae, also on the left side of the slab, but closer to the cranial cervicals (Fig. 9B), probably belong to the middle portion of the tail.

Cervical series. The atlantal intercentrum is preserved in articulation with the axial intercentrum and the odontoid process (Fig. 7A–D). The atlantal intercentrum is U-shaped in cranial view, in which the lateral tips curve upwards and bulge craniocaudally (Fig. 7E, F). The concave dorsal basin fits well with the occipital condyle of

the described skull. This concavity is shallower at the cranial margin, and deeper at the caudal border, where it receives the cranioventral margin of the odontoid process. Ventrally, the atlantal intercentrum is transversely wider than the axis (Fig. 7H). It also harbours a mediolaterally oriented shallow sulcus that is not seen in *Marasuchus* (PVL 3870) or *Silesaurus* (Piechowsky & Dzik 2010). An incomplete right rib is tightly articulated with the caudolateral and ventral margin of the atlantal intercentrum (Fig. 7A, B). The rod-like narrow shaft is parallel to the cervical column.

The left atlantal neural arch is similar to those of *Tropidosuchus* (PVL 4601), *Marasuchus* (PVL 3870) and *Silesaurus* (Piechowsky & Dzik 2010) in the presence of a robust pedicel that articulates with both the dorsolateral portion of the atlantal intercentrum and the craniolateral margin of the odontoid process. Its base is slightly wider transverselly than craniocaudally, and the ventral region is facing medially (Fig. 7A–D). As seen in *Silesaurus* (Piechowsky & Dzik 2010), the dorsal portion of the atlantal neural arch is craniocaudally elongated, with the cranial ramus projecting medially as an arched plate, roofing the laterodorsal border of the neural canal (Fig. 7E, F). The caudal ramus corresponds to the postzygapophysis plus the epipophysis, which are indiscernible from each other. The caudal ramus is a rod-like, elongated and slightly caudally flattened structure. It articulates with the dorsal margin of the reduced axial prezygapophysis, and its caudal tip does not reach the cranial edge of the axial postzygapophysis, as occurs in most archosaurs (Yates 2003).

The odontoid process (atlantal centrum, Romer 1956) is a stout piece of bone not completely co-ossified to the axial centrum (Fig. 7A, B). In right lateral view, its caudoventral margin is separated from the axial intercentrum. The dorsal margin of the odontoid process is slightly concave, and composes the rostral floor of the neural canal. As in the atlantal intercentrum, the lateral tips of the odontoid process are dorsally projected, and receive part of the ventral surface of the pedicel of the atlantal neural arch.

The axial intercentrum is completely fused with the axial centrum (Fig. 7A–D), but its caudal margin is marked by a shallow sulcus, cranioventral to which the intercentrum is bulged. The craniodorsal portion of the intercentrum is in close contact with the ventrocaudal surface of the odontoid process. By contrast, its cranioventral portion receives part of the atlantal intercentrum.

The axial centrum is transversely compressed (Fig. 7G, H). If combined with the axial intercentrum, it is craniocaudally as long as the other cervical centra, and is longer than the dorsal ones. The lateral surface of the axial centrum bears a dorsal excavation and a ventral concavity (Fig. 7C, D). The upper excavation is the deepest and extends along most of the lateral length of the centrum. It is dorsally bordered by a rugose horizontal crest, which

also demarcates the ventral edge of the neural arch. Ventrally, the excavation is bordered by another ridge that also delimits the lower concave area. The latter projects onto the ventral margin of the centrum, which possesses a sharp median keel. No lateral foramina are seen. The configuration of the lateral surface of the axial centrum described above also matches those of *Tropidosuchus* (PVL 4601), *Marasuchus* (PVL 3870) and *Silesaurus* (Piechowsky & Dzik 2010).

The parapophysis occupies a cranioventral position on the lateral surface of the centrum. Similarly to *Marasuchus* (PVL 3870), it is a bud-like area fused to the caudal margin of the axial intercentrum (Fig. 7A–D). In the right side, a rod-like rib is attached to the parapophysis. The rib is slightly expanded proximally, projects caudally as a narrower shaft, and does not reach the caudal edge of the axial centrum.

The cranial articular facet of the axis is not visible due to attachment of the odontoid process. The caudal articular facet is concave, significantly higher than wide, and with thickened borders.

Measured from the floor of the neural canal to the top of the postzygapophysis, the axial neural arch is slightly higher than the centrum (Fig. 7A–D). At mid-height, its lateral surface is laterally bulged, and bears a small crest-like prezygapophysis in the cranial portion. The postzygapophysis spans caudodorsally from the neural arch as a thin lamina, and develops a dorsomedial flange that fuses with the caudoventral margin of the neural spine. The caudodorsal surface of the postzygapophysis is slightly bulged, but there is no evidence of an epipophysis.

The transversely compressed neural spine is craniocaudally longer than the centrum. Differently from *Silesaurus* (Piechowsky & Dzik 2010), *Herrerasaurus* (PVSJ 407), *Lesothosaurus* (Sereno 1991b) and *Heterodontosaurus* (SAM-PK-1332), which possess a rather straight dorsal rim of the axial neural spine, in *Lewisuchus admixtus* this margin is strongly convex, resulting in an axe-like lateral outline. Its cranial edge is connected to the prezygapophysis by a thin lamina, and projects beyond the cranial margin of the centrum, resembling the condition of *Silesaurus* (Piechowsky & Dzik 2010). The cranial edge of the neural spine is lower than the caudal one. Two rugose ridges are seen on the lateral surface of the axial neural spine. The dorsal ridge extends along the convexity of the neural spine dorsal border. The ventral ridge extends craniocaudally along the mid-height of the neural spine. The upper ridge is present in other dinosauriforms, such as *Silesaurus* (Piechowsky & Dzik 2010) and *Heterodontosaurus* (SAM-PK-1332), but the lower one is restricted to *L. admixtus*.

The post-axial cervical centra are longer than the preserved dorsal centra (Fig. 8A, F). This is typical for basal dinosauriforms (Nesbitt *et al.* 2010), but also occurs in the enigmatic *Spondylosoma* (GPIT 479/30) and some

rauisuchians (Lautenschlager & Desojo 2011). The cervical centra are also transversely compressed and laterally concave. Contrasting with the neck vertebrae of *Tropidosuchus* (PVL 4601), rauisuchians (Benton & Walker 2002; Nesbitt 2005) and other dinosauriforms (Yates 2003; Nesbitt *et al.* 2009b), there is not a conspicuous 'keel' extending along the ventral surfaces of the cervical vertebrae of *L. admixtus*.

The transverse section of the third cervical vertebra reveals that its centrum (Fig. 8D), which is separated from the neural arch by a lateral constriction (= the upper excavation of the axis), is very low (4.2 mm high) and narrow (2.7 mm wide) if compared to the portion encasing the neural canal (6.5 mm high; 5.3 mm wide). In addition, the wall around the neural canal is broader (1.3 mm) than the outer wall of the centrum (0.7 mm). The crest that dorsally borders the upper excavation on the lateral surface of the centrum is very faint in the third cervical vertebra. It becomes more pronounced in the fourth and fifth cervical vertebrae, and is replaced by a true transverse process from the sixth cervical vertebra backwards (Fig. 8A). The thin ridge that dorsally borders the lower lateral excavation of the axial centrum is visible in all the remaining cervical vertebrae, but the lower excavation itself disappears in the fourth cervical vertebra backwards.

The caudal facet of the centrum is situated more ventrally than the cranial one, resulting in a parallelogram centrum in lateral view. As a consequence, it is ventrally offset with regard to the cranial margin of the centrum, similar to *Tropidosuchus* (PVL 4601), some crurotarsans (Nesbitt 2005), and dinosauriforms (Gauthier 1986; Sereno & Arcucci 1994b; Novas 1996).

The centrum of the third cervical vertebra bears two low knob-like processes on its cranioventral portion, the ventral of which is topologically equivalent to the parapophysis (Fig. 7C). The dorsal knob is part of the dorsolateral crest that limits the neural arch ventrally and, apparently, it serves as attachment site for the tuberculum in the third and fourth cervical vertebrae, which do not have transverse processes. In the sixth to seventh cervical vertebrae, which bear a true transverse process, the rib attaches both in the parapophyseal area and in the distal portion of the transverse process. Despite this change in the rib attachment, the dorsal knob-like process on the cranial portion of the centrum is maintained at least until the first dorsal vertebra.

