The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2011, **163**, S7–S36. With 17 figures

A new sebecid mesoeucrocodylian from the Rio Loro Formation (Palaeocene) of north-western Argentina

DIEGO POL[1]* and JAIME E. POWELL[2]

[1]*CONICET, Museo Paleontológico Egidio Feruglio, Ave. Fontana 140, Trelew CP 9100, Chubut, Argentina*
[2]*CONICET, Instituto Miguel Lillo, Miguel Lillio 205, San Miguel de Tucumán CP 4000, Tucumán, Argentina*

Received 2 March 2010; revised 10 October 2010; accepted for publication 19 October 2010

A new basal mesoeucrocodylian, ***Lorosuchus nodosus*** **gen.** et **sp. nov.**, from the Palaeocene of north-western Argentina is presented here. The new taxon is diagnosed by the presence of external nares facing dorsally, completely septated, and retracted posteriorly, elevated narial rim, sagittal crest on the anteromedial margins of both premaxillae, dorsal crests and protuberances on the anterior half of the rostrum, and anterior-most three maxillary teeth with emarginated alveolar margins. This taxon is most parsimoniously interpreted as a bizarre and highly autapomorphic basal member of Sebecidae, a position supported (amongst other characters) by the elongated bar-like pterygoid flanges, a laterally opened notch and fossa in the pterygoids located posterolaterally to the choanal opening (parachoanal fossa), base of postorbital process of jugal directed dorsally, and palatal parts of the premaxillae meeting posteriorly to the incisive foramen. *Lorosuchus nodosus* also shares with basal neosuchians a suite of derived characters that are interpreted as convergently acquired and possibly related to their semiaquatic lifestyle. The phylogenetic analysis used for testing the phylogenetic affinities of *L. nodosus* depicts Sebecidae as the sister group of Baurusuchidae, forming a monophyletic Sebecosuchia that is deeply nested within Notosuchia. Alternative phylogenetic placements of Sebecidae, such as the recently proposed affinities with peirosaurids, were also evaluated within the context of the present data matrix and found to be only marginally suboptimal.

doi: 10.1111/j.1096-3642.2011.00714.x

ADDITIONAL KEYWORDS: Crocodyliformes – Mesoeucrocodylia – phylogeny – Sebecidae – Sebecosuchia.

INTRODUCTION

In contrast to the high diversity and abundance of Cretaceous crocodyliforms from South America, the Palaeocene crocodyliform record is scarce and a limited number of well-preserved remains have been published to date. Three major groups of Crocodyliformes have been recorded so far in different Palaeocene deposits from disparate regions of South America: caimanine eusuchians (Simpson, 1937a; Bonaparte, Van Valen & Kramarz, 1993; Bona, 2007), dyrosaurids (Gasparini, 1996; Barbosa, Kellner & Sales Viana, 2008), and sebecids (Paula Couto, 1970; Buffetaut & Marshall, 1991; Gasparini, Fernández & Powell, 1993; Gasparini, 1996).

Sebecidae was originally created as a monotypic family for *Sebecus icaeorhinus* from the Eocene of Patagonia (Simpson, 1937b). Subsequently, different taxa from the Palaeogene and early Neogene of South America have been described and referred to this family, reaching up to seven named taxa (see Paolillo & Linares, 2007 for a recent review).

Sebecids were diverse, abundant, and broadly distributed in South America during the Palaeogene. The Palaeocene records include several unnamed taxa from the Itaboraí Formation of Brazil (Paula Couto, 1970; Gasparini, 1984), *Sebecus querejazus* (Buffetaut

---

*Corresponding author. E-mail: dpol@mef.org.ar

& Marshall, 1991), and *Bretesuchus bonapartei* from the Maíz Gordo Formation of north-western Argentina (Gasparini *et al*., 1993). The latter taxon was actually referred to Bretesuchidae, but for the moment, we have opted to consider this taxon as part of Sebecidae until a more robust phylogenetic placement of this taxon is achieved (following Ortega *et al*., 2000). The Eocene record includes *Se. icaeorhinus* from the Sarmiento Formation of Patagonia (Simpson, 1937b; Colbert, 1946; Gasparini, 1972), *Ayllusuchus fernandezi* from the Lumbrera Formation of north-western Argentina (Gasparini, 1984), and the poorly known *Ilchunaia parca* from the Divisadero Largo Formation of western Argentina (Rusconi, 1946; Gasparini, 1972, 1984), as well as unnamed and fragmentary remains from Eocene beds of Argentina and Colombia (Langston, 1965; Gasparini, 1984). The Oligocene record of sebecids is scarce and restricted to fragmentary material referred to this family found in Patagonia and Colombia (Langston, 1965; Gasparini, 1984).

The Neogene record of Sebecidae is restricted to the central and northern regions of South America (Peru, Venezuela, and Colombia; see Gasparini, 1984 and Paolillo & Linares, 2007 for a review) and all significant material has been found in middle Miocene beds. These records include *Sebecus huilensis* from the Villavieja Formation of Colombia (Langston, 1965; Busbey, 1986; Langston & Gasparini, 1997) and the recently described *Barinasuchus arveloi* from the Parangula Formation from Venezuela (Paolillo & Linares, 2007).

In addition to the high diversity of sebecids from South America, certain taxa found in Eocene beds of Europe and Africa have been considered by some authors as closely related to Sebecidae (e.g. *Iberosuchus*, *Bergisuchus*, *Eremosuchus*; Ortega, Buscalioni & Gasparini, 1996; Ortega *et al*., 2000; Rossmann, Rauhe & Ortega, 2000; Company *et al*., 2005; Turner & Calvo, 2005).

Sebecids have long been characterized by a suite of derived skull features such as the presence of a high and narrow rostrum, laterally directed orbits, anteriorly facing external nares, and lateromedially compressed teeth with serrated carinae (ziphodont dentition). These characters have been interpreted as evidence supporting predatory and terrestrial habits for these taxa (Gasparini, 1984; Busbey, 1995). Furthermore, given the large body size of sebecids (with skull lengths ranging between 50 and 100 cm), sebecids have been considered one of the large carnivorous components of the terrestrial ecosystems in South America during the Palaeogene and early Neogene.

Since the early description of *Se. icaeorhinus* (Simpson, 1937b; Colbert, 1946), sebecids have been interpreted as a distinct lineage within Crocodyliformes, probably stemming from Cretaceous 'mesosuchians' because of the presence of two plesiomorphic features: a 'mesosuchian' type of palate and amphicoelic vertebrae. Although this interpretation has never been challenged, different authors have disagreed on more specific hypotheses on the affinities of Sebecidae. Most authors have suggested that sebecids were closely related to Baurusuchidae, another group with high and narrow snouts and ziphodont dentition mainly recorded in the Cretaceous beds of South America (Colbert, 1946; Gasparini, 1972, 1984; Buffetaut, 1980). The group composed of Sebecidae and Baurusuchidae has traditionally been named Sebecosuchia (Colbert, 1946; Gasparini, 1972) and most cladistic analyses published to date have supported the monophyly of this group (see Phylogenetic relationships). However, alternative interpretations have been suggested, depicting Sebecidae as closely related to peirosaurids, another group with ziphodont dentition but with more platyrostral snouts that is recorded in the Cretaceous of Gondwana (Buffetaut, 1991). This alternative scenario for the origin of Sebecidae was retrieved in the recent cladistic analysis of Larsson & Sues (2007), who coined the name Sebecia for the Sebecidae + Peirosauridae clade.

Here we describe a new taxon from the Palaeocene Rio Loro Formation of north-western Argentina that represents one of the few Palaeocene records of Sebecidae and is interpreted as the most basal form of Sebecidae based on a comprehensive cladistic analysis. The new taxon is particularly interesting because it departs drastically from the characteristic rostral and dental morphology mentioned above that so far have characterized sebecids. This taxon is therefore important for understanding the morphological and ecological diversity of Sebecidae as well as the evolutionary origins of this clade. Anatomical and institutional abbreviations used throughout the text are listed in Appendices 1 and 2.

HORIZON AND LOCALITY

The material was collected at the southern end of Medina Range, 3 km east of El Cadillal Lake, from the margin of a small stream tributary of the Río Loro (26°36′06.68″S, 65°09′53.03″W), 22 km north of the city of San Miguel de Tucumán, Tucumán Province, Argentina.

The fossil was found in the Río Loro Formation (Bossi, 1969). This stratigraphical unit is integrated with fluvial light red medium to coarse sandstones, with not clearly visible stratification with intercalations of siltstones and diamictites. In the same level and site was reported the carapace of a turtle: '*Pelomedusoides*' cf. *argentinensis* (de Broin & de la Fuente, 1993). Although there are no references of absolute dating, the mammal association found in this formation has been considered as Middle or Late Palaeocene (Powell & Palma, 1981). The mammals include basal ungulates: the astrapotherian *Eoastrapostylos riolorense* (Soria & Powell, 1981), the notoptern *Notonychops powelli* (Soria, 1988), *Satshatemnus bonapartei* (Soria, 1989), and at least two undescribed taxa.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA WALKER, 1970

CROCODYLIFORMES HAY, 1930 (*SENSU* CLARK, 1986)

MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983 (*SENSU* CLARK, 1986)

SEBECOSUCHIA SIMPSON, 1937

SEBECIDAE SIMPSON, 1937

LOROSUCHUS NODOSUS **GEN.** ET **SP. NOV.**

Holotype: PVL 6219, almost complete skull found in articulation with the lower jaws and fragmentary postcranial remains.

Etymology: Loro, in reference to the Río Loro Formation in which this specimen was found, and *suchus*, Latinized from the Greek *souchos* that refers to the Egyptian crocodile god. The species name *nodosus* refers to the particular ornamentation of the dorsal surface of the skull of this taxon, which strikingly resembles the basal archosauriform *Proterochampsa nodosa*, both in the overall skull shape and ornamentation pattern.

Diagnosis: A non-eusuchian mesoeucrocodylian characterized by the following unique combination of characters (autapomorphies marked with an asterisk): rostrum approximately 65% of the longitudinal length of the skull, anterior half of the rostrum is moderately broad and high but the posterior half is much broader and higher (oreinirostral in cross-section), external nares facing dorsally, completely septated, and retracted posteriorly*, elevated narial rim*, presence of a crest on the anteromedial margins of both premaxillae*, premaxilla with a well-developed subcircular depression located just anterior to the external nares opening, presence of dorsal crests and protuberances on the anterior half of the rostrum*, buccal notch at premaxilla–maxilla contact (almost exclusively formed by the premaxilla*), supratemporal fenestrae small and longitudinally elongated, anterior-most three maxillary teeth with emarginated alveolar margins, posterior surface of distal body of quadrate bearing a ridge from the squamosal–quadrate suture to the medial quadrate condyle, which laterally borders a subtriangular concave surface, quadrate forming a large part of the posterior margin of the otic aperture, pterygoid flanges elongated, subhorizontal, and anteroposteriorly narrow, anterior margin of the pterygoid flanges separated from the choanal region of the pterygoids by a laterally opened notch of a parachoanal fossa, dentary extends for approximately 75% of the mandibular length, large slot-like foramen intramandibularis oralis, lateral surface of the angular is markedly convex, presence of an accessory glenoid facet in the surangular for reception of the quadratojugal condyle, articular glenoid facet with posterior buttress, dorsal surface of retroarticular process divided into a narrow and dorsally facing lateral and a broad concave and paddle-shaped medial flange that faces dorsomedially.

Distribution: Río Loro Formation, north-western Argentina. Age: middle–late Palaeocene.

DESCRIPTION

Skull

The skull of PVL 6219 has all its elements preserved except for the posterior region of the skull roof and the braincase floor (Figs 2–3). The rostrum is elongated and is approximately 65% of the longitudinal length of the skull. The snout broadens gradually posteriorly, towards to the orbital region. The anterior half of the rostrum is moderately broad and high (i.e. platyrostral, *sensu* Busbey, 1995), whereas the posterior half is much broader and higher, oreinirostral in cross-section (Figs 2, 4). The external nares are subcircular in shape and face dorsally. These openings are well separated from each other, being completely divided by a broad internarial bony septum. In contrast to most crocodyliforms the external nares are retracted posteriorly, being well separated from the anterior edge of the snout by an extensive anterior region of the premaxilla (Fig. 2). The antorbital fenestrae are completely obliterated and there are no signs of antorbital fossae or depression. The orbital openings are reduced in size and located on the posterior half of the skull, and facing laterodorsally. The supratemporal fenestrae are markedly small and longitudinally elongated. The infratemporal fenestra is large and subtriangular, being much longer anteroposteriorly than dorsoventrally high. Most of the external surface of the skull is heavily ornamented with a pattern that varies depending on the skull region. Interestingly, the dorsal surface of the snout and frontal bears remarkably high crests and protuberances, a unique character amongst Crocodyliformes (see below).

The premaxilla is anteroposteriorly elongated, occupying approximately the anterior third of the snout. It forms the lateral and also the anterior margin of the external nares. The anterior half of the premaxilla separates the external nares from the anterior margin of the snout. Along this region the premaxilla is dorsoventrally low and ornamented with grooves and ridges. The anteromedial ends of both premaxillae bear a tuberosity that narrows posteriorly, continuing posteriorly towards the external nares as a broad crest that elevates from the main body of the premaxilla (Fig. 5). This crest merges with the anterior end of the internarial septum. Lateral to this crest, the dorsal surface of each premaxilla bears a subcircular depression located just anterior to the external nares opening (Figs 1, 5).

The posterior half of the premaxilla is mostly occupied by the external nares, forming their anterior and lateral margins. These margins are elevated from the dorsal surface of the premaxilla, forming a well-developed narial rim. Along this region, the lateral margins of the premaxillae are slightly bulged because of the large size of the external nares and the enlarged alveolar margins of the posterior-most premaxillary tooth (see below). Posterior to this point, the premaxilla contacts the maxilla and bears a ventrally opened notch on its buccal margin (Fig. 4). Dorsally to this notch, the external surface of the snout at the premaxilla–maxilla suture is laterally concave. This notch may receive an enlarged anterior dentary tooth but the lower tooth row is badly preserved and this cannot be confirmed at the moment. The presence of a large notch at the premaxilla–maxilla suture is not an uncommon feature for a crocodyliform; however, a unique feature of *Lorosuchus* is that this notch is almost exclusively formed by the premaxilla.

The premaxilla–maxilla suture extends posterodorsally from this region, forming the posterolateral edge of a broad and extensive posterodorsal process of the premaxilla. This process is mostly exposed laterodorsally on the snout and wedges between the maxilla and nasal (Figs 4, 5). The posterior end of the premaxillary posterodorsal process bears a remarkably high crest orientated transversely to the longitudinal axis of the skull. This crest continues posteriorly on the nasal and maxilla, forming a semicircular ridge located anteriorly on the rostrum dorsal surface (Figs 4, 5; see below). The precise location of the premaxilla–nasal suture is difficult to determine in PVL 6219, although it seems to continue anteriorly from this crest, running subparallel to the longitudinal axis of the skull. The well-developed ornamentation and the poor preservation preclude clear identification of the premaxilla–nasal suture at (or near) the internarial bar. Only a single small neurovascular foramen can be observed in the specimen PVL 6219 on the lateral surface of the right premaxilla, at the level of the third premaxillary tooth.

The palatal branches of the premaxillae are smooth, elongated, and dorsoventrally thick. Their medial margins were not preserved in contact to each other. Most of the anterior halves of these margins enclose a subovoid incisive foramen (Fig. 3) and the palatal branches of the premaxillae seem to be sutured to each other anteriorly and posteriorly to this opening. The posterior margins of the palatal branches of the premaxilla are sutured to the maxilla on its lateral region. This suture encloses an elongated foramen (better preserved on left side; Fig. 3), resembling the condition of some basal mesoeucrocodylians [e.g. *Pabwehshi pakistanus* GSP-UM 2000, *Stratiotosuchus maxhechti* (Riff, 2003), *Iberosuchus macrodon*, *Hamadasuchus rebouli* (Larsson & Sues, 2007)]. Medially to this foramen, the posterior margins of the palatal shelf of the premaxilla seem to be directed anteromedially, along its contact with a distinct rhomboid element. This morphology resembles that of *Pa. pakistanus* (Wilson, Malkani & Gingerich, 2001) and *Ha. rebouli* (Larsson & Sues, 2007), in which this element was identified as an anterior palatal exposure of the vomer separating the posteromedial region of the premaxilla from the anteromedial region of the maxilla. The palatal surface of the premaxilla is flat, except for the region adjacent to the third and fourth premaxillary teeth. At this point, the palatal surface of the premaxilla is ventrally emarginated, forming distinctive platforms where the alveoli are located. Several neurovascular foramina are scattered close to the alveolar margins, being more conspicuous and numerous posteromedially to the posterior-most premaxillary alveolous.

