

The skull anatomy of *Decuriasuchus quartacolonina* (Pseudosuchia: Suchia: Loricata) from the middle Triassic of Brazil

MARCO A. G. DE FRANÇA^{1*}, MAX C. LANGER¹ & JORGE FERIGOLO²

¹Laboratório de Paleontologia de Ribeirão Preto, FFCLRP, Universidade de São Paulo, Av. Bandeirantes 3900, Ribeirão Preto, SP 14040-901, Brazil

²Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Av. Dr. Salvador França 1427, Porto Alegre, RS, 90.690-000, Brazil

*Corresponding author (e-mail: marquinhobio@yahoo.com.br)

Abstract: Unlike most raiusuchians, which are known based on partially preserved specimens, fossils attributed to *Decuriasuchus quartacolonina* include a monotonomic assemblage composed of nine associated individuals (MCN-PV10.105a–i), three with almost complete skulls (MCN-PV10.105a,c,d), and a partial disarticulated skull (MCN-PV10.004) collected in the Middle Triassic (Ladinian, *Dinodontosaurus* Biozone) beds of the Santa Maria Formation, in south Brazil. Because of its completeness and possible phylogenetic position, as one of the most basal loricatans, *D. quartacolonina* is a key taxon for anatomic, evolutionary and biomechanical studies of raiusuchians. The comparative description of its osteology reveals that the skull and mandible of *D. quartacolonina* are very similar to those of cf. *Prestosuchus chiniquensis* and *Saurosuchus galilei*, sharing a drop-shaped subnarial fenestra, a subtriangular antorbital fenestra with an elongated and narrow anterior point, a ‘roman nosed’ nasal, and a posteroventrally oriented ridge on the lateral surface of the ventral ramus of the squamosal. Among the differences are the autapomorphies of *D. quartacolonina*: numerous maxillary teeth (17), lateral expansion of the nasal/lacrimal covering the antorbital fenestra dorsally, and squamosal and quadratojugal forming a subtriangular projection that invades the lower temporal fenestra.

The study of raiusuchians began in the middle of the 20th century, when the German palaeontologist Friedrich von Huene discovered archosaur fossils in Brazil. Huene (1938b, 1942) described four new taxa currently considered as raiusuchians: *Prestosuchus chiniquensis*, *Prestosuchus loricatus*, *Procerosuchus celer* and *Raiusuchus tiradentes*. The generic name of the latter taxon, in honour of Guilherme Rau, a Brazilian-German dentist who collaborated with Huene, achieved family and class status in later works (e.g. Huene 1956; Krebs 1976; Bonaparte 1984; Parrish 1993; Brusatte *et al.* 2010; Nesbitt 2011). Since then, several further raiusuchian remains have been discovered in Brazil, including rather complete specimens such as that of cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T; Barberena 1978). However, more recently, about 70 years after Huene’s discoveries, a new taxon was proposed (França *et al.* 2011a). Named *Decuriasuchus quartacolonina*, the taxon was based on a monotonomic assemblage composed of nine associated individuals (MCN-PV10.105a–i) and a partial disarticulated skull (MCN-PV10.004). The MCN-PV10.105 assemblage included three partial articulated skulls (MCN-PV10.105a,c,d), and MCN-PV10.004 enables the observation of features unavailable in those

specimens. The phylogenetic position of *D. quartacolonina* is still controversial. Its inclusion in the data matrix of Brusatte *et al.* (2010) resulted in a position within Raiusuchoidea, closely related to *Prestosuchus chiniquensis* and *Batrachotomus kupferzellensis* (see analysis in França *et al.* 2011a). On the other hand, when incorporated into the study of Nesbitt (2011), *D. quartacolonina* is positioned as the most basal taxon of Loricata (França *et al.* 2011b). Because of its completeness, *D. quartacolonina* is a key taxon for anatomic, evolutionary and biomechanical studies of raiusuchians, and the aim of this study is to provide a comparative description of its skull remains.

Geological settings

Decuriasuchus quartacolonina was discovered in the site know as ‘Posto’, situated about 200 m north of the RS348 road within the western outskirts of Dona Francisca-RS (Fig. 1a). The type series of *D. quartacolonina* comes from two large ravines (Fig. 1b) located at 29°37’38” S 53°22’07” W (MCN-PV10.105) and 29°37’36” S 53°22’02” W (MCN-PV10.004). The latter outcrop, where the fossils were usually found isolated, is composed of

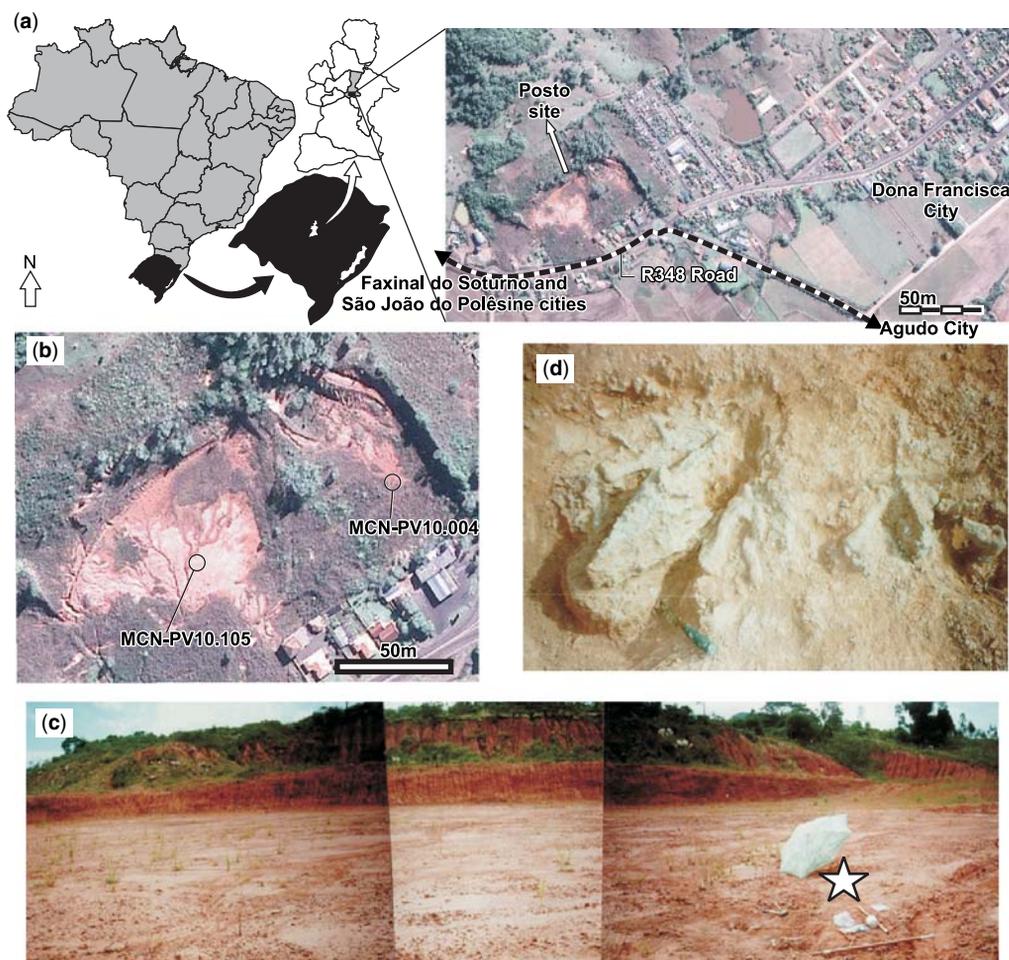


Fig. 1. Occurrence of *Decuriasuchus quartacolonia*. (a) Location of the Posto site, municipality of Dona Francisca, Quarta Colônia Area, Rio Grande do Sul State, Brazil. (b) Aerial image of the Posto site, identifying the provenience of MCN-PV10.105 and MCN-PV10.004. (c) Image of the Posto site showing the locality of excavation of MCN-PV10.105 (with star). (d) Photograph of MCN-PV10.105 during excavation.

reddish mudstones with slight gradation to coarser sediments towards the top. MCN-PV10.004 was found at its base (Mori 2005). The more southwestern outcrop is composed of *c.* 6 m of reddish mudstones, in which fossils are usually found partially articulated at the base (where MCN-PV10.105 was found) and isolated towards the top (Fig. 1c, d). These sediments belong to the Alemoa Member, Santa Maria Formation, Rosário do Sul Group, more specifically to the transgressive systems tract of the Santa Maria 1 Sequence (Zerfass *et al.* 2003). The occurrence of index fossils such as *Dinodontosaurus* and *Massetognathus* assigns the Posto site to the Middle Triassic (Ladinian) *Dinodontosaurus* Biozone, *c.* 240–235 Ma (Abdala & Ribeiro 2010). Sedimentological data and comparisons to other

localities of the Alemoa Member indicate that the Posto site was located in the distal portions of a floodplain, at some distance from the river channel. In addition, the presence of carbonate cement (nodules and mudcrack infilling) precipitation on previously exposed deposits during episodes of high phreatic level suggests contrasting dry and wet seasons (Rubert & Schultz 2004; Da Rosa 2005).

Materials and methods

The skull description presented herein is based on MCN-PV10.105a,c,d and MCN-PV10.004. The cranial remains of these specimens are similar in size (Table 1). The description does not include

Table 1. *Cranial measures of Decuriasuchus quartacolonina*

Measures	MCN-PV 10.105a (mm)	MCN-PV 10.105c (mm)	MCN-PV 10.105d (mm)	MCN-PV 10.004 (mm)
Anteroposterior length of the skull	314	260	275	–
Anteroposterior length of maxilla	150*	120*	125*	163 (left and right)
Anteroposterior length of antorbital fenestra	76	48	69	62* (right)
Anteroposterior length of frontal (in the midline)	74	64	–	80
Anteroposterior length of parietal (in the midline)	40	34	–	44

*Estimate values.

the braincase, which is concealed by the axial skeleton in MCN-PV10.105a,c,d. The comparisons were based on personal examination and on the literature for pseudosuchian archosaurs, mainly rauisuchians (Table 2).

Systematic palaeontology

Archosauria Cope 1869 (*sensu* Gauthier & Padian 1985)

Pseudosuchia Zittel 1887–1890 (*sensu* Gauthier & Padian 1985)

Suchia Krebs 1974 (*sensu* Benton & Clark 1988)

Loricata Merrem 1820 (*sensu* Nesbitt 2011)
Decuriasuchus quartacolonina (França, Langer & Ferigolo 2011)

Revised diagnosis

Medium-sized archosaur with crurotarsal ankle joint, two sacral vertebrae, roman-nose shaped nasal, external naris composed of nasal and premaxilla (maxilla excluded), subnarial fenestra dorsoventrally extended and restricted to the main body and a small part of the ascending process of maxilla, subtriangular antorbital fenestra with an elongated

Table 2. *List of comparative material*

Taxon	Specimen number and bibliographic reference
<i>Arganasuchus dutuitti</i> *	MNHN/AZA 407, 408, 900-906; MNHN/ALM1-6; Jalil & Peyer (2007)
<i>Arizonasaurus babbitti</i>	Nesbitt (2003, 2005)
<i>Batrachotomus kupferzellensis</i> *	SMNS-52970, 80260, 80261, others #; Gower (1999); Gower & Schoch (2009)
cf. <i>Prestosuchus chiniquensis</i> *	UFRGS-PV0156T; Barberena (1978)
<i>Effigia okeeffeae</i>	Nesbitt & Norell (2006); Nesbitt (2007)
<i>Fasolasuchus tenax</i> *	PVL-3850; PVL-3851; Bonaparte (1981)
<i>Luperosuchus fractus</i> *	PULR-04; PULR-057; Romer (1971); Desojo & Arcucci (2009)
<i>Ornithosuchus longidens</i> *	BMNH-R2409, 2410, 3142, 3143, others #; Walker (1964); Sereno (1991)
<i>Polonosuchus silesiacus</i> *	ZPAL-AbIII/563; Sulej (2005); Brusatte <i>et al.</i> (2009)
<i>Postosuchus kirkpatricki</i>	Chatterjee (1985); Long & Murry (1995); Weinbaum (2011)
<i>Prestosuchus chiniquensis</i> *	BSPG/ASXXV1, 28; Huene (1938b, 1942); Desojo & Rauhut (2008, 2009)
<i>Qianosuchus mixtus</i>	Li <i>et al.</i> (2006)
<i>Rauisuchus tiradentes</i> *	BSPG-ASXXV60-68, 122, 125-127; Huene (1938b, 1942); Desojo & Rauhut (2008)
<i>Riojasuchus tenuisiceps</i> *	PVL-3827; PVL-3838; Bonaparte (1971); Sereno (1991)
<i>Saurosuchus galilei</i> *	PVL-2062; PVSJ-32; Sill (1974); Alcober (2000)
<i>Shuvosaurus inexpectatus</i>	Chatterjee (1993); Long & Murry (1995); Nesbitt (2007)
<i>Stagonosuchus nyassicus</i>	Huene (1938a); Gebauer (2004); Lautenschlager & Desojo (2011)
<i>Teratosaurus suevicus</i> *	NHM-38646; Galton (1985); Benton (1986); Brusatte <i>et al.</i> (2009)
<i>Ticinosuchus ferox</i> *	PIMUZ-T2817; Krebs (1965)
<i>Tikisuchus romeri</i>	Chatterjee & Majumdar (1987)
<i>Xillosuchus sapingensis</i>	Nesbitt <i>et al.</i> (2011)
<i>Yarasuchus deccanensis</i>	Sen (2005)

*First-hand observation.

and narrow anterior portion, straight anterior region of maxillary ventral margin (anteriormost region to second alveolus), absent maxillary rostromedial foramen, U-shaped maxilla, posteroventrally oriented ridge on the lateral surface of the ventral ramus of the squamosal, and orbit not anteroposteriorly narrowed. *Decuriasuchus quartacolonina* is distinguishable from all other rauisuchians (except *Q. mixtus*) by the possession of more than 15 maxillary teeth, and characterized by the following autapomorphies: lacrimal and nasal form a lateral expansion of the skull roof that overhangs most of the antorbital fenestra; rostrally extended dorsal margin of quadratojugal and ventral margin of squamosal form the ventral portion of a subtriangular expansion that enters the lower temporal fenestra.

Description of skull and mandible

Skull

Premaxilla (Figs 2, 3 & 4). The premaxilla is better preserved in MCN-PV10.105a,d, and is partially covered by the nasal in MCN-PV10.105c (right

side), whereas the medial surface is partially exposed in the left bone. The premaxilla is composed of a main body and two dorsal slender projections, the anterodorsal and posterodorsal processes. The palatal surface of the premaxilla cannot be observed in *Decuriasuchus quartacolonina*.

The main body is subrectangular, *c.* 1.5 times longer anteroposteriorly than dorsoventrally deep (Fig. 4b, f: mb), as seen in most rauisuchians (e.g. *Polonosuchus silesiacus* [ZPAL/AbIII-563], *Fasolasuchus tenax* [PVL-3850], *Batrachotomus kupferzellensis* [SMNS-80260], *Postosuchus kirkpatricki*). Yet, this feature appears to be intraspecifically variable, because the maxillary body is subrectangular in the holotype of *Saurosuchus galilei* (PVL-2062), but quadrangular in PVSJ-32. In *Decuriasuchus quartacolonina*, the anterior margin of the premaxillary body is straight-vertical, becoming concave only at the anterodorsal process. This differs from the sinuous anterior margin seen in *Postosuchus kirkpatricki* (Weinbaum 2011) as well as from the dorsoposteriorly inclined anterior margin of main body of *Effigia okeeffeae* (Nesbitt 2007). The ventral margin of premaxilla is almost

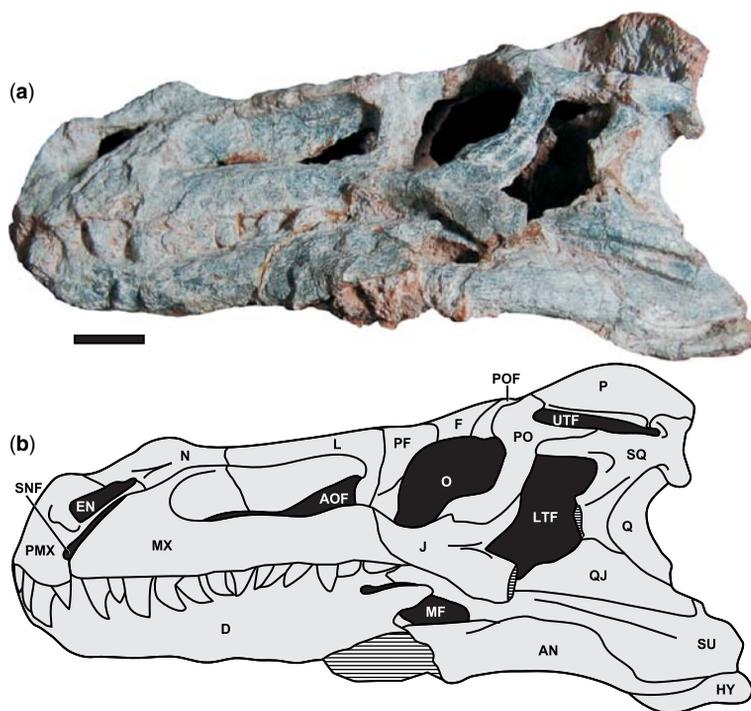


Fig. 2. Skull of *Decuriasuchus quartacolonina* (MCN-PV10.105a) in lateral view. (a) Photograph of left side. (b) Outline of left side. Scale bar, 3 cm. **Abbreviations:** AN, angular; AOF, antorbital fenestra; D, dentary; EN, external naris; F, frontal; HY, hyoid; J, jugal; L, lacrimal; LTF, lateral temporal fenestra; MF, mandibular fenestra; MX, maxilla; N, nasal; O, orbit; P, parietal; PF, prefrontal; PMX, premaxilla; PO, postorbital; POF, postfrontal; Q, quadrate; QJ, quadratojugal; SNF, subnarial fenestra; SQ, squamosal; SU, surangular; UTF, upper temporal fenestra.