The sixth cervical vertebra bears a hint of the tetraradiated pattern of lamination associated with the transverse process, a feature that becomes more conspicuous from the seventh presacral vertebra backwards (Fig. 8A). The third and fourth cervical vertebrae possess a lamina topologically equivalent to the postzygodiapophyseal lamina (*sensu* Wilson 1999) of other archosauriforms, regardless of the presence of a transverse process. This condition is similar to that of *Marasuchus* (PVL 3870), but differs

from *Silesaurus* (Piechowsky & Dzik 2010), the fourth cervical vertebra of which already shows robust laminae expanding from the transverse process. The sixth cervical vertebra of *L. admixtus* bears faint cranial and caudal centrodiapophyseal laminae. This suggests that these structures are serially homologous to the crest that dorsally borders the upper excavation of more cranial cervical vertebrae, as it is the case in *Marasuchus* (PVL 3870).

The infradiapophyseal fossa (*sensu* Harris 2006) is well developed in the sixth cervical vertebra. The cranial margin of its transverse process projects craniodorsally, but does not reach the lateral surface of the prezygapophysis. On the other hand, it forms the caudal margin of an incipient cranial infradiapophyseal fossa. The lateral area caudal to the transverse process is slightly depressed, and dorsally bordered by a robust postzygodiapophyseal lamina, which expands caudally reaching the caudal edge of the postzygapophysis.

The seventh cervical vertebra possesses a more conspicuous pattern of pneumatization. In addition to the intermediary infradiapophyseal fossa, both cranial and caudal infradiapophyseal fossae associated with the lateroventrally directed transverse process are also well developed. However, contrasting with the dorsal vertebrae, the cranial margin of the transverse process forms a prezygodiapophyseal lamina that is restricted to the base of the prezygapophysis. In the dorsal vertebrae, with the more dorsal position of the rib attachment, the cranial margin of the transverse process is confluent with the lateral margin of the prezygapophysis.

As observed in *Marasuchus* (PVL 3870) and *Silesaurus* (Piechowsky & Dzik 2010), the neural arch of the postaxial cervical vertebrae of *Lewisuchus admixtus* is significantly higher than the centrum (Fig. 8A), which partially results from the strong dorsal projection of the zygapophyses. The prezygapophysis is elongated, dorsoventrally broad at its base, and distally rounded. Its laterodorsal border is marked by a ridge that forms the prezygodiapophyseal lamina in the dorsal vertebrae. At least in the sixth and seventh cervical vertebrae, this ridge projects caudally and reaches the postzygodiapophyseal lamina. The postzygapophysis is also elongated, but less dorsally oriented than the prezygapophysis. Unlike dinosaurs (Sereno 1999; Langer & Benton 2006), there is no evidence of epipophyses in the cervical vertebrae. Instead, each postzygapophysis has a dorsal ridge that projects from the caudal margin of the neural spine.

Unfortunately, in none of the post-axial cervical vertebrae is the neural spine completely preserved. The seventh cervical vertebra preserves the basal portion of the neural spine and its distal tip may correspond to the fragment of bone situated immediately above it (Fig. 8A, B). The row of elongated pieces of bone above the cervical vertebrae was identified as dorsal 'scutes' (i.e. osteoderms) by Romer (1972c, p. 8), which is endorsed herein. These are

imbricate, with the cranial ends underlying the caudal portion of the preceding element. A conspicuous lateral furrow delimits each osteoderm. The ventral surface of these elements is flat, and their dorsal margin is bulged. A similar morphology is seen in the 15th preserved vertebra (= ninth dorsal vertebra), in which the strongly cranially expanded distal end of the neural spine is capped by an osteoderm, as in the cervical vertebrae (Fig. 8F, G). Accordingly, the distal tip of the neural spine is cranially expanded both in the cervical and dorsal series. As a result, the cranio- and caudodorsal edges of the neural spine tips in adjacent vertebrae contact one another.

Within dinosauriforms, the presence of cervical osteoderms is unambiguous in the theropod *Ceratosaurus* (Gilmore 1920) and ornithischians (Norman *et al.* 2004b). In the latter, the elements are disposed in parasagittal rows, rather than along the median line of the vertebral column. The morphology of the osteoderms in *L. admixtus* is comparable to that of *Tropidosuchus* (Fig. 8C) and *Gracilisuchus* (Brinkman 1981), in which one 'scute' is attached to each neural spine. In *Chanaresuchus* (PVL 4575), there is also a single row of osteoderms, but at least two elements associate to each cervical neural spine. The cervical vertebrae of *Marasuchus* (PVL 3870) are more similar to those of *Silesaurus* (Piechowsky & Dzik 2010), with low and apparently unroofed neural spines.

A rib is attached to the last cervical vertebra (Fig. 8A). It follows the general pattern of the archosaur cervical ribs (Romer 1956), with two cranially directed processes, the medial of which is the longest, and corresponds to the rib head (capitulum). It is cranially bulged, and contacts the cranioventral portion of the centrum. The dorsal process corresponds to the rib tubercle (tuberculum). It is shorter than the head, and attaches to the distal portion of the transverse process. The processes are orthogonal to each other. Similarly to basal dinosauriforms (Sereno 1999; Dzik 2003), the whole rib lies subparallel to the cervical vertebrae and is almost twice (1.8 ×) as long as the last cervical centrum. The lateral surface of the rib is flat on the tubercle and the cranial portion of the shaft. More caudally, the shaft is rod-like, and dorsolaterally and ventrally marked by faint longitudinal ridges.

Dorsal series. Nine dorsal vertebrae are preserved in articulation, and an isolated vertebra probably belongs to the caudal portion of the trunk. They are similar to the dorsal vertebrae of most dinosauriforms (Novas 1994; Sereno & Arcucci 1994b; Dzik 2003), and differences are concentrated in the neural spine.

The preserved dorsal centra are approximately of the same length, and considerably shorter than the cervical centra. As in the neck vertebrae, each centrum has a lateral excavation dorsally bordered by a thick crest, which marks the ventral limit of the neural arch (Fig. 8D–H). The caudal articular facet is slightly offset below the cranial facet, and at least the third and seventh dorsal centra have the caudal portion ventrally projected, similar to the last cervical. No keel or sulcus is present on the ventral surface of the dorsal centra, and no foramina pierce their lateral surface.

As in the cervical vertebrae, the neural arch is higher than the respective centrum (Fig. 8F, G), and buttressed by deep pedicels. At least until the third dorsal vertebra, the rib attaches both to the cranial portion of the centrum and to the distal tip of the transverse process. In the fourth dorsal vertebra (not shown), the rib head attaches to the limit between the centrum and the neural arch, but from the fifth element (the 12th presacral vertebra) backwards, the rib head clearly attaches on the cranial portion of the cranial centrodiapophyseal lamina, very close to the distal portion of the transverse process (which is better seen in the sixth dorsal vertebra). Accordingly, from this vertebra backwards, the rib attachment has completely shifted to the neural arch, as also described for basal saurischians (Yates 2007). Even in the three cranialmost dorsal vertebrae, the parapophyses gradually get a more dorsal position on the centra.

The transverse process is dorsoventrally deeper than those of the cervical vertebrae. They are quadrangular in dorsal view, and its craniodistal tip is more laterally projected than the caudodistal edge. As in most dinosauriforms (Welles 1984; Wilson 1999; Yates 2003; Piechowsky & Dzik 2010), the laminae associated with the transverse process are well developed. The cranial centrodiapophyseal lamina projects from the ventral surface of the transverse process to the parapophysis, i.e. the cranial margin of the centrum. With the shift of the rib head attachment to a point closer to the distal portion of the transverse process, only the cranial ramus of the lamina remains, and is equivalent to the cranial centroparapophyseal lamina (Wilson 1999).

In the first to third dorsal vertebrae, the prezygodiapophyseal lamina projects craniodorsally, but from the fourth dorsal vertebra backwards, this lamina acquires a horizontal orientation. This probably results from the less conspicuous dorsal inclination of the prezygapophysis.

