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SKULL ANATOMY OF *DAKOSAURUS ANDINIENSIS* (THALATTOSUCHIA: CROCODYLOMORPHA) AND THE PHYLOGENETIC POSITION OF THALATTOSUCHIA

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SYNOPSIS New information on *Dakosaurus andiniensis* from the Latest Jurassic and Early Cretaceous is reported here. One of the specimens described herein consists of an almost complete skull and lower jaw found in the uppermost levels of the Vaca Muerta Formation (Tithonian) of Neuquén Province, Argentina. The new material allows a more complete understanding and diagnosis of this form, previously known only from the fragmentary type specimen. The new remains show that *D. andiniensis* had an unusual morphology for a marine crocodyliform,namely a remarkably short, high snout with ziphodont dentition.

This new information allows testing of the phylogenetic relationships of this taxon, which is depicted as deeply nested within Metriorhynchidae, a clade of marine crocodyliforms with derived adaptations to the marine environment (e.g. paddle-like forelimbs, hypertrophied nasal salt glands). In particular, *D. andiniensis* is inferred to be the sister taxon of *D. maximus* from the Jurassic of Europe. This relationship repeats the phylogenetic pattern seen in other Jurassic marine crocodyliforms from South America and Europe (e.g. *Geosaurus*), demonstrating the close faunal relationship between these two distant marine basins. The phylogenetic analysis reported here results in a most parsimonious hypothesis that depicts Thalattosuchia nested within Neosuchia and the strength and character evidence supporting this position is presented. In addition, several characters traditionally postulated as dependent upon the longirostrine morphology are critically examined under the light of new evidence. Most of them show a character state distribution that is not strictly compatible with that of the longirostrine condition and, therefore, are interpreted as independent units of phylogenetic evidence.

KEY WORDS Crocodyliformes, Metriorhynchidae, longirostry, phylogeny, ziphodont, Jurassic

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INTRODUCTION

The Jurassic record of crocodyliforms is largely composed of marine forms, some of which had modified 'paddle-like' forelimbs for aquatic locomotion. These taxa were traditionally grouped in Thalattosuchia (Fraas 1902; Mook 1934; Kälin 1955; Westphal 1962; Buffetaut 1981; Gasparini 1981; Vignaud 1995) and are known from marine deposits from Europe, Asia and South and Central America (Eudes-Deslongchamps 1867–1869; Fraas 1902; Andrews 1913; Young 1948; Gasparini 1992; Gasparini & Iturralde-Vinent 2001; Frey *et al.* 2002). South American thalattosuchians are mainly known from Middle Jurassic through Late Jurassic deposits from Chile and the Middle Jurassic through Early Cretaceous beds of western Argentina (Gasparini *et al.* 2000; Gasparini & Fernández 2005). The most diverse assemblage comes from several outcrops of the Tithonian levels of the Vaca Muerta Formation (Gasparini 1981, 1996). Some crocodyliforms from this formation were referred to *Geosaurus* and *Dakosaurus*, two previously known metriorhynchid genera from the Jurassic of Europe (Gasparini & Dellapé 1976; Vignaud & Gasparini 1996).

The first of these taxa is *Geosaurus araucanensis* (Gasparini & Dellapé 1976) and represents the best-known Jurassic crocodyliform from South America. Its generic assignment was never questioned due to the presence of numerous derived characters shared with *G. suevicus* (Fraas 1902) from the Tithonian of Switzerland (Buffetaut 1981; Vignaud 1995). These forms are among the most apomorphic marine crocodyliforms, having remarkably modified postcranial anatomy (e.g. discoidal radius, ulna, hypocercal tail) and large prefrontal depressions interpreted as cavities for hypertrophied nasal salt glands (Fernández & Gasparini 2000).

The type species of the second genus is *Dakosaurus maximus* (Quenstedt 1856), originally described as *Geosaurus maximus* (Plieninger 1846). This form is mainly known from an incomplete skeleton from the Lower Tithonian beds of Germany, described in detail by Fraas (1902). This taxon was characterised and distinguished from other thalattosuchians by the presence of a short rostrum and a modified dentition composed by a low number of large teeth with serrated edges. Numerous remains (in particular isolated teeth) were later attributed to this species (for a summary of the taxonomic history of this taxon see Kuhn 1968; Vignaud 1995). Vignaud & Gasparini (1996) described *D. andiniensis*, based on a rather fragmentary specimen that represents the only remains found outside Europe that were referred to this genus. Despite the fragmentary nature of this specimen, it shares with the type specimen of *D. maximus* a set of diagnostic characters (e.g. high rostrum, great lateral development of the nasal, short longitudinal development of the dorsal part of the maxillae). Here we describe in detail a nearly complete skull of *D. andiniensis*, showing numerous autapomorphic characters. This specimen was briefly described recently (Gasparini *et al.* 2006) and represents the most complete cranial material from this genus.

The phylogenetic relationships of these marine crocodyliforms are tested here through a comprehensive cladistic analysis, increasing the taxonomic and character sampling on thalattosuchian and longirostrine forms in comparison with previous approaches to crocodyliform phylogenetics (Clark 1994; Wu *et al.* 1997; Buckley & Brochu 1999; Ortega *et al.* 2000; Pol 2003; Pol & Norell 2004*a*,*b*).

Institutional Abbreviations

AMNH = American Museum of Natural History, New York, USA
BMNH = The Natural History Museum (British Museum of Natural History), London, England
BSP = Bayerische Staatssammlung für Paläontologie und Geologie, Münich, Germany
CNRST-SUNY = Centre National de la Recherche Scientifique et Technologique de Mali – Stony Brook University, New York, USA
FMNH = The Field Museum, Chicago, USA
GPIT = Institut und Museum für Geologie und Paläontologie, Universitat Tübingen, Tübingen, Germany
MACN = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MB = Institut für Palaontologie, Museum fur Naturkunde, Humbolt-Universitat, Berlin, Germany
MHNSR = Museo de Historia Natural de San Rafael, San Rafael, Argentina
MLP = Museo de La Plata, La Plata, Argentina
MNN = Musée National du Niger, Niamey, Niger
MOZ = Museo Profesor J. Olsacher, Zapala, Argentina
MZSP-PV = Museu de Zoología, Universidade de São Paulo, São Paulo, Brazil

PVL = Instituto Miguel Lillo, Tucumán, Argentina
SMNS = Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
UA = University of Antananarivo, Madagascar

Systematic Palaeontology

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
THALATTOSUCHIA Fraas, 1901
METRIORHYNCHIDAE Fitzinger, 1843
DAKOSAURUS Quenstedt, 1856

Dakosaurus andiniensis Vignaud & Gasparini, 1996 (see Figs 2–15)

Holotype. MHNSR PV 344. An isolated rostrum slightly eroded.

Referred specimens. MOZ 6146P, skull with articulated lower jaws and fragmentary postcranial remains; MOZ 6140P, anterior mandibular fragment.

Ocurrence. The type specimen was found in Catan Lil, Barranca River, Malargüe, Mendoza Province, Argentina (Fig. 1) in sediments of the Vaca Muerta Formation (Tithonian–Berriasian) of the Mendoza Group (Legarreta & Uliana 1996; Spalletti *et al.* 2000). The other two specimens were found in the Yesera del Tromen-Pampa Tril area, northwestern Neuquén province (Fig. 1). The most complete specimen described here (MOZ 6146P) was found in the upper Tithonian levels of the Vaca Muerta Formation, and MOZ 6140P comes from the same locality but in the Berriasian level of the same formation (Neuquén Basin: Spalletti *et al.* 1999). At the Yesera del Tromen-Pampa Tril area there is a sequence in which shales, laminated mudstones and marl concretions predominate. Fifteen skeletons of marine reptiles (ichthyosaurs, pliosaurs, *Geosaurus* sp. and the specimens MOZ 6146P and MOZ 6140P) have been found in an area of 2.1 km^2. The specimens are not necessarily contemporaneous since the fossil-bearing horizons belong to a condensed sequence. However, they are the most conspicuous off-shore herpetofauna of the Jurassic–Cretaceous transition (Spalletti *et al.* 1999; Gasparini & Fernández 2005). The excellent preservation of the reptiles is attributed to the lack of both bottom predators and bottom currents, as well as to a soupy substrate composed of a thick column of water-saturated muds (Spalletti *et al.* 1999).