The premaxillary dentition of PVL 6219 consists of four well-spaced teeth with subcircular cross-section. The first two premaxillary teeth are slightly procumbent, and located anteriorly to the external nares. These elements are well separated from each other, leaving space for an anterior dentary tooth that seems to interlock between them. The second tooth is similar in length to the first element, although is approximately twice as broad. None of these elements seem to have serrations on their mesial or distal margins. The third premaxillary tooth is not preserved, although its alveolous is well preserved in the right premaxilla. The margins of this alveolous are prominent and located at the anteroposterior midpoint of the premaxilla. The interalveolar space between the second and third premaxillary teeth is the largest of the premaxilla, forming an incipient diastema and a slightly developed notch between them. In contrast, the separation between the third

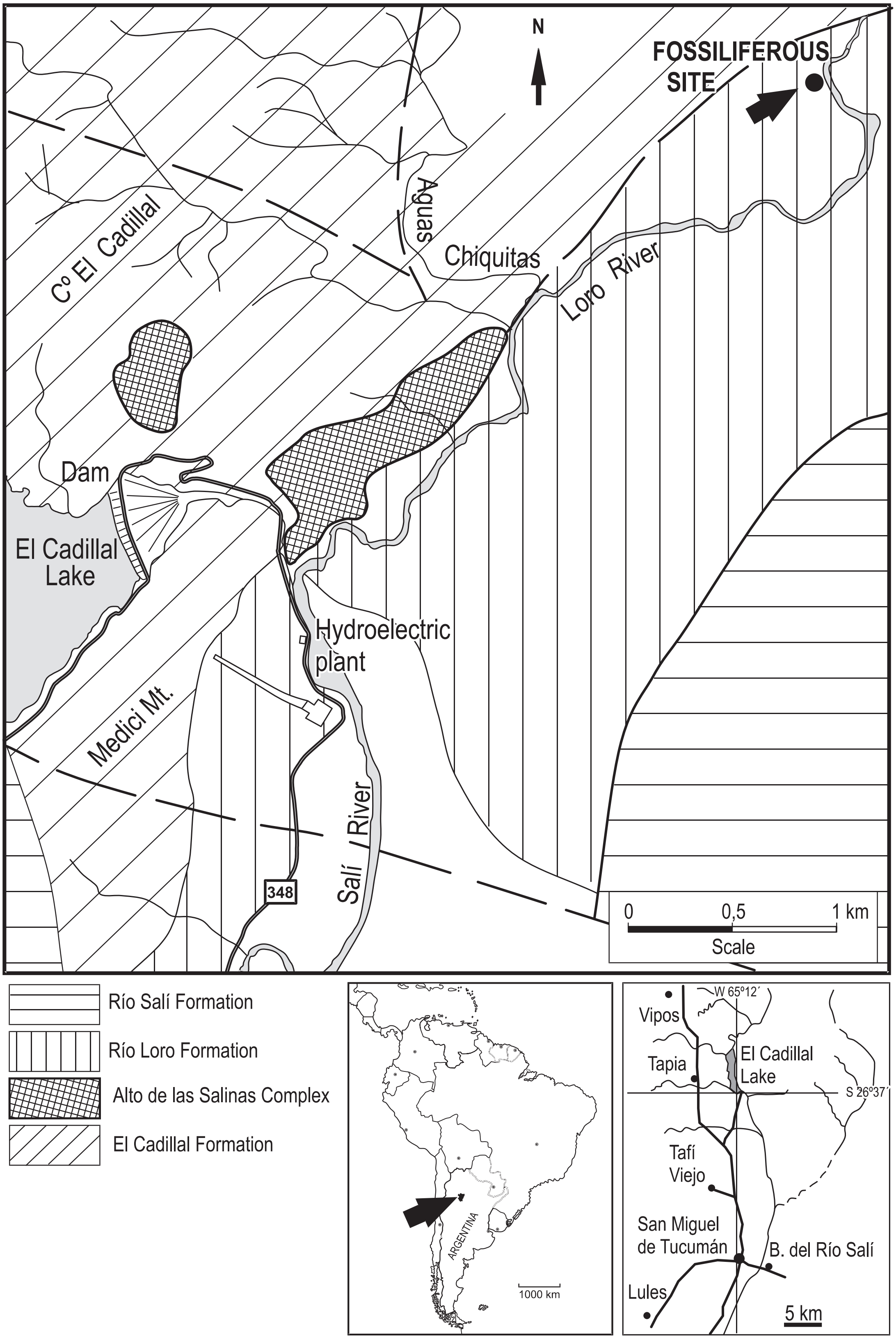

Figure 1. Geographical location of the outcrops of the Rio Loro Formation where ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) was found.

and fourth alveoli is much smaller. Only the root of the posterior-most element is preserved. This alveolous is large and its margins are slightly more emarginated than in its preceding element. As mentioned above, the lateral margins of the premaxillae are slightly bulged at this point.

The maxillae are well preserved in PVL 6219, except for the posterior-most region of their palatal branches (Figs 2–4). The external surface of the maxilla forms the posterior two thirds of the rostrum, it has two planes of exposure (a ventral region orientated vertically and a dorsal region facing dorsolaterally), and its external surface is densely ornamented. At the anterior maxillary region the rostrum is lateromedially narrower than dorsoventrally high, but towards the posterior region of the maxilla the rostrum becomes progressively broader, increasing the extension of its dorsolaterally exposed region (Figs 2, 4).

The dorsomedial margin of the maxilla contacts the nasal along a straight and parasagittally orientated suture. This region of the maxilla is more heavily ornamented than its ventral region and consequently, the maxilla–nasal suture is hard to determine in some regions. In particular, the ornamentation on the anterior half of this region differs from that of the rest of the maxilla in the presence of several well-developed crests and protuberances (Fig. 5). The most anterior of these is located at the contact between the maxilla and the posterior end of the premaxillary posterodorsal process. This crest is symmetrically present in both sides of the snout, being markedly high and semicircular shaped (with its concave side facing posteriorly). The medial extension of this crest extends onto the dorsal surface of the nasal (Fig. 5). Posterior to this crest, the dorsal region of the maxilla bears three irregular protuberances, which in contrast to the semicircular ridge are not fully symmetrical (Fig. 5). The posterior half of the maxilla–nasal suture lacks distinct ridges or protuberances, being ornamented similarly to the rest of the maxillary external surface. The presence of these crests and protuberances on the anterior half of the rostrum is an autapomorphic feature of *L. nodosus*.

The ventral region of the lateral surface of the maxilla is ornamented with a complex pattern composed of small discontinuous ridges and elongated and irregularly spaced pits. The posterior region of the lateral surface of the maxilla is laterally overlapped by the anterior process of the jugal. Dorsal to this suture, the maxilla seems to contact the lacrimal along a subvertically orientated suture located well anteriorly to the orbital opening, although the poor preservation of this region precludes a precise determination of this contact. Similarly, it cannot be determined in PVL 6219 if the posterodorsal region of the maxilla contacts the prefrontal or not.

The alveolar margin of the maxilla has an irregular profile. The buccal margin of the anterior-most three maxillary teeth have their alveolar margins emarginated and well individualized, superficially resembling the condition of some long-snouted neosuchians (e.g. *Terminonaris robusta* Wu, Russell & Cumbaa, 2001a, *Rhabdognathus aslerensis* SUNY-CNRST 190). This emargination of the anterior maxillary alveoli, however, differs from that of the above-mentioned longirostrine crocodyliforms in the morphology of the lingual surface of the alveolar margins (see below). The remainder of the buccal margin of the maxilla is rather straight along the posterior region of the tooth row (Fig. 4). The maxillary alveoli are well separated from each other, especially at the anterior region of the tooth row. These alveoli show a single wave of size variation, increasing along the three anterior maxillary elements and rapidly decreasing posterior to this point (Fig. 3). The maxillary dentition is reduced in number, having either eight or nine elements in each tooth row. The three anterior teeth are only partially preserved and have the base of their crowns subcircular in cross-section. Although none of the maxillary teeth are complete, these anterior elements seem to be significantly larger than the posterior ones. Posteriorly, the maxillary teeth are less spaced from each other and seem to be slightly compressed lateromedially at their crown's base.

The palatal shelves of the maxillae are flat along their medial region and probably contacted each other medially extending posteriorly the secondary palate, although their medial margins were preserved slightly separated from each other (Fig. 3). The palatal surface of the maxilla extends ventrally at the alveolar region. This extension covers the entire lingual margin of the maxillary alveoli, forming a continuous sheet of bone that is vertically orientated (Fig. 6). This morphology resembles that of several sebecosuchian crocodyliforms [e.g. *Se. icaeorhinus* AMNH 3160, *Baurusuchus pachecoi* DGM-R 299, *St. maxhechti* (Riff, 2003), *I. macrodon*]. This contrasts, however, with the emarginated alveolar margins of several long-snouted neosuchians (e.g. dyrosaurids). In these forms the margins of the maxillary alveoli are emarginated but are well separated from each other, forming individualized evaginations rather than a continuous sheet along the lingual alveolar margin. Medially to the alveolar margin the palatal surface of the maxilla is smooth and is pierced by several neurovascular foramina (located mainly along the anterior half of the maxillary tooth row; Fig. 6).

As mentioned above, the lateral region of the anterior margin of the palatal surface of the maxilla

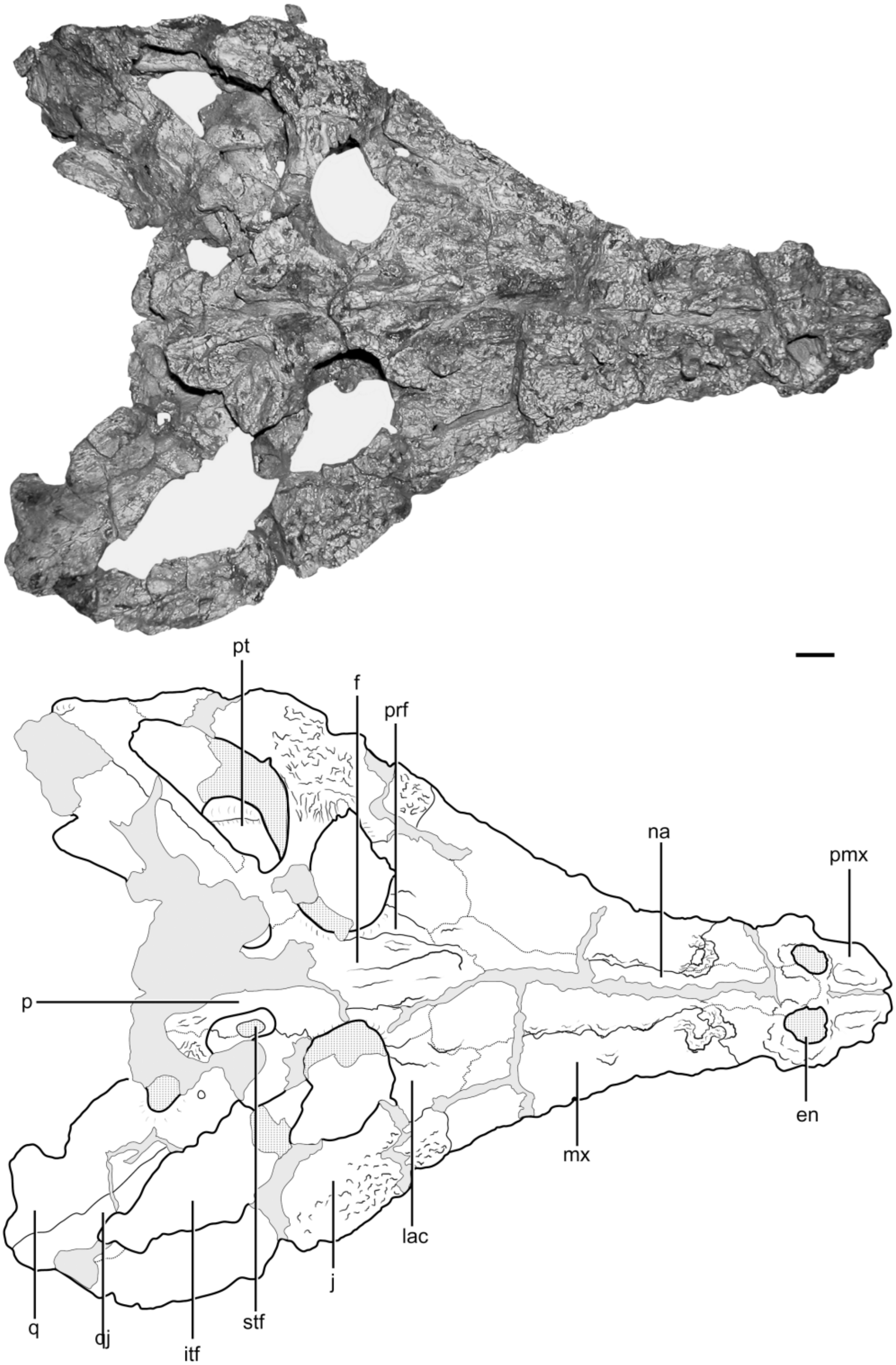

Figure 2. Skull of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) in dorsal view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

contacts the premaxilla enclosing an elongated foramen. Medially to this point, a rhomboid element (presumably the vomer) is exposed on the palate separating the maxilla from the premaxilla (Fig. 3). The anteromedial margins of the maxillae are directed posteromedially bordering the lateral margins of the rhomboid element. The palatal surface of each maxilla diverges posteriorly from each other,

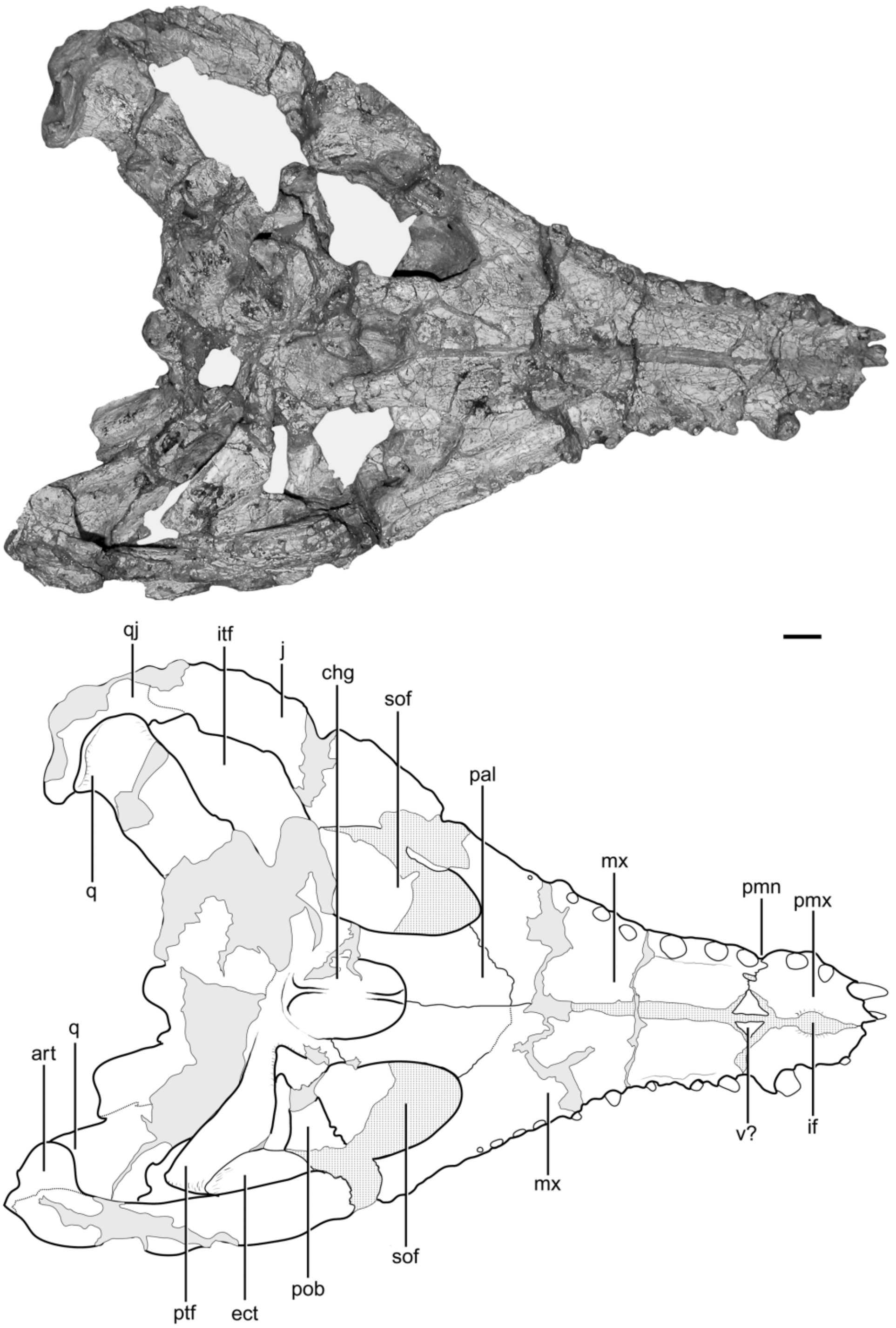

Figure 3. Skull of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) in ventral view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

receiving a large anterior process of the palatines that wedges between them (Fig. 3). The maxilla–palatine contact extends posterolaterally reaching the anterolateral margin of the suborbital fenestra. Posterior to this point, the palatal surface of the maxilla is lateromedially narrow and forms the lateral margin of this opening.