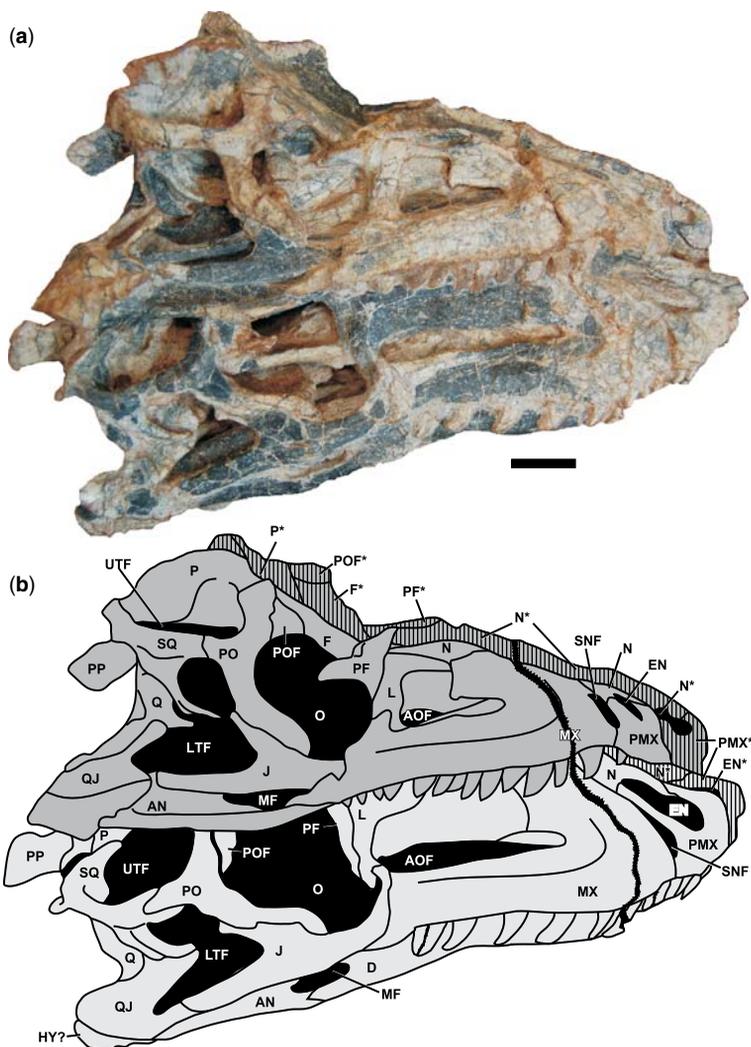


Fig. 3. Skull of *Decuriasuchus quartacolonina* (MCN-PV10.105c, above; MCN-PV10.105d, below) in lateral view: (a) photograph of right side; (b) outline of right side. Scale bar, 3 cm. *Abbreviations:* AN, angular; AOF, antorbital fenestra; D, dentary; EN, external naris; F, frontal; HY, hyoid; J, jugal; L, lacrimal; LTF, lateral temporal fenestra; MF, mandibular fenestra; MX, maxilla; N, nasal; O, orbit; P, parietal; PF, prefrontal; PMX, premaxilla; PO, postorbital; POF, postfrontal; PP, paraoccipital process of opisthotic; Q, quadrate; QJ, quadratojugal; SNF, subnarial fenestra; SQ, squamosal; UTF, upper temporal fenestra. Asterisk and hatched area indicate bones of the left side.

horizontal, bearing four teeth (MCN-PV10.105d; Figs 3 & 4e, f). A mostly rounded ventral margin is seen in *Luperosuchus fractus* (PULR-057) and ornithosuchids (PVL-3827; BMNH-R2409), whereas that of *Qianosuchus mixtus* is sinuous (Li *et al.* 2006). Few rauisuchians have more (e.g. *Qianosuchus mixtus*) or less (e.g. *Heptasuchus clarki* (Dawley *et al.* 1979)) premaxillary teeth, but some are edentulous (e.g. *Lotosaurus adentus*, *Shuvosaurus inexpectatus*, *Effigia okeeffeae*).

The elongated posterodorsal process forms an angle of 45° with the ventral margin of the premaxilla (Fig. 4b, f: pdp). Its posterior tip reaches the posterodorsal edge of the external naris (MCN-PV10.105d; Fig. 4), but does not exceed this limit as in *Saurosuchus galilei* (PVL-2062; PVSJ-32). The posteroventral margin of the posterodorsal process contacts the ascending process of the maxilla, whereas its posterodorsal margin contacts the posteroventral process of the nasal. The

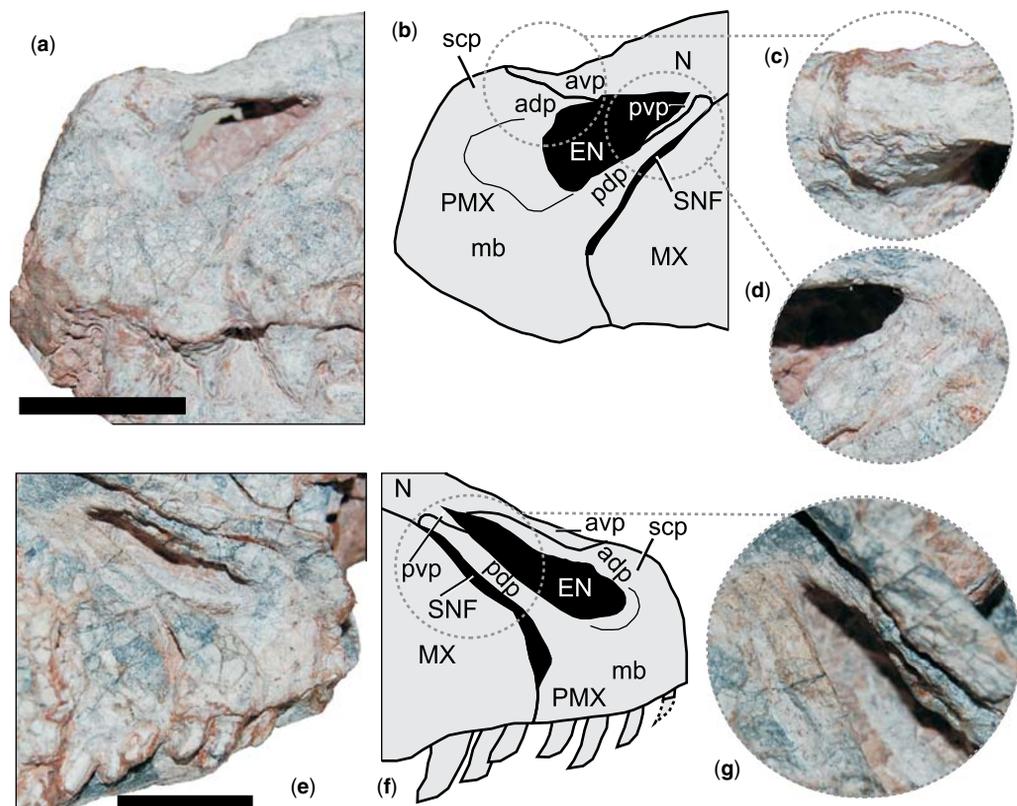


Fig. 4. Articulation among premaxilla, maxilla and nasal in *Decuriasuchus quartacolonia*. (a) Photograph of left side in lateral view of MCN-PV10.105a. (b) Outline of left side in lateral view of MCN-PV10.105a. (c) Detail of dorsal articulation of premaxilla and nasal in dorsolateral view of MCN-PV10.105a. (d) Detail of ventral articulation of premaxilla and nasal in lateral view of MCN-PV10.105a. (e) Photograph of right side in lateral view of MCN-PV10.105d. (f) Outline of left side in lateral view of MCN-PV10.105d. (g) Detail of articulation of premaxilla, maxilla and nasal in dorsolateral view of MCN-PV10.105d. Scale bar, 3 cm. *Abbreviations:* adp, anterodorsal process of premaxilla; avp, anteroventral process of nasal; EN, external naris; mb, main body; MX, maxilla; N, nasal; pdp, posterodorsal process of premaxilla; PMX, premaxilla; pvp, posteroventral process of nasal; scp, slightly convex protuberance; SNF, subnarial fenestra;

premaxilla also contacts the maxilla on the ventral portion of the main body below the subnarial fenestra. This aperture is drop-shaped, elongated dorsoventrally and arched posterodorsally (Figs 2, 3 & 4; SNF).

The shorter anterodorsal process (Fig. 4b, f: adp) forms the internarial bar and dorsally contacts the anteroventral process of the nasal. This contact is not restricted to a point, and the anterodorsal process overlaps the nasal dorsally (Fig. 4), as seen in *Saurosuchus galilei* (PVL-2062; PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T). The ventral part of the anterodorsal process in MCN-PV10.105a,d is posterodorsally arched, forming a slightly convex protuberance (Fig. 4b, f scp), and its distal region extends more posteriorly than dorsally. This is also seen in *Batrachotomus*

kupferzellensis (SMNS-52970) and *Fasolasuchus tenax* (PVL-3850), whereas the protuberance is absent in cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T), *Saurosuchus galilei* (PVL-2062; PVSJ-32), *Rauisuchus tiradentes* (BSPG/ASXXV-60) and *Postosuchus kirkpatricki*.

The external naris of *Decuriasuchus quartacolonia* is drop-shaped and oblique relative to the anteroposterior axis of the skull (Figs 2, 3 & 4: EN). The premaxilla borders the external naris almost completely, except by a small posterodorsal region of that aperture, bordered by the nasal bone. Therefore, the maxilla does not contribute to form the external naris. This is common among rauisuchians (e.g. *Luperosuchus fractus* [PULR-057], *Saurosuchus galilei* [PVL-2062; PVSJ-32], cf. *Prestosuchus chiniquensis* [UFRGS-PV0156T], *Fasolasuchus*

tenax [PVL-3850], *Heptasuchus clarki*, whereas the maxilla borders the external naris in *Lotosaurus adentus* (Parrish 1993; Brusatte *et al.* 2010), *Batrachotomus kupferzellensis* (SMNS-52970; SMNS-80260), *Qianosuchus mixtus* (Li *et al.* 2006) and *Effigia okeeffeae* (Nesbitt 2007).

Maxilla (Figs 2, 3, 4 & 5). The maxilla of *Decuriasuchus quartacolonina* is composed of a main body plus posterior, ascending and palatal processes. It articulates with the premaxilla, nasal, jugal and lacrimal in lateral view, and possibly meets the vomer and palatine medially. The lateral surface is better preserved in the articulated specimens (Figs 2 & 3), whereas the other surfaces are better preserved in MCN-PV10.004 (Fig. 5).

The medial surface of maxilla (Fig. 5b, e) lacks both the fossae and sculpture seen in *Saurosuchus galilei* (PVL-2062; PVSJ-32) and the vertical grooves of the interdental gaps of *Fasolasuchus tenax* (PVL-3851). Likewise, its lateral surface (Figs 2, 3 & 5a, f) lacks the pronounced longitudinal ridge below the antorbital fossa present in *Effigia okeeffeae* (Nesbitt 2007), *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Rauisuchus tiradentes* (BSPG/ASXXV-122). More ventrally, the lateral surface (MCN-PV10.004) is depressed in relation to the rest of the bone (Fig. 5d, h: vd). This depression is dorsoventrally low, and extends along almost the entire anteroposterior length of the main body and posterior process. Semicircular grooves occur dorsal to this depression (Fig. 5d: scg), subtler versions of which are also observed in *Saurosuchus galilei* (PVL-2062; PVSJ-32). In addition, the lateral surface of the maxilla (MCN-PV10.004) bears nutrient foramina scattered across the main body and posterior process, which do not form rows (Fig. 5d, h: nfo). The ventral margin of the maxilla of *Decuriasuchus quartacolonina* is generally convex anteriorly and straight posteriorly. However, as better observed in the right side of MCN-PV10.004, this margin is straight anterior to the second alveolus (Fig. 5a), and convex posterior to that, between alveoli 2–5. This configuration forms a step also seen in *Saurosuchus galilei* (PVL-2062; PVSJ-32), but not in *Batrachotomus kupferzellensis* (SMNS-80260) and *Polonosuchus silesiacus* (ZPAL/ABIII-563). Likewise, the straight posterior part of the ventral margin in *Decuriasuchus quartacolonina* is interrupted by a very small convexity between alveoli 10–11.

The maxilla of MCN-PV10.105c has 12 preserved teeth, but empty alveoli are present in the posterior region. The computed tomography (CT) scan of MCN-PV10.105a revealed 17 alveoli, as also seen in both isolated maxilla of MCN-PV10.004 (Fig. 5c). Among rauisuchians, only *Decuriasuchus quartacolonina* and *Qianosuchus*

mixtus (Li *et al.* 2006) have more than 15 maxillary teeth, but the latter taxon also has a higher number of premaxillary teeth. Together with the dental groove (Fig. 5m: ig), maxillary interdental plates are seen in the medial side of both maxillae of MCN-PV10.004 (Fig. 5b, e, m: ip). These are not fused as in most rauisuchians such as *Teratosaurus suevicus* (BMNH-R35646), *Saurosuchus galilei* (PVL-2062; PVSJ-32), *Postosuchus kirkpatricki* (Weinbaum 2011) and *Fasolasuchus tenax* (PVL-3851). Plates 3–5 have anterior and posterior margins not parallel to one another, as also seen in *Arganasuchus dutuiti* (ALM-1; *contra* Jalil & Peyer 2007), but in *Decuriasuchus quartacolonina* more anterior plates are higher than long, whereas all plates are longer than high in *Arganasuchus dutuiti* (ALM-1). The shallow dental groove of *Decuriasuchus quartacolonina* (MCN-PV10.004) is continuous along the maxilla. In the left side, it is straight above alveoli 1–2, but ventrally deflected in the right side (Fig. 5m). Likewise, the first alveolus is smaller than the second in the right side of MCN-PV10.004, but they are the same size in the left side. The two last traits are shared with *Saurosuchus galilei* (PVL-2062).

As in most rauisuchians, the anterior border of the maxilla, composed of the ascending process and main body of the bone, is slightly concave, forming a U-shaped bone. Conversely, the anterior projection is separated from the ascending process by a concave step (Y-shaped maxilla) in *Arganasuchus dutuiti* (ALM-1), *Arizonasaurus babbitti* (Nesbitt 2005), *Batrachotomus kupferzellensis* (SMNS-52970), *Effigia okeeffeae* (Nesbitt 2007), *Fasolasuchus tenax* (PVL-3851), *Ticinosuchus ferox* (PIMUZ-T2817) and *Xilousuchus sapingensis* (Nesbitt *et al.* 2011). The dorsal region of the posterior process and the posteroventral portion of the ascending process house, respectively, the ventral and anterior regions of the antorbital fossa/fenestra. The fossa is similar to that of *Saurosuchus galilei* (PVL-2062; PVSJ-32), and less developed than that of *Fasolasuchus tenax* (PVL-3850). The fenestra is subtriangular, with a tapering anterior portion (Figs 2, 3 & 5: AOF). In MCN-PV10.105a,c (Figs 2 & 3), that anterior extremity has subparallel dorsal and ventral margins, with the posterior tip of the dorsal margin projected posterodorsally, as also seen in *cf. Prestosuchus chiniquensis* (UFRGS-PV0156T) and *Saurosuchus galilei* (PVL-2062; PVSJ-32). The medial surface of the ascending process has a deep subtriangular fossa (Fig. 5b, e, i: aos), named the antorbital sinus (Witmer 1997). It is deeper in *Decuriasuchus quartacolonina* than in *Polonosuchus silesiacus* (ZPAL/ABIII-563). The maxillary body (MCN-PV10.004) has about the same thickness as the posterior process, as seen in *Saurosuchus galilei* (PVL-2062; PVSJ-32)

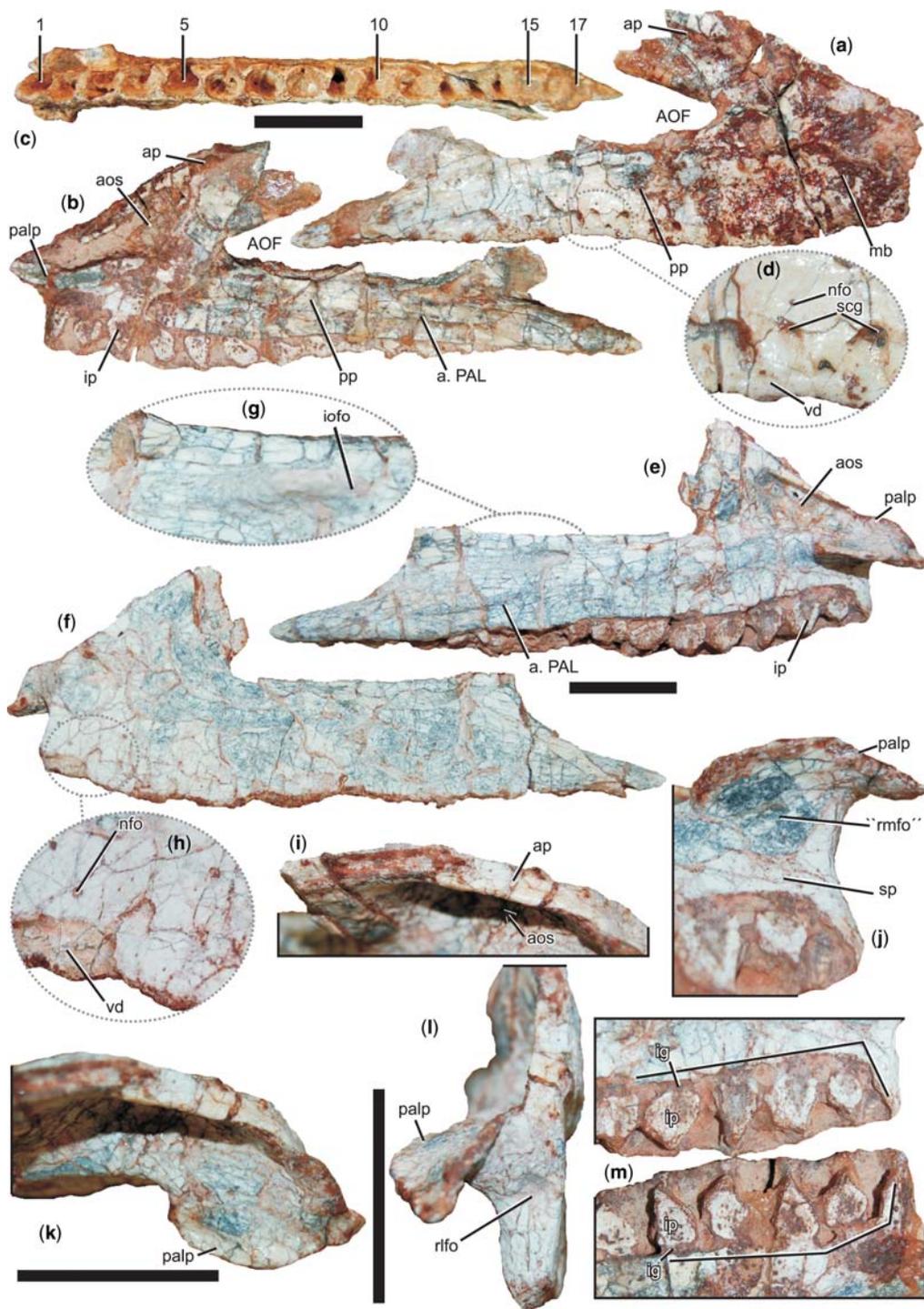


Fig. 5. Isolated maxillae of MCN-PV10.004: (a) right side in lateral view; (b) right side in medial view; (c) right side in ventral view; (d) detail of lateral surface of right maxilla; (e) left side in medial view, (f) left side in lateral view; (g) detail of posterior process of maxilla in dorsomedial view; (h) detail of ventral region of lateral surface of maxillar

and *Fasolasuchus tenax* (PVL-3851). A rostralateral foramen (Fig. 5l: rlfo) pierces the anterior surface of the maxillary body of *Decuriasuchus quartacolonina*, whereas the rostromedial foramen is absent (see below).