Diagnosis. A metriorhynchid crocodyliform with the following unique combination of characters (autapomorphic characters are indicated by an asterisk): rostrum proportionately high and short; anterior tips of the nasals nearly meet the premaxillae but are not in contact; dorsal surface of rostrum at the same level as the skull roof*; antorbital fossa deep and anteroposteriorly elongated (subovoid), with its major axis obliquely orientated at approximately 30° with respect to the longitudinal axis; internal antorbital fenestra formed by the lacrimal (posteriorly), nasal (dorsally) and maxilla (ventrally); lacrimal dorsoventrally low occupying approximately 20% of the orbital height; aligned set of large foramina extending posteroventrally from the antorbital fossa*; markedly sigmoidal anterior end of jugal*; extending anterior to the orbit; mandibular and maxillary teeth buccolingually compressed with well-developed denticles on their anterior and posterior margins.

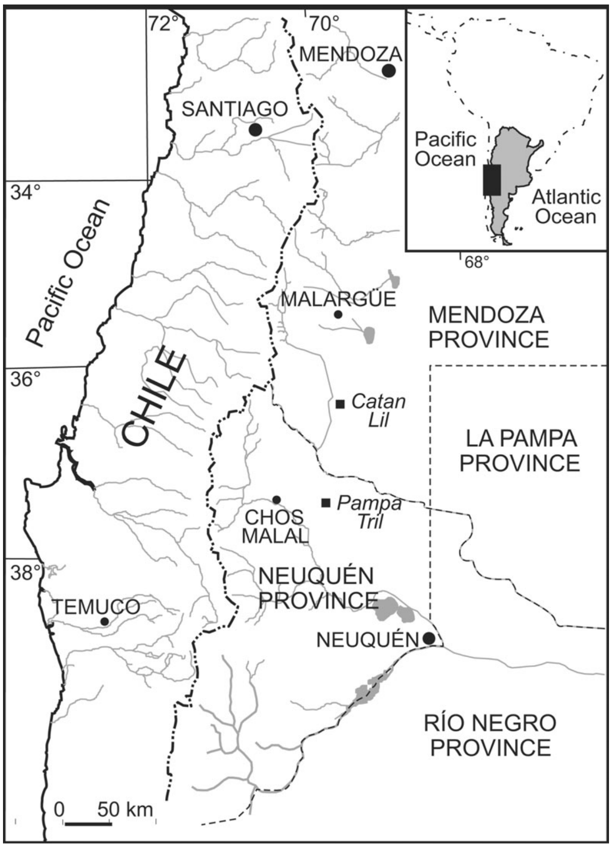


Figure 1 Map of western Argentina, showing the localities where the holotype (MHNSR PV34) and the new specimen (MOZ 6146P) of *Dakosaurus andiniensis* were found (indicated by the solid rectangles). Major cities in the area are indicated by solid circles.

Description

Skull

MOZ 6146P consists of an almost complete skull found in articulation with its lower jaws. The rostral end of the snout is weathered and parts of the external surface of the premaxilla and maxilla are partially damaged. The posterior region of MOZ 6146P is plastically deformed, being asymmetrical in its orbital and temporal regions. The occipital table is also damaged due to the lateromedial crushing, having its right elements facing posteromedially rather than posteriorly. The right side of MOZ 6146P suffered only a slight deformation on its supratemporal and occipital regions, whereas the left side was severely affected. In line with this interpretation, most of the description is based on the right side of this specimen.

The external surface of the skull bones is smooth, although the dorsal surface of the nasals has a faint ornamentation pattern. The snout is proportionately high and

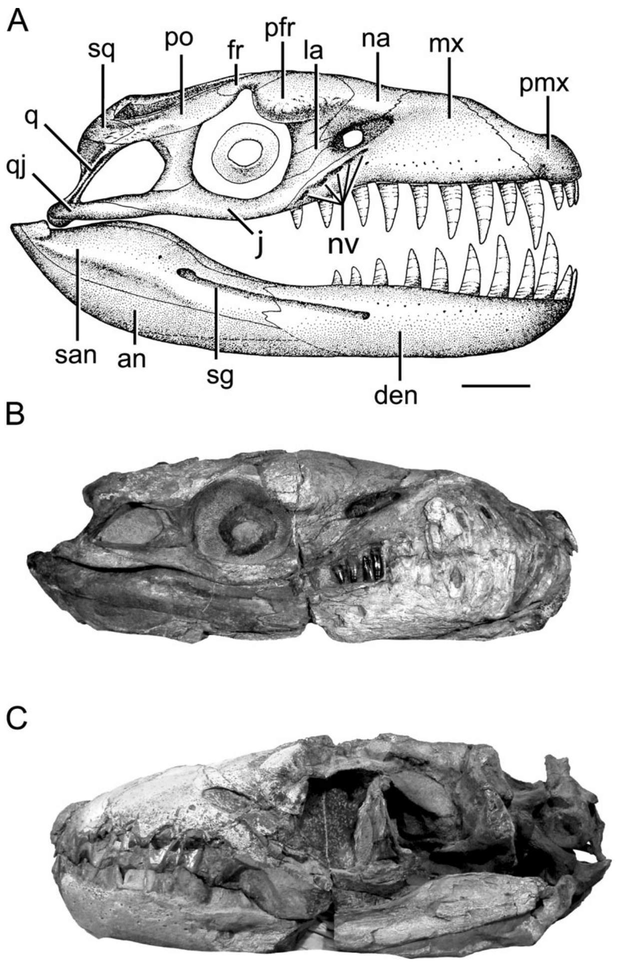


Figure 2 Skull of *Dakosaurus andiniensis* in lateral view. **A**, reconstruction of the right side based on information from available specimens. **B**, right side of MOZ 6146P. **C**, left side of MOZ 6146P. Abbreviations: **an**, angular; **den**, dentary; **fr**, frontal; **j**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **pfr**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **q**, quadrate; **qj**, quadratojugal; **san**, surangular; **sg**, surangular groove; **sq**, squamosal. Scale bar = 10 cm.

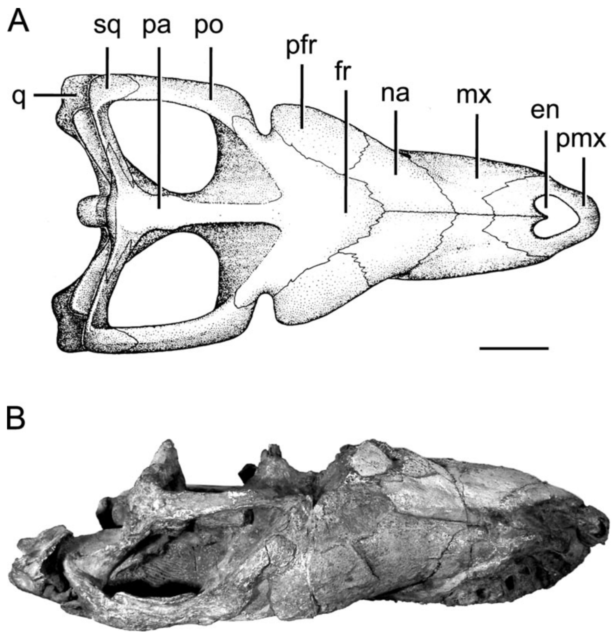


Figure 3 Skull of *Dakosaurus andiniensis* in dorsal view. **A**, reconstruction based on information from available specimens and **B**, specimen MOZ 6146P. Abbreviations: **en**, external nares; **fr**, frontal; **mx**, maxilla; **na**, nasal; **pa**, parietal; **pfr**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **q**, quadrate; **sq**, squamosal. Scale bar = 10 cm.