The nasals of PVL 6219 are poorly preserved and highly ornamented. These two factors make the precise delimitation of their sutural contacts difficult.

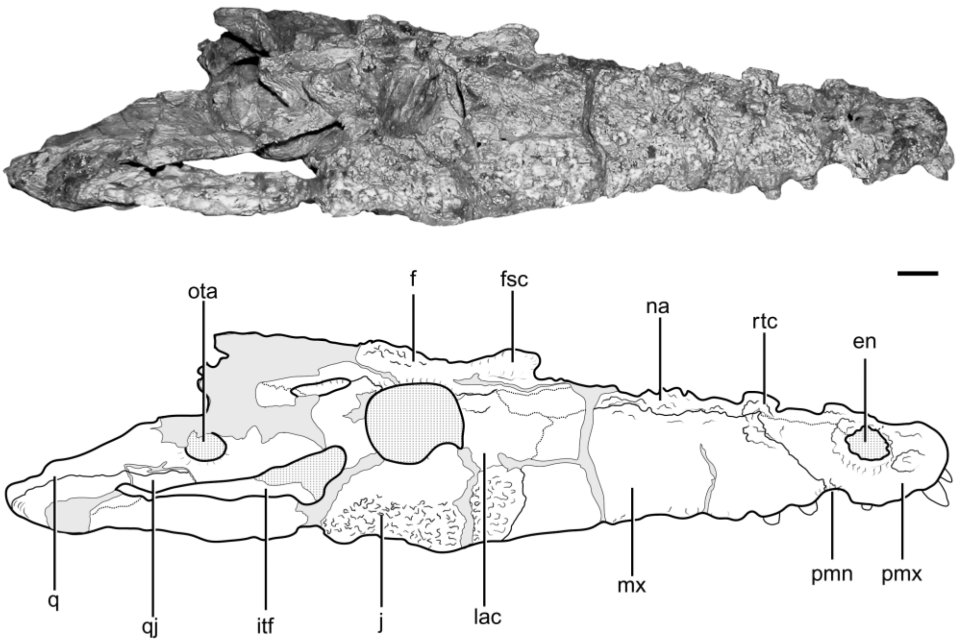

Figure 4. Skull of ***Lorosuchus nodosus*** **gen.** et **sp. nov.** (PVL 6219) in lateral view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

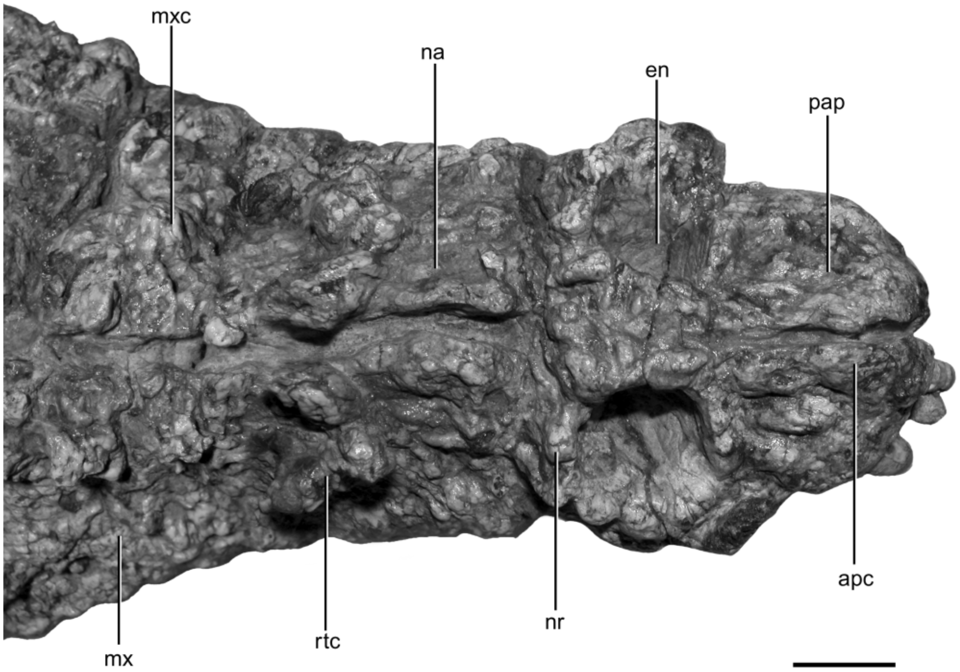

Figure 5. Rostrum of ***Lorosuchus nodosus*** **gen.** et **sp. nov.** (PVL 6219) in dorsal view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

These elements form the dorsal surface of the rostrum and, as the maxilla, bear an irregular pattern of high crests and protuberances on their anterior half. The posterior region of the nasals has a similar ornamentation pattern as the rest of the skull. The anterior extension of the nasals cannot be precisely determined, although they certainly contact the posterodorsal process of the premaxillae. As in most

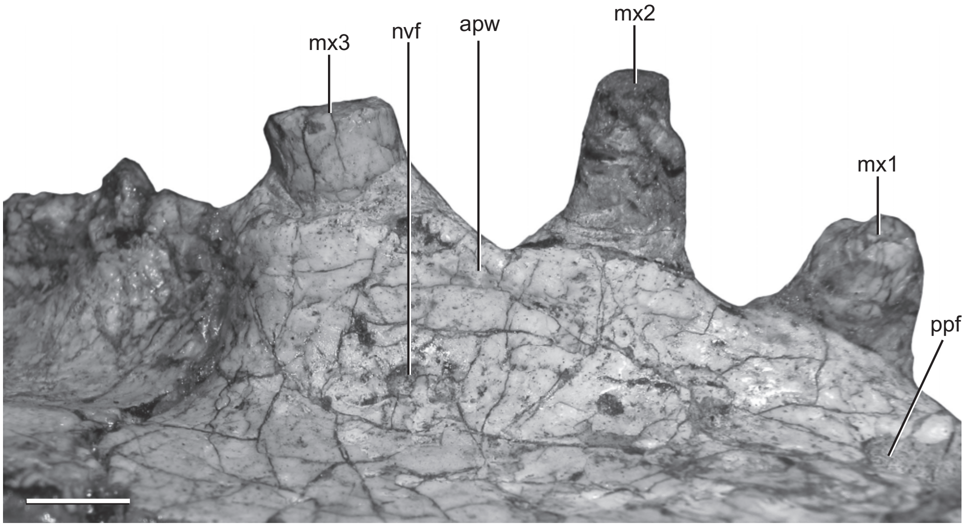

Figure 6. Lingual surface of the first three maxillary alveoli of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) in anteromedial view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

nonlongirostrine crocodyliforms the nasals seem to form part of the narial opening and internarial septum, although this cannot be corroborated with certainty. The medial margins of the nasals have not been preserved in contact to each other and therefore there is a narrow space between them filled with matrix (as in the palatal branches of the maxillae).

The lateral margins of the nasals slightly diverge posteriorly along their contact with the maxillae (Fig. 2). The distinct protuberances described above for the maxilla are partially formed by the nasal, and in some of them the nasal–maxilla suture passes through them (Fig. 5). Most of the posterior region of the nasals is dorsally exposed; however, a reduced posterolateral flance is exposed laterally or laterodorsally (extending onto the lateral surface of the rostrum). A similar character is present in some Palaeogene sebecids [e.g. *Se. icaeorhinus* AMNH 3160, *B. bonapartei* (Gasparini *et al*., 1993)] and in the baurusuchid *St. maxhechti* (Riff, 2003), and much more developed in metriorhynchid thalattosuchians (e.g. *Geosaurus araucaniensis* MACN-N 195). The sutural contacts on the posterior margin of the nasal are not well preserved, although they seem to contact the anterior process of the frontals.

The lacrimal forms the anterior margin of the orbital opening and is sutured to the prefrontal, maxilla, and jugal. This element is extensively exposed anterior to the orbit, as in most crocodyliforms that lack an enlarged antorbital opening [e.g. *Sphagesaurus huenei* RCL-100, *Baurusuchus pachecoi* DGM-R 299, *St. maxhechti* (Riff, 2003), *Se. icaeorhinus* AMNH 3160, *Lomasuchus palpebrosus* MOZ P 4084, *Sarcosuchus hartii* MNN 604, *Goniopholis simus* BMNH 41098, Crocodylia]. The external surface of the lacrimal is ornamented with a similar pattern to that of the lateral surface of the rostrum.

The anterior margin of the lacrimal contacts the maxilla along a vertical interdigitated suture. As noted above, the specimen studied here seems to lack an antorbital opening or fenestra, although the ventral end of the maxilla–lacrimal contact is poorly preserved and a reduced fenestra may have been present. The ventral margin of the lacrimal is laterally overlapped by the jugal along an anteroposteriorly directed suture that reaches the anteroventral margin of the orbit. The posterodorsal region of the lacrimal contacts the prefrontal at the anterodorsal corner of the orbital opening and directs medially onto the dorsal surface of the skull. The lacrimal bears a well-developed protuberance located anterolaterally to the prefrontal-lacrimal suture (Fig. 7). As a result of the poor anterior extension of the prefrontals, the lacrimal probably contacted the posterolateral region of the nasal, although this contact is not preserved in PVL 6219.

The prefrontals of *L. nodosus* are anteroposteriorly short and form the anterior half of the dorsal margin of the orbit. The anterior prefrontal process is short and curves laterally following the orbital margin. Posteriorly the prefrontals are sutured to the lateral margins of the frontal and their lateral margins are only slightly elevated, forming poorly developed orbital rims. The dorsal surface of the prefrontals is slightly ornamented and does not seem to have well-developed articular surfaces for an anterior palpebral (not preserved, or absent, in *L. nodosus*). Inside the

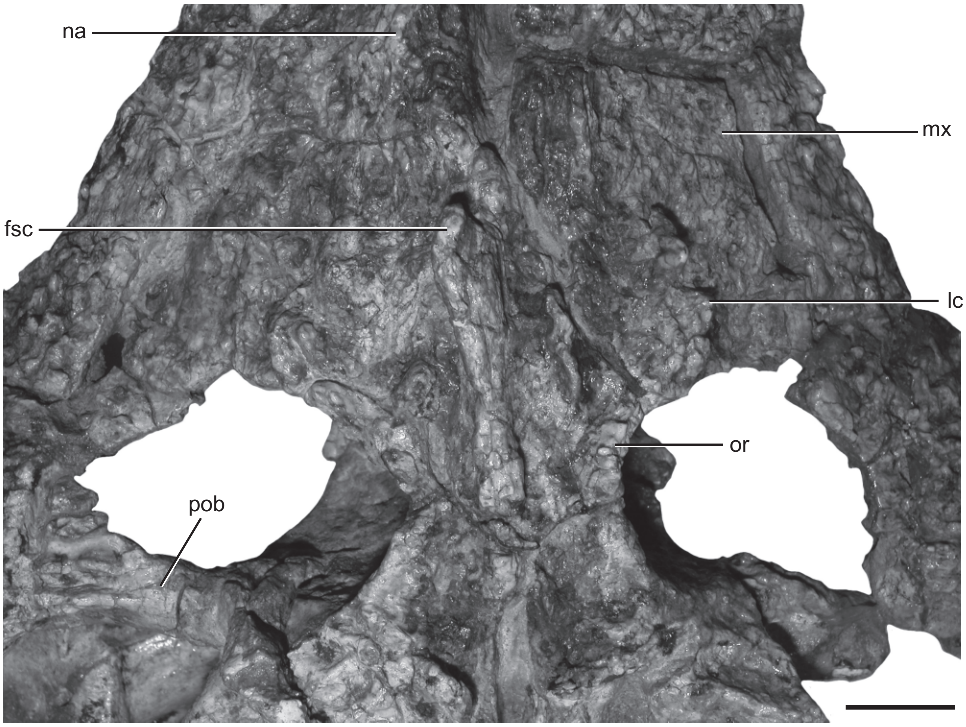

Figure 7. Orbital and antorbital region of ***Lorosuchus nodosus*** **gen.** et **sp. nov.** (PVL 6219) in dorsal view. Anterior is to the top. See Appendix 1 for anatomical abbreviations. Scale bar equals 1 cm.

orbital cavity the prefrontal is poorly preserved and details on the pillars cannot be observed in PVL 6219.

The frontals are fused to each other as in all adult mesoeucrocodylian crocodyliforms (Clark, 1994). The most conspicuous feature of this unpaired element is an extremely well-developed sagittal crest (Fig. 7). The presence of a sagittal ridge is not very uncommon in crocodyliforms [e.g. *Sichuanosuchus shuhanensis* IVPP V 10594, *Simosuchus clarki* UA 8679, *Notosuchus terrestris* MACN-RN 1041, *Se. icaeorhinus* AMNH 3160, *Rugosuchus nonganensis* (Wu, Cheng & Russell, 2001b), *Shamosuchus djadochtaensis* AMNH 6412]. However, this crest is remarkably high in *L. nodosus*, resembling only the condition of the sebecosuchian *I. macrodon*. Some differences, however, exist between the frontal crests of these two taxa. In *I. macrodon* it increases in height and width towards the posterior end of the frontals (at the frontal–parietal suture), being low or disappearing anterior to the orbits. The frontal crest of *L. nodosus* reaches its maximum height at the anterior end of the frontal (located anteriorly to the orbit), decreasing posteriorly to this point (Fig. 7). Unfortunately, the posterior end of this crest has not been preserved in PVL 6219.

The anterior end of the frontal tapers anteriorly to the orbits and was probably in contact with the posterior margin of the nasals. The lateral margins of the frontal form the posterior half of the dorsal margin of the orbits, expanding posteriorly towards its contact with the postorbital. The frontal–postorbital contact is directed posteriorly from the posteromedial corner of the orbit to the anterior margin of the supratemporal fossa. Therefore, the frontal forms part of the margin of this fossa, although it is not clear in PVL 6219 if the frontal enters extensively into this depression and if it forms part of the anterior margin of the supratemporal fenestra. As for most of the dorsal surface of the skull roof, the frontal–parietal contact has not been preserved in the specimen studied here.

Most of the dorsal surface of the parietals has been lost in PVL 6219 and only the surface of the medial region of the right supratemporal fossa has been preserved. The medial margin of this depression is formed by a ridge, being the only preserved region of the parietal's dorsal surface (Fig. 8). The squamosal is also damaged in PVL 6219 and only its anteromedial region has been preserved. This element forms most of the posterior region of the supratemporal fossa, where it is sutured to the parietal and anterodorsal process of the quadrate. Only a fragment of the squamosal's dorsal surface has been preserved posterior to the supratemporal fossa. This surface is dorsally flat and sculpted, as in most crocodyliforms. The postorbital also has a poorly preserved dorsal surface and no details of its contact with the squamosal and

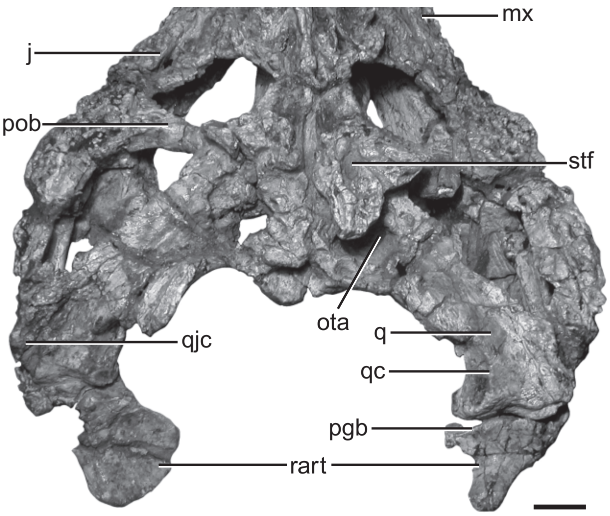

Figure 8. Temporal region of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) in dorsal view. See Appendix 1 for anatomical abbreviations. Scale bar equals 1 cm.

quadratojugal could be determined. The descending process of this element, however, is better preserved (on the left side). This process extends ventrally, forming the dorsal part of the robust and subcylindrical postorbital bar. This bar meets the ascending process of the jugal but their suture cannot be precisely identified. Posteriorly, the postorbital forms the dorsal apex of the infratemporal fenestra, being sutured to the dorsal process of the quadratojugal and quadrate in the otic recess.