The three fossae ventral to the transverse process and their laminae are well developed and deeper in the dorsal vertebrae than in the seventh cervical vertebrae. The caudal infradiapophyseal fossa is medially walled by the neural arch pedicel, and unlike some dinosauriforms such as *Silesaurus* (Piechowsky & Dzik 2010), *Guaibasaurus* (MCN-PV 2355, UFRGS PV-0725-T) and *Plateosaurus* (GPIT mounted skeletons), there is no evidence of a vertical lamina within it (Langer *et al*. 2010). In *Lewisuchus admixtus* the postzygapophysis articular facet is caudal to the caudal edge of neural arch pedicel. Similarly to the prezygapophysis, the postzygapophysis of the three cranialmost dorsal vertebrae is more inclined dorsally than in the more caudal vertebrae. No hyposphene–hypanthrum

articulation was recognized, but this may be an artefact as the region is not well preserved or exposed in any dorsal vertebra.

The neural spine of the dorsal vertebrae is only slightly higher than the neural arch (measured from the floor of the arch to the top of the postzygapophysis). Its cranial margin is straight and inclined forward due to a strong cranial projection of its craniodorsal edge, forming a wedge-like structure in lateral view. In the eighth dorsal vertebra, the cranial margin of the neural spine is strongly notched and its craniodorsal tip contacts the caudodorsal edge of the preceding neural spine (Fig. 8F, G), similar to the dorsal vertebrae of *Marasuchus* (PVL 3870). A modified version of this configuration is also seen in *Lagerpeton* (Arcucci 1986; Sereno & Arcucci 1994a). In *Silesaurus* (Piechowsky & Dzik 2010), the neural spine of some dorsal vertebrae also contacts adjacent neural spines, but these structures are rectangular (Dzik 2003; Piechowsky & Dzik 2010) rather than subtriangular as in *L. admixtus* and *Marasuchus* (PVL 3870).

The distal portion of all preserved neural spines is laterally bulged, probably for articulation with the osteoderms. Although this is possibly homologous to the spine tables of other archosauriforms (Walker 1961; Nesbitt 2011), it is less expanded than in crurotarsans (Gower & Schoch 2009) and some dinosauriforms (Novas 1994). As previously mentioned, the neural spine of the eighth dorsal vertebra is capped by an elongated bone, which is very similar to the cervical osteoderms mentioned by Romer (1972c). This is separated from the neural spine by a ventral furrow, suggesting that these are independent ossifications.

The isolated possible dorsal vertebra is similar to the remaining elements of the vertebral column. The centrum is elongated; the lateral margin of the postzygapophysis is crested, and the distal end of the neural spine is bulged (Fig. 8H). Yet, conspicuous differences with more cranial dorsal vertebrae include: reduction of the lateral excavation of the centrum; transverse process (although incomplete) continuous with a cranial lamina with no evidence of a rib attachment; less conspicuous set of laminae associated with the transverse process; elongated neural spine, forming a rectangular plate rather than a wedge-like structure, with its caudodorsal tip slightly projected backwards. Other features of this vertebra include a wider than high neural canal, quite different from those of the cranial cervical vertebrae. The cranial articular facet is slightly excavated, as seen in all other preserved vertebrae.

Several dorsal ribs are scattered in the slab, but these are articulated, even if partially, in the first to third dorsal vertebrae (Fig. 8A). The shaft is more robust than in the cervical series. The head is cranially bulged and contacts the cranioventral portion of the centrum at least in the first and second dorsal vertebrae. As in the last cervical vertebra, the tubercle is also shorter than the head, and both

converge to the distally elongated shaft. The margin between the tubercle and the shaft is concave, whereas the margin between the latter and the head is convex. Indeed, the proximal portion of the rib is curved. The first dorsal rib is only slightly angled laterally to the longitudinal axis of the column. The shaft of trunk ribs second to fourth are gradually more laterally and ventrally directed. They are caudally concave at the proximal portion, and the concavity becomes a slim sulcus due to the distal narrowing of the shaft. No ribs are clearly preserved from the fifth dorsal vertebra backwards, but an element embedded within the slab belongs to the middle portion of the dorsal series. It provides an estimate of the rib length, which is at least five times the length of the longest preserved dorsal vertebra.

Caudal series. Three possible proximal caudal vertebrae are preserved close to the left scapula. The centra are about as long as the dorsal centra (Fig. 9A), and both the proximal and distal articular facets are more excavated than in other vertebrae. The ventral margin of the distal facet has flat lateroventral surfaces for the articulation with haemal arch. The neural arch is as high as in the previously described vertebrae. The prezygapophysis is strongly inclined dorsally, and the postzygapophysis is similar to those of the dorsal vertebrae, i.e. horizontally directed, with lateroventrally facing articular surface, and lateral surface marked by a strong ridge. In none of the caudal vertebrae is the transverse process well preserved, but they are transversely deep and rounded at the proximal end. Both the prezygodiapophyseal and cranial centrodiapophyseal laminae are present. The cranial, intermediary and caudal infradiapophyseal fossae are present, but quite smaller in comparison to those of the dorsal vertebrae. The condition is similar to the proximal caudal vertebrae described for *Silesaurus* (Piechowsky & Dzik 2010).

The neural spine of the caudal vertebrae is distinct from those of the presacral vertebrae. It does not possess a proximal expansion at the dorsal tip, nor has osteoderms associated to it. The neural spine as a whole is restricted to the caudal portion of the neural arch, as also seen in the middle caudal of *Silesaurus* (Piechowsky & Dzik 2010). In the third preserved caudal vertebra, the proximal portion and the dorsodistal edge of the neural spine are missing. Its apex is lateromedially bulged, as in the presacral vertebrae. The caudal margin of the neural spine is concave, and merges with the dorsomedial surface of the postzygapophyses, forming a spinopostzygapophyseal lamina.

On the right side of the slab, close to the cranial cervical vertebrae, a sequence of five incomplete vertebrae is seen (Fig. 9B). The centra are as long and as high as the dorsal centra; the incomplete transverse process is deep, and the base of the neural spine appears axially elongated, with a hint of a dorsal projection in the distal portion. Although a distinct ventrodistal facet for haemal arch attachment is not conspicuous, given the overall resemblances with the
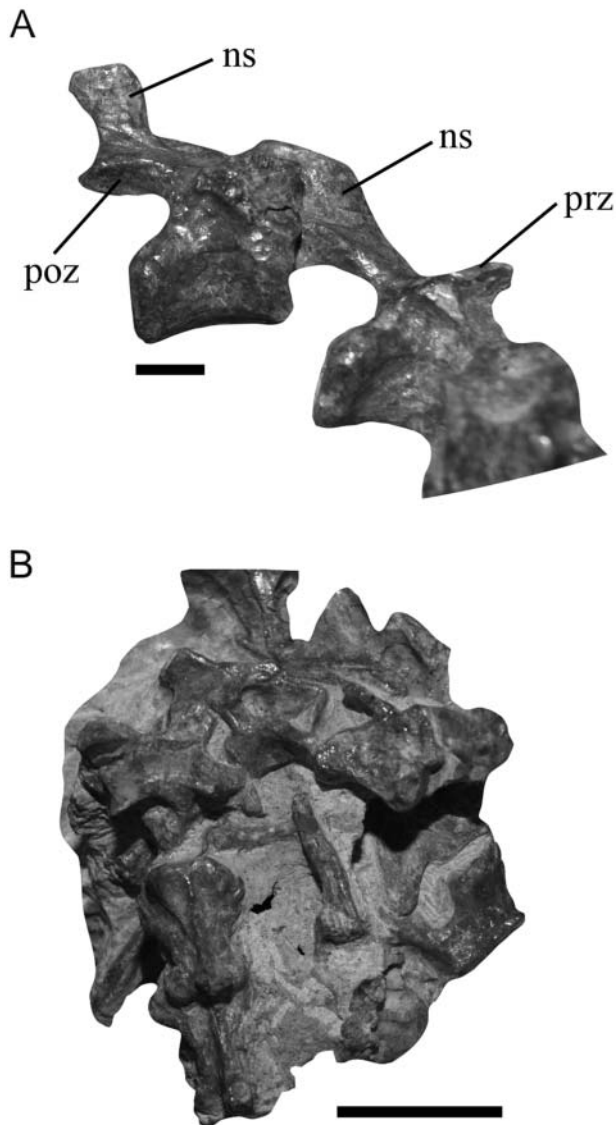
Figure 9. *Lewisuchus admixtus*, PULR 01. Isolated caudal vertebrae in **A,** right lateral and **B,** dorsolateral views. Abbreviations: ns, neural spine; poz, postzygapophysis; prz, prezygapophysis. Scale bars: A = 5 mm; B = 20 mm.

caudal vertebrae previously described, these elements are tentatively identified as proximal to middle caudal vertebrae of *Lewisuchus admixtus*. One of these vertebrae bears a foramen on the lateral surface of the centrum. Due to poor preservation, this occurrence cannot be confirmed in the remaining vertebrae.