short in comparison with other thalattosuchians. The rostrum height is approximately 36% of the anteroposterior length (Fig. 2). This lateromedial width of the rostrum is approximately equal to the dorsoventral depth, although the ratio could be distorted by the lateromedial post-mortem crushing that deformed the temporal and occipital regions. The rostrum occupies approximately half the skull length, being thus a brevirostral form according to the categorisation proposed by Busbey (1995), who proposed categorising rostra using the ratio of rostral length versus basal skull length, establishing the boundary between brevirostral and mesorostral forms at 0.55. Therefore, the condition of *D. andiniensis* falls right below the brevirostral/mesorostral boundary. The snout's dorsal surface is located approximately at the same level as the frontal and supratemporal region (Fig. 2), instead of descending ventrally as in most crocodylomorphs. Most of the rostral region has a constant lateromedial width, except for its anterior end, which tapers along the anterior region of the maxillae and the premaxillae (Fig. 3). In contrast to most crocodyliforms, the skull of MOZ 6146P does not widen lateromedially posterior to the orbital region, although this feature might be accentuated by the lateromedial compression. As in metriorhynchids and other thalattosuchians, the skull lacks the flat, wide and horizontally exposed dorsal surface surrounding laterally and posteriorly the supratemporal fossae (present in other crocodyliforms). The frontal and parietal, instead, have a flat surface dorsally exposed between the supratemporal openings as in all crocodyliforms, although this region is only partially preserved.

The right orbit is subcircular and rather large compared with *Steneosaurus bollensis* (BSP 1945.XV.1), but slightly smaller than *Geosaurus araucanensis* (MLP 72-IV-7-1) and *Metriorhynchus superciliosus* (SMNS 10116), occupying 18% of the skull's anteroposterior length (Fig. 2). This opening faces laterally as in other metriorhynchids, in contrast to the dorsolaterally orientated orbit of *Steneosaurus bollensis* (MB 1921.12) and other thalattosuchians. Inside the orbit, MOZ 6146P has a preserved sclerotic ring, formed by plates that overlap each other counter-clockwise (Fig. 4). On the right orbit, the internal edges of these plates are slightly projected laterally with respect to their external margins, producing a slightly telescoped sclerotic ring. The external circumference of the sclerotic ring occupies 56% of the dorsoventral height of the orbit, whereas the dorsoventral extension of its internal opening occupies 25% of the orbit.

The antorbital fossa (*sensu* Witmer 1997) is rather low and elongated, similar to the condition of metriorhynchids (e.g. *Geosaurus araucanensis* MLP 72-IV-7-1, *Metriorhynchus casamiquelai* Gasparini & Chong Díaz 1977). The major axis of the antorbital fossa is orientated obliquely, having its anterior end located more dorsally than

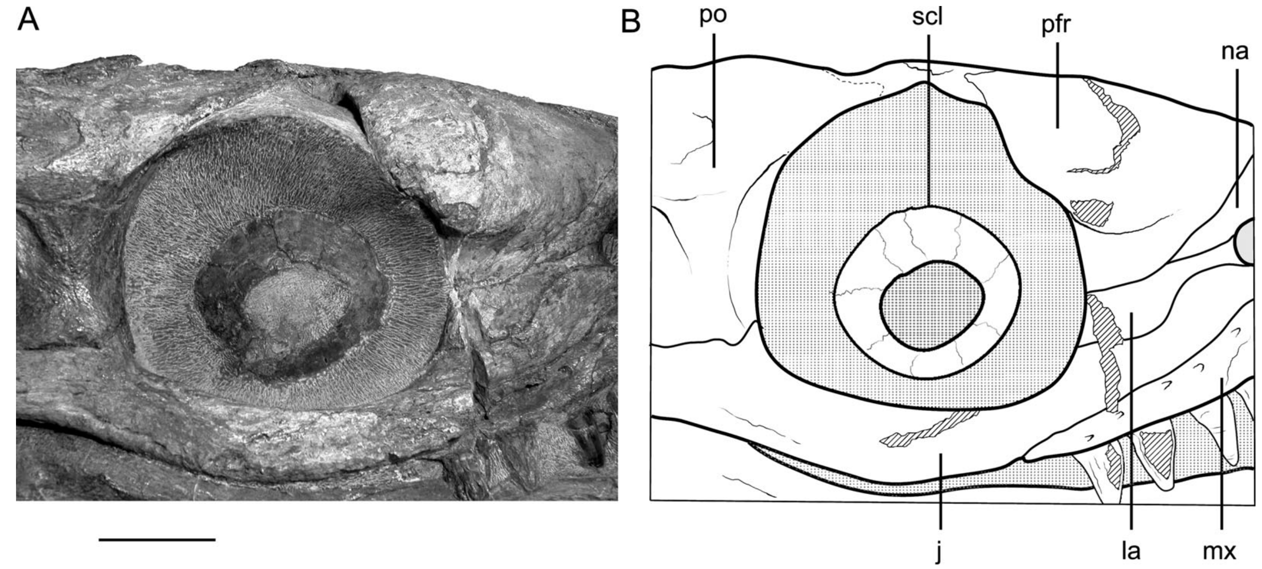


Figure 4 Right orbit of *Dakosaurus andiniensis*. **A**, right side of MOZ 6146P, **B**, reconstruction. Abbreviations: **j**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **pfr**, prefrontal; **po**, postorbital; **scl**, scleral ring. Scale bar = 5 cm.

its posterior end (the former being approximately at the level of the dorsal margin of the orbits). The fossa that surrounds the internal antorbital fenestra is deep and its walls are orientated perpendicular to the external surface of the snout (Fig. 5), instead of the shallow fossa present in most crocodylomorphs. As in metriorhynchid crocodyliforms the nasal and jugal of MOZ 6146P contribute to the margins of the antorbital fossa, instead of being exclusively formed by the maxilla and lacrimal. The internal antorbital fenestra (*sensu* Witmer 1997) is subcircular, small (approximately 15 mm high), and is located on the posterior half of the antorbital fossa (Fig. 5). Its posterior margin is formed by the lacrimal, whereas the maxilla and nasal form its ventral and dorsal margins, respectively.

The right infratemporal fenestra faces laterally and is longer than high. This opening is tear-drop shaped, having its anterior end rounded and its posterior end forming an acute angle (Fig. 2). The margins of both supratemporal fossae are deformed. However, the right opening seems to be only deformed on its posterolateral region, where the squamosal is broken and displaced. When this displacement is corrected, the supratemporal fossa has a subtriangular shape (Fig. 3A). The supratemporal fenestra closely follows the margins of the supratemporal fossa, except for its anteromedial region,