The palatal process of the right maxilla of MCN-PV10.004 is complete (Fig 5e, j, l: palp). It is leaf-shaped in dorsal view, with the curved medial border posteriorly continuous to the maxillary body. The anterior portion is laterally convex and medially concave, resulting on a pointed tip. In lateral view, only one-third of the process exceeds the anterior edge of the maxillary body. The process is also slightly sloped anteroventrally, so that its smooth ventral surface is seen in medial view (Fig. 5j: 'rmfo'). This differs from the more medioventrally sloped process, separated by a deep pit from the maxillary body, as in *Saurosuchus galilei* (PVL-2062). *Decuriasuchus quartacolonina* lacks a rostromedial foramen as in *Polonosuchus silesiacus* (ZPAL-AbIII/563) and *Teratosaurus suevicus* (NHM-38646), but bears a shallow pit on the medial surface of the maxillary body (Fig. 5j: sp), positioned between the palatal process and the dental groove, like that of *Fasolasuchus tenax* (PVL-3851). The dorsal and lateral surfaces of the palatal process of *Decuriasuchus quartacolonina* lack grooves or pits. Comparing the extension of the palatal processes of MCN-PV10.004 with the lateral dimensions of the MCN-PV10.105 skulls, it seems that the palatal process of *Decuriasuchus quartacolonina* did not contact its contralateral part.

The dorsolateral portion of the posterior process of the maxilla (MCN-PV10.004) is composed of a thin blade, with a straight dorsal margin that forms the antorbital fenestra (Fig. 5e, f). Its posterior lacrimal/jugal articulation (Fig. 5a, b) extends dorsoposteriorly as a thin blade (anteroposteriorly long and lateromedially narrow), placed dorsal to alveoli 11–13. Its dorsal margin contacts the descendent process of the lacrimal, whereas its posterior part meets the jugal, which covers the maxilla laterally. As a result, in a lateral view of the skull of MCN-PV10.105, the posterior region of the maxilla is not totally visible. This morphology makes it difficult to know whether or not the jugal participates in the antorbital fenestra. In dorsomedial view, the maxilla of MCN-PV10.004 has a deep

and lateromedially narrow furrow that extends anteroposteriorly ventral to the antorbital fenestra. This leads anteriorly to the infraorbital foramen, positioned at the level of alveoli 9–11 (Fig. 5e, g: iofo). In MCN-PV10.004, the maxilla–palatine contact is indicated by an elongated shallow pit on the medial surface of posterior process, at the levels of alveoli 10–12 (Fig. 5b, e: a. PAL) and the posterior part of the infraorbital foramen. The tapering tip of the posterior process of the maxilla (MCN-PV10.004) has an oval cross-section (Fig. 5).

Nasal (Figs 2, 3, 4, 6, 7 & 8). The nasals are seen in all MCN-PV10.105 skulls, but they are best preserved in MCN-PV10.105a, which served as the basis for its description. The elongated nasal of *Decuriasuchus quartacolonina* occupies the anterior part of the skull roof and contacts its counterpart medially. It has two anterior projections (MCN-PV10.105d; Fig. 4). The anteroventral process (Fig. 4b, f: avp) is more anteriorly placed, and contacts the anterodorsal process of premaxilla composing the dorsal border of external naris in lateral view. The posteroventral process contacts the posterodorsal process of the premaxilla (Fig. 4b, f: pvp). It is shorter than the anteroventral process, forming about one-third of the posteroventral length of the external naris. In articulated skulls (MCN-PV10.105a,c,d), the posteroventral process is often only represented by its anterodorsal region, which overlaps the posterodorsal process of the premaxilla. Inversely, the posteroventral part of this process is laterally overlapped by the maxillary ascending process, as also seen in *Saurosuchus galilei* (PVSJ-32). The posteroventral process is not totally exposed in any specimen of *Decuriasuchus quartacolonina*, so its general shape is unknown.

Defined as the area between the anterior (which articulates with the premaxilla) and the posterior (which contacts the frontal and prefrontal) processes, the main body of the nasal of *Decuriasuchus quartacolonina* has an entirely laminar lateral margin (MCN-PV10.105c; Fig. 8d: fm), lacking the rugose ridge seen in *Batrachotomus kupferzellensis* (SMNS-80260), *Postosuchus kirkpatricki* (Weinbaum 2011), *Polonosuchus silesiacus* (ZPAL/AbIII-563) and *Rauisuchus tiradentes* (BSPG/ASXXV-65). Its anterior third lacks a lateral

Fig. 5. (Continued) main body of left side; (i) detail of ascendant process of left side in dorsal view; (j) detail of medial surface of maxillar main body of left side in ventromedial view; (k) detail of maxillar palatal process of left side in dorsal view; (l) left side in anterior view; (m) detail of interdental groove of left side (above) and right side (below) in medial view. Scale bar, 3 cm. *Abbreviations:* 'rmfo', position of rostromedial foramen in other rauisuchians; 1–17, number of alveolus; a., articulation with; AOF, antorbital fenestra; aos, antorbital sinus; ap, ascendant process of maxilla; ig, interdental groove; iofo, infraorbital foramen; ip, interdental plate; mb, main body of maxilla; nfo, nutrient foramen; PAL, palate; palp, palatal process of maxilla; pp, posterior process of maxilla; rlfo, rostralateral foramen; scg, semicircular groove; sp, shallow pit; vd, ventral depression.

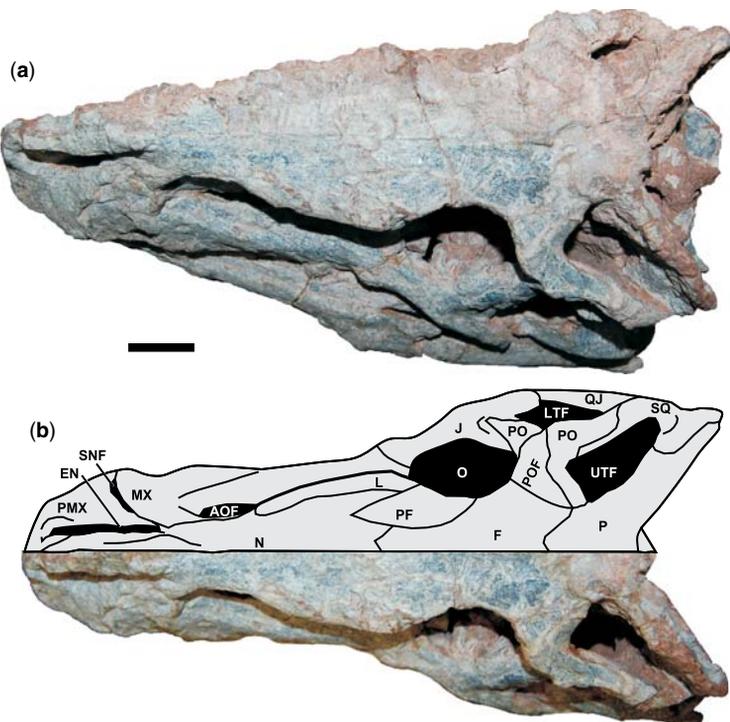


Fig. 6. Skull of *Decuriasuchus quartacolonía* (MCN-PV10.105a) in dorsal view. (a) Photograph of laterodorsal view. (b) Dorsal view with photograph (above) and outline (below). Scale bar, 3 cm. *Abbreviations:* AOF, antorbital fenestra; EN, external naris; F, frontal; J, jugal; L, lacrimal; LTF, lateral temporal fenestra; MX, maxilla; N, nasal; O, orbit; P, parietal; PF, prefrontal; PMX, premaxilla; PO, postorbital; POF, postfrontal; QJ, quadratojugal; SNF, subnarial fenestra; SQ, squamosal; UTF, upper temporal fenestra.

projection where it contacts the maxilla ventrally. The posterior two-thirds of that margin are hidden laterally by the lacrimal in MCN-PV10.105a, but the partially disarticulated bone of MCN-PV10.105c reveals that it is also laminar (Fig. 8d).

At the level between the external naris and the antorbital fenestra, the dorsal surface of the nasal of *Decuriasuchus quartacolonía* is convex in lateral view (MCN-PV10.105a; Fig. 2, 8b, e: rn). Romer (1971) described a similar structure in *Luperosuchus fractus* (PULR-04), naming it as the ‘romanosed stout’, which is also seen in cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T), *Saurosuchus galilei* (PVL-2062; PVSJ-32) and *Riojasuchus tenuisiceps* (PVL-3827). Posterior to this structure, the dorsal surface of the nasal in *Decuriasuchus quartacolonía* has a medially restricted shallow concavity (posteromedial depression of nasal; MCN-PV10.105a; Fig. 8e: pmd). The nasal is flat lateral to this depression (Fig. 8d: fm), but rises posteriorly to reach the same level as the rest of the skull roof, as in *Saurosuchus galilei* (PVL-2062; PVSJ-32) and cf. *Prestosuchus chiniquensis*

(UFRGS-PV0156T). This morphology differs from that of some other rauisuchians (e.g. *Batrachotomus kupferzellensis* [SMNS-80260] and *Postosuchus kirkpatricki* [Weinbaum 2011]), in which the entire medial portion of the nasal is depressed.

Posteriorly, the nasal contacts the frontal, prefrontal and lacrimal (Figs 6, 7 & 8c), where the more lateral projection is placed between the lacrimal and prefrontal. More medially, it forms an M-shaped suture with the prefrontal and frontal, like *Saurosuchus galilei* (PVSJ-32). This is formed by a more posteriorly projected lateral apex, which contacts the prefrontal (laterally) and frontal (medially), a rounded posterior projection that contacts the frontal, and a small apex that contacts the frontal and the other nasal. This is also observed in the dorsal view of the frontal in MCN-PV10.004 (Fig. 9a, b), although its ventral and anterior surfaces are composed of several Z-shaped sutures.

Lacrimal (Figs 2, 3, 6, 7 & 8). This inverted-L shaped bone is formed by an anterior ramus and the descendent process (Fig. 8b, d: ar, dp). It is

SKULL ANATOMY OF *DECURIASUCHUS QUARTACOLONIA*

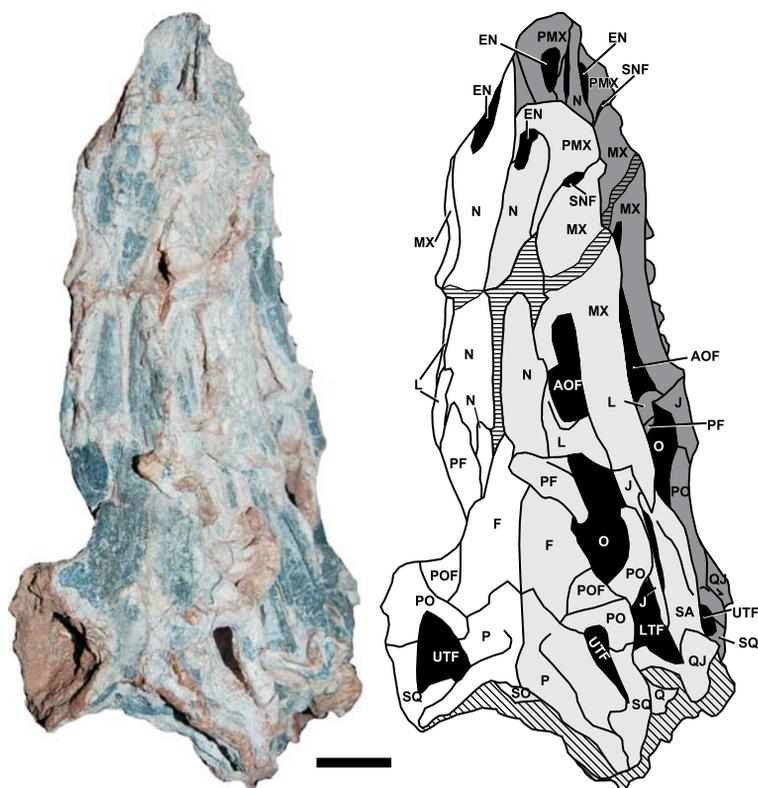


Fig. 7. Skull of *Decuriasuchus quartacolonina* (MCN-PV10.105c, above; MCN-PV10.105d, below) in dorsal view: (a) photograph and (b) outline (white area indicates the left side and light grey the right side of MCN-PV10.105c; dark grey indicates the MCN-PV10.105d). Scale bar, 3 cm. *Abbreviations:* AOF, antorbital fenestra; EN, external naris; F, frontal; J, jugal; L, lacrimal; LTF, lateral temporal fenestra; MX, maxilla; N, nasal; O, orbit; P, parietal; PF, prefrontal; PMX, premaxilla; PO, postorbital; POF, postfrontal; Q, quadrate; QJ, quadratejugal; SA, surangular; SNF, subnarial fenestra; SO, supraoccipital; SQ, squamosal; UTF, upper temporal fenestra.

preserved on three MCN-PV10.105 skulls, with sutures most evident in MCN-PV10.105c,d. The dorsal region is better preserved in the left side of MCN-PV10.105c, where it is exposed on the skull roof, whereas the ventral region is better visualized in MCN-PV10.105d.

The anterior ramus is much longer than the descending process, like most rauisuchians, but unlike a shorter ramus seen in *Postosuchus kirkpatricki* (Weinbaum 2011) and *Polonosuchus silesiacus* (ZPAL/AbIII-563). The anterior ramus of *Decuriasuchus quartacolonina* can be divided into two portions. An anteriorly directed flattened blade, exposed in lateral view, contacts the ascending process of the maxilla, forming the posterodorsal margin of the antorbital fenestra (Fig. 8b, e: fb). This is dorsoventrally narrower posteriorly, giving a subtriangular shape to the antorbital fenestra, and has a slight sinuous ventral margin (MCN-PV10.105a). Dorsal to this blade, the anterior ramus

has a slightly rugose dorsal ridge (Fig. 8b, e: sdr). This is continuous to the flattened lateral margin of the nasal and to the maxillary ascending process. This ridge extends anteroposteriorly, contacting the prefrontal posteriorly and the nasal medially (Fig. 8c). The anterior blade is depressed relative to the dorsal ridge, forming part of the antorbital fossa (Fig. 8e), as seen in cf. *Prestosuchus chini-quensis* (UFRGS- PV0156T), *Saurosuchus galilei* (PVL-2062; PVSJ-32) and *Luperosuchus fractus* (PULR-04). However, whereas these taxa have the lateral margin of the skull roof expanded only above the lacrimal/prefrontal bar, this structure expands more anteriorly in MCN-PV10.105a, covering almost the entire length of the antorbital fenestra (Fig. 6, 8c, d). This elongated lateral expansion is considered autapomorphic of *Decuriasuchus quartacolonina*.

The descending process of the lacrimal is a columnar structure, about four times dorsoventrally

Frontal (Figs 2, 3, 6, 7, 8 & 9). The frontal is preserved in MCN-10.105 and MC-PV10.004, with its limits better seen in MCN-10.105c and the ventral surface available in MCN-PV10.004. It forms an M-shaped anterior suture with the nasal (Fig. 8c), and contacts the prefrontal and the postfrontal laterally. Between the pre- and postfrontal contacts the frontal is laterally exposed, forming a small dorsal part of the orbit (Figs 2, 3, 6, 7 & 9b). This contrasts with the frontal excluded from the orbit in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Saurosuchus galilei* (PVL-2062; PVSJ-32), and its larger participation in *Effigia okeeffeae* (Nesbitt 2007). In addition, the frontal is not rugose at the orbital margin, as in *Arizonasaurus babbitti* (Nesbitt 2005) and *Effigia okeeffeae* (Nesbitt 2007). The posterior contact with the parietal is S-shaped, medially concave and laterally convex (Fig. 9a, b). Similarly to *Saurosuchus galilei* (PVSJ-32), the dorsal surface of the frontal in *Decuriasuchus quartacoloniam* (MCN-PV10.105a,d; MCN-PV10.004) has a small sagittal crest on its posterior third (Fig. 9l: c.F) and two small circular pits (better seen in the left side of MCN-PV10.004; Fig. 9a, b, c: cp).

In ventral view (MCN-PV10.004), each frontal has an anteroposteriorly blunt ridge extending along its anterior half, medial to which lies a shallow fossa. These structures are related to the olfactory tract (Gower 1999; Fig. 9d, e: ot). Immediately posterior to that, each frontal also has another anterolateral to posteromedial oriented ridge. Its anterolateral portion is flanked by two shallow depressions, whereas its posteromedial portion is confluent with the protruding contact of the frontals, which is ventrally projected relative to the rest of the ventral surface of the bone. More posteriorly, the ventral surface of the frontal contacts the laterosphenoid. This bone forms part of the braincase; it is ventrally projected and medially arched, forming an anteriorly tapering tube.

Postfrontal (Figs 2, 3, 6, 7, 8 & 9). The postfrontal is preserved in MCN-PV10.105a,c and MCN-PV10.004, but only its lateral extremity is visible in MCN-PV10.105d. This bone takes part in the orbit/upper temporal fenestra bar and, unlike in *Postosuchus kirkpatricki* (Weinbaum 2011), reaches the lateral margin of the skull roof. In addition, the postfrontal of *Decuriasuchus quartacoloniam* is at least as medially extensive as the postorbital (MCN-PV10.105a; Fig. 6b; MCN-PV10.105d; Fig. 7b), differing from that of *Batrachotomus kupferzellensis* (SMNS-80260), which is smaller and more laterally restricted. The bone is subtriangular, contacting the frontal medially and the postorbital posterolaterally. In MCN-PV10.004, the left postfrontal also contacts the parietal posteromedially,

but this is not seen on the right side (Fig. 9a, b). Its dorsal and ventral surfaces have no ornamentations or foramina. In lateral view, the postfrontal forms a small dorsal margin of the orbit.