The jugal of *L. nodosus* is anteriorly elongated, exceeding the anterior margin of the orbital opening. Its external surface is markedly ornamented (mainly with irregularly shaped pits), being smooth only at the dorsal end of the ascending process of the jugal. This element is rather low dorsoventrally along the infratemporal region and abruptly increases its depth at the orbital region. Most mesoeucrocodylians have the suborbital region of the jugal approximately twice as deep as its infratemporal region (Clark, 1994). Anterior to the orbit, the jugal is dorsoventrally broad, instead of being acute as in most crocodyliforms. A dorsoventrally high jugal, extending anterior to the orbits is also present in *Sp. huenei* (RCL-100) and sebecosuchians (e.g. *Baurusuchus pachecoi* DGM-R 299, *I. macrodon*, *Se. icaeorhinus* AMNH 3159, *B. bonapartei* PVL 4735).

The ascending postorbital process is located slightly anteriorly to the anteroposterior midpoint of the jugal (Fig. 2). The ascending process of the jugal forms the ventral part of the postorbital bar that separates the orbit from the enlarged infratemporal fenestra. The base of this process is ornamented on its lateral surface as in basal crocodyliforms (Clark, 1994), but contrasting with the unornamented condition of most mesoeucrocodylians (including all sebecosuchians and peirosaurids). At this region, the ascending process of the jugal is markedly robust and subquadrangular in cross-section, bearing a distinct concavity on its posterior surface. Its dorsal end, however, is smooth and subcylindrical. As a result of poor preservation of this region of PVL 6219, details of the jugal–postorbital contact could not be determined. The infratemporal bar of the jugal is slightly flattened in cross-section and extends posteriorly, forming most of the ventral margin of the infratemporal fenestra contacting the quadratojugal at its posterior end.

The quadratojugal is ornamented on its external surface, except for the anterodorsal process that forms the posterior margin of the infratemporal fenestra. The anterior branch contacts the posterior end of the jugal and probably formed the posteroventral corner of the infratemporal fenestra. The ascending process of the quadratojugal extends dorsally and is ornamented and moderately broad at its base. This process tapers dorsally and its lateral surface becomes smooth along the dorsal half of the infratemporal fenestra towards the posteroventral margin of the descending process of the postorbital. The anterodorsal process of the quadratojugal is sutured to the quadrate along a straight suture. Posteroventrally, the quadratojugal is sculpted and reaches the lateral condyle of the quadrate, overlapping it laterally. Although this region is not perfectly preserved in PVL 6219, the quadratojugal seems to have a rounded protuberance at its posteroventral end that would form an accessory articular condyle (Figs 8, 9). The participation of the quadratojugal (and surangular) in the craniomandibular joint is a relatively widespread character amongst basal mesoeucrocodylians, being present in some sebecids (e.g. *Se. icaeorhinus* AMNH 3160), peirosaurids (e.g. *Montealtosuchus* MPMA 16-0007–04), *Araripesuchus gomesii* (AMNH 24450), and dyrosaurs (*Rhabdognathus aslerensis* SUNY-CNRST 190). Such articulation, however, is absent in most notosuchians (including baurusuchids).

The quadrates are well preserved in PVL 6219, except for their dorsal end and their anterodorsal branch. This process of the quadrate has its lateral surface smooth and constitutes most of the posterior surface of the otic recess (Fig. 8). The anterodorsal ends of both quadrates seem to be pierced by a subcircular foramen, resembling the anterior siphoneal foramen of extant crocodyliforms. Posterior to this point, the anterodorsal branch of the quadrate forms the anterior, ventral, and posteroventral margins of the otic aperture. This opening is notably large and subcircular shaped (Fig. 4). The quadrate contributes to a large part of the posterior margin of this opening

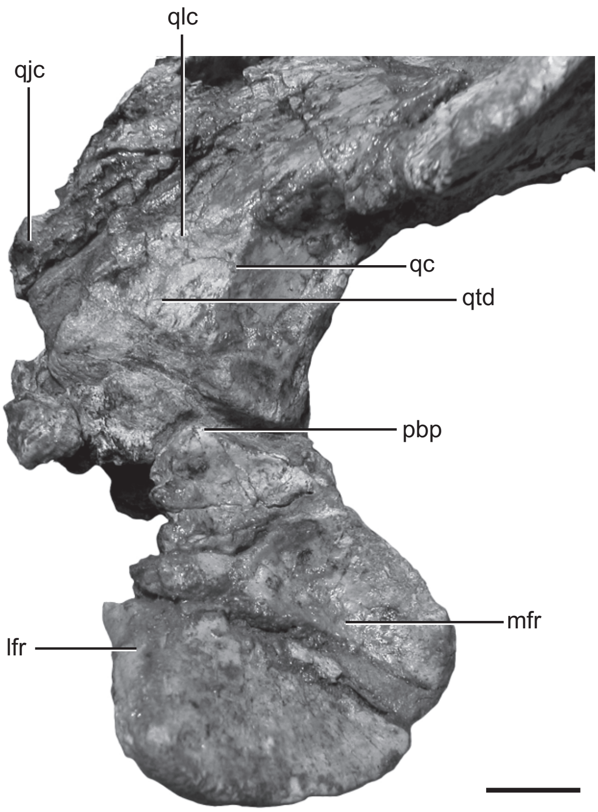

Figure 9. Left quadrate and articular region of mandible of ***Lorosuchus nodosus*** **gen.** et **sp. nov.** (PVL 6219) in posterior view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

in comparison to the condition of most neosuchian crocodyliforms in which most of this margin is formed by the squamosal.

The distal body of the quadrate is well developed, elongated, and directed posteroventrally. This region of the quadrate is lateromedially broad and anteroposteriorly thin, resembling the condition present in neosuchian crocodyliforms as well as sebecids and related forms (e.g. *Se. icaeorhinus* AMNH 3160, *I. macrodon*) but differing from the quadrate of most notosuchians (including baurusuchids), which is subquadrangular in cross-section. In posterior view the entire distal body of the quadrate is markedly curved medially towards the condylar end (Fig. 9), as in sebecids and *I. macrodon*. The posterior surface of the quadrate body bears a sharp ridge running from the squamosal–quadrate suture posterior to the otic aperture to the medial quadrate condyle (Fig. 9). A similar sharp crest is present in *Se. icaeorhinus* (AMNH 3160) although this feature also resembles that of other mesoeucrocodylians [*Hsisosuchus chungkingensis* CNM V 1090, *Ha. rebouli* (Larsson & Sues, 2007), *Montealtosuchus* MPMA 16-0007-04]. Lateral to this ridge, the posterior surface of the quadrate has a subtriangular concave surface bounded laterally by a slightly developed ridge (which runs from the squamosal–quadrate contact to the lateral condyle of the quadrate; see Fig. 9). A similar triangular depression is present in most notosuchians (e.g. *Araripesuchus gomesii* AMNH 24450, *Libycosuchus brevirostris* BSP 1912.VIII.574, *Si. clarki* UA 8679, *Notosuchus terrestris* MACN-RN 1037, *Mariliasuchus amarli* MZSP-PV 50), including sebecosuchians (*Stratiotosuchus* URC R73, *I. macrodon*, *Se. icaeorhinus* AMNH 3160). The dorsomedial extension of the quadrate and its contact with the exoccipital is not well preserved, although this region seems to be dorsoventrally low below the occipital opening of the cranioquadrate passage.

The ectopterygoids are only partially preserved in PVL 6219. The posterior branch of these elements is sutured to the lateral end of the pterygoid flanges. Their suture extends anteromedially from the posterolateral end of the pterygoid flanges, with the ectopterygoid increasingly exposed on the anterior region of the flanges (Figs 10, 11). Unfortunately, it is not possible in PVL 6219 to determine if the ectopterygoid contacted the palatines or the morphology of the anterolateral process of this element and its suture to the jugal.

The pterygoids of *L. nodosus* are completely fused to each other as in all mesoeucrocodylians. The palatal surface of these elements is complex and divided into a medial region and two posterolateral extensions (i.e. the pterygoid flanges). Its medial region is smooth and markedly depressed, forming a rather wide choanal groove (Fig. 10). In contrast to the condition of most other crocodyliforms, the anteromedial region of this groove is distinctly depressed. This depression within the choanal groove bears a low and thin choanal septum that runs along the sagittal plane of the skull (Fig. 10). The anterolateral margins of the choanal groove are subvertically orientated and divide this depression from the posteromedial region of the suborbital opening. The anterior end of this region of the pterygoids is sutured to the posterolateral region of the palatines, which form the anterolateral and anterior margins of the choanal opening. The posterior end of the choanal groove lies close to the posterior margin of the pterygoids and is bounded by a buttress (Figs 10, 11).

Posterolaterally, the pterygoid projects elongated, subhorizontal, and anteroposteriorly narrow flanges. The medial region of the pterygoid flanges of *L. nodosus* has a particularly interesting morphology. Its ventral surface is anteroposteriorly narrow and slightly convex. This curved surface continues onto the rounded and dorsoventrally high anterior surface (Fig. 11). In contrast, the posterior edge of the medial

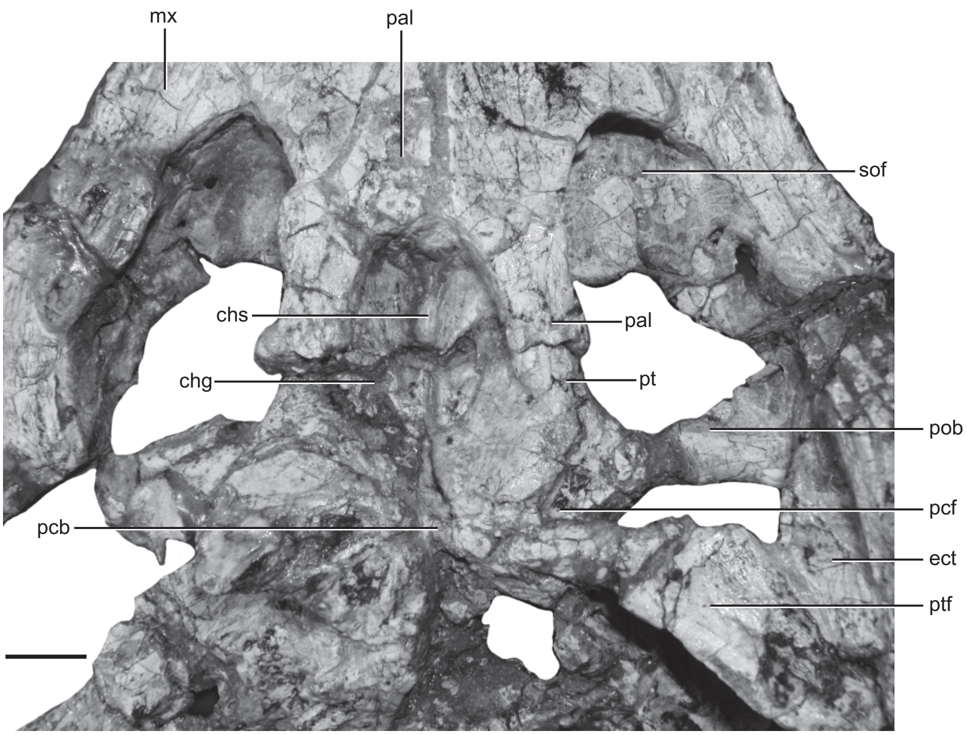

Figure 10. Choanal region of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) in ventral view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

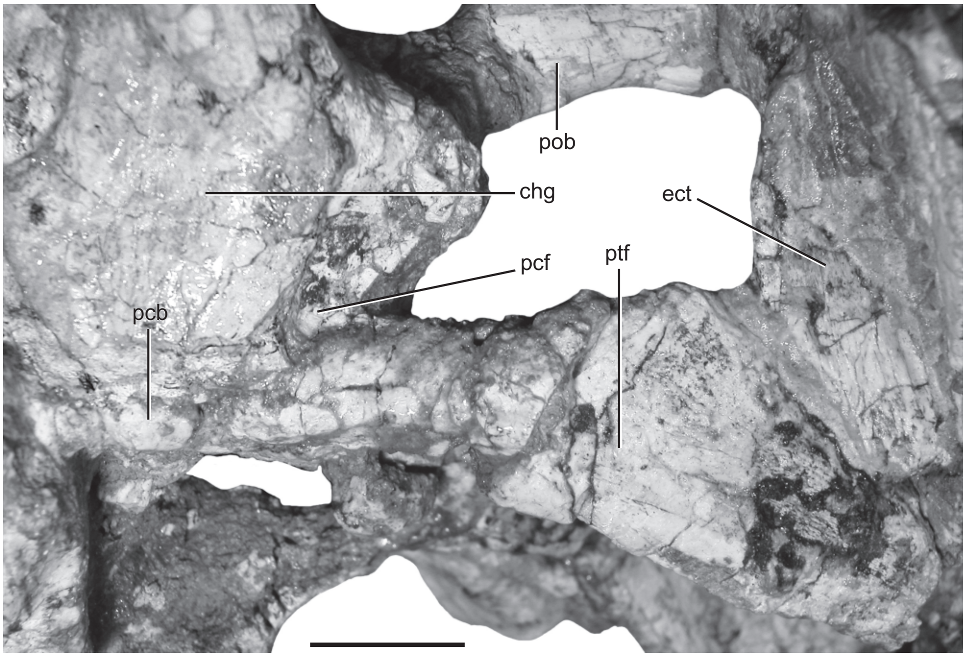

Figure 11. Right pterygoid of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219) in ventral view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

region of the pterygoid flanges is sharp and thin. Thus, the base of the pterygoid flanges of *L. nodosus* are tear-drop shaped in cross-section, with the acute apex pointing posteriorly. The rounded anterior margin of the pterygoid flanges is separated from the medial region of the pterygoids (i.e. the choanal groove) by a laterally opened notch that forms the medial margin of a parachoanal fossa (*sensu* Andrade & Bertini, 2008). This region has only been preserved on the left side of PVL 6219 (Figs 10, 11) as the right side is severely damaged and crushed. The posterior margin of the parachoanal fossa is formed by the anterior margin of the pterygoid flanges. The parachoanal fossa is a depressed surface that extends anterior to the pterygoid flange and laterally to the choanal groove. The floor of this fossa is located dorsally with respect to the choanal margin and the pterygoid flange. A parachoanal fossa located posterolaterally to the choanal groove, at the base of the pterygoid flanges, is also present in derived notosuchians (e.g. *Sp. huenei*, *Sphagesaurus montealtensis*) including baurusuchids (*Baurusuchus salgadoensis*, *St. maxhechti*). *Notosuchus*, *Mariliasuchus*, and more basal notosuchians (e.g. *Araripesuchus* AMNH 24450, *Simosuchus* UA 8679, *Malawisuchus* MAL-49) and peirosaurids [e.g. *Lomasuchus palpebrosus* (Gasparini, Chiappe & Fernández, 1991); *Ha. rebouli* (Larsson & Sues, 2007)], instead, lack this depression. Some sebecids have an anteroposteriorly narrow and laterally elongated opening located posterolaterally to the choana located at the anterior margin of the pterygoid (e.g. *B. bonapartei* PVL 4735). This has been referred to as an accessory pterygoid fenestra but is here putatively interpreted as a perforated parachoanal fossa (*sensu* Andrade & Bertini, 2008). The presence of this structure in the sebecosuchian *I. macrodon* from the Eocene of Europe is currently unknown, although it shares with *L. nodosus* the presence of anteroposteriorly narrow and elongated pterygoid flanges. This peculiar morphology differs from the anteroposteriorly expanded pterygoid flanges of other crocodyliforms [except for the probably convergent condition of some dyrosaurids (e.g. *Rhabdognathus aslerensis* SUNY-CNRST 190)].

Towards the lateral end, the ventral surface of the pterygoid flange becomes flat and slightly expanded anteroposteriorly, close to its sutural contact with the ectopterygoid (Figs 10, 11). The lateral end of this flange is remarkably swollen, being dorsoventrally broader than the rest of the flanges. Based on this specimen, it is not clear if the pterygoid flange had enclosed air cavities, as in some non-neosuchian crocodyliforms [e.g. *Edentosuchus tienshanensis* (Pol *et al*., 2004), *Araripesuchus buitreraensis* MPCA-PV 235, *Notosuchus terrestris* MACN-RN 1037].

The palatines are almost completely preserved in PVL 6219. These elements are relatively broad and contact each other medially forming a posteriorly extended secondary palate characteristic of mesoeucrocodylians. Anterior to the suborbital openings, the palatines are triangular shaped, having their lateral margins sutured to the posterior end of the palatal branches of the maxillae (Fig. 3). This process is remarkably extensive, and rostrally largely exceeds the suborbital openings, as in sebecids [e.g. *Se. icaeorhinus* AMNH 3160, *B. bonapartei*, *Se. querejazus* (Buffetaut & Marshall, 1991)], *Araripesuchus*, peirosaurids, and most neosuchian crocodyliforms. The palatines form the entire anterior margin of the suborbital fenestra, extending up to its anterolateral corner, where the obliquely orientated maxilla–palatine suture reaches this opening (Fig. 10).