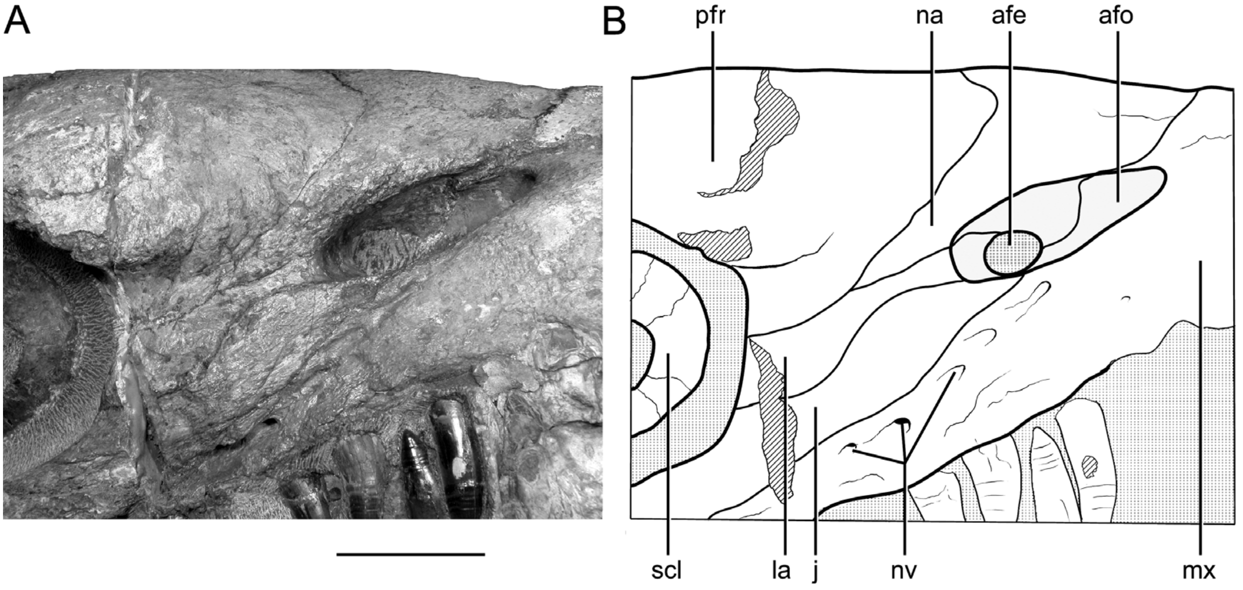


Figure 5 Right antorbital region of *Dakosaurus andiniensis*. **A**, right side of MOZ 6146P, **B**, reconstruction. Abbreviations: **afo**, antorbital fossa; **afe**, (internal) antorbital fenestra; **j**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **pfr**, prefrontal; **nv**, neurovascular foramina. Scale bar = 5 cm.

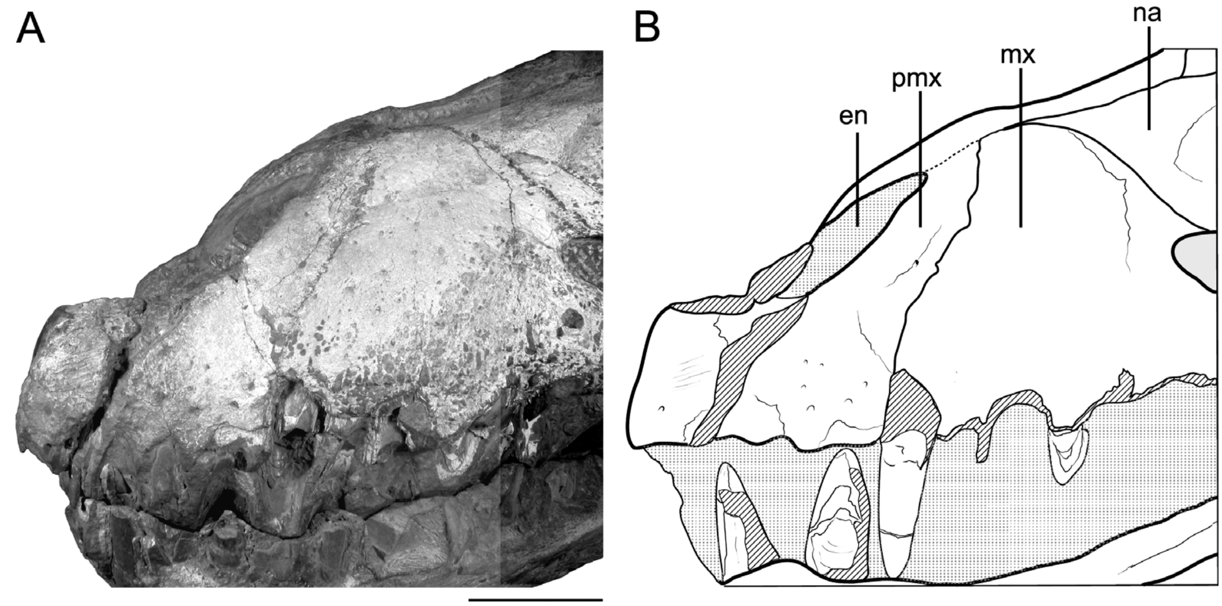


Figure 6 **A**, Left premaxilla of *Dakosaurus andiniensis* (MOZ 6146P) in anterolateral view, **B**, reconstruction. Abbreviations: **en**, external nares; **mx**, maxilla; **na**, nasal; **pmx**, premaxilla. Scale bar = 5 cm.

where the frontal and postorbital extend as a wide and flat shelf that forms the floor of the supratemporal fossa.

The choanal opening is short and wide, being subcircular in contour, and lacks an internal septum. Its posterior margin is formed by the pterygoids and its V-shaped anterior edge is formed by the palatines. The external mandibular fenestra is completely obliterated (Fig. 2).

The external surface of the rostrum is weathered on the right side. Therefore, details of the morphology of the external nares and most of the snout cannot be determined on this side. The left premaxilla of MOZ 6146P has been preserved almost without damage. The external surface of this element is smooth and slightly convex, being vertically orientated at its alveolar edge and facing dorsolaterally at its dorsalmost region. Its posterior margin contacts the anterior margin of the maxilla through a strongly interdigitated suture directed posterodorsomedially on the lateral surface of the snout (Fig. 6). The medial margin of the premaxillae should have been in contact with each other enclosing the external nares, because the nasals do not reach the premaxillae as in most thalattosuchians (Vignaud 1995). As in *D. maximus*, the suture between the premaxillae and the maxillae forms a broad U-shaped, rather than a posteriorly pointed V-shaped, suture.

The left maxilla is preserved entirely while only the posterior region of the right element is present in MOZ 6146P. The left maxilla is notably short, high and subtriangular in lateral view (Fig. 2). As with the premaxilla, the external surface of the maxilla is smooth and convex, facing laterally near the alveolar edge and curving to face dorsally on the dorsal midline of the snout. Posterior to its contact with the posterodorsal process of the premaxilla, the dorsal edge of the maxilla contacts its counterpart through a brief suture extending along the sagittal plane (between the posterior tip of the premaxillae and the anterior end of the nasals: Fig. 7). The posterior margin of the maxilla is bordered by

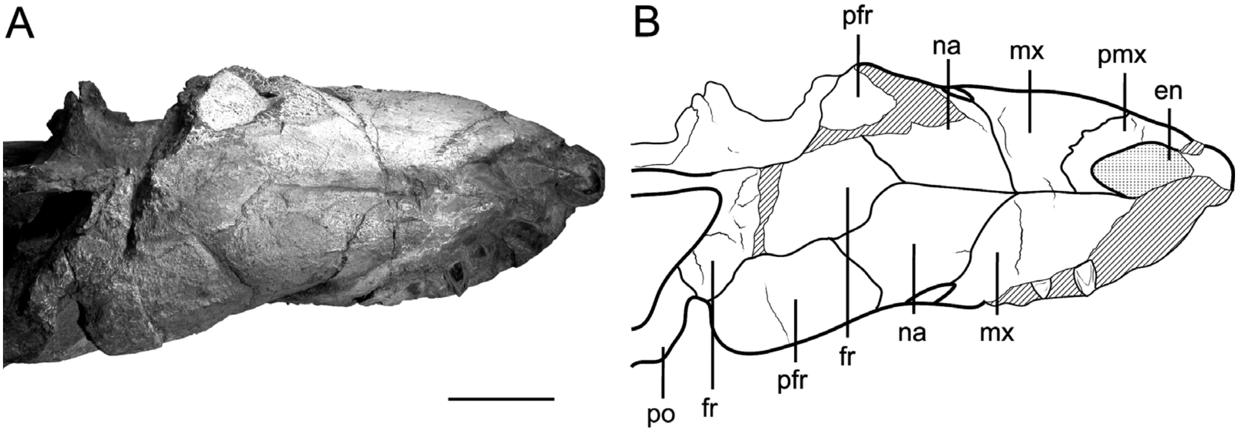


Figure 7 **A**, Rostrum and interorbital region of *Dakosaurus andiniensis* (MOZ 6146P) in dorsal view, **B**, reconstruction. Abbreviations: **en**, external nares; **fr**, frontal; **mx**, maxilla; **na**, nasal; **pfr**, prefrontal; **pmx**, premaxilla; **po**, postorbital. Scale bar = 10 cm.