Parietal (Figs 2, 3, 6, 7 & 9). The parietal is preserved in MCN-PV10.105 and MCN-PV10.004, with the ventral surface exposed in the latter. In lateral view, the bone is partially hidden by the squamosal and postorbital (Figs 2 & 3). Its flat ventral surface contacts the laterosphenoid (MCN-PV10.004, Fig. 9d, e) and its middle posterior margin contacts the supraoccipital. The anterior portion of the parietal pair forms the medial plate between upper temporal fenestrae, composing the most posterior part of the skull roof. More posteriorly, each bone has a posterolaterally projected occipital/transverse process (Gower 1999; parietal crest of Alcober 2000; Fig. 9b, e, g: ocp) that posteromedially borders the upper temporal fenestra. The parietal participation in the skull roof of *Decuriasuchus quartacoloniam* is about as anteroposteriorly long as lateromedially broad, whereas this is much broader in *Saurosuchus galilei* (PVSJ32) and slightly longer in cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T). In addition, its anterior margin is only slightly broader than its midlength, so the medial margin of the upper temporal fenestra is slightly concave. This differs from the condition in *Saurosuchus galilei* (PVSJ-32), the parietal of which is significantly narrower anteriorly. The parietal is dorsally flat on the skull roof, except for a medial prominence in the posterior portion (Fig. 9i: c.P), also seen in *Batrachotomus kupferzellensis* (SMNS-52970), *Saurosuchus galilei* (PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T).

As in *Batrachotomus kupferzellensis* (SMNS-52970) and *Saurosuchus galilei* (PVSJ-32), the anterior margin of each parietal of *Decuriasuchus quartacoloniam* (MCN-PV10.004, Fig. 9a, b) projects slightly into the frontal, differing from the condition in *Postosuchus kirkpatricki* (Weinbaum 2011) where the medialmost margin of the pairs is convex. In addition, *Postosuchus kirkpatricki* also has a lateral projection on the anterior region of parietal, absent in *Decuriasuchus quartacoloniam*. In dorsal view, the lateral surface of the parietal is concave, forming the medial margin of the upper temporal fenestra. This concavity is more angled in MCN-PV10.105a,c than in MCN-PV10.004, but an even more angled excavation is seen in *Saurosuchus galilei* (PVSJ-32). In *Batrachotomus kupferzellensis* (SMNS-52970) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011), this margin is more rounded than in *Decuriasuchus quartacoloniam*. The long occipital process (as long as the midline anteroposterior length of the bone) extends from the posterolateral margin of the skull

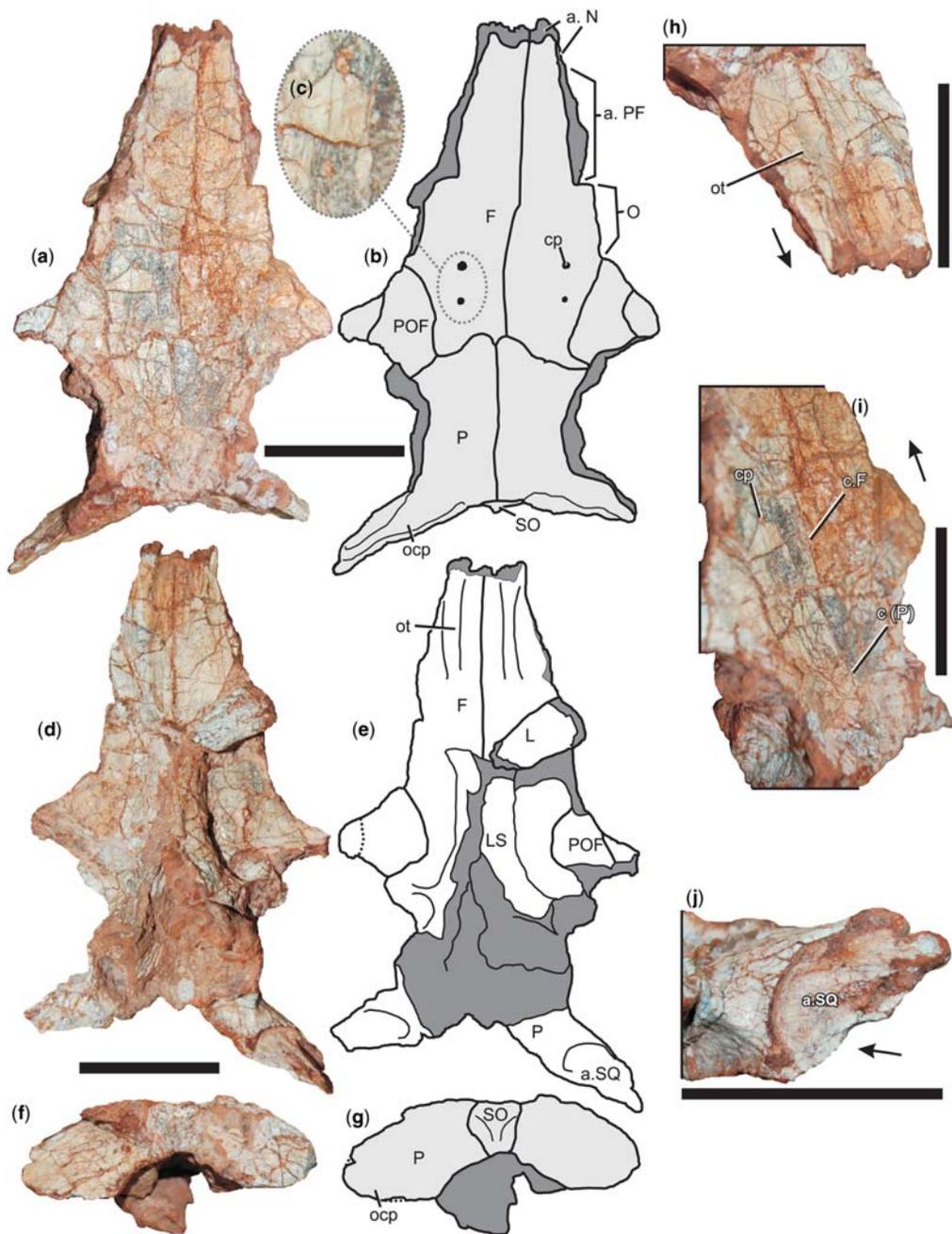


Fig. 9. Frontal, parietal and postfrontal of *Decuriasuchus quartacolonia* (MCN-PV10.004): (a) photograph in dorsal view; (b) outline in dorsal view; (c) detail of circular pit on dorsal surface of frontal; (d) photograph in ventral view; (e) outline in ventral view; (f) photograph in posterior view; (g) outline in posterior view; (h) detail of olfactory tract on ventral surface of frontal in anterolateral view; (i) detail of crests on dorsal surface of frontal and parietal in laterodorsal view; (j) detail of anterior surface of occipital process of parietal in lateroventral view, showing the articulation area with squamosal. Scale bar, 3 cm. *Abbreviations:* a., articulation with; c., crest of; cp, circular pits on frontal; F, frontal; L, lacrimal; LS, laterosphenoid; N, nasal; O, orbit; ocp, occipital process of parietal; ot, olfactory tract on frontal; P, parietal; PF, prefrontal; POF, postfrontal; SO, supraoccipital; SQ, squamosal. The arrow in (h, i, j) indicates the anterior region.

roof. In dorsal view, the processes form an angle of 90–100° to one another, whereas a larger (120–130°) angle is seen in *Batrachotomus kupferzellensis* (SMNS-52970), *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Arizonasaurus babbitti* (Nesbitt 2005).

In posterior view, the occipital process is only slight lateroventrally inclined (Fig. 9f, j). It has a sinuous ventral margin, a slightly concave posteromedial surface and a convex anterolateral surface. In its anterolateral surface a more distal semicircular depression on its anterolateral surface articulates with the squamosal (Fig. 9j: a.SQ). This articulation is smooth in MCN-PV10.004 and the squamosal is present but partially disarticulated in MCN-10.105d, which may indicate a kinetic junction. The posteromedial part of the upper temporal fenestra is formed by the occipital process of the parietal, whereas its posterolateral half is composed of the squamosal (Fig. 6). Because the squamosal articular area in the parietal does not reach the dorsal surface, the dorsal margin of the upper temporal fenestra is solely composed of the occipital process of the parietal.

Postorbital (Figs 2, 3, 6, 7 & 10). The postorbital is preserved in all MCN-105 skulls, plus the isolated left bone in MCN-PV10.004. It is T-shaped in lateral view, with medial, posterior and descending (or ventral) processes (Figs 2, 3 & 10a: mp, pp, dp). The first two processes are more dorsal, and form an angle of *c.* 120° to one another. In dorsal view, the medial process forms an angle of *c.* 45° to the sagittal line, unlike the 90° angle observed in *Saurosuchus galilei* (PVSJ-32). The contact area between medial and posterior processes bears a shallow furrow on the dorsal surface of the element, with a more protuberant lateral region (Fig. 10a, f: msf, lp). The descending process is perpendicular to the anteroposterior axis of the skull. The lateral margin of the dorsal surface is slightly rugose, but not as much as in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Batrachotomus kupferzellensis* (SMNS-52970; SMNS-80260). The short, cylindrical medial process contacts the postfrontal along an excavated anterior surface (MCN-PV10.105d, Fig. 10e, f). The medial process forms the anterolateral border of the upper temporal fenestra. The also cylindrical posterior process has an excavated distal area overlapped laterally by the squamosal (Fig. 10e, f). The small flat area that ventrally extends from the contact between the posterior and descending process seen in *Saurosuchus galilei* (PVL-2062; PVSJ-32) is absent in *Decuriasuchus quartacolonina*.

The posterior process articulates to the squamosal, forming the anterodorsal border of the lower temporal fenestra and the anterolateral border of

the upper temporal fenestra. In MCN-PV10.105 it has the same proximodistal length as the medial process, whereas in *Saurosuchus galilei* (PVL-2062; PVSJ-32) the posterior process is significantly shorter. The slender descending process has the anteroventrally directed distal half forming a smooth angle of *c.* 45° to the rest of the process, which is responsible for the keyhole shape of the orbit. The proximal portion of the process is subtriangular in cross-section, with posterior, lateral and medial surfaces. The elongated jugal articulation is posterior to the tapering distal part of the process (Fig. 10a, d), in the form of a dorsoventrally elongated furrow with a deep depression on the distal extremity. The descending process forms the posterodorsal margin of the orbit and the anterodorsal margin of the lower temporal fenestra. The dorsoventral ridge seen in *Arizonasaurus babbitti* (Nesbitt 2005) is absent in the descending process of *Decuriasuchus quartacolonina*.

Squamosal (Figs 2, 3, 6, 7 & 11). The squamosal is a four-pronged bone preserved in all MCN-PV10.105 skulls. A right isolated squamosal is preserved in MCN-PV10.004, in which all views of the bone are available (Fig. 11b: ap, pp, vp, mp). The blunt anterior process is circular in cross-section (Fig. 11d), as in *Saurosuchus galilei* (PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T), and unlike the suboval shape seen in *Batrachotomus kupferzellensis* (SMNS-80260) and *Polonosuchus silesiacus* (ZPAL/AbIII-563). In MCN-PV10.004 this anterior process is hollow, as seen in Fig. 11d. Its anterior margin articulates with the posterior process of the postorbital, forming the bar between upper and lower temporal fenestrae. The squamosal participation in that bar is not as extensive as in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011), but more than in *Batrachotomus kupferzellensis* (SMNS-80260). Its distal articulation has a notch on the ventral surface (Fig. 10), where the squamosal covers the postorbital dorsally, as in *Batrachotomus kupferzellensis* (SMNS-80260), *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Saurosuchus galilei* (PVSJ-32).

The lateral surface of the anterior process (MCN-PV10.105, MCN-PV10.004) lacks the thick rugose ridge seen in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011), *Polonosuchus silesiacus* (ZPAL/AbIII-563) and *Batrachotomus kupferzellensis* (SMNS-80260), whereas its dorsal surface has a small, circular, deep and rugose pit near its distal end (Fig. 11e, f: cp), a slight version of which is seen in *Saurosuchus galilei* (PVSJ-32), but not in *Effigia okeeffeae* (Nesbitt 2007), *Shuvosaurus inexpectatus* (Chatterjee 1993), *Batrachotomus kupferzellensis* (SMNS-80260) and

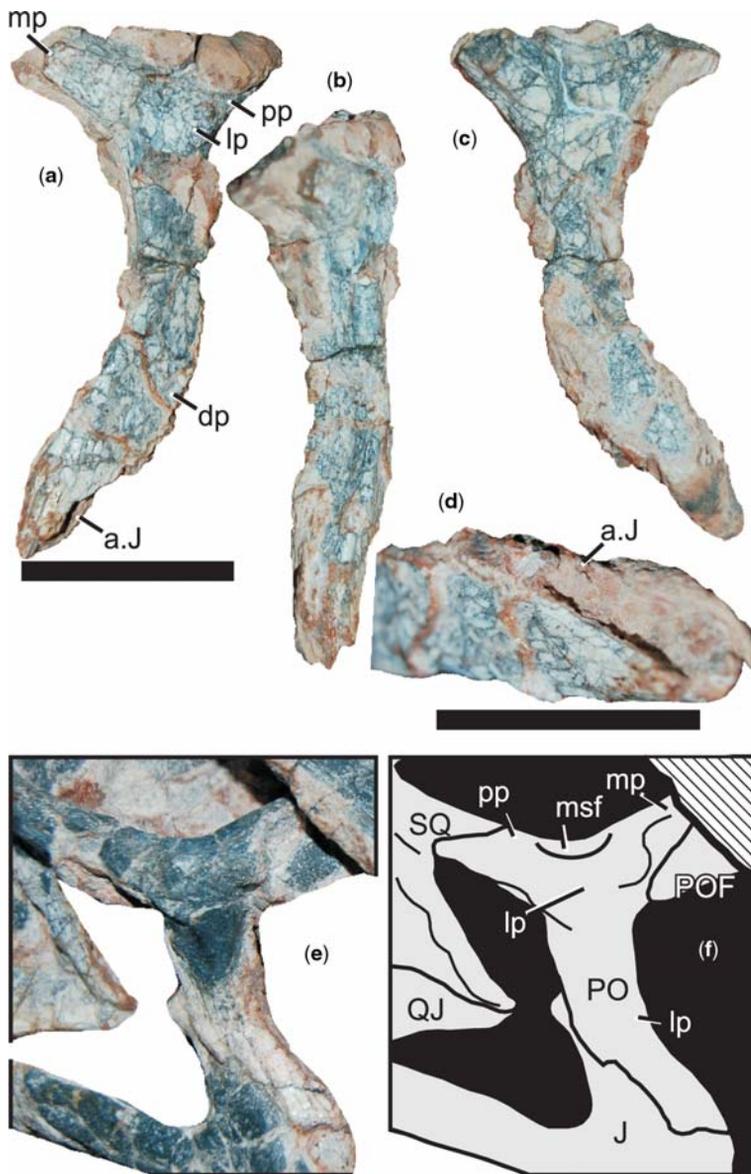


Fig. 10. Postorbital of *Decuriasuchus quartacolonia*: (a) left side of MCN-PV10.004 in lateral view; (b) left side of MCN-PV10.004 in anterior view; (c) left side of MCN-PV10.004 in medial view; (d) detail of distal extremity of descendant process of postorbital of left side of MCN-PV10.004; (e) photograph of MCN-PV10.105d in lateral view and (f) outline of MCN-PV10.105d in lateral view. Scale bar, 3 cm. *Abbreviations:* a., articulation with; dp, descendant process of postorbital; J, jugal; lp, lateral protuberance of dorsal surface of postorbital; mp, medial process of postorbital; msf, medial shallow furrow on dorsal surface of postorbital; PO, postorbital; POF, postfrontal; pp, posterior process of postorbital; QJ, quadratojugal; SQ, squamosal.

Postosuchus kirkpatricki (Chatterjee 1985; Weinbaum 2011). In some rauisuchians (e.g. *Batrachotomus kupferzellensis* [SMNS-80260], *Rauisuchus tiradentes* [BSPG/ASXXV-62], *Polonosuchus silesiacus* [ZPAL/AbIII-563], *Postosuchus kirkpatricki*

[Weinbaum 2011]), this process bears a ventral blade that articulates with the postorbital, which is absent in *Decuriasuchus quartacolonia*, *Saurosuchus galilei* (PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T).

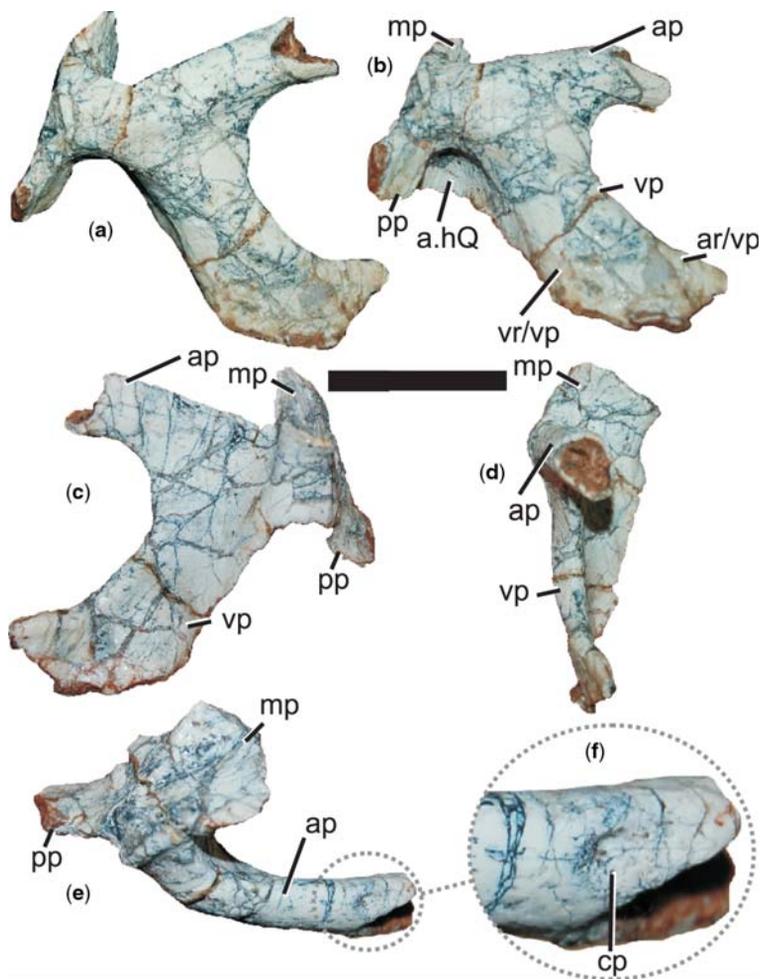


Fig. 11. Right squamosal of *Decuriasuchus quartacolonia* (MCN-PV10.004): (a) lateral view; (b) lateroventral view; (c) medial view; (d) anterior view; (e) dorsal view; (f) detail of circular pit on dorsal surface of anterior process of squamosal. Scale bar, 3 cm. *Abbreviations:* a., articulation with; ap, anterior process of squamosal; ar, anterior ramus of ventral process of squamosal; cp, circular pit; hQ, head of quadrate; mp, medial process of squamosal; pp, posterior process of squamosal; vp, ventral process of squamosal; vr, ventral ramus of ventral process of squamosal.