Scapular girdle and forelimb. Romer (1972c) described two scapulocoracoids and humeri associated with the holotype of *Lewisuchus admixtus* (Fig. 10A–D). The right scapulocoracoid, now isolated, was attached to the fourth and fifth cervical vertebrae, with its medial area facing laterally (Romer 1972c, fig. 6). A portion of the humeral head was close to it, but not articulated to the glenoid.
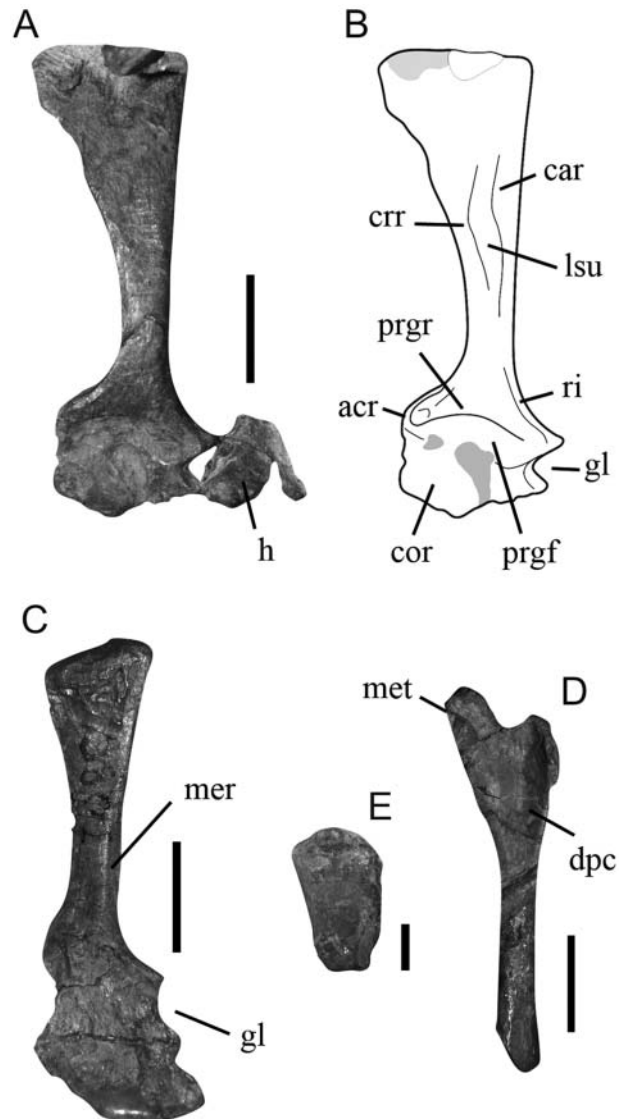
Figure 10. *Lewisuchus admixtus*, PULR 01. **A, B,** left and **C,** right scapulae, respectively, in lateral and medial views; **D,** left and **E,** right humerus, respectively in medial and lateral views. Abbreviations: acr, acromial process; car, caudal ridge; cor, coracoid; crr, cranial ridge; dpc, deltopectoral crest; gl, glenoid; h, humerus; Isu, lateral sulcus; mer, medial ridge; met, medial tuberosity; prgf, preglenoid fossa; prgr, preglenoid ridge. Scale bars: A–D = 30 mm; E = 10 mm.

Both are rather different from the left elements, which are articulated to each other and in the expected position relative to the vertebral column. Therefore, the description of the scapular girdle and limb will be based on the left elements, and the differences with the right ones are stressed along.

Scapulocoracoid. The lateral surface of the left scapulocoracoid is exposed (Fig. 10A, B). It is relatively well preserved, but the ventral margin of the coracoid is

missing, and the distal scapular blade is concealed by sediment associated with the caudal vertebrae.

In general, the scapula is very similar to that of *Silesaurus* (ZPAL AbIII/362). It is elongated, medially curved, and its body is ventrally excavated by a deep preglenoid fossa (*sensu* Langer *et al.* 2007a). At the ventral margin of the glenoid, a short and incomplete ridge marks the limit between scapula and coracoid, although they are co-ossified. Contrasting with *Chanaresuchus* (PVL 4575), in which the scapula and coracoid are not fused, the co-ossification of the scapula and coracoid is seen in dinosauriforms such as *Marasuchus* (PVL 3871), *Silesaurus* (ZPAL AbIII/362), *Heterodontosaurus* (SAM-PK-1332), and partially in *Herrerasaurus* (PVSJ 53) and *Saturnalia* (MCP 3844-PV). A craniocaudal preglenoid ridge (*sensu* Langer *et al.* 2007a) borders the dorsal margin of the preglenoid fossa and projects both cranially and caudally onto the lateral surface of the scapula.

The acromial process has a pyramid-like shape and is ventrally bordered by the cranial extension of the preglenoid ridge (Fig. 10A, B). Its lateral surface is bulged and its dorsal margin forms an angle of 120° to the cranial margin of the scapular blade. This is distinct from the condition seen in basal dinosaurs (e.g. *Herrerasaurus*, *Saturnalia*; Sereno 1994; Langer *et al.* 2007a; Remes 2007), in which that angle is lower. In contrast, this configuration agrees with that of silesaurids (Dzik 2003; Ferigolo & Langer 2007). The scapular glenoid is composed of a ventrocaudal projection of the scapular body, continuous with the caudal margin of the blade. Dorsolaterally, it bears a short ridge, which corresponds to the reduced tubercle for the triceps tendon, as observed in dinosauriforms (Langer *et al.* 2007a; Remes 2007; Yates 2007). In contrast, this structure is far more expanded in crurotarsans (Chatterjee 1978; Gower & Schoch 2009), probably due to the enhanced extensor capability of the antebrachium promoted by the triceps-group muscles (Meers 2003). The articular surface is directed ventrocaudally and displays a thickened outer rim.

As in *Silesaurus* (ZPAL AbIII/362), the scapular blade is concave along the cranial margin and nearly straight on the caudal border (Fig. 10A, B). Its minimal craniocaudal width is in the ventral portion. Dorsally, the blade expands craniocaudally, achieving its maximal breadth at the dorsal end. The width of the dorsal expansion accounts for less than one quarter of the total scapular length, differently from the strongly enlarged dorsal margin of the scapula attributed to *Marasuchus* (Bonaparte 1975; Sereno & Arcucci 1994b; but see Remes 2007).

The scapular blade is also transversely wider in the ventral portion (Fig. 10A, B). In this region, its caudal margin is flattened, laterally bound by a craniocaudally wide and dorsoventrally elongated crest extending along the laterocaudal portion of the blade. On the cranial portion, a faint vertical ridge also extends along the scapular blade. Both ridges border a dorsoventrally elongated and somewhat depressed area on the central portion of the lateral surface of the blade. This morphology is similar to that of *Herrerasaurus* (PVSJ 53), although its blade differs from that of *L. admixtus* because it is craniocaudally short, and has relatively straight cranial and caudal margins.

The coracoid/scapula contact is nearly indistinguishable, but along with the caudal glenoid crest, the ventral limit of the preglenoid fossa marks more cranially the dorsal edge of the coracoid (Fig. 10A, B). The lateral surface of the coracoid is damaged, and the exact position of the coracoid foramen is not clear. The preserved portions suggest that the coracoid was elliptical, and as deep and as long as the scapular body. The articular surface of the glenoid is caudodorsally oriented and possesses a faint ridge bordering its lateral rim. Its subglenoid portion is not preserved, and the presence of a caudoventral process cannot be determined.