the nasal dorsal to the antorbital fossa and overlapped by the jugal ventral to this opening. The maxilla forms the anterior and most of the ventral margin of the elongated antorbital fossa and extends medially forming its anterior and ventral walls. Within the deep antorbital fossa, the maxilla is sutured to the nasal dorsally and to the lacrimal posteriorly. Deep into the fossa, the maxilla forms the ventral and most of the anterior margins of the subcircular antorbital fenestra (Fig. 5). The posteroventral region of the maxilla extends posteriorly as an acute process ending at the anterior margin of the orbit. Along this region, the maxilla is pierced by five large foramina aligned in a row extending parallel to the maxilla–jugal suture. These foramina are interconnected through a shallow groove that extends from the ventral margin of the antorbital fossa to the posterior end of the maxillary alveolar edge (Fig. 5). Anterior to this point, the alveolar margin is poorly preserved and, therefore, it is not possible to determine if it was straight or festooned as in non-longirostrine neosuchians. The palatal processes of the maxillae cannot be observed in MOZ 6146P.

The nasals are highly modified, being extremely short and broad. These elements form the posterior third of the snout's dorsal surface contacting each other along their medial edges (Figs 3, 7). Their anterior end is acute and does not reach the premaxillae, as in other thalattosuchian crocodyliforms (e.g. *Geosaurus araucanensis* MLP 72-IV-7-1; *Metriorhynchus* SMNS 10116; *Steneosaurus bollensis* SMNS 15951). The lateral part of each nasal extends broadly onto the lateral surface of the snout, reaching the antorbital opening (Fig. 5). It contacts the maxillae through an interdigitated suture. This suture is not symmetrical in MOZ 6146P (Fig. 3B). The right suture is anteriorly concave and directed posterolaterally towards the anterodorsal margin of the antorbital fossa. The left suture is less posteriorly directed, forming an angle of approximately 30° with the transverse plane, and is straight instead of being anteriorly concave. This difference is probably due to post-mortem crushing since the left suture also reaches the anterodorsal margin of the antorbital fossa. Posteriorly on the dorsal surface of the skull, the nasals are sutured to the frontal and prefrontals (Fig. 7). The nasal–frontal suture is directed posterolaterally forming a 45° angle with the sagittal plane since the frontal has a wide anterior process that wedges between the two nasals. The nasal–prefrontal suture is only clearly preserved on the right side of MOZ 6146P. This interdigitated suture extends anterolaterally on the dorsal surface of the snout and curves posteriorly on the lateral surface of the snout, where it is directed posteroventrally (Figs 5, 7).

The nasals are widely exposed on the lateral surface of the skull as an acute process projecting posteriorly along the dorsal margin of the antorbital fossa, resembling the condition of most metriorhynchid crocodyliforms (*Metriorhynchus superciliosus* (Wenz 1968); *Geosaurus suevicus* (Fraas 1902); *Geosaurus araucanensis* MLP 72-IV-7-1). The posterior margin of this process is bordered posterodorsally by the prefrontals (also widely exposed on the lateral surface of the snout). The ventral margin of the lateral extension of the nasals forms the dorsal margin of the antorbital fossa. The nasal enters this fossa and forms the dorsal margin of the antorbital fenestra.

The right lacrimal is perfectly preserved while the left element is badly damaged. The lacrimal is exposed exclusively on the lateral surface of the skull due to the large ventral extension of the nasal and prefrontal, a character shared with metriorhynchids (e.g. *Metriorhynchus superciliosus* (Wenz 1968); *Geosaurus araucanensis* MLP 72-IV-7-1; *Metriorhynchus casamiquelai* (Gasparini & Chong Díaz 1977)). The posterior end of the lateral surface of the lacrimal forms the middle third of the orbital anterior margin and extends anteriorly reaching the antorbital fossa (Fig. 5). Its ventral margin is sigmoid along its suture with the anterior process of the jugal. Its dorsal margin, instead, is straight and is sutured on its posterior half to the ventral margin of the prefrontal. The anterior half of its dorsal margin is sutured to the acute posterolateral process of the nasal. Due to the sigmoid shape of its ventral edge, the lateral surface of the lacrimal is dorsoventrally high on its posterior half and rapidly tapers anteriorly, at the level of its contact with the nasal (Fig. 5). This low anterior region is notably smooth and slightly recessed with respect to the lateral surface of the nasal and jugal, which bound the lacrimal dorsally and ventrally at this point.

Inside the antorbital fossa, the lacrimal's dorsoventral extension increases progressively toward the posterior margin of the antorbital fenestra (Fig. 5). The lacrimal extends medially into the fossa, facing anteriorly and being perpendicular to the external surface of the snout. Inside the fossa, the dorsal margin of the lacrimal contacts the nasal and the ventral margin is sutured to the maxilla. The jugal does not contact the lacrimal within the fossa since it fails to enter this depression. The lacrimal forms the posterior margin of the antorbital fenestra.

The right prefrontal of MOZ 6146P is completely preserved, whereas the left element has most of its external surface badly damaged. As in all metriorhynchids the prefrontals are extremely enlarged (Figs 5, 7), extending onto the lateral surface of the snout and projecting laterally (overhanging the anterodorsal region of the orbit). They form the anterior half of the dorsal margin and the dorsal half of the anterior orbital margin (Fig. 4). Unfortunately, the presence of prefrontal pillars cannot be currently determined in MOZ 6146P, although they are present in other metriorhynchids (e.g. *Geosaurus araucanensis* MLP 72-IV-7-1).

The dorsal surface of the prefrontal is broad, slightly convex and exposed laterodorsally. Its medial margin is strongly and extensively sutured to the frontal, excluding most of this element from the orbital margin (Fig. 7). The posterolateral region of the broad dorsal surface of the prefrontal overhangs the anterior half of the orbit. Its anterior margin is sutured to the nasal, extending anterolaterally on the dorsal surface of the skull and posteroventrally on the lateral surface of the snout (Fig. 5).

The prefrontal extends onto the lateral surface of the snout, between the orbit and the antorbital opening. The ventral end of this region is slightly recessed with respect to the bulging posterolateral process of the prefrontal that overhangs the orbit and is sutured to the dorsal margin of the lacrimal (Fig. 5). This region of the prefrontal of MOZ 6146P might have been slightly deformed due to preservational causes, possibly being more horizontally orientated as in other metriorhynchids (e.g. *Metriorhynchus* SMNS 10116, *Geosaurus araucanensis* MLP 72-IV-7-1).