The posterior process is short, lateromedially flattened and cone-shaped in laterodorsal view (Fig. 11: pp). Distally, it is articulation-free and extends posteriorly to the parietal and quadrate. Its ventromedial surface, near the body, has a deep pit that articulates with the quadrate (Fig. 11b: a.hQ) and possibly with the dorsomedial region of the opisthotic. The medial part of this pit is occupied by a flat lamina that connects the posterior and ventral processes (Fig. 11b). In lateral view, the posterior process is ventrally angled in relation to the anterior process, unlike in *Arizonasaurus babbitti* (Nesbitt 2005), where these processes form a continuous line. The medial process of the squamosal

in MCN-PV10.105 and MCN-PV10.004 articulates with a semicircular depression of the occipital process of the parietal, forming the posterolateral margin of the upper temporal fenestra. As in *Effigia okeeffeae* (Nesbitt 2007) and *Saurosuchus galilei* (PVSJ-32), *Decuriasuchus quartacolonia* lacks a fossa in this area as seen in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011). In dorsal view, the medial process forms an angle of c. 30° in relation to the anterior process. In postero-medial view, this process has a subtriangular shape, flattened lateromedially.

The ventral process of the squamosal in *Decuriasuchus quartacolonia* has a singular morphology

among rauisuchians, which is best observed in MCN-PV10.105c,d (Fig. 3). Its tapering end projects anteriorly, reaching half the anteroposterior breadth of the lower temporal fenestra. The more dorsal part of the process is flat and medially displaced compared to the anterior projection. It contacts the quadrate posteriorly and is slightly posteromedially projected, forming a depressed area in relation of that bone. This contact is anterovertrally inclined, forming an angle of 45° in relation to the anterior process of the squamosal. Its ventral region has a straight margin that contacts the quadratojugal, and both bones form a triangular projection that invades the lower temporal fenestra. However, the anterior contact with the postorbital seen in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011), *Polonosuchus silesiacus* (ZPAL-AbIII-563) and *Tikisuchus romeri* (Chatterjee & Majumdar 1987) is lacking.

Jugal (Figs 2, 3, 10 & 12). This bone is present in all the MCN-PV10.105 skulls, and an isolated left jugal is also preserved in MCN-PV10.004. The jugal is a lateromedially flattened bone composed of elongate posterior, anterior and ascending (or dorsal) processes (Fig. 12a: pp, ap, asp). The

anterior is the thicker of the processes, and contacts the maxilla and possibly the lacrimal, forming the ventral margin of the orbit. It is not possible to determine the shape of its anterior margin, because it is either incomplete (MCN-PV10.004) or laterally covered by the maxilla (MCN-PV10.105). As in *Saurosuchus galilei* (PVL-2062; PVSJ-32) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011), the anterior process of the jugal in *Decuriasuchus quartacolonia* has a dorsal blade forming part of the posteroventral margin of the antorbital fenestra (MCN-PV10.105a). In lateral view, its distal half is anterodorsally deflected at an angle of 45°, in contrast to the broader angle in *Saurosuchus galilei* (PVL-2062; PVSJ-32). The process is deeper (dorsoventrally) distally than proximally, and its dorsal margin is concave. An anteroposteriorly directed ridge is seen in the ventral portion of the lateral surface (Fig. 12c: apr), subtler and stronger versions of which are seen respectively in *Saurosuchus galilei* (PVL-2062; PVSJ-32) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011).

The thin ascending process is the shortest of the jugal. It is directed dorsoposteriorly, forming a 45° angle with the posterior process, as seen in

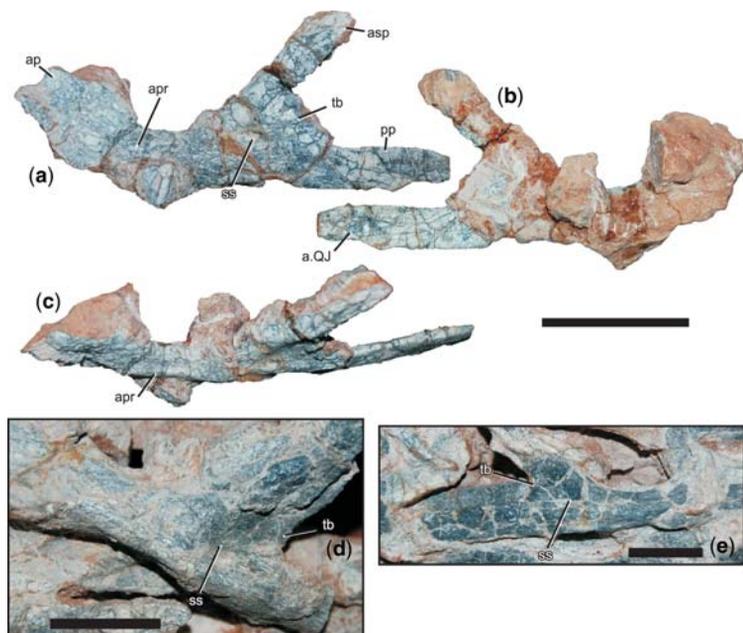


Fig. 12. Jugal of *Decuriasuchus quartacolonia*: (a) left side of MCN-PV10.004 in lateral view; (b) left side of MCN-PV10.004 in medial view; (c) left side of MCN-PV10.004 in laterodorsal view; (d) left side of MCN-PV10.105d in lateral view; (e) right side of MCN-PV10.105d in lateral view. Scale bar, 3 cm. *Abbreviations:* a., articulation with; ap, anterior process of jugal; apr, anteroposterior ridge on lateral surface of jugal; asp, ascendant process of jugal; pp, posterior process of jugal; QJ, quadratojugal; ss, shallow surface on lateral surface of main body of jugal; tb, thin blade between posterior and ascendant process of jugal.

Postosuchus kirkpatricki (Chatterjee 1985; Weinbaum 2011), *Arizonasaurus babbitti* (Nesbitt 2005) and *Effigia okeeffeae* (Nesbitt 2007), in contrast to the 80° angle of *Batrachotomus kupferzellensis* (SMNS-52970), *Saurosuchus galilei* (PVL-2062; PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T). This process contacts the descending process of the postorbital via a slit in the latter bone (Figs 10e, f & 12d, e). This articulation extends along almost the entire length of this process, as in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Saurosuchus galilei* (PVL-2062; PVSJ-32), but unlike the process in *Batrachotomus kupferzellensis* (Gower 1999), which has a higher participation in the orbit margin. In the lower temporal fenestra, the ascending process extends over approximately half of its anterior margin, as in *Batrachotomus kupferzellensis* (Gower 1999), whereas the process is more extensive in *Saurosuchus galilei* (PVL-2062; PVSJ-32). Near the jugal body, the lateral surface of the ascending process has a shallow excavation (Fig. 12a, d, e: ss), as also seen in cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T) and *Saurosuchus galilei* (PVL-2062; PVSJ-32), but not in *Batrachotomus kupferzellensis* (SMNS-52970). *Decuriasuchus quartacolonina* has a bone lamina connecting the ascending and posterior processes, forming a fossa at the anteroventral corner of the lower temporal fenestra (Fig. 12a, e, f: tb), which extends more posteriorly in *Batrachotomus kupferzellensis* (SMNS-52970) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011).

The posterior process of the jugal is lateroventrally flattened, lacking the rugose ridge seen in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011). Its dorsal and ventral margins are almost parallel, except for a step along the ventral margin near the distal end, also seen in *Batrachotomus kupferzellensis* (SMNS-52970), *Saurosuchus galilei* (PVL-2062; PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T). A tapering posterior process as in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) is, however, lacking. In medial view, MCN-PV10.004 has a semicircular shallow depression in the posteroventral portion of the process (Fig. 12b: a.QJ), which is also present in *Batrachotomus kupferzellensis* (SMNS-52970). In this area, the posterior process covers the quadratojugal laterally. In addition, the posterior process of *Decuriasuchus quartacolonina* does not comprise the entire ventral border of the lower temporal fenestra as in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011).

Quadratojugal (Figs 2, 3 & 7). The quadratojugal is preserved only in the MCN-PV-10.105 skulls, and its anterior and ascending processes form the

posteroventral border of the lower temporal fenestra. The short anterior process has dorsal and ventral margins almost parallel to one another, and contacts the jugal anteriorly at the ventromedial surface of that bone. In lateral view, the ascending process is composed of a triangular blade with a slightly concave lateral surface. It contacts the quadrate posteriorly and the ventral ramus of the ventral process of the squamosal dorsally. As discussed above, this region forms the triangular projection that reaches the lower temporal fenestra, as more clearly seen in the left side of MCN-PV10.105a and the right side of MCN-PV10.105d. The partial disarticulation observed in the other sides/skulls suggests that the quadratojugal/squamosal articulation is fragile. The anterior and ascending processes form an angle of *c.* 30°. The main body of the quadratojugal, formed by the confluence of the anterior and ascending processes, is expanded posteriorly to the quadrate, and has convex lateral and concave medial surfaces (Fig. 3a, b).

Quadrate (Figs 2, 3, 7 & 13). The quadrate is preserved in both sides of MCN-PV10.105a, but better seen in the posterior and lateral view of the left side, except for the ventral and dorsal extremities, which are covered by other cranial bones. The bone in MCN-PV10.105c,d is observed only partially in the right side, whereas it is almost completely preserved isolated in the left side of MCN-PV10.004, except for its dorsal portion. Accordingly, the quadrate head is not available in any specimen. The quadrate is anterodorsally inclined in lateral view and slightly dorsomedially inclined in posterior view. The bone articulates dorsally with the squamosal, ventrally with the articular, laterodorsally with the squamosal, lateroventrally with the quadratojugal, and medially with the pterygoid (Fig. 13).

The ventral articulation of the quadrate is subrectangular in ventral view (Fig. 13 g), with the long axis forming an angle of *c.* 45° relative to the anteroposterior axis of the skull (the lateral region is more anteriorly situated, and the medial more posteriorly). The lateral and medial condyles are separated by a well-defined groove, and have almost the same shape and height. The medial condyle is slightly more oval in shape, whereas the lateral condyle is more subrectangular, as also described for *Arizonasaurus babbitti* (Nesbitt 2005). In addition, the medial condyle is slightly more ventrally projected (MCN-PV10.004), and both are more ventrally projected than the quadratojugal (MCN-PV10.105a), as also seen in *Batrachotomus kupferzellensis* (SMNS-80260) and *Saurosuchus galilei* (PVSJ-32).

The quadrate body is a pillar nearly dorsoventrally oriented in posterior view and posterodorsally

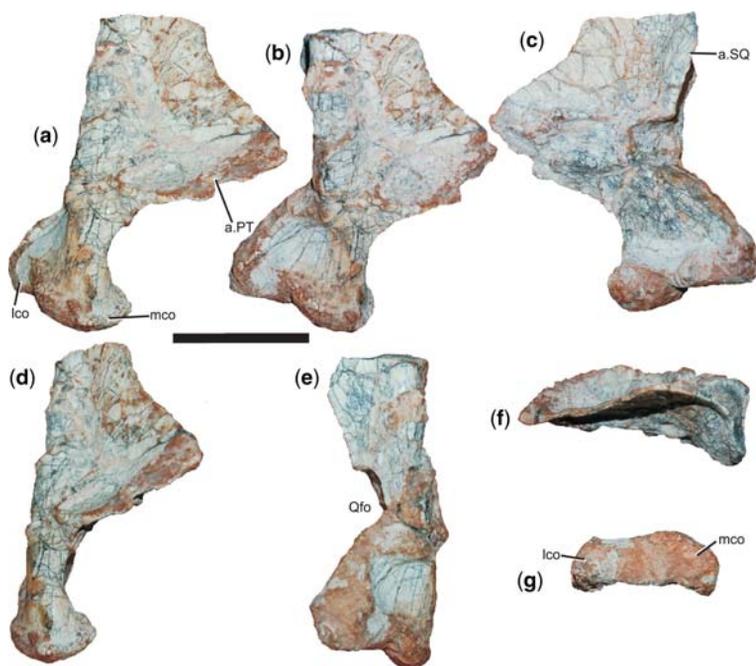


Fig. 13. Left quadrate of *Decuriasuchus quartacolonina* (MCN-PV10.004): (a) medial view; (b) posteromedial view; (c) anterolateral view; (d) anterior view; (e) posterior view; (f) dorsal view; (g) ventral view. Scale bar, 3 cm. Abbreviations: a., articulations with; lco, lateral condyle of quadrate; mco, medial condyle of quadrate; PT, pterygoid; Qfo, quadrate foramen; SQ, squamosal.

inclined in lateral view. Its distal third is posterolaterally to anteromedially flattened and its most lateral surface bears a thin blade that articulates with the quadratojugal (MCN-PV10.105c), lacking the thick lateral ridge seen in *Saurosuchus galilei* (PVSJ-32). Dorsal to that, the quadrate foramen is seen in lateral view (MCN-PV10.105c,d). It is ventrally, dorsally and medially limited by the quadrate, and laterally by the quadratojugal (Fig. 13e: Qfo). At the dorsal two-thirds of the body, in lateral view, the lateral flange of the quadrate corresponds to a thin, anteriorly directed blade that articulates with the ventral margin of the squamosal (Fig. 13c, e: a.SQ). Walker (1990) considered this flange in *Sphenosuchus acutus* homologous to the anterodorsal process of crocodylians, suggesting that it limited mandible protraction. In posterior view, the lateral flange is partially covered by the columnar body, as also seen in *Saurosuchus galilei* (PVSJ-32) but not in *Batrachotomus kupferzellensis* (Gower 1999), the flange of which is well seen in posterior view. The flange in *Decuriasuchus quartacolonina* has a convex lateral margin, like *Saurosuchus galilei* (PVSJ-32). This is evident in the posterolateral view of MCN-PV10.105c,d, but covered by the squamosal in MCN-PV10.105a and missing in MCN-PV10.004. Its posteriormost

region, immediately anterior to the columnar body, has a dorsoventrally directed thin groove, which appears to reach the quadrate foramen (MCN-PV10.105c,d, MCN-PV10.004).

In posteromedial view, the pterygoid flange of MCN-PV10.004 occupies the dorsal two-thirds of the bone (Fig. 13a). This is lateroposteriorly bounded by the columnar body and ventromedially by a rugose ridge. In MCN-PV10.004, the pterygoid and lateral flanges form an angle of *c.* 45°, whereas a greater angle of *c.* 80° is seen in *Saurosuchus galilei* (PVSJ-32). The anteromedial surface of the quadrate is only seen in MCN-PV10.004. In anterior view, on the ventral third of the body, there is a well-defined rugose protuberance, also seen in *Batrachotomus kupferzellensis* (Gower 1999), *Arizonasaurus babbitti* (Nesbitt 2005) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011), and more subtly in *Saurosuchus galilei* (PVSJ-32). In the dorsal third of the pterygoid flange, a medially directed ridge forms an angle of 45° to the lateral flange. In the medial surface of the columnar body, at its dorsal region portion and between the pterygoid and lateral flanges, a well-defined groove is seen, as is also the case for *Saurosuchus galilei* (PVSJ-32). In the anterodorsal view of MCN-PV10.004, although most of its dorsal region is

not preserved, the lateral and pterygoid flanges form an angle of 50°; an angle smaller than that is seen in *Saurosuchus galilei* (PVSJ-32). *Batrachotomus kupferzellensis* has a posteromedial groove in the ventral third of the body, possibly correlated to the tympanic insertion (Gower 1999). This structure is not observed in the specimens of *Decuriasuchus quartacolonina*.

Vomer. The vomer cannot be observed in any skull of *Decuriasuchus quartacolonina*, including the part of the palate exposed in MCN-PV10.105a (Fig. 14). In addition, the manipulation of the two maxillae preserved in MCN-PV10.004, and comparison to the articulated skulls of MCN-PV10.105, suggest that the palatal processes of those bones were medially separated by the vomer.

Palatine (Fig. 14). The left partial palatine is visible in MCN-PV10.105a, but only in ventral view. The bone contacts the maxilla laterally and the pterygoid medially, and the area between these articulations is anteroposteriorly expanded as in like *Batrachotomus kupferzellensis* (SMNS-80260) and *Saurosuchus galilei* (PVSJ-32). The ventral surface bears protuberances and depressions that may have been taphonomically produced (Fig. 14c: prt, sha). The posterior region that borders the suborbital fenestra is incomplete. Likewise, the anterior region that forms the choanal border is not observed because this region is covered by the dentary teeth and encrustations.

Pterygoid (Fig. 14). The triradiate pterygoid is only visible in the ventral view, in the left side of MCN-PV10.105a, and is composed of anterior, posteroventral and quadrate rami (Fig. 14b: ar, pvr, qr). The anterior ramus is almost complete and contacts the palatine laterally, but the anterior contact with the vomer is not visible. Its ventral surface is flat, with a concave medial margin along the midline, whereas the lateral margin is slightly sinuous and bends medially in the anterior region. The posterior region of the anterior ramus of the pterygoid is expanded laterally, forming an angle of nearly 90° with the anterior portion of the bone, as in *Batrachotomus kupferzellensis* (SMNS-80260) and *Saurosuchus galilei* (PVSJ-32). In other rauisuchians, as *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Polonosuchus silesiacus* (ZPAL/AbIII-563), this angle is more obtuse.

The posterior margin of the posteroventral ramus of the pterygoid is almost perpendicular to the anteroposterior skull axis. The ramus does not appear to expand ventrally, but this is probably due to taphonomic deformation. Its ventral surface has an S-shaped 'suture' (Fig. 14b, d: sss), lateral to which

the ramus is dorsally depressed. The posteromedial region of the posteroventral ramus has a small conical midline posterior projection, a subtler version of which is seen in *Saurosuchus galilei* (PVL-32). In addition, the posteroventral ramus of the pterygoid of *Saurosuchus galilei* (PVSJ-32) is more laterally expanded than that of *Decuriasuchus quartacolonina*.