The right scapulocoracoid (Fig. 10C) has some marked differences relative to its counterpart, such as a less pronounced preglenoid fossa and ridge; a deeper glenoid cavity, a narrower and shorter blade; a more pronounced notch between the caudal margin of the blade and the glenoid; a craniocaudally wider bulged area on the ventral portion of the scapular blade rather than a caudal thick crest, and the absence of the dorsoventral central depression on the blade. These differences may be taphonomic, as noted for the maxilla. Conversely, several resemblances with the left scapulocoracoid suggest that it actually belongs to the holotype. These include: a scapular blade with a concave cranial margin, nearly straight caudal margin, and a more projected caudodorsal edge; a caudolateral ridge above the glenoid, corresponding to the reduced triceps tubercle, and a laterally bulged acromial process. The association of the right pectoral girdle with the holotype close to the neck–trunk contact reinforces this conclusion.

Humerus. The left humerus of *Lewisuchus admixtus* is partially articulated to the scapulocoracoid, but displaced from its original position (Fig. 10D). The bone is incomplete, lacking the proximalmost surface of the head, parts of the deltopectoral crest and the distal portion. It has a straight shaft, as seen in *Silesaurus* (ZPAL AbIII/362) and *Marasuchus* (PVL 3871), and the relatively stout medial tuberosity articulates with the glenoid as in the latter form and basal dinosaurs (Sereno 1994).

The proximal margin of the humerus is not entirely preserved, but its transverse section is cranially concave (Fig. 10D). This cranial excavation is deeper and closer to the lateral portion of the bone than to the medial, extending ventrally until the level of the ventral edge of the deltopectoral crest.

The deltopectoral crest projects craniolaterally from the proximal end of the humerus and is not as prominent as in *Chanaresuchus* (PVL 4575), *Marasuchus* (PVL 3871), and

especially basal dinosaurs (Santa Luca 1980; Sereno *et al.* 1993; Langer *et al.* 2007a; Nesbitt *et al.* 2009b). It forms an angle of 160° to the transverse axis of the proximal end of the humerus in proximal view. Its caudal surface is excavated by a longitudinal sulcus along most of its extension, and its distal projection reaches between 45 and 50% of the total preserved length of the humerus (4.7 cm), but the stouter portion is located within the 25% of that length, as also seen in *Silesaurus* (ZPAL AbIII/362). Although both the proximal and distal portions of the humerus are not preserved, these proportions are reasonably accurate.

The humeral shaft is proximodistally well elongated if compared to that of some early dinosaurs (e.g. *Saturnalia*), but resembles the condition of *Marasuchus* (PVL 3871), *Agnosphitys* (Fraser *et al.* 2002) and *Silesaurus* (ZPAL AbIII/362). In transverse section, the shaft is nearly rounded at mid-length, but becomes transversely expanded distally. The incomplete distal part of the left humerus bears a slight rotation with regard to the proximal portion (Remes 2007).

The proximal fragment of the right humerus associated with the holotype (Fig. 10E) is more robust than the articulated left bone, and the deltopectoral crest appears to be less distally projected.

Hindlimb. Romer (1972c) referred a femur, a tibia, and metapodial elements to the holotype of *Lewisuchus admixtus*. However, the described structures of the femur, i.e. 'femoral head' and the 'greater trochanter', are more properly interpreted as the cnemial crest and the caudoproximal condyles of a tibia (Fig. 11A–D; Arcucci 1998; Nesbitt 2011). Additional evidence for this interpretation is the absence of cranial and fourth trochanters, variably observed in archosaurs. The identification of the other elongated bone as a tibia (Romer 1972c) is probably correct. The metapodial remains probably belong to a proterochampsid.

There is no definitive evidence that the preserved tibiae belong to the holotype of *L. admixtus*. However, the morphology of the tibia is comparable to that of basal dinosauriforms (Fig. 11E), with a stout cnemial crest and a nearly straight and slender shaft. In addition, they are of the dimensions expected for the pelvic epipodium of *L. admixtus*, if this is scaled with an updated reconstruction of *Silesaurus* (Piechowsky & Dzik 2010). In the latter, the cervical series is about 10% longer than the tibia, and an equivalent proportion is observed in *L. admixtus*.

Tibia. The left tibia is more complete than the right one, and will serve as a reference to the following description (Fig. 11A–D). The proximal portion of the tibia is crushed, and parts of the proximal and distal regions are missing. The cnemial crest is stout, craniolaterally projected, and conspicuously separated from the proximal portion of the shaft by a lateral sulcus. By contrast, the
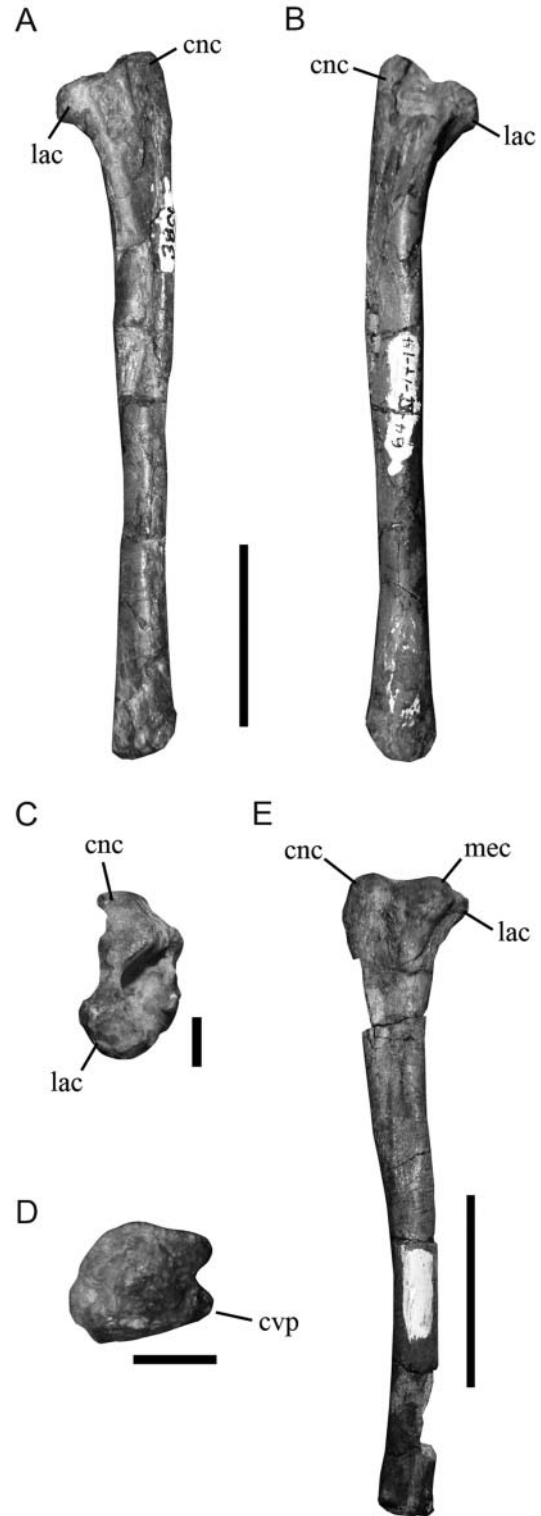
Figure 11. *Lewisuchus admixtus*, PULR 01, and cf. *Pseudolagosuchus*, 'UPLR 53'. Right tibia of *L. admixtus* in **A,** lateral, **B,** medial, **C,** proximal and **D,** distal views; **E,** left tibia assigned to *Pseudolagosuchus* in lateral view. Abbreviations: cnc, cnemial crest; cvp, caudoventral process; lac, lateral condyle; mec, medial condyle. Scale bars: A, B, E = 30 mm; C, D = 5 mm.

cnemial crest of typical silesaurids is straight and poorly expanded (Irmis *et al.* 2007a; Nesbitt *et al.* 2010). The lateral sulcus extends proximodistally along the cranial portion of the lateral surface of the tibia. Caudal to this sulcus, there is a thick and low distinct area that cranially borders another proximodistal sulcus, which marks the cranial limit of the fibular condyle. Both lateral sulci and the bulged low area lie within a large fossa that occupies most of the lateral surface of the proximal third of the tibia. The lateral condyle of the proximal tibia is expanded and caudally rounded. The tibial condyle is not preserved, and its position relative to the caudal edge of the fibular condyle cannot be assessed. The medial surface of the proximal end of the tibia is convex.