Distinct palpebral elements are not preserved and there are no signs of sutures for these elements, commonly found in other crocodyliforms on the prefrontal and/or postorbital. This suggests that palpebrals were absent in this taxon, or

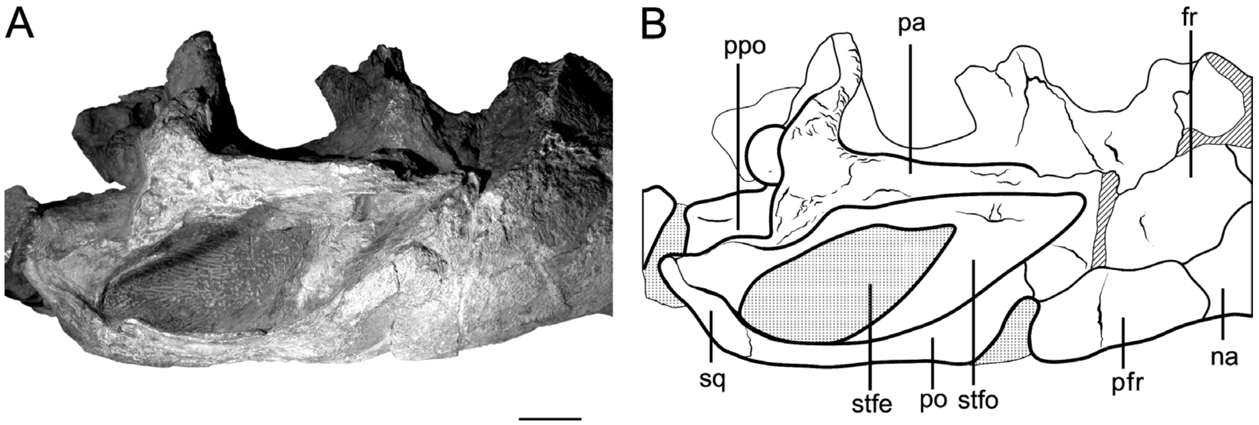


Figure 8 **A**, Right supratemporal opening of *Dakosaurus andiniensis* (MOZ 6146P) in dorsal view, **B**, reconstruction. Abbreviations: **fr**, frontal; **na**, nasal; **pa**, parietal; **po**, postorbital; **ppo**, paroccipital process; **pfr**, prefrontal; **sq**, squamosal; **stfe**, supratemporal fenestra; **stfo**, supratemporal fossa. Scale bar = 5 cm.

alternatively completely fused with the skull elements. The absence of distinct palpebrals was also noted for other thalattosuchians (Clark 1986).

The frontals are completely fused into a single element, as in all adult mesoeucrocodylians (Clark 1994). Its posterior and left posterolateral regions are poorly preserved. Like the rest of the skull, its dorsal surface is smooth and slightly convex. The lateral margins of this element converge anteriorly along the orbit and their contact with the prefrontals, ending in a pointed process sutured to the nasals (Fig. 7). The anterior end of the frontals extends beyond the orbital anterior margin separating the posterior margin of the nasals along a V-shaped suture. The naso–frontal suture is straight and forms an angle of 45° with the sagittal plane, resembling the condition of *D. maximus* (SMNS 8203, BSP AS.VI.1), but contrasting with that of other metriorhynchids, which have a wide diversity of morphologies in the frontal–nasal suture (Vignaud 1995).

Posteriorly, the frontal enters extensively on the large supratemporal fossa and fenestra. This element forms the acute anterior end of the left supratemporal fossa, as well as most of its anterolateral margin (Figs 3, 8). The frontal forms most of the anterior floor of the supratemporal fossa, which restricts the anterior extension of the supratemporal fenestra. The dorsal surface of the frontal is poorly preserved between the supratemporal fossae, although it seems to have a narrow but flat dorsal surface at its contact with the parietal (Fig. 8). The posterolateral region of the frontal is a rather narrow bar that separates the supratemporal opening from the orbit. At its end, it is strongly sutured to the postorbital.

The parietals are also completely fused into a single element, as in all crocodylomorphs. Unfortunately, the dorsal surface of the parietal is damaged and its contact with the frontal and squamosals cannot be precisely determined in MOZ 6146P. This element has an elongated and narrow dorsal surface between the supratemporal fossae that slightly widens posteriorly. Despite the narrowness of this surface, it is clearly flat (Fig. 8), rather than being crest-like as in adult specimens of *Steneosaurus bollensis* (MB 1921.12, BSP 1945.XV.1), some dyrosaurids (e.g. *Rhabdognathus* CNRST-SUNY 190: Jouve 2005*a*) and non-crocodyliforms. The lateral surface of the parietal extends ventrally as a vertical wall towards the medial margins of the supratemporal fenestra (Fig. 8). This condition resembles that of some metriorhynchids (*Geosaurus araucanensis* MLP 72-IV-7-1; *Metriorhynchus superciliosus* SMNS 10116) and dyrosaurids (e.g. *Rhabdognathus* CNRST-SUNY 190) but contrasts with the morphology of most crocodyliforms (including some longirostrine forms such as *Steneosaurus bollensis* BSP 1945.XV.1; *Pelagosaurus typus* BSP 1890.I.5; *Sarcosuchus imperator* MNN 604), in which the parietal widens ventrally as a broad shelf that forms the medial floor of the supratemporal fossa. At its posterior end, the parietal broadens forming the posteromedial margins of the supratemporal fenestra, where it contacts the squamosal (Fig. 8). The parietal forms the medial region of the occipital margin of the skull table.

The right squamosal is entirely preserved in MOZ 6146P although it is broken and displaced on its posterolateral region. Unfortunately, the left element is missing from this specimen. The dorsal surface of the squamosal is markedly narrow (Fig. 8), in contrast to the broad and flat condition that characterises the skull table of most crocodyliforms. Such morphology is also present in metriorhynchids (*Geosaurus araucanensis* MACN-N 95; *Metriorhynchus* GPIT Auer1909-s.281-f.15), *Steneosaurus bollensis* (SMNS 15951, BSP 1945.XV.1) and crocodyliform outgroups. The posteromedial branch of the squamosal forms most of the posterior margin of the supratemporal fossa. The orientation of this branch has been modified due to the lateromedial compression that distorted the skull (Figs 3, 8), being directed even more posteriorly than in other metriorhynchids, in which this branch is orientated slightly obliquely to the transverse axis (e.g. *Geosaurus araucanensis* MACN-N 95, BSP AS.I.504; *Metriorhynchus* GPIT Auer1909-s.281-f.15). In other crocodyliforms, including *Pelagosaurus typus* (e.g. BSP 1890.I.5, BSP 1925.I.34) and *Steneosaurus bollensis* (SMNS 15951), the posteromedial branch of the squamosal is orientated transversally to the longitudinal axis of the skull. Within the supratemporal fossa, the squamosal extends ventrally as a vertical wall, lacking the subhorizontal shelf present in other crocodyliforms. Therefore, in MOZ 6146P, as in most metriorhynchids, the posterior margin of the supratemporal fenestra closely follows that of the supratemporal fossa. The posteromedial branch of the squamosal is briefly exposed on the occipital surface of the skull as a

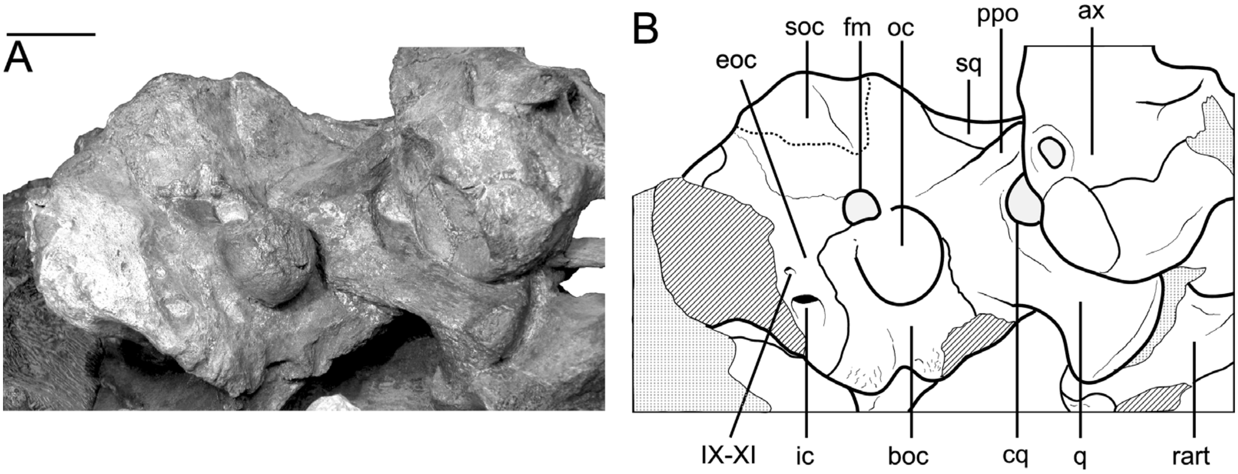


Figure 9 **A**, Occipital surface of *Dakosaurus andiniensis* (MOZ 6146P), **B**, reconstruction. Abbreviations: **ax**, axis; **cq**, cranioquadrate opening; **boc**, basioccipital; **eoc**, exoccipital; **fm**, foramen magnum; **ic**, internal carotid foramen; **oc**, occipital condyle; **ppo**, paroccipital process; **q**, quadrate; **rart**, retroarticular process; **soc**, supraoccipital; **sq**, squamosal; **IX–XI**, posterior opening for cranial nerves IX through XI. Scale bar = 5 cm.