The posterolaterally directed quadrate ramus is not well preserved in the pterygoid of *Decuriasuchus quartacolonina*. Its anterior and posterior extremities are more expanded than its waisted middle portion, which is almost oval in cross-section, forming a columnar structure. The posterior half of the bone is flattened, forming the contact with the quadrate and the dorsal contact with the basisphenoid. The quadrate ramus of the pterygoid of *Decuriasuchus quartacolonina*, *Saurosuchus galilei* (PVSJ-32) and *Batrachotomus kupferzellensis* (SMNS-80260) has a shaft more anteroposteriorly elongated than in *Postosuchus kirkpatricki* (Weinbaum 2011).

Ectopterygoid (Fig. 14). Only the ventral surface of the posterior region of the left ectopterygoid is visible in *Decuriasuchus quartacolonina* (MCN-PV10.105a), but the anterior and lateral regions are covered by the hyoid. The ectopterygoid contacts the pterygoid medially and is similar to *Batrachotomus kupferzellensis* (SMNS-80260) and *Postosuchus kirkpatricki* (Weinbaum 2011). Because of preservational issues, some characteristics cannot be observed, such as the length of the articular facet with the jugal and the number of heads on the jugal process.

Mandible

Articular (Fig. 15). Although preserved in MCN-PV10.105a,c,d, the articular is only completely seen in MCN-PV10.004. It is a complex bone that composes the posterior portion of the mandible, dorsomedial to the surangular. In dorsal view, its most anterior region bears the medial and lateral mandible glenoids, which articulate to the medial and lateral condyles of the quadrate (Fig. 15b, g: mgl, lgl; see also Sampson & Witmer 2007). The drop-shaped lateral glenoid is more anteriorly placed, so that the condyles are oblique in relation to the anteroposterior axis of the skull, whereas *Fasolasuchus tenax* (PVL-3850), *Batrachotomus kupferzellensis* (SMNS-80260), *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Polonosuchus silesiacus* (ZPAL/AbIII-563) have lateromedially aligned condyles. The anterior margin of the lateral glenoid has a sharp ridge that is lateromedially directed for most of its length (Fig. 15b, j: dsr), except for a minor, posteromedially directed

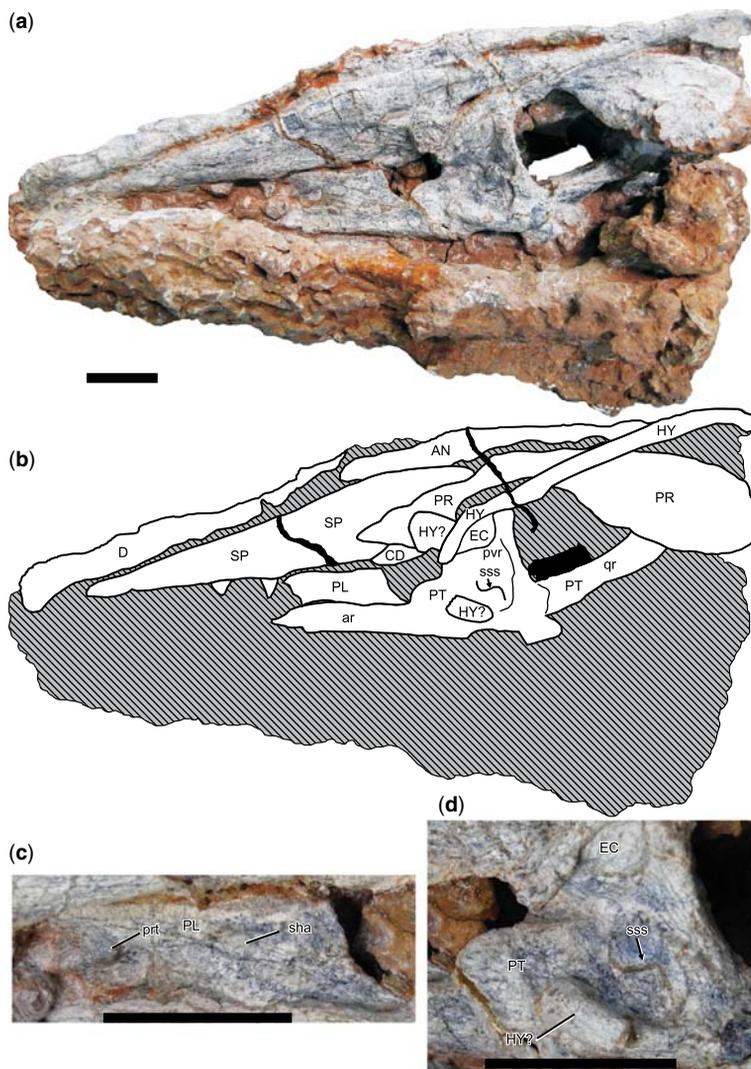


Fig. 14. Skull of *Decuriasuchus quartacolonina* (MCN-PV10.105a) in ventral view: (a) photograph; (b) outline; (c) detail of palate; (d) detail of pterygoid and ectopterygoid. Scale bar, 3 cm. *Abbreviations:* AN, angular; ar, anterior ramus of pterygoid; CD, coronoid; D, dentary; EC, ectopterygoid; HY, hyoid; PL, palate; PR, prearticular; prt, protuberance on palatine; PT, pterygoid; pvr, posteroventral ramus of pterygoid; qr, quadrate ramus of pterygoid; sha, shallow area on palatine; SP, splenial; sss, s-shaped suture on pterygoid. Hatched area indicated the concretion that involves the fossil.

medial portion. Anteriorly, this ridge delimits the articulation with the surangular. The lateral margin of the lateral glenoid is slightly concave, and marks the anterolateral articulation with the surangular. Its medial margin forms the interglenoid ridge (Fig. 15b, j: igr), which is anteromedially directed, almost straight, slightly pronounced and concave. The lateral and medial margins of the lateral glenoid form a posterior apex, which is dorsally

projected (Fig. 15c, d). The medial glenoid is reniform in dorsal view, and is almost parallel to the anteroposterior skull axis (Fig. 15b: mgl). The anterior and posterior margins are convex, with the posterior more dorsally expanded. The medial margin is also parallel to the anteroposterior skull axis, although its midlength is excavated. The anterior region of the medial glenoid is a subrectangular flattened area that forms the anterior border of

the bone, and its largest edges are almost lateromedially directed. The lateral glenoid is dorsally displaced relative to the medial glenoid (Fig. 15f, g).

The retroarticular region of *Decuriasuchus quartacolonina* is composed of six distinct structures, seen well in dorsal view: an anteroposterior projection, situated anterolaterally (Fig. 15b, j: app); a longitudinal groove, immediately lateral to the anteroposterior projection (Fig. 15b, j: lg); a lateromedially elongated deep groove, immediately posterior to the medial glenoid and medial to the anteroposterior projection (Fig. 15b, j: tg); a retroarticular fossa on the posterolateral region (Fig. 15b, g, j: raf), with a dorsal ridge on the lateral margin (Fig. 15b, g, j: dr); and an ascending process, on the posteromedial region (Fig. 15b, g, j: asp). The columnar anteroposterior projection contacts the lateral glenoid on its anterior tip. It laterally delimits the articular anteroposteriorly and contacts the surangular, from which it is separated by an anteroposteriorly elongated narrow groove. Posteriorly, it contacts the retroarticular fossa, and medially the groove and the ascending process. Similar structures have not been described for any rauisuchians. The well-developed longitudinal groove of the retroarticular region lies immediately lateral to the anteroposterior projection. It is narrow and anteroposteriorly elongated. The transverse groove is rectangular-shaped and lateromedially directed between the medial condyle and the ascending process. A similar groove is present in *Postosuchus alisonae* (Peyer *et al.* 2008), *Polonosuchus silesiacus* (ZPAL/AbIII-563) and *Effigia okeeffeae* (Nesbitt 2007), and a deeper and oval-shaped groove in *Batrachotomus kupferzellensis* (SMNS-80260). The ascending process is the most dorsal area of the articular and is an anteroposteriorly directed, lateromedially compressed rugose protuberance. This contacts the transverse groove anteriorly and the retroarticular fossa laterally. The latter contact bears a posterior notch between the ascending process and the retroarticular fossa, forming a hook-shaped structure in dorsal view, as also seen in *Arizonasaurus babbitti* (Nesbitt 2005) and *Batrachotomus kupferzellensis* (SMNS-80260). The subquadrangular retroarticular fossa is laterally and posteriorly limited by a distinct rugose ridge, which is probably associated with the insertion of muscle depressor mandibulae (Sampson & Witmer 2007). The surface of the fossa is composed of two slightly depressed areas, the more posterior of which is wider and deeper, separated by a slightly lateromedially directed rugosity that occupies the anterior third of the fossa. *Batrachotomus kupferzellensis* (SMNS-80260) has a single depression on the retroarticular fossa, which is relatively smaller and deeper than that of MCN-PV10.004. In dorsal view, the retroarticular region of *Postosuchus*

kirkpatricki (Chatterjee 1985; Weinbaum 2011) has a lateroposterior projection, absent in *Decuriasuchus quartacolonina*, as well as in *Batrachotomus kupferzellensis* (SMNS-80260), *Fasolasuchus tenax* (PVL-3850; PVL-3851) and *Polonosuchus silesiacus* (ZPAL/AbIII-563).

In lateral view, the dorsal and ventral margins of the posterior articular form an angle of 30° (Fig. 15c, d). Only the dorsal margin of the ridge of the retroarticular fossa and the columnar structure between the retroarticular fossa and lateral glenoid are observed in this view, whereas the ventral region bears a lateral rugosity and another columnar structure, both of which, as well as the entire posterolateral surface of the articular, have scars possibly representing muscle insertions. The lateral rugosity is suboval in shape and located approximately mid-length along the posterior margin of the articular (Fig. 15d, i, k: lr). The ventral columnar structure is more posteroventrally placed (Fig. 15i, k: vcs), occupying the posterolateral region of the articular, separated from the lateral rugosity by a groove (better seen in lateroventral view).

The ventral surface of the articular is almost flat, except for the above-mentioned columnar structure on its posterolateral region and the also columnar and medioventrally directed medial process of the articular (Fig. 15 g, i, k: mp). A more ventrally directed medial process is seen in *Arizonasaurus babbitti* (Nesbitt 2005), whereas that of *Batrachotomus kupferzellensis* (SMNS-80260) approaches the condition described here. In *Rauisuchus tiradentes* (BSPG/ASXXV-68), this process is perpendicular to the lateromedial axis in posterior view, and more vertical than in MCN-PV10.004. The medial process of *Decuriasuchus quartacolonina* is circular in cross-section, with a broader base. Its medial surface has the oval deep fossa often associated with the *chorda tympani* foramen (Fig. 15 g: ctfo) (Chatterjee 1985; Gower 1999; Nesbitt 2005; Peyer *et al.* 2008). In *Arizonasaurus babbitti* (Nesbitt 2005) and *Stagonosuchus nyassicus* (Gebauer 2004), this foramen is smaller and more dorsal than in *Decuriasuchus quartacolonina*, *Batrachotomus kupferzellensis* (SMNS-80260) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011). The lateral contact of the articular with the surangular is evident in ventral view, where the articular bears a L-shaped shallow groove, just anterior to the medial process (Fig. 15i, k: lssg). One facet of this groove forms the lateroanterior margin of the medial process, and the other is anterolaterally directed. More anteriorly, the articular has a lateromedial straight margin, which is depressed along with the surangular flap, forming the posterior portion of the adductor fossa. The area between the L-shaped groove and the depressed margin corresponds to the articulation with the

prearticular, on the anteromedial of the articular ventral surface. Following the considerations of Sampson & Witmer (2007), the *M. pterigoideus ventralis* probably inserted in the ridges around the retroarticular fossa, as well as in the lateral rugosity and columnar structure on the posterolateroventral portion of the articular of *Decuriasuchus quartacolonina*, whereas *M. pterigoideus dorsalis* would be associated with the medial process of the articular.

Surangular (Figs 2, 3 & 15). This bone is exposed in lateral view on the left side of MCN-PV10.105a and on the right side of MCN-PV10.105c,d. In MCN-PV10.004, the surangular is firmly articulated with the articular, which covers its posteromedial portion. In general, the surangular occupies most of the posterolateral region of the mandible and is composed of lateral and dorsal flat portions, which project dorsoventrally and lateromedially, respectively (Fig. 15b, d, g; lfs, dfs), forming an angle of 90° to one another. The anterior portion of the surangular forms the entire posterior and dorsal margins and part of the ventral margin of the lateral mandibular fenestra. It contacts the dentary anterodorsally, the angular ventrally and the articular posteriorly and medially. In lateral view, the margin between the dorsal and lateral flat structures is almost anteroposteriorly oriented, except its posterior tip. This margin has an anteroposteriorly elongated protuberance that projects laterally and dorsally, concealing the lateral flat structure in dorsal view. This protuberance is positioned at the level of the lateral glenoid of the articular (Fig. 15d: SAls), and corresponds to the surangular lateral shelf of Sampson & Witmer (2007). Ventral to that, the lateral flat structure has a small excavated area, possibly related to the insertion of *M. adductor mandibulae externus* (Sampson & Witmer 2007). This area bears a very small aperture placed at the anteroposterior level of the lateral glenoid, probably representing the posterior foramen of the surangular (Fig. 15e: pfo). In dorsal view, the surangular lateral shelf is lateromedially narrow (Fig. 15a, b), with a sinuous lateral

margin: the lateral edge is convex except for a concave region just anterior to the lateral glenoid.

The dorsal flat structure of the surangular has an almost flat dorsal surface, lateromedially narrow and anteroposteriorly elongated, and contacts the anterior ridge of the lateral glenoid. Anteriorly, the surface has a deep groove (MCN-PV10.004) on its laterodorsal corner (Fig. 15b: a.DE) that articulates to the posterodorsal process of the dentary (Gower 1999), as seen in *Batrachotomus kupferzellensis* (SMNS-80260) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011). However, the contact area is not completely preserved, lacking the anterior tip of the surangular (MCN-PV10.004). The posteromedial surface of the lateral flat structure has a hook-shaped medial projection, seen in dorsal and ventral views. This is dorsoventrally flattened and forms the posteromedial portion of the adductor fossa of the mandible (Fig. 15b, g, i, k: a.PR). The ventral surface of the dorsal flat structure of surangular has an anteroposterior ridge on its posterior two-thirds, whereas the medial surface of the lateral structure bears an oval depression situated on its intermediate third, which fits to the central process of the dentary (Fig. 15 g: a.DE; Gower 1999). The area just anterior to that depression bears two pits that possibly indicate the articulation of the coronoid (Fig. 15i: a.CD; Gower 1999).

In lateral view, the ventral margin of the surangular is convex, and MCN-PV10.004 shows an articular area with the angular bone along its anterior two-thirds (Fig. 15i: a.AN). The reconstructed mandibular fenestra of *Decuriasuchus quartacolonina* is smaller than that of *Batrachotomus kupferzellensis* (SMNS-80260) and *Rauisuchus tiradentes* (BSPG/ASXXV-68). The ventral region of the fenestra is occupied by a small tapering projection of the surangular (MCN-PV10.105d). Comparing the anteroposterior length with the dorsoventral height, the surangular of MCN-PV10.004 is almost five times longer than it is high. A similar condition is seen in *Batrachotomus kupferzellensis* (SMNS-80260), whereas the bone is bulkier in *Rauisuchus tiradentes* (BSPG/ASXXV-68) and more slender in *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum

Fig. 15. (Continued) of surangular; (f) photograph in medial view; (g) outline in medial view; (h) photograph in ventral view; (i) outline in ventral view; (j) detail of glenoids and retroarticular region of articular in dorsal view; (k) detail of ventral surface of articular in lateroventral view. Scale bar, 3 cm. *Abbreviations:* a., articulation with; app, anteroposterior projection of retroarticular region of articular; AN, angular; AR, articular; asp, ascendant process of retroarticular region of articular; CD, coronoid; ctfo, *chorda tympani* foramen; DE, dentary; dfs, dorsal flat structure of surangular; dr, dorsal ridges of retroarticular region of articular; dsr, dorsal sharp ridge of surangular/articular; igr, interglenoid ridge; lfs, lateral flat structure of surangular; lgr, longitudinal groove of retroarticular region of articular; lgl, lateral glenoid of articular; lr, lateral rugosity of articular; lssg, L-shaped shallow groove of ventral surface of articular; MF, mandibular fenestra; mgl, medial glenoid of articular; mp, medial process of articular; pfo, posterior foramen of surangular; PR, prearticular; raf, retroarticular fossa of retroarticular region of articular; SA, surangular; SAls, surangular lateral shelf; tg, transverse groove of retroarticular region of articular; vcs, ventral columnar structure of articular.

2011), *Effigia okeeffeae* (Nesbitt 2007) and *Shuvosaurus inexpectatus* (Chatterjee 1993). In addition, the posterior portion of the mandible (in ventral view), which is mainly composed of the surangular and articular, is less medially oriented in *Decuriasuchus quartacolonius* than in *Rauisuchus tiradentes* (BSPG/ASXXV-68). In the latter taxon, the posterior region forms an angle of 30° with the anteroposterior axis of the dorsal flat structure of the surangular, whereas in MCN-PV10.004 this margin is more gently convex, as in *Batrachotomus kupferzellensis* (SMNS-80260) and *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011).

Angular (Figs 2, 3 & 14). Only the lateral surface of the angular is exposed in the MCN-PV10.105a,c,d skulls, but its ventral and medial surfaces are partially seen in MCN-10.105a. In lateral view, the angular forms the posteroventral margin of the lateral mandibular fenestra. Its slender anterior projection forms a V-shaped articulation with two small expansions of the dentary (MCN-PV10.105d), surpassing the level of the anterior edge of the fenestra. Posteriorly, the also slender posterior projection of the angular contacts the surangular along the ventral margin of mandible. Between the two projections, the angular body is more dorsoventrally expanded, laterally covering the articular region with the surangular. The dorsal margin of the body is convex in lateral view. The anteromedial region of the angular contacts the splenial dorsally, whereas the posteromedial region contacts the prearticular (MCN-PV10.105a; Fig. 14a). The angular of *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) has anterior and posterior projections that are less elongated than those of *Decuriasuchus quartacolonius*. In addition, *Postosuchus kirkpatricki* has a thickened and rugose ventral surface, whereas this surface is subtly convex in *Decuriasuchus quartacolonius* and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T).