The palatines extend posteriorly between the suborbital fenestrae, forming their medial margins (Fig. 10). Along this region, the secondary palate extends briefly, because of the rather anterior position of the anterior margin of the choana (located just anteriorly to the midpoint of the suborbital openings). The posterior margin of the palatines forms a markedly concave anterior choanal margin. The posterolateral branches of these elements diverge slightly posteriorly (Fig. 10) but do not have the distal ends preserved in PVL 6219. These branches are ventrally offset respect to the level of the ventral surface of the pterygoids (Fig. 10), resembling the condition of forms that have the posterolateral branch of the palatine forming a 'palatine bar' (*sensu* Zaher *et al*., 2006). The presence of a palatine bar in *Lorosuchus*, however, cannot be confirmed or rejected at the moment.

Unfortunately, the braincase and occipital region of PVL 6219 are poorly preserved and we can only interpret that the entire occiput was probably dorsoventrally low in comparison with other crocodyliforms.

Mandible

The mandible of PVL 6219 is long and slender in comparison with those of most basal mesoeucrocodylians, including all sebecosuchians and peirosaurids. The mandibular symphysis is dorsoventrally low and lateromedially narrow, forming an elongated region of the mandible with parallel margins (Figs 12, 13). Posteriorly to the mandibular symphysis the mandibular rami diverge from each other at an angle of 45°. The rami are straight for most of their length but deflect medially close to the articular region.

The dentary is extremely low at the symphyseal region, with completely flat dorsal and ventral surfaces. This region was probably affected by dorsoventral crushing that exaggerated the dorsoventral compression of the anterior tip of the lower jaw, but

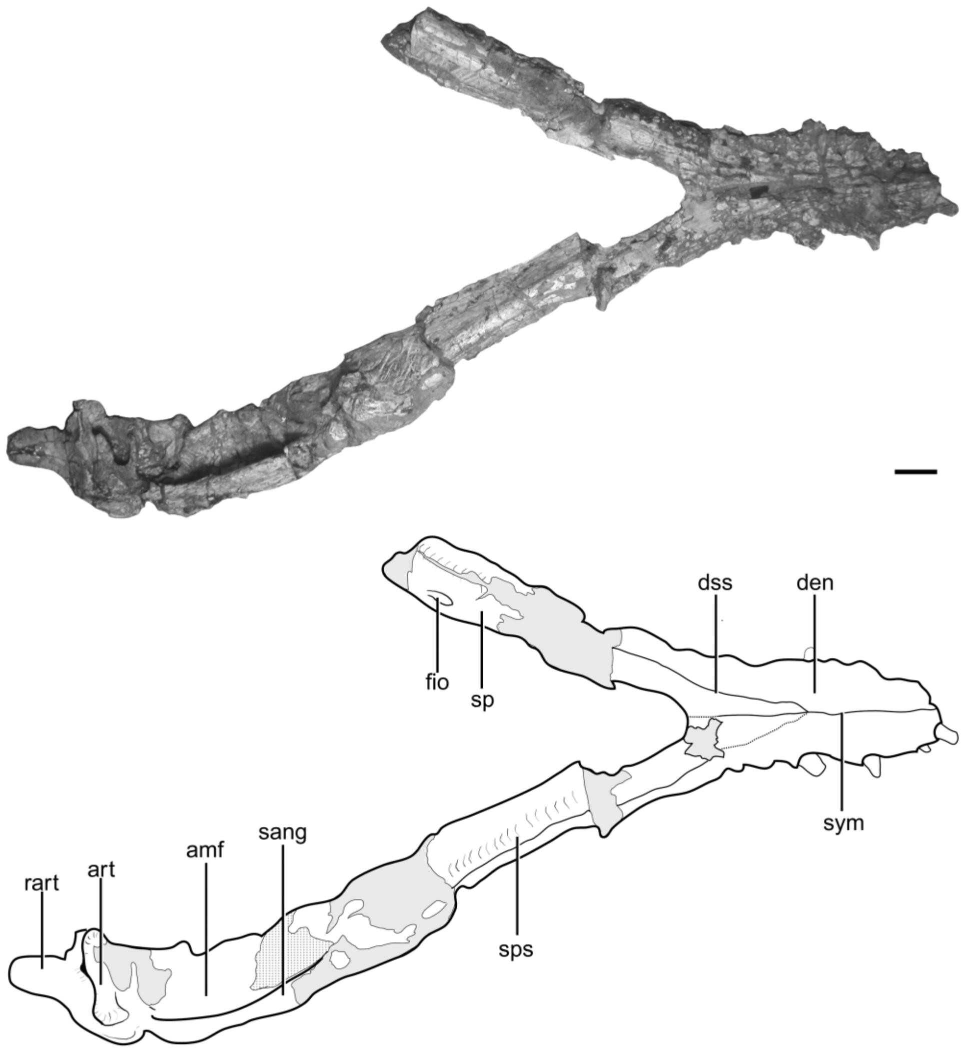

Figure 12. Mandible of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219), in dorsal view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

the original condition must have been nonetheless markedly different from the deep mandibular symphysis present in other sebecids. The dorsal surface of the lower jaw has not been perfectly preserved and parts of the lateral margins of the dentary are broken. The ventral surface is also partially damaged but has preserved an ornamentation pattern formed by short and sinuous grooves and crests (Fig. 13). The rostral tip of the symphysis is narrow and rounded (contrasting with the pointed anterior symphyseal tip of some notosuchians). Along the symphyseal region the dentaries are firmly sutured to each other and to the splenials that participate significantly in the dorsal and ventral surfaces of the symphysis (Figs 12, 13).

Posterior to the mandibular symphysis the dentaries form the lateral and most of the ventral surfaces of the lower jaw. This region of dentaries is dorsoventrally low anteriorly but increases its depth posteriorly. The lateral surface of the dentary is markedly convex in cross-section (as in neosuchian crocodyliforms) and the surface immediately below the alveolar margin seems to be medially located with respect with the rest of the lateral surface of the dentary. The ventral and most of the lateral surface of the dentaries bear an ornamentation pattern of grooves and crests that are longer and straighter than those of the symphyseal region of the mandible. The precise suture with the angular and surangular is hard to determine because of the extensive ornamentation of the lateral surface of the dentary, but this bone seems to extend posteriorly up to the external mandibular fenestra that is located close to the articular region of the mandible. Only a fragment of the right dentary is preserved anteriorly to the

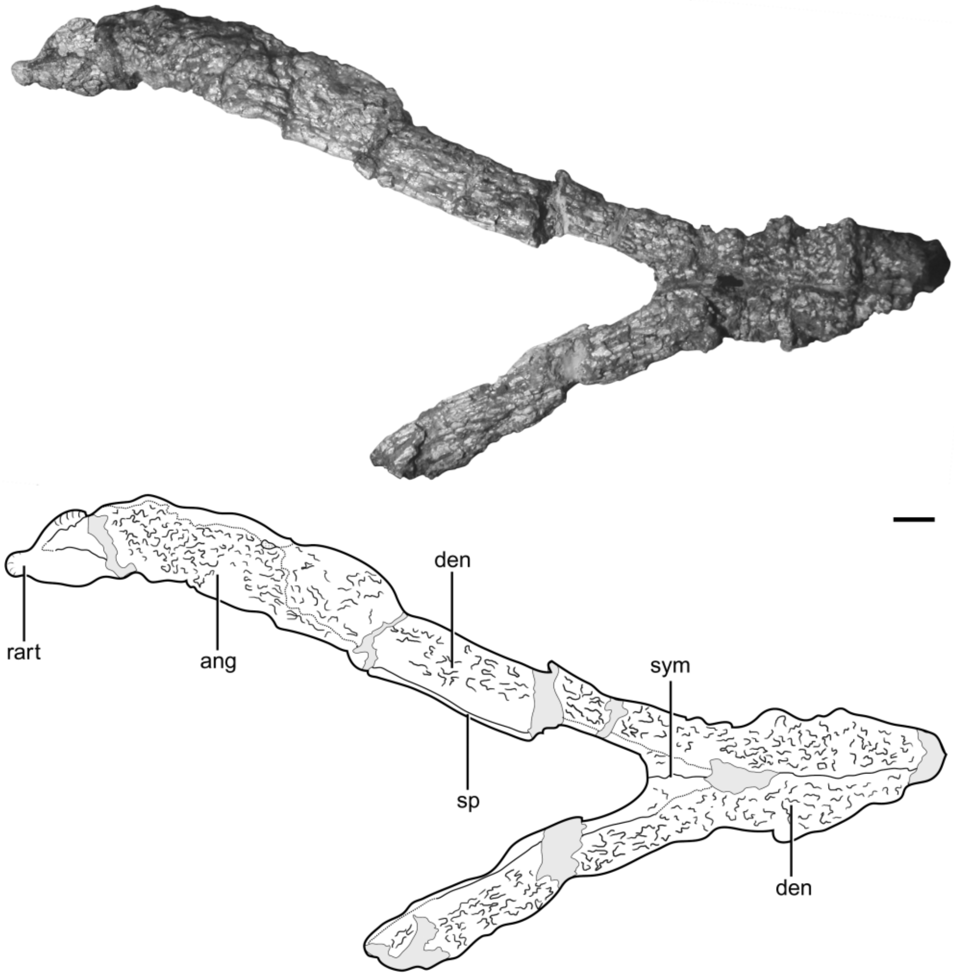

Figure 13. Mandible of ***Lorosuchus nodosus*** **gen.** et **sp. nov.** (PVL 6219), in ventral view. See Appendix 1 for anatomical abbreviations. Scale bar = 1 cm.

external mandibular fenestra, forming the anteroventral margin of this opening (Fig. 15). Thus, the dentary of *L. nodosus* could have extended for approximately 75% of the mandibular length, which is a condition frequently found in longirostrine taxa but is rare amongst basal mesoeucrocodylians.

The dentition of the lower jaw is only partially preserved. The lower tooth row is relatively short in comparison with the mandibular length, extending only along the anterior third of each mandibular ramus. This feature is common amongst basal mesoeucrocodylians (including sebecids) but not amongst neosuchian crocodyliforms, which have more extensive tooth rows. The most anterior right tooth is slightly procumbent and projects anterolaterally from the anterior rounded margin of the dentary. This tooth is similar to the procumbent premaxillary teeth, being conical and slightly recurved with a poorly developed constriction between the crown and the root. Although other teeth are poorly preserved in the symphyseal region, the lateral swellings of the alveolar margin indicate the presence of at least nine teeth in the symphyseal region. Only two postsymphyseal teeth have been preserved on the left mandibular ramus and they are well spaced from each other. These postsymphyseal teeth are set in distinct alveoli although these are not evaginated as in the maxilla. One of the crowns of the two preserved teeth is well preserved and shows a subcircular cross-section in the root and a well-developed constriction between the crown and the root (Fig. 14B). The crown is relatively low and lateromedially compressed, especially towards the mesial and distal margins. There are no denticles preserved in this crown, and most of the enamel is poorly preserved.

The splenial has an extensive participation in the mandibular symphysis and posteriorly covers the medial surface of the mandibular ramus. On the

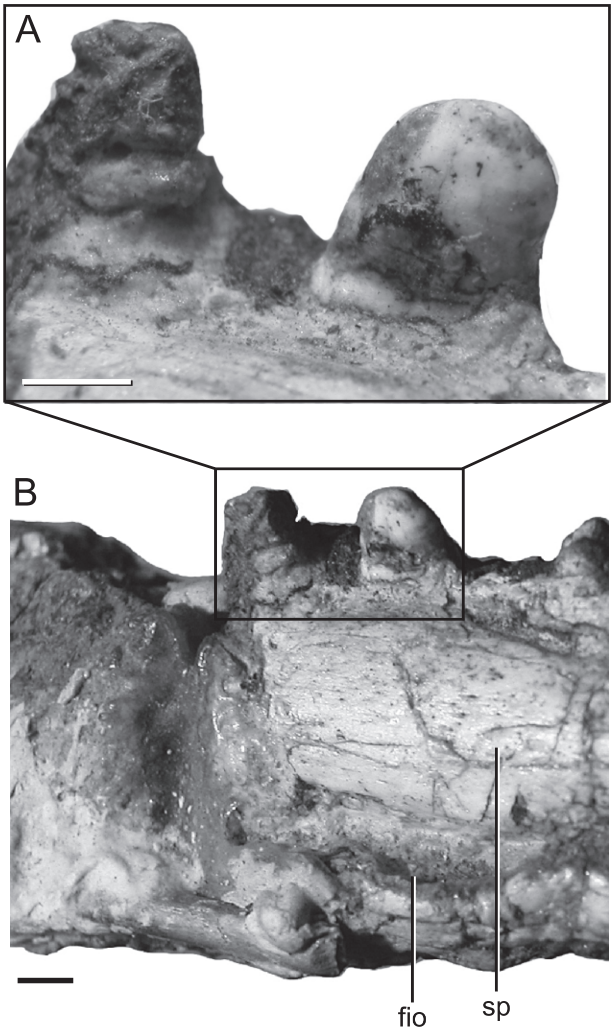

Figure 14. Mandible of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219). A, post-symphyseal tooth in buccal view. B, splenial medial surface in anteromedial view. See Appendix 1 for anatomical abbreviations. Scale bars = 5 mm.

dorsal surface of the mandibular symphysis the splenials are firmly sutured to each other and wedge between the dentaries forming an acute and narrow V-shaped process. The rostral tip of this process reaches the anteroposterior midpoint of the mandibular symphysis. On the ventral surface of the symphysis, the splenials are poorly preserved, but they seem to have a more reduced symphyseal participation than in the dorsal surface, being restricted to the posterior third of the mandibular symphysis. The postsymphyseal lamina of the splenials covers the entire medial surface of the tooth-bearing region of the mandibular ramus. This lamina is slightly convex at its anterior region and gradually flattens posteriorly. Posterior to the symphysis, in the anterior third of the mandibular ramus, the splenial bears a remarkably large slot-like foramen intramandibularis oralis (Fig. 14A), a feature only found in sebecosuchians (Ortega *et al*., 1996).

The dorsal margin of the splenial deflects laterally to form a shelf that extends lingually to the alveoli (Fig. 12). This shelf broadens lateromedially and is more robust toward the posterior end of the tooth row, so that at the posterior end this shelf is a flat horizontal surface that forms an angle of 90° with the vertical lamina of the splenial. Such a broad dorsal exposure of the splenials medial to the posterior alveoli is found both in sebecosuchians (Ortega *et al*., 1996) and in peirosaurids (e.g. *Lomasuchus palpebrosus* MOZ P 4084, *Mahajangasuchus insignis* UA 8654, *Peirosaurus* MOZ P 1750).

The angular is deeply ornamented and forms most of the ventral margin of the minute external mandibular fenestra (Fig. 15A). The ornamentation of the external surface of the angular forms a vermiform pattern composed of sinuous grooves and ridges, which extends for most of the lateral and ventral surface of the angular except for its posterior-most tip. The external surface of the angular does not have features indicating the insertion area of the m. pterygoideus posterior, which could be partially caused by the poor preservation of this region of the mandibular ramus.

The lateral surface of the angular is markedly convex in comparison with that of most crocodyliforms and is medially deflected towards its posterior end (Fig. 12). The lateral convexity and curvature of the angular creates a large and deep mandibular adductor fossa on the medial surface of the posterior end of the mandibular ramus (Fig. 15B, D). The posterior end of the angular seems to extend underneath the articular, reaching the base of the retroarticular process (Fig. 15C).

The surangular is a low and elongated bone that covers the dorsal surface of the posterior half of the mandibular ramus and forms the entire dorsal margin of the external mandibular fenestra (Fig. 15A). The surangular has only a moderate dorsoventral extension and its external surface is less ornamented in comparison with the angular. The dorsal edge of the surangular is horizontal for most of its length and close to the articular region the surangular is slightly upturned. The dorsal surface of the surangular is flat and smooth, facing dorsally along its anterior half. Posteriorly this surface tapers lateromedially and bears a ridge along its lateral margin, which increases its development and height close to the articular region.