As in several gracile archosauriforms, including *Tropidosuchus* (PVL 4601), *Gracilisuchus* (Brinkman 1981), *Lagerpeton* (PULR 06, PVL 4619) and *Marasuchus* (PVL 3870, 3871), the tibial shaft of *Lewisuchus admixtus* is elongated, straight and, where not crushed (distal midlength), rounded in cross section. A distinct edge extends proximodistally along the caudal surface of the shaft.

The distal surface bears a shallow concavity for the reception of the astragalar ascending process. The caudoventral process (*sensu* Novas 1996) is not expanded laterally as in dinosaurs, but this portion of the distal tibia is incomplete.

Inclusivity of *Lewisuchus admixtus*

Archosauriform remains found together with the holotype

An incomplete right dentary (Fig. 12A–C) was also originally referred to *L. admixtus* (Romer 1972c), based on its size and morphology of the teeth. Indeed, the dentary teeth are similar to those of the maxillae in the presence of labiolingually compressed and caudally curved crowns with nine serrations per mm (left maxilla). However, no unambiguous evidence supports its assignment to the holotype. Besides the fact that this dentary was found isolated from the other cranial remains, it shares a potential synapomorphy with the dentary of *Chanaresuchus* (PULR 07): the low and rostrocaudally elongated crest on the lateral surface of the bone. This character cannot be evaluated in other proterochampsids due to the lack of more complete specimens (Trotteyn *et al.* 2013). Pseudosuchians in general lack this feature (Nesbitt 2011). Within dinosauriforms, ornithischians possess a pronounced bevelled eminence (Norman *et al.* 2011) on the lateral surface of the dentary rather than an elongated and low crest. Some early sauropodomorphs (e.g. *Panphagia*, PVSJ 874) also have a lateral crest on the dentary, but in this case it is more pronounced and begins further caudally on the dentary. Additional characters shared with the dentary of *Chanaresuchus* reinforce a possible proterochampsids

affinity for the isolated dentary. These include the rostrocaudally long and dorsoventrally low profile of the bone and the foramen-sized rostral excavations aligned close to its alveolar margin.

The assignment of the pedal elements found within the slab to *L. admixtus* (Romer 1972c, fig. 8) is also dubious (Fig. 12H–J). In fact, they share a unique combination of characters with the proterochampsid pes (e.g. *Chanaresuchus*, PVL 4575), including the elongated metatarsals and phalanges, enlarged metatarsal II, and narrow unguals with straight flexor margin (Romer 1972a; Arcucci 1990). Thus, the isolated partial pes is referred to an indeterminate proterochampsid until further evidence is available.

A small left astragalus is associated with the type material of *L. admixtus* (Fig. 12E–G). It was not described by Romer (1972c), and no reference to it was found in the literature. Its overall morphology suggests archosauriform affinities (Arcucci 1990; Sereno 1991a; Sereno & Arcucci 1994b), but its association to *L. admixtus* is uncertain. The astragalus is transversely wider than craniocaudally long. The laterocranial portion bears a stout pyramidal ascending process, which is buttressed by four laminae: two are caudally directed, and two located on the cranial portion. This pattern is also present in other gracile archosauriforms from the Chañares Formation, including *Tropidosuchus* (PVL 4601), *Marasuchus* (PVL 3870) and *Pseudolagosuchus* (MACN 18954). In contrast, the ascending process of the astragalus associated with the specimen PVL 3454 (*Pseudolagosuchus*; Supplemental Table 1; Arcucci 1987), is strongly craniocaudally elongated.

The craniomedial lamina merges with the cranioproximal border of the astragalus, and the craniolateral lamina composes the cranial wall of the articular surface that receives the distal end of fibula (Fig. 12E, F). The cranial surface of the ascending process bears a fossa, the depth and mediolateral breadth of which compare with those of *Tropidosuchus* (PVL 4601). In *Marasuchus* (PVL 3870) and other basal dinosauriforms (Dzik 2003), this excavation is considerably smaller. Similarly to *Tropidosuchus* (PVL 4601), the caudomedial lamina merges with the thick caudoproximal border of the astragalus body, and the caudolateral lamina terminates right medial to the caudolateral margin of the bone. Between the caudal laminae, the caudal surface of the ascending process possesses a shallow concavity, which in proximal view appears like a triangular notch, being followed by the vertical caudal surface of the astragalus. Consequently, a caudal basin for reception of the tibial caudoventral process is not seen, suggesting a different type of articulation with the pelvic epipodium than that described for early dinosauriforms (Novas 1989, 1996; Dzik 2003).

The proximal surface of the astragalus has two depressed areas. The lateral one is short and narrow, and corresponds to the surface for fibular articulation. This area is caudoventrally limited by a transverse sulcus,
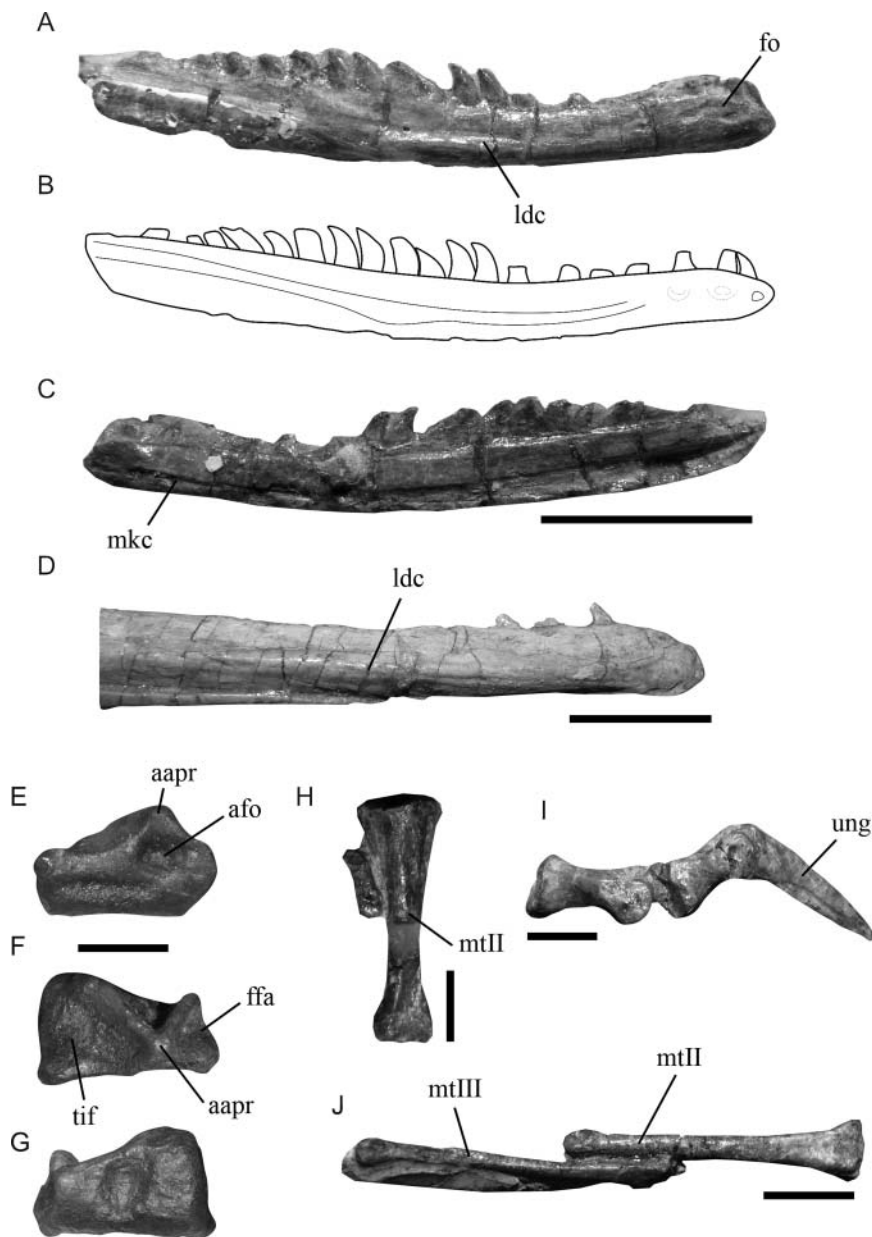
Figure 12. Archosauriform remains found in *Lewisuchus* concretion. Dentary in **A, B,** lateral and **C,** medial views; mandible of *Chanaresuchus* (PULR 07) in **D,** lateral view; left astragalus in **E,** cranial, **F,** dorsal and **G,** ventral views; pedal elements, including **H, J,** isolated metatarsals and **I,** distal portion of digit. Abbreviations: aapr, astragalar ascending process; afo, astragalar foramen; ffa, fibular facet; fo, foramen; ldc, lateral dentary crest; mkc, Meckelian channel; mt metatarsal; tif; tibial facet; ung, ungual. Scale bars: A–D = 20 mm; E–H = 5 mm; I = 10 mm.

similar to the condition of *Chanaresuchus* (Sereno 1991a). The medial area is transversely and craniocaudally longer, and receives the distal tibia. In dorsal view, the medial rim of the astragalus is significantly longer craniocaudally than the lateral rim. The craniomedial corner bears a small dorsal process, which does not match the strongly dorsally curved medial portion of the astragalus of PVL 3454 (Arcucci 1987). A transversely oriented shallow sulcus divides the cranial portion of the astragalus in a shallower upper portion and a deeper ventral portion.