Splenial (Fig. 14). Only the medial surface of the splenial is observable in MCN-PV10.105a. Its surface is flat, but with some taphonomic protuberances, and the anterior portion is not fully prepared. The ventral margin is rounded, thicker than the dorsal margin, and covered by the ventral margin of the dentary not forming the ventral margin of the mandible. Those bones are separated by a deep anteroposteriorly elongated groove (MCN-PV10.105a), as seen in *Prestosuchus chiniquensis* (BSPG/ASXXV-1). The only region that apparently participates in the ventral margin of the mandible is the angular process of the splenial, similar to the arrangement in *Prestosuchus chiniquensis* (BSPG/AS-XXV-1). This is the greater of the two posterior processes of the splenial of *Decuriasuchus*

quartacolonius that border the anterior region of the internal mandibular fenestra. The process has a ventral margin that is continuous to the blade region of the bone, whereas the dorsal margin is anterodorsally directed and tapers posteriorly. The smaller dorsal (coronoid) process is about one-third the length of the angular process. This is also triangular, but both margins are posteriorly confluent. The contact with the coronoid is restricted to the dorsal region of the process, and does not extend anteriorly along the blade region of the splenial, as reconstructed in *Batrachotomus kupferzellensis* (Gower 1999).

Coronoid (Fig. 14). The coronoid is only partial visible in MCN-PV10.105a, and is mostly covered by encrustation. It is posteriorly restricted by the splenial, dorsally covering the anterior region of the prearticular.

Prearticular (Fig. 14). This bone is preserved in MCN-PV10.105a, but covered by the hyoid and encrustations on its posterior portion. In general, it is a gently curved bone, which contacts the splenial anteriorly, the coronoid anterodorsally and the articular posteromedially. At its midpoint, the bone apparently has an oval cross-section, whereas anterior and posterior extremities are mediolaterally flattened. Its ventral margin is covered by the angular, so it is restricted to the medial surface of the jaw. The dorsal margin forms the ventral border of the internal mandibular fenestra. Its anterior portion is more anteroposteriorly extended than that of *Rauisuchus tiradentes* (BSPG/AS-XXV-68).

Dentary (Figs 2, 3, 14 & 16). The dentary is partially or entirely preserved in all specimens of *Decuriasuchus quartacolonius*. In lateral view, the bone contacts the surangular posterodorsally, the angular posteroventrally and the splenial, coronoid and angular medially. The dentary is a slender, anteroposteriorly elongate bone, corresponding to c. 60% of the mandible length (MCN-PV10.105a,d), as inferred for *Batrachotomus kupferzellensis* (Gower 1999). In *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) the bone is relatively longer (75% of the mandible length), and in *Effigia okeeffeae* (Nesbitt 2007) and *Shuvosaurus inexpectatus* (Chatterjee 1993) much shorter (25% of the mandible length). The ventral margin of the dentary of *Decuriasuchus quartacolonius* is slightly convex as in *Saurosuchus galilei* (PVSJ-32), in contrast to the straight margin seen in *Prestosuchus chiniquensis* (BSPG/ASXXV-1), *Batrachotomus kupferzellensis* (SMNS-80260), *Arganasuchus* (Jalil & Peyer 2007) and *Arizonasaurus babbitti* (Nesbitt 2005), and the sinuous ventral margin of *Postosuchus kirkpatricki* (Weinbaum 2011). The

SKULL ANATOMY OF *DECURIASUCHUS QUARTACOLONIA*

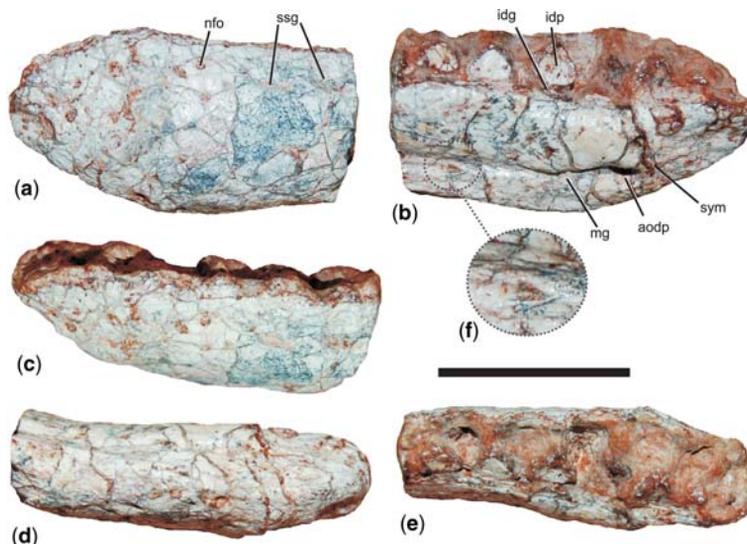


Fig. 16. Fragment of left dentary of *Decuriasuchus quartacolonina* (MCN-PV10.004): (a) lateral view; (b) medial view; (c) laterodorsal view; (d) ventral view; (e) dorsal view; (f) detail of medial surface in medial view. Scale bar, 3 cm (except f). *Abbreviations:* aodp, anterior oval deep fit on meckelian groove; idg, interdental groove; idp, interdental plates; mg, meckelian groove; nfo, nutrient foramen; ssg, semilunar shaped grooves; sym, symphysis mandibular region.

dorsal margin is almost parallel to the ventral margin for almost its entire extension. This resembles the condition in *Saurosuchus galilei* (PVSJ-32) and *Prestosuchus chiniquensis* (BSPG/ASXXV-1), which lack the dorsoventral expansion of both margins seen in *Batrachotomus kupferzellensis* (SMNS-80260; Gower 1999) and the dorsal margin expansion of *Arizonasaurus* (Nesbitt 2005), *Postosuchus kirkpatricki* (Weinbaum 2011) and *Polonosuchus silesiacus* (ZPAL-AbIII-563; Sulej 2005).

In MCN-PV10.004, the dorsal and ventral margins of the dentary converge to a tapering anterior point. In lateral view, the dorsal margin slopes anteroventrally, reaching the level of the dentary groove, whereas the ventral margin is more arched (Fig. 16a), as in *Saurosuchus galilei* (PVSJ-32) and *Prestosuchus chiniquensis* (BSPG/ASXXV-1). However, the anterior margin in *Decuriasuchus quartacolonina* is less angular in the former taxon and more rounded in the latter. The anterior dentary tip of *Decuriasuchus quartacolonina* has striations (MCN-PV10.004, MCN-PV10.105d), mainly on the anterodorsal portion, as observed in *Prestosuchus chiniquensis* (BSPG/ASXXV-1) and *Polonosuchus silesiacus* (ZPAL/AbIII-563). Posteriorly, the dentary forms the anterior border of the lateral mandible fenestra, contacting the surangular dorsally and the angular ventrally. The contact with the surangular is formed by two posterodorsal projections, better seen and partially disarticulated

in MCN-PV10.105a (Fig. 2). The ventral projection extends medially into a fossa in the surangular. The dorsal projection contacts the surangular via a groove in its dorsal surface. The contact with the angular also has two projections, although these are more slender and posteriorly elongated (MCN-PV10.105d). The dorsal projection is slightly shorter and occupies the anteroventral half of the lateral mandible fenestra. The ventral projection is more posteriorly extended, reaching the level of the mid-length of that fenestra.

The anterior portion of the dentary of MCN-PV10.004 shows striations over its dorsal margin. These limit the anterior region of the dentary, which is depressed in relation to the rest of the bone. Similar striations are absent in *Prestosuchus chiniquensis* (BSPG/ASXXV-1), *Postosuchus kirkpatricki* (Chatterjee 1985; Long & Murry 1995; Weinbaum 2011), *Batrachotomus kupferzellensis* (SMNS-80260), *Saurosuchus galilei* (PVSJ-32), *Arizonasaurus babbitti* (Nesbitt 2005), *Polonosuchus silesiacus* (ZPAL/AbIII-563) and *Arganasuchus dutuiti* (ALM-2,3,6). In the medial surface, the depressed area indicates the posterior limit of the mandibular symphysis. The symphyseal area is narrow and occupies a small region on the anterior tip of the dentary, showing striations and rugosities. The symphysis appears to be 'loose', possibly allowing some kineticism among the hemimandibles. The lateral surface of the dentary

(MCN-PV10.004) has several nutrient foramina (Fig. 16a: nfo) scattered over the anterodorsal and anteroventral regions, as seen on the anterodorsal dentary surface of *Batrachotomus kupferzellensis* (SMNS-80260), whereas the dentary of *Prestosuchus chiniquensis* (BSPG/ASXXV-1) appears to lack these foramina. The most posterior portion of the fragmentary dentary of MCN-PV10.004 has two anteroposteriorly aligned semilunar-shaped grooves on the dorsal portion of the lateral surface (Fig. 16a: ssg), which are dorsally open and convex ventrally. Posteroventral to these, the dentary has two other grooves. In posterior view, the most posterior of the grooves extends onto the lateral wall of the dentary. It is drop-shaped in cross-section, dorsally tapering, and with a rounded portion projected into the lateral groove. Two rows of grooves are also present in *Batrachotomus kupferzellensis* (SMNS-80260), differing from *Saurosuchus galilei* (PVSJ-32), *Polonosuchus silesiacus* (ZPAL/AbIII-563) and *Prestosuchus chiniquensis* (BSPG/ASXXV-1), which have a singular row of grooves.

In the medial view, the fragmentary dentary of MCN-PV10.004 reveals a deep meckelian groove anteroposteriorly elongated along the ventral third of the dorsoventral height of the bone (Fig. 16b: mg). It approaches the symphyseal area, forming an anterior oval deep pit (Fig. 16b: aodp), as seen in *Polonosuchus silesiacus* (ZPAL/AbIII-563). The meckelian groove is not as anteriorly extensive in *Arizonasaurus babbitti* (Nesbitt 2005), *Arganasuchus dutuiti* (ALM-2, 3, 6) and *Postosuchus kirkpatricki* (Weinbaum 2011). In addition, the latter taxon has a ventral flange that articulates with the splenial (Chatterjee 1985; Weinbaum 2011). Ventral to the meckelian groove, *Decuriasuchus quartacolonina* has two small slit-shaped pits (Fig. 16f) similar to those described for *Arganasuchus dutuiti* (Jalil & Peyer 2007), which are lacking in *Batrachotomus kupferzellensis* (SMNS-80260), *Saurosuchus galilei* (PVSJ-32) and *Polonosuchus silesiacus* (ZPAL/AbIII-563).

Except for the third, MCN-PV10.004 has the first six interdental plates preserved (Fig. 16b: idp). These are subtriangular in shape, with a ventral surface parallel to the anteroposterior axis of the dentary, and two confluent dorsal surfaces. The internal surface is slightly concave, as seen better in the fourth element. In dorsomedial view, these plates are separated from the dentary by a deep dentary groove (Fig. 16b: idg). Unlike *Decuriasuchus quartacolonina*, the dentary plates in *Saurosuchus galilei* (PVSJ-32), *Postosuchus kirkpatricki* (Chatterjee 1985; Long & Murry 1995; Weinbaum 2011) and *Arganasuchus* (ALM-2, 3, 6) are fused. *Polonosuchus silesiacus* (ZPAL/AbIII-563) has unfused interdental plates, but these are

subpentagonal shaped, like in *Prestosuchus chiniquensis* (BSPG/ASXXV-1). Unfortunately, no specimen of *Decuriasuchus quartacolonina* preserves the complete tooth series of the dentary.

Hyoid apparatus (Figs 2, 3 & 14). The left hyoid is observed in ventral view in MCN-PV10.105a, whereas MCN-PV10.105d shows a small region exposed in lateral view. The hyoid is a slightly curved rod-like structure (MCN-PV10.105a), similar to that of *Qianosuchus mixtus* (Li *et al.* 2006). Another rod-like element is preserved near the left posteroventral ramus of the pterygoid in that same specimen (Fig. 14: HY?), but it not clear if it is a part of the left or right hyoid.

Dentition. Unfortunately, a hard concretary matrix covers the fossil, and details of most teeth were not made available by the mechanical preparation. However, MCN-PV10.105d has four premaxillary teeth. These are laterally compressed (although less than the maxillary teeth), recurved and serrated along both edges. It is not possible to externally determine the number of maxillary teeth in MCN-PV10.105a,c,d. The well-preserved maxilla of MCN-PV10.004 shows 17 alveoli, although few of them have preserved teeth. In addition, a preliminary CT scan analysis of MCN-PV10.105a also shows 17 maxillary and four premaxillary teeth.

Discussion

The well-preserved specimens of *Decuriasuchus quartacolonina* clarify the skull morphology of rauisuchians, providing hints into the evolution of cranial characters within the group. A subnarial fenestra is evident in *Decuriasuchus quartacolonina* (MCN-PV10.105a,c,d), but was considered absent in cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T) and *Saurosuchus galilei* (Jul 1994; Gower 2000; Nesbitt 2011). However, despite some taphonomic distortion in UFRGS-PV0156T, the subnarial fenestra is obvious on its right side, although not totally prepared on the left side. Nesbitt (2011) argued that the left side of a young specimen of *Saurosuchus galilei* (PVSJ-32) preserves the original morphology, which is devoid of a subnarial fenestra, but the similarity between the right side of PVSJ-32 and the holotype, both sides of which bear the fenestra, suggests that the structure is indeed present. Among other rauisuchians, a small rounded subnarial fenestra is seen in *Batrachotomus kupferzellensis* (SMNS-80260), *Polonosuchus silesiacus* (ZPAL/AbIII-563), *Postosuchus kirkpatricki* (Weinbaum 2011; *contra* Chatterjee 1985) and *Effigia okeeffeae* (*contra* Nesbitt 2007). The antorbital fenestra of *Decuriasuchus quartacolonina* is subtriangular, with an elongated and narrow

anterior portion, as seen in *Saurosuchus galilei* (PVL-2062; PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-0156T). In other suchians with a subtriangular antorbital fenestra, the dorsal and ventral margins diverge from the anteriormost region, as seen in *Riojasuchus tenuisiceps* (PVL-3827), *Ticinosuchus ferox* (PIMUZ-T2817), *Batrachotomus kupferzellensis* (SMNS-52970), *Fasolasuchus tenax* (PVL-3851), *Arganasuchus dutuitti* (ALM-1), *Luperosuchus fractus* (PULR-04; PULR-057), *Polonosuchus silesiacus* (ZPAL/AbIII-563) and *Teratosaurus suevicus* (BMNH-R35646).

The area between the anterior margin of the maxilla and the second alveolus is ventrally straight in *Decuriasuchus quartacolonina* (Fig. 5a, f) and *Saurosuchus galilei* (PVL-2062; PVSJ-32), posteriorly to which both taxa share a convex ventral margin of the maxilla. By contrast, in some rauisuchians (e.g. *Batrachotomus kupferzellensis* [SMNS-52970; SMNS-80260], *Polonosuchus silesiacus* [ZPAL/AbIII-563], *Arizonasaurus babbitti* (Nesbitt 2005), *Postosuchus kirkpatricki* (Weinbaum 2011)) this convex ventral margin extends to the anterior tip of the bone. Brusatte *et al.* (2009) argued that the anteroposterior orientation of the dental groove distinguishes *Polonosuchus silesiacus* from *Teratosaurus suevicus*: in the left maxilla of *Polonosuchus silesiacus* the anterior part of the groove is straight, whereas the right maxilla of *Teratosaurus suevicus* has an anteroventral deflected groove above alveoli 1–2. In *Decuriasuchus quartacolonina* (MCN-PV10.004) the left maxilla has a straight dental groove, whereas the right bone has a deflected groove, as also seen in *Saurosuchus galilei* (PVL-2062). Similar variation may also be present in *Polonosuchus silesiacus*, given that its right maxilla is not well preserved in this area. Similarly, as discussed by Brusatte *et al.* (2009), *Teratosaurus suevicus* has a smaller first alveolus in the maxilla, as in the right bone of MCN-PV10.004, whereas the first alveolus is similar in size to other alveoli in *Polonosuchus silesiacus*, as in the left maxilla of MCN-PV10.004. Again, as also seen in *Saurosuchus galilei* (PVL-2062), this difference between *Polonosuchus silesiacus* and *Teratosaurus suevicus* may also represent lateral (left–right) variation.

The maxillary rostromedial foramen is absent in *Decuriasuchus quartacolonina*, but a small depression is seen at the medial surface of the maxilla between the palatal process and the dental groove (Fig. 5j: sp). In addition, the palatal process of *Decuriasuchus quartacolonina* is only slightly medioventrally sloped, and its dorsal surface is exposed in medial view (Fig. 5e, l). On the other hand, in *Saurosuchus galilei* (PVL-2062; PVSJ-32) this structure is more medioventrally sloped and a deep pit is seen on the ventral surface of the

palatal process, whereas that of *Decuriasuchus quartacolonina* is flat (Fig. 5j: ‘rmfo’). In contrast, *Saurosuchus galilei* lacks the depression on the medial surface of the maxillary body, which is deeper in *Fasolasuchus tenax* (PVL-3851) and also seen in *Postosuchus kirkpatricki*, (Chatterjee 1985; Weinbaum 2011). In addition, the rostromedial foramen Brusatte *et al.* (2009) described for *Polonosuchus silesiacus* and *Teratosaurus suevicus* is only slightly more dorsal and deep, as well as restricted to the palatal process. In any case, these appear to represent different states of the same character. *Decuriasuchus quartacolonina*, *Saurosuchus galilei* (PVSJ-32) and cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T) share a dorsal depression on the nasal, restricted to the area just posterior to the ‘roman nose’ (Fig. 8e: pmd), but the lateral margin of the bone lack a rugose lateral ridge. Gower (1999) considered that a medial depression along the entire posterior portion of the nasal resulted from the presence of the lateral ridge, as seen in *Batrachotomus kupferzellensis* (SMNS-80260), *Postosuchus kirkpatricki* (Weinbaum 2011) and *Polonosuchus silesiacus* (ZPAL/AbIII-563). Yet, *Rauisuchus tiradentes* (BSPG/ASXXV-65) has both the rugose lateral ridge and a restrict postero-medial depression, shallower than that of MCN-PV10.105a. Accordingly, the presence of an extensive depression on the nasal does not seem strictly related to the presence of its rugose lateral ridge.