At the articular region, this ridge forms the lateral margin of an accessory glenoid facet, presumably for the quadratojugal. The dorsal surface of the

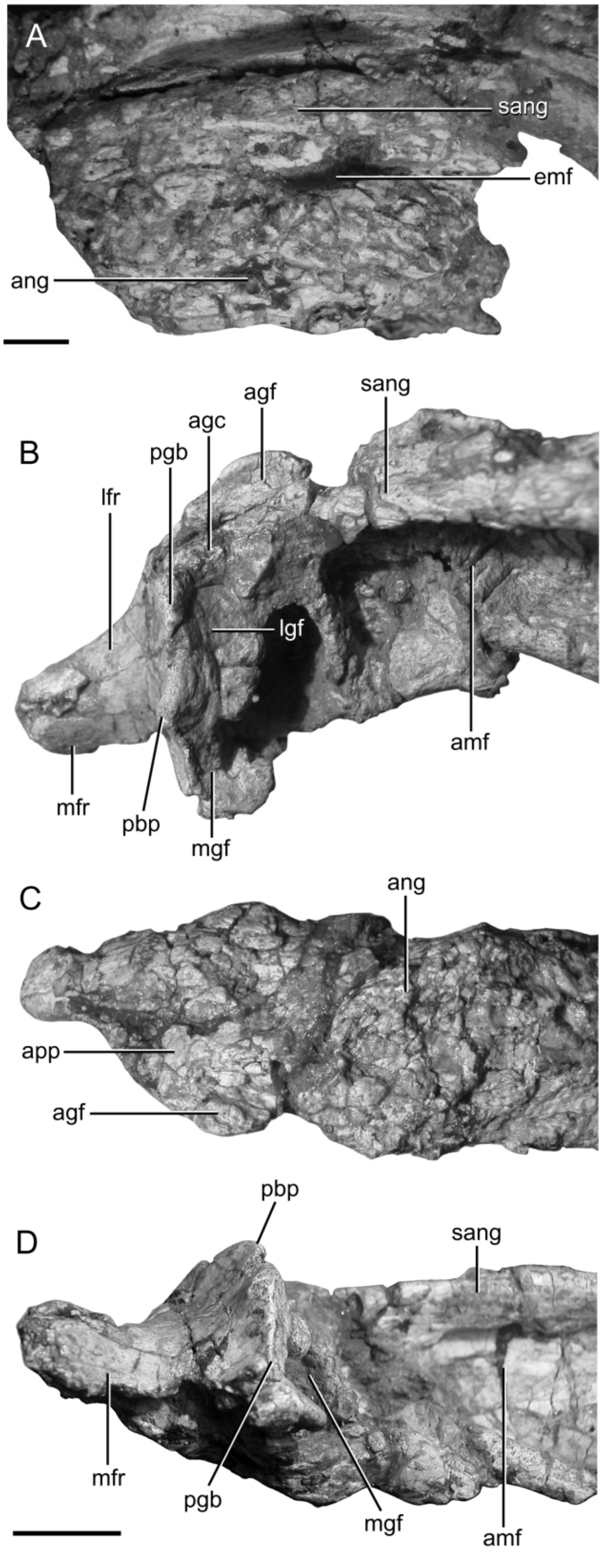

Figure 15. Posterior region of the mandibular ramus of ***Lorosuchus nodosus* gen.** et **sp. nov.** (PVL 6219). A, external mandibular fenestra in lateral view. B–D, right articular region (inverted view) in B, dorsal; C, ventral; and D, medial views. See Appendix 1 for anatomical abbreviations. Scale bars = 1 cm.

surangular in this region is distinctly concave forming a rounded depression bounded laterally by the above-mentioned ridge and medially and posteriorly by a broad crest that delimits the lateral edge of the glenoid facet of the articular (Fig. 15B). The surangular accessory glenoid facet is not continuous with the glenoid facet of the articular bone, not only because of the presence of this broad crest but also because it is set ventrally and slightly anteriorly to the glenoid facet of the articular (Fig. 15B). The surangular glenoid facet projects laterally from the rest of the lateral surface of the mandibular ramus, so that it forms a shelf visible in ventral view (Fig. 15C). An accessory glenoid facet formed by the surangular is present in several groups of basal mesoeucrocodylians, including peirosaurids (*Lomasuchus* MCF PVPH 160, *Mahajangasuchus* UA8 456), *Araripesuchus gomesii* (AMNH 24450), and *Uruguaysuchus aznarezi* (FC-DPV 2320).

The broad crest that delimits the medial margin of the surangular accessory facet is mainly formed by the surangular and its suture with the articular runs medially to it. At the posterior end of the articular facet for the quadrate condyles the broad crest curves medially forming the posterolateral corner of a well-developed posterior buttress of the glenoid facet (Fig. 15B). Posteriorly to the glenoid facet the surangular has a large participation in the retroarticular process. The surangular forms the external half of the lateral flange of the retroarticular process (see below). Along the retroarticular process the dorsal surface of the surangular is smooth and concave, curving dorsally towards its posterior end. The lateral surface of the retroarticular projection of the surangular is dorsoventrally low and tapers posteriorly covering the entire lateral surface of the elongated retroarticular process (Fig. 15B).

The left and right articulars are partially preserved and both lack their process anterior to the glenoid articular facets. However, the glenoid region and the retroarticular process can be completely reconstructed based on the left and right articulars (Figs 9, 15). The glenoid facet is lateromedially wide and anteroposteriorly short, matching the morphology of the quadrate condyles. The glenoid region has a slightly marked distinction between the medial and lateral articular facets and faces anterodorsally, having a well-developed posterior buttress that prevents the posterior excursion of the quadrate condyles during occlusion (Fig. 15B, D). This morphology differs markedly from that of most notosuchians (including baurusuchids) but resembles the condition of other mesoeucrocodylians, including sebecids (e.g. *Se. icaeorhinus* AMNH 3160), peirosaurids (e.g. *Lomasuchus* MCF-PVPH 160, *Montealtosuchus* MPMA-16-0007-04), and neosuchians. The posterior buttress of the glenoid facet has a well-developed peg that projects posterodorsally at the level of the intercondylar groove of the quadrate condyles (Fig. 15B).

The retroarticular process of *Lorosuchus* is dorsoventrally low and posteriorly elongated, and the articular forms the medial two-thirds of this process. The dorsal surface of this process is smooth and divided into a lateral and a medial flange. The medial flange is well preserved in the left articular (Fig. 9), whereas the lateral flange is best preserved in the right articular (Fig. 15). The lateral flange is triangular shaped and formed by the articular and the surangular, both of which contribute equally to its dorsal surface (Fig. 15B). In lateral view, the dorsal surface of this flange is markedly concave, being directed posteroventrally at its proximal half and slightly recurved dorsally along its distal half (Fig. 15D). The posterior end of the retroarticular process bears a slightly developed bulge that is mostly formed by the articular. The lateral flange of the retroarticular process faces dorsally and is distinguished from the medial flange because the latter has a distinct dorsomedial orientation. These two flanges are not divided by a longitudinal ridge as in some crocodyliforms but their boundary forms a straight line between the posterodorsal peg of the glenoid posterior buttress and the bulged posterior tip of the retroarticular process (Fig. 9). The medial flange of the retroarticular process is paddle shaped because of the semicircular outline of its medial edge that extends from the posteromedial corner of the glenoid posterior buttress to the rounded posterior tip of the retroarticular process (Fig. 9). The dorsal surface of the medial flange is depressed and concave, forming a rounded basin that faces dorsomedially (and slightly posteriorly). This particular morphology of the medial flange of the retroarticular process is only found in notosuchians (including baurusuchids) and peirosaurids (e.g. *Montealtosuchus* MPMA-16-0007-04). These forms also share a similar morphology in the lateral flange although its morphology represents the generalized condition of most mesoeucrocodylians.

PHYLOGENETIC RELATIONSHIPS

The available remains of *L. nodosus* clearly indicate that this new taxon is a non-eusuchian mesoeucrocodylian, an assemblage of forms referred to as 'mesosuchians' in the precladistic literature and traditionally characterized by the presence of two plesiomorphic features (choanal opening bounded by palatine and pterygoids and amphicoelic vertebrae). Although non-eusuchian mesoeucrocodylians were extremely diverse and abundant in the Cretaceous (especially in the southern hemisphere), only a small fraction of this diversity survived the Cretaceous/Palaeogene extinction. Amongst them, non-eusuchian crocodyliforms have been recognized as belonging to Dyrosauridae and Sebecidae (and possibly related forms such as *Iberosuchus*). *Lorosuchus* has evaginated and well-spaced alveoli (a synapomorphic character of dyrosaurids) and shares several derived features with sebecids in the choanal and temporal regions; however, its general craniomandibular anatomy is remarkably different from that of dyrosaurids, sebecids, or other clades of Mesoeucrocodylia. The described features indicate *Lorosuchus* is highly autapomorphic, representing a challenging taxon to place within a phylogenetic context. In order to test the phylogenetic affinities of *Lorosuchus* we have expanded the taxon and character sampling scheme of a data set that includes a broad sampling of non-eusuchian mesoeucrocodylians (Pol, Turner & Norell, 2009). The complete data set includes 295 characters and 89 taxa, 63 of which are non- eusuchian mesoeucrocodylians (see Supporting Information for the complete list of characters and data set).

This phylogenetic data set was analysed with equally weighted parsimony using TNT v. 1.0 (Goloboff, Farris & Nixon, 2008a, b). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences) followed by tree bisection-reconnection (TBR) branch swapping (holding ten trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (i.e. rule 1 of Coddington & Scharff, 1994). This analysis resulted in 216 most parsimonious trees of 1209 steps (consistency index = 0.304, retention index = 0.717), found in 30 out of the 1000 replicates. TBR branch swapping of these 216 trees did not find additional optimal topologies. Branch support of clades was evaluated examining the most parsimonious trees in which the monophyly of a given group was rejected (Bremer, 1994) and several exploratory runs were conducted using negative and positive constraints in TNT, in order to test how suboptimal were alternative positions of *L. nodosus*.

All the most parsimonious hypotheses of this analysis placed *L. nodosus* as the most basal taxon of Sebecidae, and this clade is deeply nested within

Notosuchia forming a monophyletic Sebecosuchia (Fig. 16).

In the present analysis Sebecidae, *Iberosuchus*, and *Bergisuchus* were retrieved as a monophyletic group in all the most parsimonious trees (MPTs; node 5 in Fig. 16), forming a clade of Cenozoic sebecosuchians. The latter two taxa are known from the Eocene of Europe and were originally referred to Sebecosuchia or Baurusuchidae (Kuhn, 1968; Steel, 1973; Antunes, 1975) but previous phylogenetic studies depicted *Iberosuchus* as closely related to Sebecidae (Ortega *et al.*, 1996, 2000) and the sebecid affinities of *Bergisuchus* have been supported in some of the MPTs in the analysis of Company *et al.* (2005; see also Rossmann *et al.*, 2000), resembling the position obtained in this study for both taxa. This clade is diagnosed by 11 unambiguous synapomorphies, six of which are preserved in *L. nodosus*. One of the most remarkable modifications of this clade is their elongated bar-like pterygoid flanges (character 179.1), a condition recorded in *Iberosuchus*, *Bretesuchus*, *Se. icaeorhinus*, and *Lorosuchus* (subsequently modified in *Se. querejazus* according to the MPTs of this analysis). Most mesoeucrocodylians instead have pterygoid flanges that are markedly expanded anteroposteriorly at their lateral ends. The other five characters optimized as synapomorphies of this clade that are present in *Lorosuchus* represent reversals to the condition found in several mesoeucrocodylians but are interpreted as such because of the deeply nested position of this clade within Notosuchia. These include the presence of more than eight maxillary teeth (character 108.0); posteroventral corner of the quadratojugal reaching the quadrate condyles (character 141.0); major axis of the quadrate directed posteroventrally and laterally projected from the otoccipital–quadrate (characters 149.0 and 212.1); and distal body of quadrate lateromedially broad and anteroposteriorly narrow in cross section (character 192.0). The remaining unambiguous synapomorphies of this clade are features not preserved in *Lorosuchus* (see Supporting Information for a full list of unambiguous synapomorphies of all clades). Bremer support values for this clade are minimal, given that the clade collapses in the strict consensus of trees with one extra step. This is because of the unstable position of three highly incomplete sebecosuchian taxa (*Pehuenchesuchus enderi*, *Cynodonthosuchus rothi*, and *Se. huilensis*). However, ignoring the alternative positions of these three taxa in trees with one extra step the monophyly of this clade holds in trees up to two extra steps.

Lorosuchus is depicted as the most basal member of Sebecidae, a clade that clusters all taxa from South America (Fig. 16). Sebecidae is diagnosed by seven synapomorphies, most of which are unknown in *Bergisuchus* and therefore are optimized as ambiguous synapomorphies of this South American clade when *Bergisuchus* is depicted as its sister taxon. These synapomorphic features are the palatal parts of the premaxillae meet posteriorly to the incisive foramen, along the contact with the premaxillae (character 7.1; paralleled in *Hamadasuchus* and neosuchians); absence of antorbital fenestra (character 67.2; optimized as convergently acquired in baurusuchids given their presence in most notosuchians, *Iberosuchus*, and *Bergisuchus*); lateral surface of the jugal flat, lacking a broad shelf on its suborbital/antorbital region (character 121.0); absence of a small neurovascular foramen located on the lateral surface of the premaxilla–maxilla suture (character 135.0; a reversal from the derived notosuchian condition); base of postorbital process of jugal directed dorsally (character 142.1); surangular forming approximately one-third of the mandibular glenoid fossa for its articulation with the accessory condyle of the quadratojugal (character 156.1; paralleled in *Araripesuchus* and peirosaurids); and a restricted extension of the perinarial fossa (character 226.0; a reversal from the derived condition of notosuchians). Bremer support for Sebecidae is also minimal as there are trees with one extra step that place *Bergisuchus* within this clade. Ignoring the position of this taxon (as well as *Pehuenchesuchus*, *Cynodonthosuchus*, and *Se. huilensis*), the South American clade of sebecids collapses in trees up to two steps longer than the MPTs.

Lorosuchus is depicted as the sister taxon of all other sebecids (node 4 in Fig. 16), a position supported by the presence of a pterygoid septum that partially divides the choanal opening (character 69.1) that is completely lost in *Barinasuchus*, *Bretesuchus*, and *Se. icaeorhinus*. The presence of this septum in *Se. querejazus* is optimized as a reversal to the condition found in *Lorosuchus* and more basal notosuchians. Two sister clades of South American sebecids are retrieved in the strict consensus in a more derived position than *Lorosuchus* and *Barinasuchus*: a clade formed by *Bretesuchus* and *Ayllusuchus*, and a *Sebecus* clade (including an undescribed form from the Lumbrera Formation of north-western Argentina). These two clades form a monophyletic group (node 3 in Fig. 16) because they share the presence of a posterolateral process of the nasal that deflects abruptly, forming an almost 90° angle with the dorsal surface of the nasal (character 288.1).

The monophyly of the clade formed by *Bretesuchus* and *Ayllusuchus* (node 2 in Fig. 16) is supported by two unambiguous synapomorphies: the presence of a large concave perinarial fossa that extends anteroventrally from the nares toward the alveolar margin of the premaxilla (character 226.2; a feature optimized as convergently acquired with baurusuchids) and the absence of an incisive foramen

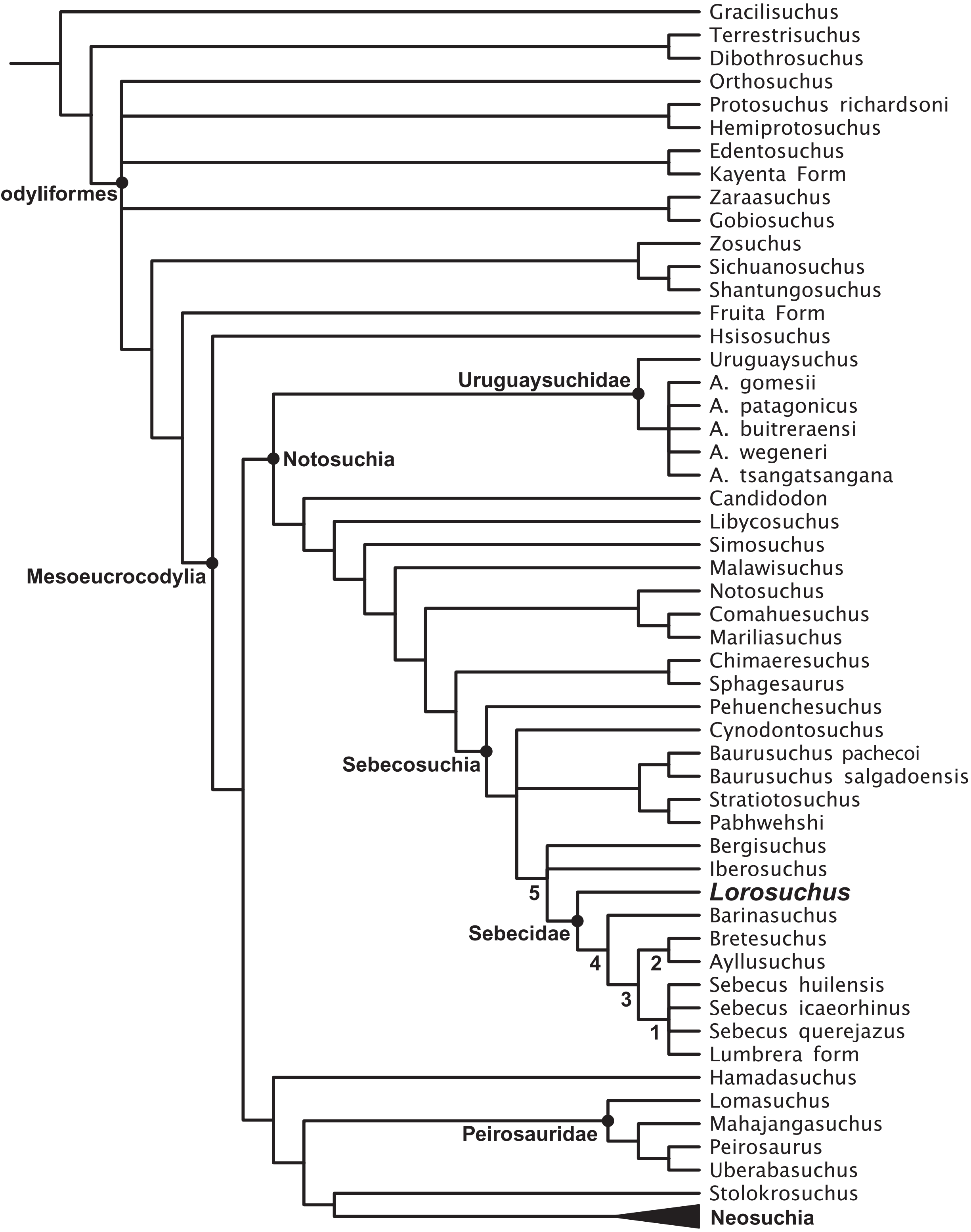

Figure 16. Summary of the strict consensus of the most parsimonious trees (tree length = 1209 steps) obtained in the cladistic analysis using TNT (Goloboff *et al*., 2008a, b). Neosuchians have been collapsed into a single clade in this figure (see Supporting Information for a complete strict consensus). Node numbers indicate the clades for which synapomorphic features are discussed in the text.

on the palate (character 285.2; a unique feature amongst crocodyliforms). The monophyly of the clade formed by the three described species of *Sebecus* (*Se. icaeorhinus, Se. querejazus*, and *Se. huilensis*) and the undescribed taxon from the Lumbrera Formation (node 1 in Fig. 16) is supported by two unambiguous synapomorphies: mid to posterior elements of the tooth row highly compressed buccolingually (character 140.2) and presence of a small notch at the alveolar edge of the premaxilla–maxilla suture (character 9.1; similar to the condition of *Lorosuchus* but contrasting with the enlarged notch present in *Bretesuchus, Barinasuchus, Iberosuchus*, and baurusuchids).