dorsoventrally low and elongated process that extends laterally (Fig. 9). Ventrally, it borders the dorsal margin of the paroccipital process. As in metriorhynchids (e.g. *Metriorhynchus* GPIT Auer1909-s.281-f.15; *Geosaurus araucanensis* MLP 72-IV-7-1), the dorsal margin of the squamosal occipital flange is sharp and markedly concave, delimiting the dorsal edge of the occipital surface (Fig. 9). The post-temporal fenestra cannot be observed in MOZ 6146P, probably due to the deformation suffered by this specimen.

As mentioned above, the squamosal is broken posterolaterally. Therefore, the anterior branch of the squamosal forms an artificially acute angle with the posteromedial branch (Fig. 8). Lateral to the distal end of the paroccipital process, the squamosal has a distinct subcircular surface facing posterolaterally (Fig. 10). This surface is smooth and is slightly concave. A similar morphology is present in metriorhynchids (e.g. *Geosaurus araucanensis* MACN-N 95; *Metriorhynchus* GPIT Auer1909-s.281-f.15) but seems to be absent in other crocodyliforms. *Steneosaurus bollensis* (SMNS 15951; BSP 1990.VIII.68) and *Pelagosaurus typus* (BSP 1890.I.5) have a similar surface although in these forms it is notably smaller and located more ventrally than in metriorhynchids.

This surface forms a small shelf that overhangs the quadrate, forming a distinct otic recess (Fig. 10). This recess is extremely reduced in comparison to that of most mesoeucrocodylians and, like the squamosal, is restricted to a narrow region located posteriorly to the infratemporal fenestra (as in *Geosaurus araucanensis* MACN-N 95; *Metriorhynchus casamiquelai* IIG.1.080573; *Metriorhynchus superciliosus* (Wenz 1968); *Pelagosaurus typus* BSP 1890.I.5; *Steneosaurus bollensis* BSP 1945.XV.1). In other crocodyliforms, however, the squamosal extends further anteriorly, forming at least the posterior half of the temporal region, it projects laterally as a wide shelf that overhangs a deep otic recess that extends dorsally to the infratemporal fenestra. The descending process of the squamosal within the otic recess is occluded by the axis and, therefore, its relationship with the quadrate, cranioquadrate passage and the otic notch cannot be observed in MOZ 6146P.

Anterior to this point, the anterior branch of the squamosal is notably short, overlapping the posterior process of the postorbital. Its dorsal surface is markedly narrow and its lateral surface is dorsoventrally deep (Figs 8, 11). An extremely short anterior branch of the squamosal is also present in some metriorhynchids (*D. maximus* BSP AS.VI.1; *Geosaurus araucanensis* MACN-N 95). Other metriorhynchids (e.g. *Metriorhynchus* GPIT Auer1909-s.281-f.15) and *Pelagosaurus typus* (BSP 1890.I.5) have a slightly longer anterior branch. However, most other crocodyliforms, including *Steneosaurus bollensis* (SMNS 18878), have an extensive squamosal anterior branch that reaches the anteroposterior midpoint of the supratemporal fossa.

The right postorbital of MOZ 6146P is completely preserved while the left element is fragmentary and crushed inside the orbit. This element forms the posterior half of the dorsal margin and the entire posterior margin of the orbit. Anteriorly, the postorbital contacts the frontal through an interdigitated suture. The orbital region of the postorbital tapers anteriorly, is laterodorsally exposed and lacks ornamentation as the rest of the skull. Posterior to the orbit, the postorbital extends ventrally as the postorbital bar and posteriorly separating the infratemporal and supratemporal fenestrae (Fig. 11). As in other thalattosuchians (e.g. *Geosaurus araucanensis* MACN-N 95; *Pelagosaurus typus* BSP 1890.I.5; *Steneosaurus bollensis* SMNS 15951) the postorbital bar and the dorsal margin of the infratemporal fenestra are not inset with respect to the dorsal surface of the postorbital. In *D. andiniensis* the postorbital bar is only separated from the dorsal surface of the postorbital by a slightly developed ridge (Fig. 11). This condition contrasts with the morphology of other crocodyliforms in which the postorbital is horizontally exposed on the skull roof and forms the anterior end of the shelf that overhangs extensively the deep otic recess located dorsally to the infratemporal fenestra. In these forms, the postorbital has a distinct descending process that delimits the infratemporal fenestra and forms the postorbital bar (Clark 1994).

In MOZ 6146P, the postorbital bar is almost entirely formed by the postorbital, a condition also present in other thalattosuchians (e.g. *Geosaurus araucanensis* MACN-N 95;