The prefrontal of *Decuriasuchus quartacolonina* is similar to that of *Saurosuchus galilei* (PVL-2062; PVSJ-32), cf. *Prestosuchus chiniquensis* (UFRGS-PV0156T) and *Batrachotomus kupferzellensis* (SMNS-80260), but differs from the small bone seen in *Postosuchus kirkpatricki* (Weinbaum 2011), which is restricted to the skull roof due to the presence of a palpebral. Recently, the presence of a palpebral was suggested for some rauisuchians like *Postosuchus kirkpatricki* and *Polonosuchus silesiacus* (Brusatte *et al.* 2010; Nesbitt 2011). Yet, *contra* Nesbitt (2011), there is no evidence of such a bone in *Saurosuchus galilei* (PVL-2062; PVSJ-32), and there are *Batrachotomus kupferzellensis* specimens well preserved enough to confirm the absence of the palpebral. The parietal–postfrontal contact in *Decuriasuchus quartacolonina* is present in the left side of MCN-PV10.004, but not in the right side (Fig. 9a, b). Among rauisuchians, *Batrachotomus kupferzellensis* (SMNS-52970; Gower 1999) and *Arizonasaurus babbitti* (Nesbitt 2005) lack this contact. In *Luperosuchus fractus* (PULR-04; PULR-057) the morphology of this area resembles that on the left side of *Decuriasuchus quartacolonina*, whereas *Postosuchus kirkpatricki* (Chatterjee 1985; Weinbaum 2011) and *Saurosuchus galilei* (PVL-2062; PVSJ-32) have a discrepant morphology. In the former taxon,

the postfrontal is situated more medially than most raiusuchians and this region is modified due to the presence of a palpebral. In *Saurosuchus galilei* (PVL-2062; PVSJ-32), the postfrontal, as considered by Alcober (2000), is only visualized in ventral view (but see Nesbitt 2011).

Conclusion

The skull morphology of *Decuriasuchus quartacolonina* is very similar to that of some other South American raiusuchians, such as cf. *Prestosuchus chiniquensis* and *Saurosuchus galilei*, but differs more substantially from those of *Raiusuchus tiradentes* and *Fasolasuchus tenax*. Along with the other Raiusuchidae, *Raiusuchus tiradentes* and *Fasolasuchus tenax* have a well-developed depression on the dorsal surface of the nasal, absent in *Decuriasuchus quartacolonina*. Other traits that occur variously in putative raiusuchids, but are absent in *Decuriasuchus quartacolonina*, include a rostralateral foramen on the maxilla (*Polonosuchus silesiacus*, *Teratosaurus suevicus*), a dorsolateral ridge on the nasal (*Batrachotomus kupferzellensis*, *Raiusuchus tiradentes*, *Polonosuchus silesiacus* and *Postosuchus kirkpatricki*), a divided lateral temporal fenestra (*Tikisuchus romeri*, *Raiusuchus tiradentes*, *Polonosuchus silesiacus* and *Postosuchus kirkpatricki*), a lateral ridge on maxilla and jugal (*Raiusuchus tiradentes*, *Polonosuchus silesiacus* and *Postosuchus kirkpatricki*), a Y-shaped maxilla with a shallow anterior area for the premaxillary articulation and a concave protuberance on the dorsal margin of the ascending process (*Arganasuchus dutuiti*, *Batrachotomus kupferzellensis* and *Fasolasuchus tenax*), strongly suggesting that *Decuriasuchus quartacolonina* is not deeply nested within Raiusuchidae. Similarly, the skull of *Decuriasuchus quartacolonina* also differs markedly from those of Poposauroidea. This is obvious regarding the edentulous forms (*Lotosaurus adentus*, *Shuvosaurus inexpectatus* and *Effigia okeeffeae*), which have a longer premaxilla and parietals inclined dorsoventrally. In addition, other poposauroid traits absent in *Decuriasuchus quartacolonina* also suggest that it is not included within the group; for example, the posterior process of the squamosal aligned with the anterior process (*Arizonasaurus babbitti*, *Shuvosaurus inexpectatus*, *Effigia okeeffeae* and *Lotosaurus adentus*), the premaxilla with anterodorsal process longer than the posterodorsal process (*Qianosuchus mixtus*, *Lotosaurus adentus*, *Effigia okeeffeae* and *Shuvosaurus inexpectatus*), maxilla participating in the external naris (*Xilousuchus sapingensis*, *Qianosuchus mixtus*, *Lotosaurus adentus*, *Effigia okeeffeae* and *Shuvosaurus inexpectatus*), and external naris larger than the

antorbital fenestra (*Qianosuchus mixtus*, *Xilousuchus sapingensis* and *Lotosaurus adentus*).

In addition to its autapomorphies, *Decuriasuchus quartacolonina* also differs from *Ticinosuchus ferox* in having a C-shaped maxilla without a lateral ridge; from *Luperosuchus fractus*, in having the subnarial fenestra not dorsally positioned and with nasal participation, no diastema and notch between the premaxilla and maxilla, dorsoventrally elongated descending process of the prefrontal, and dorsal bar of the lateral temporal fenestra less than 50% the length of the ventral bar; from *Saurosuchus galilei*, in having the posterodorsal process of the maxilla not extending posterior to the level of the external naris, unfused maxillary interdental plates, and not anteroposteriorly narrow orbit; and from cf. *Prestosuchus chiniquensis*, in having an anterodorsal process with evident angle between proximal and distal regions, and not an anteroposteriorly narrow orbit. Of these, resemblances are more obvious with *Saurosuchus galilei* and cf. *Prestosuchus chiniquensis*. They share with *Decuriasuchus quartacolonina* a subnarial fenestra dorsoventrally extended and restricted to the body and a small part of the ascending process of the maxilla, a subtriangular antorbital fenestra with an elongated and narrow anterior point, a deep antorbital sinus on the medial surface of the body/ascending process of the maxilla (convergent with *Polonosuchus silesiacus* and *Postosuchus kirkpatricki*), a 'roman nosed' nasal (convergent with *Luperosuchus fractus* and ornithosuchids), a subtle parietal crest (*Batrachotomus kupferzellensis* and *Postosuchus kirkpatricki* have a well-developed crest, which is absent in most Poposauroidea), and a posteroventrally oriented ridge on the lateral surface of the ventral ramus of the squamosal (convergent with *Batrachotomus kupferzellensis*). In this context, these three taxa (*Decuriasuchus quartacolonina*, *Saurosuchus galilei* and *Prestosuchus chiniquensis*) may form a monophyletic Prestosuchidae, although it was not recovered when *Decuriasuchus quartacolonina* was incorporated into assorted phylogenetic analyses (França et al. 2011a, b).

This article is a part of modified version of MAGF Doctoral Thesis at the FFCLRP-USP, supervised by MCL. We thank A. M. Ribeiro, curator at MCN FZB-RS. Additional financial support was provided by FAPESP (scholarship 2007/54695-9 and 2011/23834-9, a grant to MAGF; project 2009/54645-7, a grant to MCL). Thanks also go to C. L. Schultz (UFRGS), J. Powell (PVL), S. Martin (PULR), R. Martinez (PVSJ), O. Rauhut (BSPG), S. Chapman (BMNH), R. Schoch (SMNS), J. Dzik and T. Sulej (ZPAL), H. Furrer (PIMUZ) and R. Allain (MNHN) for permission to examine specimens under their care. We thank the editor and two anonymous reviewers for helpful reviews that engendered substantial improvement to this paper.

Appendix I

Institutional abbreviations

BMNH-R, NHM, Natural History Museum, London, England; BSPG/ASXXV, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; MCN-PV, Museu de Ciências Naturais – Fundação Zoológica do Rio Grande do Sul, Porto Alegre, Brazil; MNHN/AZA, MNHN/ALM, Museum National d’Histoire Naturelle, Paris, France; PIMUZ-T, Paläontologisches Institut und Museum der Universität, Zürich, Switzerland; PULR, Museo de Ciencias Naturales – Universidad Nacional de La Rioja, La Rioja, Argentina PVL, Instituto Miguel Lillo, Tucuman, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UFRGS-PV, Instituto de Geociências – Universidade Federal do Rio Grande Do Sul, Porto Alegre, Brazil; ZPAL, Instytut Paleobiologii – Polska Akademia Nauk, Warsaw, Poland.

References

- ABDALA, F. & RIBEIRO, A. M. 2010. A new traversodontid cynodont from the Santa Maria Formation (Ladinian-Carnian) of Southern Brazil, with a phylogenetic analysis of Gowndwana traversodontids. *Zoological Journal of the Linnean Society*, **139**, 529–545.
- ALCOBER, O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). *Journal of Vertebrate Paleontology*, **20**, 302–316.
- BARBERENA, M. C. 1978. A huge thecodont skull from the Triassic of Brazil. *Pesquisas*, **7**, 111–129.
- BENTON, M. J. 1986. The Late Triassic reptile *Teratosaurus* a rauisuchian not a dinosaur. *Palaeontology*, **29**, 293–301.
- BENTON, M. J. & CLARK, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: BENTON, M. J. (ed.) *The Phylogeny and Classification of the Tetrapods. Vol 1: Amphibians and Reptiles*. Clarendon Press, Oxford, 295–338.
- BONAPARTE, J. F. 1971. Los tetrapodos del sector superior de la Formacion Los Colorados, La Rioja, Argentina. *Opera Lilliana*, **XXII**, 1–183.
- BONAPARTE, J. F. 1981. Descripción de *Fasolasuchus tenax* y su significado en la sistemática y evolución de los Thecodontia. *Revista del Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’*, **3**, 55–101.
- BONAPARTE, J. F. 1984. Locomotion of the thecodonts. *Journal of Vertebrate Paleontology*, **3**, 210–218.
- BRUSATTE, S. L., BUTLER, R. J., SULEJ, T. & NIEDZWIEDZKI, G. 2009. The taxonomy and anatomy of rauisuchian archosaurs from the Late Triassic of Germany and Poland. *Acta Palaeontologica Polonica*, **54**, 221–230.
- BRUSATTE, S. L., BENTON, M. J., DESOJO, J. B. & LANGER, M. C. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology*, **8**, 3–47.
- CHATTERJEE, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. *Philosophical Transactions of the Royal Society of London B*, **309**, 395–460.
- CHATTERJEE, S. 1993. *Shuvosaurus*, a new theropod. *National Geographic Research and Exploration*, **9**, 274–285.
- CHATTERJEE, S. & MAJUMDAR, P. K. 1987. *Tikisuchus romeri*, a new rauisuchid reptile from the Late Triassic of India. *Journal of Paleontology*, **61**, 784–793.
- COPE, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. *Transactions of the American Philosophical Society (New Series)*, **14**, 1–252.
- DA ROSA, A. A. S. 2005. *Paleoalterações de depósitos sedimentares de planícies aluviais do Triássico Médio a superior do sul do Brasil: caracterização, análise estratigráfica e preservação fóssilífera*. Unpublished PhD dissertation. Unisinos, São Leopoldo.
- DAWLEY, R. M., ZAWISKIE, J. M. & COSGRIFF, J. W. 1979. A rauisuchid thecodont from the Upper Triassic Popo Agie Formation of Wyoming. *Journal of Paleontology*, **53**, 1428–1431.
- DESOJO, J. B. & ARCUCCI, A. B. 2009. New material of *Luperosuchus fractus* (Archosauria: Crurotarsi) from the Middle Triassic of Argentina: the earliest known South American rauisuchian. *Journal of Vertebrate Paleontology*, **29**, 1311–1315.
- DESOJO, J. B. & RAUHUT, O. W. M. 2008. New insights in ‘rauisuchian’ taxa (Archosauria: Crurotarsi) from Brazil. *Symposium of Vertebrate Palaeontology and Comparative Anatomy Annual Meeting*, Lugar, Dublin, Ireland.
- DESOJO, J. B. & RAUHUT, O. W. M. 2009. The taxonomic status and phylogenetic position of the Late Triassic Brazilian rauisuchian *Prestosuchus*. *Journal of Vertebrate Paleontology*, **29**(sp1), 87A.
- FRANÇA, M. A. G., FERIGOLO, J. & LANGER, M. C. 2011a. Associated skeletons of a new middle Triassic ‘Rauisuchia’ from Brazil. *Naturwissenschaften*, **98**, 389–395.
- FRANÇA, M. A. G., FERIGOLO, J. & LANGER, M. C. 2011b. Incorporating *Decuriasuchus Quartacolonina* (Pseudo-suchia) into the Archosaur phylogeny. In: *IV Congreso Latinoamericano de Paleontología de Vertebrados, Abstracts and Program*. Museo de Ciencias Naturales, Universidad Nacional de San Juan.
- GALTON, P. M. 1985. The poposaurid thecodontian *Teratosaurus suevicus* v. Meyer plus referred specimens mostly based on prosauropod dinosaurs from the Middle Stubensandstein Upper Triassic of Nordwürttemberg West Germany. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Palaeontologie)*, **116**, 1–29.
- GAUTHIER, J. & PADIAN, K. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: HECHT, M. K., OSTROM, J. H., VIOHL, G. & WELLNHOFER, P. (eds) *The Beginning of Birds*. Freunde des Jura Museums, Eichstatt, 185–197.
- GEBAUER, E. V. I. 2004. Neubeschreibung von *Stagonosuchus nyassicus* v. Huene, 1938 (Thecodontia, Rauisuchia) from the Manda Formation (Middle Triassic) of southwest Tanzania. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **231**, 1–35.
- GOWER, D. J. 1999. The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle

- Triassic of southern Germany. *Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)*, **280**, 1–49.
- GOWER, D. J. 2000. Rausuchian archosaurs (Reptilia, Diapsida): an overview. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **218**, 447–488.
- GOWER, D. J. & SCHOCH, R. 2009. Postcranial anatomy of the rausuchian archosaur *Batrachotomus kupferzellensis*. *Journal of Vertebrate Paleontology*, **29**, 103–122.
- HUENE, F. VON. 1938a. Ein grosser Stagonolepide aus der jüngeren Trias Ostafrikas. *Neues Jahrbuch für Geologie und Paläontologie, Beilage-Bände Abteilung B*, **80**, 264–278.
- HUENE, F. VON. 1938b. Die fossilen Reptilien des südamerikanischen Gondwanalandes. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B*, **1938**, 142–151.
- HUENE, F. VON. 1942. Eine Reptilfauna aus der ältesten Trias Nordrusslands. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B*, **84**, 1–23.
- HUENE, F. VON. 1956. *Paläontologie und Phylogenie der niederen Tetrapoden*. VEB Gustav Fischer-Verlag, Jena.
- JALIL, N.-E. & PEYER, K. 2007. A new rausuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco. *Palaeontology*, **50**, 417–430.
- JUUL, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana*, **31**, 1–38.
- KREBS, B. 1965. Die Triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox*, nov. gen. nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. *Schweizerische Palaontologische, Abhandlungen*, **81**, 1–140.
- KREBS, B. 1974. Die Archosaurier. *Naturwissenschaften*, **61**, 17–24.
- KREBS, B. 1976. Pseudosuchia. In: KUHN, O. (ed.) *Handbuch der Paläoherpologie, Teil 13, Thecodontia*. Gustav Fischer Verlag, Stuttgart, 40–98.
- LAUTENSCHLAGER, S. & DESOJO, J. B. 2011. Reassessment of the Middle Triassic ‘rausuchian’ archosaurs *Ticinosuchus ferox* and *Stagonosuchus nyassicus*. *Paläontologische Zeitschrift*, **85**, 357–381.
- LI, C., WU, X.-C., CHENG, Y.-N., SATO, T. & WANG, L. 2006. An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften*, **93**, 200–206.
- LONG, R. A. & MURRY, P. A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *New Mexico Museum of Natural History and Science Bulletin*, **4**, 1–254.
- MERREM, B. 1820. *Versuch eines Systems der Amphibien. Tentamen systematis amphibiorum*. Johann Christian Krieger, Marburg.
- MORI, A. L. O. 2005. *Tafonomia em sistemas fluviais: um estudo de caso na Formação Santa Maria, Triássico do RS*. Unpublished master’s thesis, Instituto de Geociências, Universidade Federal do Rio Grande do Sul.
- NESBITT, S. J. 2003. *Arizonasaurus* and its implications for archosaur divergences. *Proceedings of the Royal Society of London, B*, **270**, S234–S237.
- NESBITT, S. J. 2005. The osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Historical Biology*, **17**, 19–47.
- NESBITT, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), the theropod convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History*, **302**, 1–84.
- NESBITT, S. J. 2011. The early evolution of Archosauria: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**, 1–292.
- NESBITT, S. J. & NORELL, M. A. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society of London B*, **273**, 1045–1048.
- NESBITT, S. J., LIU, J. & LI, C. 2011. A sail-backed suchian from the Heshanggou Formation (Early Triassic: Olenekian) of China. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **101**, 271–284.
- PARRISH, J. M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology*, **13**, 287–308.
- PEYER, K., CARTER, J. G., SUES, H.-D., NOVAK, S. E. & OLSEN, P. E. 2008. A new suchian archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology*, **28**, 363–381.
- ROMER, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. VIII. A fragmentary skull of a large thecodont, *Luperosuchus fractus*. *Breviora*, **373**, 1–8.
- RUBERT, R. R. & SCHULTZ, C. L. 2004. Um novo horizonte de correlação para o Triássico Superior do Rio Grande do Sul. *Pesquisas*, **31**, 71–88.
- SAMPSON, S. D. & WITMER, L. M. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Memoirs of the Society of Vertebrate Paleontology* 8, *Journal of Vertebrate Paleontology*, **27**, 32–102.
- SEN, K. 2005. A new rausuchian archosaur from the Middle Triassic of India. *Palaeontology*, **48**, 185–196.
- SERENO, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology*, **10**, 1–53.
- SILL, W. D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rausuchid thecodonts. *Bulletin of the Museum of Comparative Zoology*, **146**, 317–362.
- SULEJ, T. 2005. A new rausuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. *Journal of Vertebrate Paleontology*, **25**, 78–86.
- WALKER, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London B*, **248**, 53–134.
- WALKER, A. D. 1990. A revision of *Sphenosuchus acutus* Haughton, crocodylomorph reptile from the Elliot Formation (Late Triassic or Early Jurassic) of South Africa. *Philosophical Transactions of the Royal Society of London B*, **330**, 1–120.
- WEINBAUM, J. C. 2011. The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. *PaleoBios*, **30**, 18–44.
- WITMER, L. R. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in

SKULL ANATOMY OF *DECURIASUCHUS QUARTACOLONIA*

the fossil record with an analysis of the function of pneumaticity. *Memoirs of the Society of Vertebrate Paleontology. Journal of Vertebrate Paleontology*, **17**, 1–73.

ZERFASS, H., LAVINA, E. L., SCHULTZ, C. L., GARCIA, A. J. V., FACCINI, U. F. & CHEMALE, F. J. 2003.

Sequence stratigraphy of continental Triassic strata of Southernmost Brazil: a contribution to Southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology*, **161**, 85–105.

ZITTEL, K. A. VON 1887–1890. *Handbuch der Palaeontologie*. R Oldenbourg, München & Leipzig.