In a more general aspect, all sebecids and the two taxa from the Eocene of Europe cluster as the sister clade of Baurusuchidae (i.e. Sebecosuchia; see Fig. 16), being supported in this analysis by only two unambiguous synapomorphies: the enlarged anterior caniniform in the dentary (character 80.1) and the presence of denticulated carinae in the posterior teeth (character 120.0). Baurusuchids, sebecids, and *Pehuenchesuchus enderi* form a monophyletic Sebecosuchia (as retrieved by Turner & Calvo, 2005). Sebecosuchia also has minimal support in this study but is supported by four unambiguous synapomorphies: the presence of a mandibular symphysis that is deep and anteriorly convex in lateral view (character 103.2), presence of an unsculpted region in the dentary below the tooth row (character 155.0; paralleled in neosuchians), dorsal edge of the dentary with a single dorsal expansion and concave posterior to this (character 159.2), and lateral surface of the dentaries below alveolar margin vertically orientated and continuous with the rest of the lateral surface of the dentaries (character 193.0; paralleled in *Araripesuchus* and neosuchians).

Alternative positions for Lorosuchus

As noted above, the anatomy of *Lorosuchus* is significantly different from the generalized cranial morphology of sebecids (and sebecosuchians), which are generally characterized as having narrow and high snouts bearing blade-like ziphodont teeth. The absence of such morphology in *Lorosuchus* indicates that this taxon is highly autapomorphic and the retrieved phylogenetic position of this taxon implies a large number of character transformations along the terminal branch leading to it. This fact is exemplified by the dramatic tree length decrease when *Lorosuchus* was pruned from all MPTs, which resulted in trees of 1192 steps (17 steps shorter than the length of the MPTs when *Lorosuchus* was included). Furthermore, the extremely low Bremer support values of all sebecosuchian nodes also prompted us to evaluate carefully character support for alternative phylogenetic positions of *Lorosuchus* amongst mesoeucrocodylians. This was carried out through exploratory heuristic tree searches in TNT using monophyly constraints, forcing *Lorosuchus* to fall outside different clades of Mesoeucrocodylia.

Forcing *Lorosuchus* to fall outside a clade formed by all other sebecids plus *Bergisuchus* and *Iberosuchus* resulted in MPTs with two extra steps in the constrained search (in comparison with those of the unconstrained search). In these trees *Lorosuchus* is depicted in two highly distinct positions, either as the sister taxon of the clade of *Bergisuchus* + *Iberosuchus* + Sebecidae [which is placed as the sister clade of Peirosauridae, forming a monophyletic Sebecia *sensu* Larsson & Sues, (2007)] or as the sister taxon of Neosuchia (with sebecids in its original position, allied to Baurusuchidae and deeply nested within Notosuchia). The latter position of *Lorosuchus* was also obtained when the constrained analysis forced this taxon to fall outside Notosuchia. These results indicate that, although *Lorosuchus* is best interpreted at the moment as the most basal Sebecidae (this clade being part of Sebecosuchia), it takes only two extra steps to allocate the new taxon in a markedly different position (allied to neosuchian crocodyliforms). Thus, the low support for the inclusion of *Lorosuchus* in Sebecidae illustrates how difficult is to define with confidence the phylogenetic affinities of such a highly autapomorphic taxon. It must be noted that placing *Lorosuchus* as the sister taxon of Neosuchia would imply a novel lineage of crocodyliforms that survived the Cretaceous/Palaeogene mass extinction event, given the Palaeocene age of *Lorosuchus*.

Alternative positions for Sebecidae

In the constrained searches detailed above, some marginally suboptimal topologies depict the entire clade Sebecidae in a markedly different phylogenetic position with respect to the one obtained in the unconstrained searches (Fig. 16). These results highlight one of the major current problems in mesoeucrocodylian phylogeny: the phylogenetic affinities of Sebecidae. Recent phylogenetic analyses have alternatively retrieved the Cenozoic clade Sebecidae as the sister taxon of two distinct groups of crocodyliforms from the Cretaceous of Gondwana (implying two major alternative positions within Mesoeucrocodylia). The first of these depicts Sebecidae as the sister clade of Baurusuchidae, forming a monophyletic Sebecosuchia that is deeply nested within Notosuchia or Ziphosuchia (e.g. Gasparini *et al*., 1991, 1993; Ortega *et al*., 1996, 2000; Buckley & Brochu, 1999; Buckley *et al*., 2000; Sereno *et al*., 2001, 2003; Pol, 2003; Pol *et al*., 2004, 2009; Turner & Calvo, 2005; Turner & Buckley, 2008; Pol & Gasparini, 2009). This hypothesis is consistent with the traditional classification that grouped sebecids and baurusuchids within Sebecosuchia (Colbert, 1946; Gasparini, 1972, 1984; Langston, 1973) and the suggestion made by Buffetaut (1980) that sebecosuchians evolved from the notosuchian crocodyliforms recorded in the Cretaceous of Gondwana. The second depicts Sebecidae as the sister group of Peirosauridae, forming a monophyletic Sebecia that is more closely related to Neosuchia than to Notosuchia (e.g. Larsson & Sues, 2007). This hypothesis was also advanced by Buffetaut (1991), who suggested the origin of Sebecidae may have been in peirosaurids and/or 'trematochampsids'. Different suites of apomorphic features have been proposed in the above-cited studies supporting these two alternative positions. The phylogenetic data set used in this study incorporates the derived characters shared by sebecids with both baurusuchids and peirosaurids in order to test as thoroughly as possible the phylogenetic position of Sebecidae. Although all the MPTs of the unconstrained search of this study retrieved Sebecidae as closely allied to Baurusuchidae, a secondary phylogenetic signal clearly exists, supporting a close relationship of sebecids and peirosaurids (see for instance that several synapomorphic features of sebecid notes given in the phylogenetic section are noted to be convergently acquired with peirosaurids).

In order to test specifically the support for an alternative position of Sebecidae within the context of this data set, several exploratory runs were conducted using monophyly constraints to find the best topologies that either reject the monophyly of Sebecosuchia or that support the monophyly of Sebecia (i.e. Sebecidae + Peirosauridae). When Sebecosuchia was forced to be nonmonophyletic (by forcing the monophyly of a Notosuchia, including Baurusuchidae but excluding Sebecidae), the resultant MPTs were two steps longer than in the unconstrained search. In these topologies the monophyly of Sebecia is not supported but Sebecidae (together with *Bergisuchus* and *Iberosuchus*) is depicted as the sister taxon of the clade formed by (some) peirosaurids and Neosuchia (Fig. 17A). Forcing Sebecia (Sebecidae + Peirosauridae) to be monophyletic resulted in MPTs that are three steps longer than the unconstrained searches. Interestingly, in these trees, Sebecia is not depicted as closely related to Neosuchia (as originally proposed by Larsson & Sues, 2007) but is placed as the sister group of Notosuchia (Fig. 17B), forming a clade that clusters a large assemblage of basal mesoeucrocodylians mostly recorded in the Cretaceous and Cenozoic of Gondwana (i.e. notosuchians, peirosaurids, sebecids). A large clade of similar taxonomic content has been dubbed Gondwanasuchia by Carvalho, Ribeiro & Avilla (2004). Finally, when Sebecia was forced to be monophyletic and located as the sister group of Neosuchia (as originally proposed by Larsson & Sues, 2007), the resulting MPTs required five extra steps (Fig. 17C). This implies that, within the context of this phylogenetic data set, if Sebecia is deemed as monophyletic it is most parsimoniously depicted as closer to notosuchians than to neosuchians, lending support to the monophyly of Gondwanasuchia.

CONCLUSIONS

The new basal mesoeucrocodylian *L. nodosus* has been described here and its phylogenetic affinities evaluated. This bizarre taxon is most parsimoniously interpreted as the most basal member of Sebecidae (an endemic clade recorded in the Cenozoic of South America), although it lacks the narrow and high rostrum and ziphodont dentition that are characteristic of other sebecids. In particular, the rostral anatomy of *Lorosuchus* shares derived rostral characters with neosuchians that have been traditionally interpreted as adaptations to the semiaquatic mode of life, such as the dorsally directed external nares positioned at the same dorsoventral level as the orbits and the platyrostral section of the anterior half of the snout. One of the most outstanding autapomorphies of *L. nodosus* is its skull ornamentation pattern, composed of large and sinuous crests extending on the dorsal surface of the premaxillae, nasals, and frontal. Interestingly, these crests are exclusively located above the level of the orbits and nares, which in extant crocodylians is the water–air interface level when the animals are resting or swimming in the water. If the sebecid affinities of *Lorosuchus* are correct, the presence of this rostral morphology reveals that the morphological diversity of Sebecidae was much higher than previously recorded and suggests that some members of this group evolved amphibious habits convergently with neosuchians.

Some of these possible aquatic adaptations of *Lorosuchus* are indeed similar to the condition found in Neosuchia and provide an alternative secondary phylogenetic signal that places this taxon allied to Neosuchia in trees with only two extra steps (within the context of the phylogenetic analysis presented here). It may be argued that these marginally suboptimal topologies are biased by characters with adaptive value. However, the derived similarities between *Lorosuchus* and neosuchians do exist and should not be ignored when evaluating the phylogenetic position of this new taxon solely based on the subjective interpretation of their adaptive value.

The uncertainty in the phylogenetic placement of *Lorosuchus* is further enhanced by the problematic position of Sebecidae within the context of Mesoeucrocodylia. As discussed above this group has been alternatively allied to peirosaurids or baurusuchids in recent phylogenetic analyses and these two

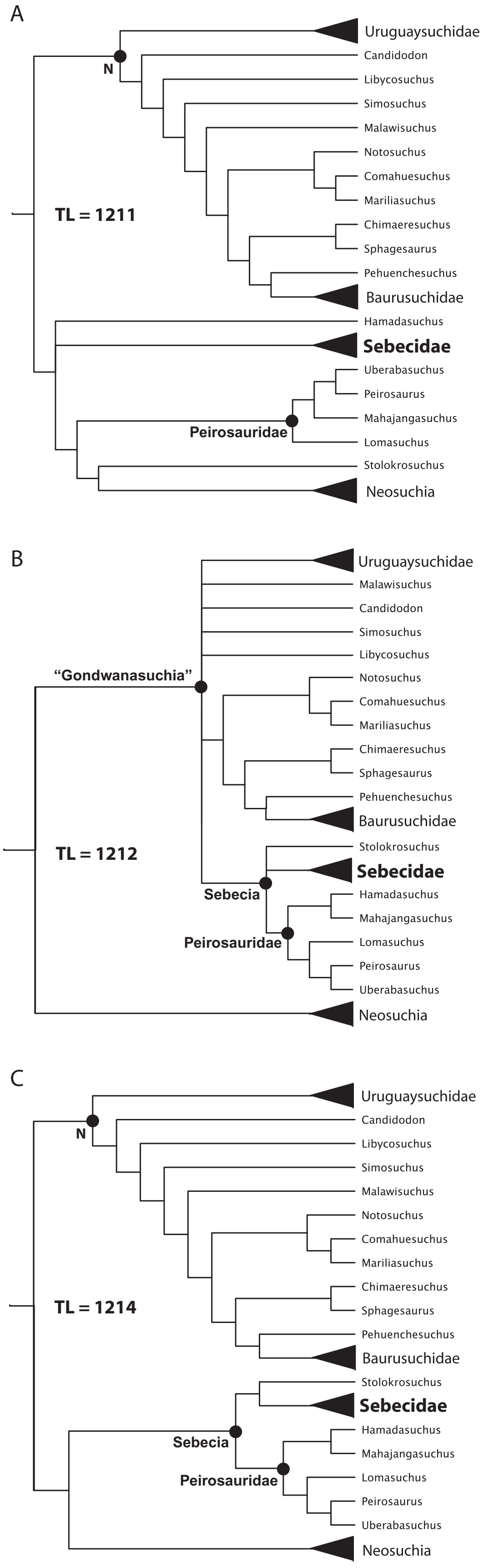

Figure 17. Summary of the strict consensus of the most parsimonious trees obtained in the constrained searches testing the alternative positions of Sebecidae (only the relationships within Mesoeucrocodylia are shown). A, Sebecosuchia forced to be nonmonophyletic by forcing the monophyly of a Notosuchia, including Baurusuchidae but excluding Sebecidae (tree length = 1211 steps). B, Sebecia (Sebecidae + Peirosauridae) forced to be monophyletic (tree length = 1212 steps). C, Sebecia forced to be monophyletic and located as the sister group of Neosuchia (tree length = 1214 steps). Major mesoeucrocodylian clades have been collapsed into a single terminal for this figure. Node N indicates the clade Notosuchia. TL, tree length.

phylogenetic signals are present in our data set. The phylogenetic placement of Sebecidae represents one of the major current problems in mesoeucrocodylian systematics. This problem is partially caused by the lack of comprehensive studies on sebecids, including the lack of detailed anatomical descriptions of most of their members. In particular, the poor current knowledge on the most primitive and ancient sebecids from the Palaeocene could be one of the major causes of this problem, as they could be the most informative taxa for understanding the evolutionary origins of Sebecidae. The present study has included a detailed description of a new basal sebecid and a phylogenetic analysis with an improved taxon sampling regime on sebecids. The new information included in this contribution supports the placement of Sebecidae as the sister clade of Baurusuchidae (deeply nested within Notosuchia) but is by no means a definitive solution to the problematic position of this clade.

Furthermore, the problem of the phylogenetic position of Sebecidae is enhanced by the current lack of extensive knowledge and understanding on the anatomy of their putative relatives from the Cretaceous of Gondwana: peirosaurids and baurusuchids. Peirosaurids are a group of disputed monophyly and few detailed studies have been published on the anatomy of their members, with only recent contributions providing a wealth of new information on some beautifully preserved taxa (e.g. Larsson & Sues, 2007; Turner & Buckley, 2008). Baurusuchids, instead, are presumably monophyletic and are known from highly complete remains of this group from the Cretaceous Bauru Group of Brazil, but detailed studies on their anatomy are scarce in the published literature (but see Nascimento & Zaher, 2011, and Riff & Kellner, 2011, both this volume). Such studies are needed to shed light on not only the morphology of the group but also on their relationships with other taxa, such as notosuchians and sebecids.

Finally, there is also a current lack of knowledge on the postcranial anatomy of all these forms (i.e.

sebecids, peirosaurids, baurusuchids), which could provide useful phylogenetic data given the remarkably high divergence and morphological disparity present in the skull anatomy of these three groups of basal mesoeucrocodylians. The slightly more conservative postcranium can therefore be highly influential for resolving the higher-level relationships amongst these groups of basal mesoeucrocodylians in future studies.