The ventrolateral margin of the astragalus is craniocaudally deeper than the ventromedial margin (Fig. 12G). This condition is similar to that of *Tropidosuchus* (PVL 4601), reinforcing the proterochampsid affinities for this element.

Comparisons with *Pseudolagosuchus major*
Arcucci (1987) erected *P. major* based on the holotype plus three referred specimens (the hypodigm *sensu* Simpson 1940). Novas (1996, p. 727) referred to this species a non-numbered specimen mislabelled as 'UPLR 53',

which includes a complete femur and tibia. This specimen is probably a silesaurid and may represent another individual of *P. major*. Other authors (Hutchinson 2001; Carrano 2006) ascribed an additional specimen (PVL 3456) from the Chañares Formation to *Lewisuchus* in the context of its possible synonym with *Pseudolagosuchus* (Arcucci 1987; Arcucci 1998). Another specimen collected from the Chañares Formation (PVL 3455) resembles those mentioned by Arcucci (1987), but its affinities are unclear. The aforementioned material is summarized in Supplemental Table 2, and will be reviewed elsewhere.

The only bone of the holotype of *L. admixtus* also preserved in the holotype of *P. major* is the tibia. There is a size difference between these (*P. major* is about 20% larger), but both are badly preserved at their proximal and distal portions, hampering comparisons. Other tibiae referred to *P. major*, including those of the specimens PVL 3454, PULR 53 and 'UPLR 53' are also smaller than that of its holotype (PVL 4269), but their distal portion are in general similar. Yet, a set of diagnostic characters that unites all of them in the same taxon cannot be constructed. Nonetheless, the tibia of 'UPLR 53' is the best-preserved one (Fig. 11E), and differs from that of *L. admixtus* in the presence of a conspicuous cranial curvature of the ventral part of the shaft, which is also seen in *Silesaurus* (ZPAL AbIII/363).

Apart from the tibia, other bones preserved in the holotype of *L. admixtus*, as well as in the specimens attributed to either that taxon or *P. major* include only an incomplete axis and the articulated third and fourth cervical vertebrae of PULR 53 (Arcucci 1987). These are superficially similar to the vertebrae of *L. admixtus* in their size and the presence of a broad excavation on the lateral surface of the centrum. Yet, these characters are variously present in proterochampsids, as well as in *Marasuchus* (Sereno & Arcucci 1994b). In addition, PULR 53 is very poorly preserved and its assignment to any small bodied archosaur from the Chañares Formation is not clear. In this sense, the available information from the material attributed to any of these taxa is not enough for a formal synonymization between them (see discussion of Nesbitt *et al.* 2010). For this reason, they are coded as independent taxonomic operational units in the phylogenetic analyses conduct herein.

Phylogenetic analysis

Dataset and procedure
A new character–taxon data matrix for Dinosauromorpha was assembled (Supplemental Appendices 1, 2), mostly based on the comprehensive study of Nesbitt (2011), in an attempt to infer the position of *Lewisuchus admixtus* on the light of the reinterpretation of its anatomical traits presented above. Its pseudosuchian affinity has been tested,

and rejected, by other authors, and the matrix presented herein does not include representatives of this clade. Accordingly, only characters that show variation amongst dinosauromorphs (i.e. they are phylogenetic informative) were selected from Nesbitt (2011). Characters from other datasets dealing with early dinosauromorphs have been added, including new observations (Supplemental Appendix 1). We also added recently described new basal dinosaur taxa (Supplemental Table 1).

The assembled new data matrix is composed of 32 taxa and 291 characters. The basal archosauriform *Euparkeria capensis* was employed for rooting purposes. This is a fairly complete taxon, which allows the polarization of a reasonable amount of characters. The scoring of Nesbitt (2011) has all been double-checked and corrected according to our own observation of the specimens. The specimens that were not analysed first-hand were coded based either on unpublished photographs, recent literature, or following previous authors with first-hand access to the material (the case of *Diodorus scytobrachion* and *Dromomeron*). *Pseudolagosuchus major* has been coded based only on its holotype, and treated as distinct of *L. admixtus*. Missing entries totalled 46% of the scoring in the matrix.

The matrix was analysed with the software TNT 1.1 (Goloboff *et al.* 2008). No characters have been ordered. Search for the most parsimonious trees (MPTs) were conducted via the 'Traditional search' (RAS + TBR), with the following options: 10,000 random addition sequences, random seed = 0 (time), hold = 20 (number of trees saved per replicate), and tree bisection and reconnection (TBR) for branch swapping. Trees were collapsed under the 'rule 1' of TNT 1.1 (default). We also applied the method IterPCR (Pol & Escapa 2009) to the MPTs, in order to identify floating taxa.