ACKNOWLEDGEMENTS

We would like to thank the technician José Aguilar for the preparation of this specimen and geologist A. Gutierrez for the geological map figured here. The work was financially supported by de Consejo de Investigaciones of the University of Tucuman, through several successive projects. Additional support was provided by ANPCyT (PICT 2006–381) and CONICET (PIP 0781). Access to collection specimens was possible thanks to: J. Maisey and M.A. Norell (AMNH), M. Moser (BSP), M. Maisch (GPIT), X. Xu (IVPP), J.M. Clark (GWU), A. Kramarz (MACN), E. Gomani (MAL), D. Unwin (MB), Z. Gasparini and M. Reguero (MLP), F.L. de Broin (MNHN), A. Kellner (MNUFRJ), S. Cocca (MOZ), J.O. Calvo and L. Salgado (MUC-PV), C. Cartelle (RCL), S. Kaal (SAM), B. Rubidge (BPI), R. Wild (SMNS), D. Krause and G. Buckley (UA), F. Jenkins (MCZ), W. Simpson (FMNH), J.A. Wilson, A. Buscalioni and F. Ortega (UAM), H. Zaher (MZUSP), P.C. Sereno (UC), I.S. Carvalho (UFRJ), R. Bertini (UNESP), and J. Tadeu Arruda and S. Tavares (MPMA).

REFERENCES

Andrade MB, Bertini RJ. 2008. A new *Sphagesaurus* (Mesoeucrocodylia: Notosuchia) from the Upper Cretaceous of Monte Alto City (Bauru Group, Brazil), and a revision of Sphagesauridae. *Historical Biology* **20:** 101–136.

Antunes MT. 1975. *Iberosuchus*, crocodile Sebecosuchien nouveau, l'Eocene iberique au Nord de la Chaine Centrale, et l'origine du canyon de Nazare. *Comunicaçoes dos Serviços Geológicos de Portugal* **59:** 285–330.

Barbosa JA, Kellner AWA, Sales Viana MS. 2008. New dyrosaurid crocodylomorph and evidences of a faunal turnover at the K-P transition in Brazil. *Proceedings of the Royal Society of London, Series B* **275:** 1385–1391.

Bona P. 2007. Una nueva especie de Eocaiman Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. *Ameghiniana* **44:** 435–445.

Bonaparte JF, Van Valen LM, Kramarz A. 1993. La fauna local de Punta Peligro, Paleoceno Inferior, de la Provincia del Chubut, Argentina. *Evolutionary Monographs* **14:** 1–61.

Bossi GE. 1969. Geología y estratigrafía del sector sur del Valle de Choromoro. *Acta geologica Lilloana* **10:** 141–160.

Bremer K. 1994. Branch support and tree stability. *Cladistics* **10:** 295–304.

de Broin FL, de la Fuente MS. 1993. Les tortues fossiles d'Argentina: synthéses. *Annales de Paléontologie (Invert-Vert)* **79:** 169–232.

Buckley GA, Brochu CA. 1999. An enigmantic new crocodile from the Upper Cretaceous of Madagascar. *Special Papers in Palaeontology* **60:** 149–175.

Buckley GA, Brochu CA, Krause DW, Pol D. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature* **405:** 941–944.

Buffetaut E. 1980. Histoire biogéographique des Sebecosuchia (Crocodylia, Mesosuchia): un essai d'interprétation. *Annales de Paléontologie (Vertébrés)* **66:** 1–18.

Buffetaut E. 1991. Fossil crocodilians from Tiupampa, (Santa Lucía Formation, Early Paleocene) Bolivia: a preliminary report. In: Suárez-Soruco R, ed. *Fósiles y Facies de Bolivia*, Vol. I. *Vertebrados 12*. Santa Cruz: Revista Técnica de YPFB, 541–544.

Buffetaut E, Marshall C. 1991. A new crocodilian, *Sebecus querejazus*, nov. sp. (Mesosuchia, Sebecidae) from the Santa Lucía Formation (Early Paleocene) at Vila Vila, Southcentral Bolivia. In: Suárez-Soruco R, ed. *Fósiles y Facies de Bolivia*, Vol. **I.** *Vertebrados 12*. Santa Cruz: Revista Técnica de YPFB, 545–557.

Busbey AB III. 1986. New material of *Sebecus* cf. *huilensis* (Crocodilia: Sebecosuchidae) from the Miocene La Venta Formation of Colombia. *Journal of Vertebrate Paleontology* **6:** 20–27.

Busbey AB III. 1995. Structural consequences of skull flattening in crocodilians. In: Thomason J, ed. *Functional morphology and vertebrate paleontology*. Cambridge: Cambridge University Press, 173–192.

Carvalho IS, Ribeiro LCB, Avilla LS. 2004. *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research* **7:** 975–1002.

Clark JM. 1986. Phylogenetic relationships of the crocodylomorph archosaurs. PhD dissertation, University of Chicago.

Clark JM. 1994. Patterns of evolution in Mesozoic Crocodyliformes. In: Fraser NC, Sues H-D, eds. *The shadow of the dinosaurs: early Mesozoic tetrapods*. New York: Cambridge University Press, 84–97.

Coddington JA, Scharff N. 1994. Problems with zero-length branches. *Cladistics* **10:** 415–423.

Colbert EC. 1946. *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. *Bulletin of the American Museum of Natural History* **87:** 221–270.

Company J, Pereda Suberbiola X, Ruiz-Omeñaca JI, Buscalioni AD. 2005. A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *Journal of Vertebrate Paleontology* **25:** 343–353.

Gasparini ZB. 1972. Los Sebecosuchia (Crocodilia) del territorio argentino. Consideraciones sobre su 'status' taxonómico. *Ameghiniana* **9:** 23–34.

Gasparini ZB. 1984. New Tertiary Sececosuchia (Crocodylia:Mesosuchia) from Argentina. *Journal of Vertebrate Paleontology* **4:** 85–95.

Gasparini ZB. 1996. Biogeographic evolution of the South

American crocodilians. *Münchner Geowissenschaftliche Abhandlungen* **30:** 159–184.

Gasparini ZB, Chiappe LM, Fernández M. 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodilians. *Journal of Vertebrate Paleontology* **11:** 316–333.

Gasparini ZB, Fernández F, Powell JE. 1993. New Tertiary sebecosuchians (Crocodylomorpha) from South America: phylogenetic implications. *Historical Biology* **7:** 1–19.

Goloboff PA, Farris JS, Nixon KC. 2008a. TNT, a free program for phylogenetic analysis. *Cladistics* **24:** 774–786.

Goloboff PA, Farris JS, Nixon KC. 2008b. *TNT: tree analysis using new technologies*. Program and documentation available from the authors. Available at http://www.zmuc.dk/public/phylogeny/TNT

Hay OP. 1930. *Second bibliography and catalogue of the fossil Vertebrata of North America 2*. Washington, DC: Carnegie Institute Washington.

Kuhn O. 1968. *Die Vorzeitlichen Krokodile*. München: Verlag Oeben.

Langston W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University California Publication Geological Sciences* **52:** 1–157.

Langston W. 1973. The crocodilian skull in historical perspective. In: Gans C, Parsons T, eds. *Biology of the Reptilia*, Vol. 4. London: Academic Press, 263–284.

Langston W, Gasparini ZB. 1997. Crocodilians, *Gryposuchus*, and the South American gavials. In: Kay R, Madden R, Cifelli R, Flynn J, eds. *Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*. Washington: Smithsonian Institution Press, 113–154.

Larsson HCE, Sues HD. 2007. Cranial osteology of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society* **149:** 533–567.

Nascimento P, Zaher H. 2011. The skull of the Upper Cretaceous baurusuchid crocodile *Baurusuchus albertoi* Nascimento & Zaher, 2010, and its phylogenetic affinities. *Zoological Journal of the Linnean Society* **163:** S116–S131.

Ortega F, Buscalioni AD, Gasparini ZB. 1996. Reinterpretation and new denomination of *Atacisaurus crassiproratus* (Middle Eocene; Issel, France) as cf. *Iberosuchus* (Crocodylomorpha: Metasuchia). *Geobios* **29:** 353–364.

Ortega F, Gasparini ZB, Buscalioni AD, Calvo JO. 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology* **20:** 57–76.

Paolillo A, Linares OJ. 2007. Nuevos cocodrilos Sebecosuchia del Cenozoico suramericano (Mesosuchia: Crocodylia). *Paleobiologia Neotropical* **03:** 1–25.

Paula Couto C. 1970. Evoluçao de comunidades, modifcaçoes e integraçoes biovenóticas dos vertebrados cenozóicos de Brasil. *IV Congreso Latinoamericano de Zoología* **1968:** 743–758.

Pol D. 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Journal of Vertebrate Paleontology* **23:** 817–831.

Pol D, Gasparini ZB. 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology* **7:** 163–197.

Pol D, Ji SH, Clark JM, Chiappe LM. 2004. Basal crocodyliforms from the Early Cretaceous Tugulu Group (Xinjiang, China), and the phylogenetic position of *Edentosuchus*. *Cretaceous Research* **25:** 603–622.

Pol D, Turner AH, Norell MA. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. *Bulletin of the American Museum of Natural History* **324:** 1–103.

Powell JE, Palma RM. 1981. Primer hallazgo de mamíferos en la Formación Río Loro, Provincia de Tucumán y su significado cronológico. *Revista de la Asociación Geológica Argentina* **26:** 208–212.

Riff D. 2003. Descrição morfológica do crânio e mandíbula de *Stratiotosuchus maxhechti* (Crocodylomorpha, Cretáceo Superior do Brasil) e seu posicionamento filogenético. MSc dissertation, Universidade Federal do Rio de Janeiro.

Riff D, Kellner AW. 2011. Baurusuchid crocodyliforms as theropod mimics: clues from the appendicular morphology of *Stratiotosuchus maxhechti* (Upper Cretaceous of Brazil). *Zoological Journal of the Linnean Society* **163:** S37–S56.

Rossmann T, Rauhe M, Ortega F. 2000. Studies on Cenozoic crocodiles 5. Description of *Bergisuchus dietrichbergi* Kühn (Sebecosuchia: Bergisuchidae n. fam.) from the Middle Eocene of Germany, and some new systematic and biological conclusions. *Paläontologische Zeitschrift* **74:** 379–392.

Rusconi C. 1946. Ave y reptil oligocenos de Mendoza. *Boletin Paleontologia Buenos Aires* **21:** 1–3.

Sereno PC, Larsson HCE, Sidor CA, Gado B. 2001. The giant crocodyliform *Sarco*suchus from the Cretaceous of Africa. *Science* **294:** 1516–1519.

Sereno PC, Sidor CA, Larsson HCE, Gado B. 2003. A new notosuchian from the Early Cretaceous of Niger. *Journal of Vertebrate Paleontology* **23:** 477–482.

Simpson GG. 1937a. An ancient eusuchian crocodile from Patagonia. *American Museum Novitates* **965:** 1–20.

Simpson GG. 1937b. New reptiles from the Eocene of South America. *American Museum Novitates* **927:** 1–3.

Soria MF. 1988. Notopterna: un nuevo orden de mamíferos ungulados eogenos de América del sur. Parte II. *Notonychops powelli* gen. et sp. Nov. (Notonychopidae nov.) de la Formación Río Loro (Paleoceno Medio), Provincia de Tucumán, Argentina. *Ameghiniana* **25:** 259–272.

Soria MF. 1989. El primer Notoungulata de la Formación Río Loro (Paleoceno medio), Provincia de Tucumán, República Argentina. *Ameghiniana* **26:** 145–151.

Soria MF, Powell JE. 1981. Un primitivo Astrapotheria (Mammalia) y la edad de la Formación Río Loro, prov. de Tucumán, República Argentina. *Ameghiniana* **18:** 155–168.

Steel R. 1973. Crocodylia. In: Kuhn O, ed. *Handbuch der Palaoherpetologie Part 16*. Portland: Gustav Fischer, 1–116.

Turner AH, Buckley GA. 2008. *Mahajangasuchus insignis* (Crocodyliformes: Mesoeucrocodylia) cranial anatomy and new data on the eusuchian-style palate. *Journal Vertebrate Paleontology* **28:** 382–408.

Turner AH, Calvo JO. 2005. A New Sebecosuchian Crocodyliform from the Late Cretaceous of Patagonia. *Journal Vertebrate Paleontology* **25:** 87–98.

Walker AD. 1970. A revision of the Jurassic reptile Hallopus victor (Marsh), with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society of London B* **257:** 323–372.

Whetstone KN, Whybrow PJ. 1983. A 'cursorial' crocodilian from the Triassic of Lesotho (Basutoland), southern Africa. *Occasional Papers of the Museum of Natural History, University of Kansas* **106:** 1–37.

Wilson JA, Malkani MS, Gingerich PD. 2001. New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous Pab Formation of Vitakri, Balochistan (Pakistan). *Contributions from the Museum of Paleontology University of Michigan* **30:** 321–336.

Wu X-C, Russell AP, Cumbaa SL. 2001a. *Terminonaris* (Archosauria: Crocodyliformes): New material from Saskatchewan, Canada, and comments on its phylogenetics relationships. *Journal of Vertebrate Paleontology* **21:** 492–514.

Wu X-C, Cheng ZW, Russell AP. 2001b. Cranial anatomy of a new crocodyliform (Archosauria: Crocodylomorpha) from the Lower Cretaceous of Song-Liao plain, northeastern China. *Canadian Journal of Earth Sciences* **38:** 1653–1663.

Zaher H, Pol D, Carvalho AB, Riccomini C, Campos D, Nava W. 2006. Redescription of the cranial morphology of *Mariliasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). *American Museum Novitates* **3512:** 1–40.

APPENDIX 1

ANATOMICAL ABBREVIATIONS

agc	crest separating the accessory from the glenoid facet
agf	accessory glenoid facet
ang	angular
apc	anterior premaxillary crest
app	angular posterior process
apw	anterior palatal wall
art	articular
chg	choanal groove
chs	choanal septum
den	dentary
dss	dentary-splenial suture
ect	ectopterygoid
emf	external mandibular fenestra
en	external nares
f	frontal
fio	foramen intramandibularis oralis
fsc	frontal sagittal crest
pgb	posterior glenoid buttress
if	incisive foramen
itf	infratemporal fenestra
j	jugal
lac	lacrimal
lc	lacrimal crest
lgf	lateral glenoid facet of the articular
lfr	lateral flange of retroarticular process
mfr	medial flange of retroarticular process
mgf	medial glenoid facet of the articular
mx	maxilla
mxc	maxillary crests
na	nasal
nr	elevated narial rim
nvf	neurovascular foramen
or	orbital rim
ota	otic aperture
p	parietal
pal	palatine
pap	premaxillary anterior depression

APPENDIX 1 *Continued*

pbp	central peg of posterior glenoid buttress
pcb	posterior choanal buttress
pcf	parachoanal fossa
pgb	posterior glenoid buttress
pmn	premaxilla–maxilla notch
pmx	premaxilla
po	postorbital
pob	postorbital bar
ppf	premaxilla–maxilla palatal foramen
prf	prefrontal
pt	pterygoid
ptf	pterygoid flange
q	quadrate
qc	quadrate crest
qj	quadratojugal
qjc	quadratojugal condyle
qlc	quadrate lateral crest
qtd	quadrate triangular depression
rart	retroarticular process
rtc	rostral transverse crest
sang	surangular
sof	suborbital fenestra
sp	splenial
sps	splenial medial alveolar shelf
stf	supratemporal fenestra
sym	mandibular symphysis
v?	vomer?

APPENDIX 2

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, USA
BMNH	British Museum of Natural History, London, England
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, Münich, Germany
DGM	Departamento de Produção Mineral, Rio de Janeiro, Brazil
FC-DPV	Facultad de Ciencias, Colección de Vertebrados Fósiles, Montevideo, Uruguay
GSP-UM	Geological Survey of Pakistan-University of Michigan, Quetta, Pakistan
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MAL	Malawi Department of Antiquities, Malawi
MCF-PVPH	Museo Carmen Funes, Plaza Huincul, Argentina
MNN	Musée National du Niger, Niamey, Niger
MOZ	Museo Profesor J. Olsacher, Zapala, Argentina
MPCA	Museo Carlos Ameghino, Cipoletti, Argentina
MPMA	Museu de Paleontologia de Monte Alto, Monte Alto, Brazil
MZSP	Museu de Zoología, Universidade de São Paulo, São Paulo, Brazil.
PVL	Instituto Miguel Lillo, Tucumán, Argentina
RCL	Museo de Ciencias Naturales, Pontificia Universidade Catolica de Minas Gerais, Brazil
SUNY-CNRST	Centre National de la Recherche Scientifique et Technologique de Mali – Stony Brook University, New York, USA
UA	University of Antananarivo, Madagascar
URC	Universidade Estadual Paulista, Rio Claro, Brazil

SUPPORTING INFORMATION

Additional Supporting Information related to the phylogenetic analysis may be found in the online version of this article:

Appendix S1. Complete strict consensus obtained in the phylogenetic analysis.
Appendix S2. Character list corresponding to the data matrix used in the phylogenetic analysis.
Appendix S3. Data matrix used in the phylogenetic analysis.
Appendix S4. Fossil taxa used in the phylogenetic analysis.
Appendix S5. List of unambiguous synapomorphies of the most parsimonious trees of the phylogenetic analysis.
Appendix S6. List of references used in the supplementary appendices.