Results
The numeric analysis resulted in 27 MPTs (Consistency Index = 0.43; Retention Index = 0.60) of 781 steps (Fig. 13A). As expected, the strict consensus shows Lagerpetidae and *Marasuchus lilloensis* as the earliest splittings of Dinosauromorpha and Dinosauriformes, respectively. In all trees, *Lewisuchus admixtus* is recovered as basal to the dichotomy Silesauridae and Dinosauria (see Discussion for the apomorphies that support this phylogenetic hypothesis), but it collapses with other dinosauriforms because of the erratic position of *Pseudolagosuchus major* (see reduced consensus of Fig. 13B). *Asilisaurus kongwe* may be a silesaurid or basal to silesaurids plus dinosaurs, although it is always more derived than *L. admixtus*. These results contrast with recent works in which these species were found as unambiguous silesaurids (Brusatte *et al.* 2010; Nesbitt *et al.* 2010; Nesbitt 2011). Constraining *L. admixtus* as the sister taxon to
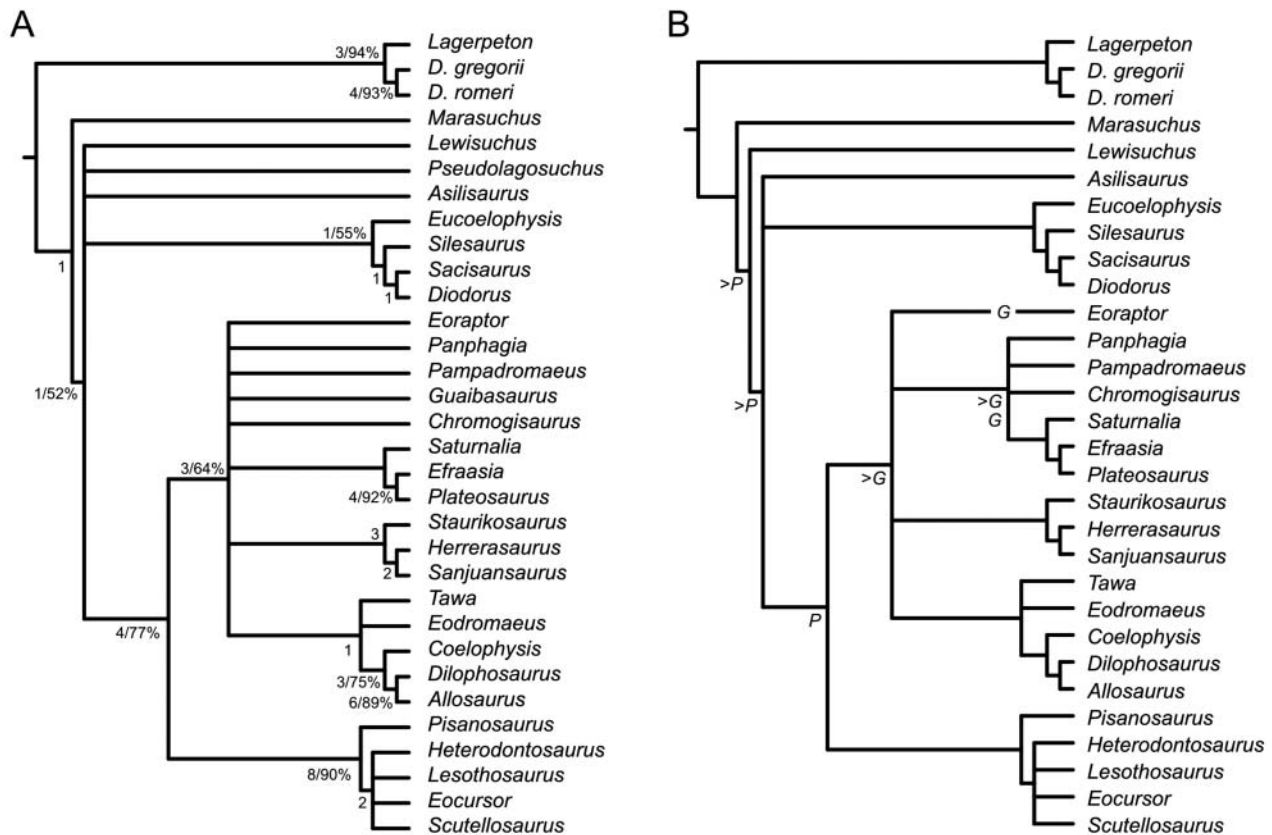
Figure 13. Cladograms depicting the phylogenetic position of *Lewisuchus admixtus*. **A,** strict consensus of 27 most parsimonious trees with 701 steps; **B,** reduced consensus derived from the application of IterPCR method of Pol & Escapa (2009). In the strict consensus, values associated with nodes are Bremer support and bootstrap proportions (above 50%). The letter associated with node in the IterPCR cladogram means that the taxon implied is sister group to that clade in some topologies. The symbol > means that the pruned taxon is located within that clade in some topologies, but it is not shown due to collapse. *P, Pseudolagosuchus major*; *G, Guaibasaurus candelariensis*.

P. major does not change the results, because it is one of the possible topologies found in the original MPTs. However, the clade formed by these taxa collapses due to lack of synapomorphies supporting it. Nesbitt *et al.* (2010) performed an analysis in which *L. admixtus* and *P. major* were treated as separated taxa. Even in this case, both species were still nested within Silesauridae, but they collapse with *Asilisaurus* at the base of that clade.

Within dinosaurs, relationships amongst ornithischians more derived than *Pisanosaurus mertii* are elusive. Within Saurischia, three monophyletic entities (Herrerasauridae, Theropoda and Sauropodomorpha) are found within a polytomy that also includes problematic basal saurischians such as *Guaibasaurus candelariensis*, *Eoraptor lunensis*, *Pampadromaeus barberenai*, *Chromogisaurus novasi* and *Panphagia protos*, which were previously attributed to Sauropodomorpha (Ezcurra 2010; Cabreira *et al.* 2011). Bremer support and bootstrap ratios are generally low, indicating weak support for several clades.

The reduced consensus derived from IterPCR analysis identified *P. major* and *G. candelariensis* as the main floating taxa (Fig. 13B). By pruning them, the result is that *L.*

admixtus falls basal to silesaurids plus dinosaurs, and *P. barberenai*, *C. novasi* and *P. protos* remain positioned within Sauropodomorpha, which is in accordance with each of the 27 MPTs. Alternative positions of *E. lunensis* and *G. candelariensis* include basal saurischian, theropod or sauropodomorph (Ezcurra 2010; Langer *et al.* 2011; Martínez *et al.* 2011), whereas herrerasaurids may be basal saurischians or basal theropods (see discussion of Nesbitt *et al.* 2009b). The recently described *Sanjuansaurus gordilloi* is sister taxon to *Herrerasaurus ischigualastensis*, and both *Tawa hallae* and *Eodromaeus murphi* are basal theropods (Nesbitt *et al.* 2009b; Martínez *et al.* 2011).

Discussion

The analysis recovered *Lewisuchus admixtus* as a basal dinosauriform outside the silesaurid and dinosaur split. The characters that minimally support a closer relationship of *L. admixtus* to the clade formed by silesaurids + dinosaurs rather than to more basal dinosauromorphs include the presence of a rostral tympanic recess on the

lateral side of the parabasisphenoid/prootic; a concave atlantal articulation facet in axial intercentrum, with upturned lateral borders; and the third cervical vertebra with centrum longer than those of axis and mid-dorsal vertebrae (Nesbitt 2011).

Silesaurids plus dinosaurs share apomorphies to the exclusion of *L. admixtus*. In the trees which *Pseudolagosuchus major* collapses with *L. admixtus* outside the dichotomy Silesauridae + Dinosauria, these apomorphies include minimally the presence of a craniocaudally short distal portion of the dorsal neural spine and the low neural arch of the dorsal vertebrae. Instead, if *P. major* is positioned within silesaurids or closer to dinosaurs than to other dinosauriforms, two additional apomorphic characters shared by silesaurids and dinosaurs, such as the reduction in the number of maxillary teeth and the loss of pterygoid teeth, draws *L. admixtus* to a more basal position. However, it should be noted that the characters mentioned above are highly homoplastic within dinosauriforms.

In light of the above anatomical and phylogenetic data, some characters previously considered to support the position of *L. admixtus* as a basal silesaurid (Nesbitt 2011) have to be reconsidered. These characters include the subvertically aligned exits of the hypoglossal nerve, which are also present in *M. lilloensis* (PVL 3872), and the rugose ridge on the craniolateral edges of the supraoccipital, also noted in one specimen of *Euparkeria capensis* (SAM-PK-5867), and some dinosaurs (Langer & Ferigolo 2013). Furthermore, the character 'cervical centra 3–5 longer than mid-trunk centra', turned out as a synapomorphy of *L. admixtus* plus other dinosauriforms, excluding *M. lilloensis*.

A taxonomic issue recently created by using Silesauridae, rather than Lewisuchidae, for naming a family-ranked taxon of ecologically distinct basal dinosauriforms (Langer *et al.* 2010; Nesbitt *et al.* 2010) becomes pointless with *L. admixtus* not belonging to that group. Names that entered the literature including Lewisuchinae and Lewisuchidae (Paul 1988; Olshevsky 1991) are redundant by including only the type species.

Relations within early dinosaurs remain poorly resolved except for the persistence of the three major clades Theropoda, Sauropodomorpha and Ornithischia. The erratic positions of herrerasaurids, *G. candelariensis* and *E. lunensis* are compatible with recent disputes concerning the phylogeny of Saurischia (Nesbitt *et al*. 2009b; Ezcurra 2010; Langer *et al*. 2011; Martínez *et al*. 2011), and reflect present knowledge of its early evolution.

Conclusions

The Middle Triassic *Lewisuchus admixtus* is a basal dinosauriform, which cannot be synonymized with its coeval *Pseudolagosuchus major* due to lack of data. Accordingly,

until further evidence is available, we recommend that they are treated as a distinct taxa in evolutionary studies.

The holotype of *L. admixtus* is less complete than presumed by Romer (1972c), because some attributed bones (lower jaw and pes) are more consistently referable to proterochampsids. The inclusion of the isolated maxilla in the holotype is tentative and should be treated with caution. Features that are peculiar for basal dinosauromorphs are confirmed or reported for the first time in this specimen, such as osteoderms and palatal teeth. The phylogenetic analyses suggest that *L. admixtus* is a dinosauriform that branched prior to the split between silesaurids and dinosaurs.

Supplemental material

Supplemental material for this article can be accessed here: http://dx.doi.org/10.1080/14772019.2013.878758

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