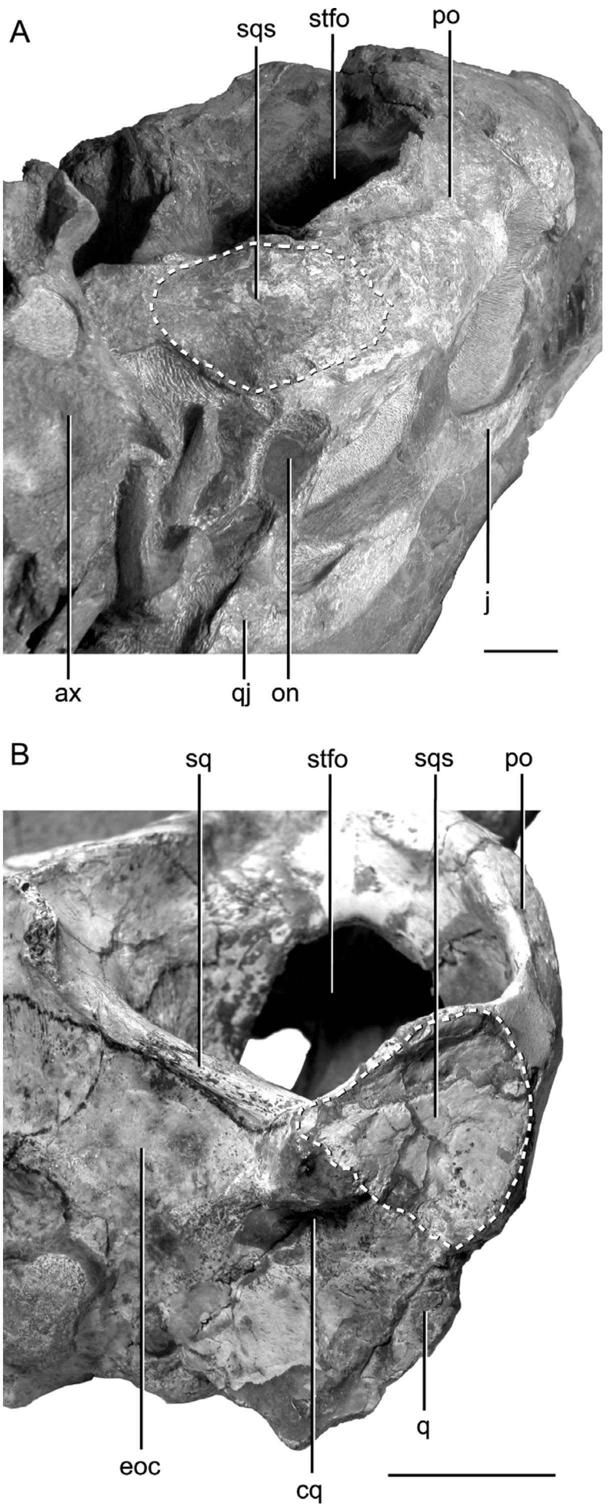


Figure 10 Posterolateral region of squamosal in metriorhynchid crocodyliforms in posterolateral view. **A**, *Dakosaurus andiniensis* (MOZ 6146P) and **B**, *Geosaurus araucanensis* (MLP 72-IV-7-1). Abbreviations: **ax**, axis; **cq**, cranioquadrate opening; **eoc**, exoccipital; **j**, jugal; **on**, otic notch; **po**, postorbital; **qj**, quadratojugal; **sq**, squamosal; **sqs**, squamosal flat surface; **stfo**, supratemporal fossa. Scale bars = 2 cm.

Pelagosaurus typus BSP 1925.I.34; *Steneosaurus bollensis* SMNS 15951, BSP 1945.XV.1, MB 1921.12). This bar is anteroposteriorly long, lateromedially narrow and lacks any ornamentation (Fig. 11). There is a poorly developed ridge on its lateral surface extending from the anterodorsal margin of the infratemporal fenestra to the middle of the postorbital bar. Its anterior and posterior margins are concave, giving this process an hourglass shape. The posteroventral end of the postorbital bar extends as a rather long and acute process that overlaps the infratemporal bar of the jugal (as in *Geosaurus araucanensis* MACN-N 95). Anteroventrally, the postorbital embraces laterally and medially a reduced ascending process of the jugal. As in most non-neosuchian crocodyliforms the lateral surface of the postorbital bar is superficial, being continuous with the lateral surface of the jugal (Fig. 11).

Posteriorly, along the temporal region, the sharp dorsal margin of the postorbital forms most of the lateral border of the supratemporal fossa, as in metriorhynchids. Its posterior end overlaps the short anterior branch of the squamosal. The temporal bar of the postorbital is a broad lamina that extends from the lateral margin of the supratemporal fossa down to the posterodorsal margin of the infratemporal fenestra (Fig. 11). At this point, the external surface of the postorbital is dorsoventrally high and exposed laterodorsally.

The right jugal of MOZ 6146P is complete and in natural articulation with the maxilla, lacrimal and postorbital. Its posterior end, however, is slightly displaced from its natural contact with the quadratojugal. Unfortunately, the left element is fragmentary and poorly preserved. The jugal is a low and elongated bar, as in other thalattosuchians, which lacks the extensive ascending process that contributes to the postorbital bar in other crocodyliforms. The suborbital region of the jugal is dorsoventrally low, being similar in depth to the infratemporal bar (Fig. 4), in contrast to the condition of mesoeucrocodylians (Clark 1994).

The anterior end of the jugal extends anterodorsally beyond the anterior orbital margin as a sigmoid-shaped process. The ventral margin of this process is dorsally concave along its suture with the maxilla. Its dorsal margin is sigmoid along its suture with the lacrimal, being dorsally concave on its posterior half and convex on its anterior region (Fig. 5). Thus, the dorsoventral extension of this process tapers anteriorly, then markedly increases and tapers again at its anterior end. The acute anterior tip of this process reaches the antorbital fossa, forming its posteroventral margin. A similar participation of the jugal on the antorbital fossa is also present in metriorhynchids (e.g. *Metriorhynchus superciliosus* (Wenz 1968); *Geosaurus araucanensis* MLP 72-IV-7-1). The jugal participation in the antorbital fossa is absent in *Steneosaurus bollensis* (BSP 1973.VII.592, SMNS 20283) and uncertain in other thalattosuchians (e.g. *Pelagosaurus typus* BSP 1925.I.34).

The jugal forms the entire ventral margin of the orbit extending posteriorly as a curved bar, which is dorsoventrally low and unsculpted (Fig. 4). At the posterior margin of the orbit, the jugal of MOZ 6146P extends dorsally as an extremely small postorbital process. This fits between the lateral and medial branches of the anteroventral end of the extensive descending process of the postorbital. Posterior to this point, the postorbital overlaps extensively the lateral surface of the jugal, as in other thalattosuchians. The infratemporal region of the jugal becomes laminar and tapers posteriorly

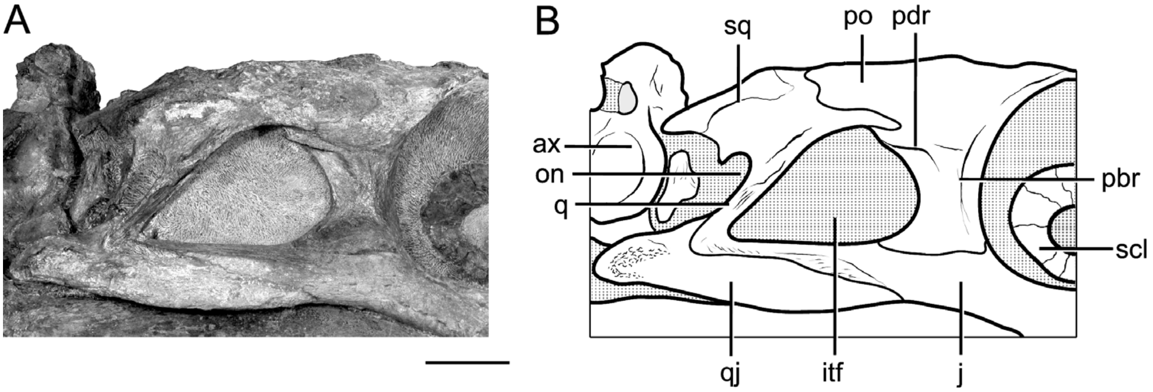


Figure 11 **A**, Right infratemporal region of *Dakosaurus andiniensis* (MOZ 6146P) in lateral view, **B**, reconstruction. Abbreviations: **ax**, axis; **itf**, infratemporal fenestra; **j**, jugal; **on**, otic notch; **pbr**, ridge on lateral surface of postorbital bar; **pdr**, postorbital dorsal ridge separating the postorbital bar; **po**, postorbital; **q**, quadrate; **qj**, quadratojugal; **scl**, scleral ring; **sq**, squamosal. Scale bar = 5 cm.

forming the entire ventral margin of the infratemporal fenestra (Fig. 11). Its dorsal margin is straight and reaches the posteroventral corner of this opening. The ventral edge is ventrally convex along its overlapping contact with the anterior process of the quadratojugal.

Only the right quadratojugal has been preserved in MOZ 6146P. This element, however, lacks the dorsal end of its ascending process and is slightly disarticulated from the quadrate and the infratemporal bar of the jugal. The anterior branch of the quadratojugal is laminar, being lateromedially thin and dorsoventrally high (Fig. 11). Its ventral margin is slightly convex while its dorsal edge is straight. The lateral surface of this region is rugose, where the jugal would articulate overlapping this element laterally. The quadratojugal forms a rounded posteroventral corner of the infratemporal fenestra and projects anterodorsally forming the posterior margin of this opening. This region, the quadratojugal ascending process, is anteroposteriorly narrow and would overlap the anterodorsal branch of the quadrate. The lateral surface of the ascending process is smooth and slightly recessed with respect to the quadratojugal's anterior branch. Unfortunately, the dorsal region of the ascending process has not been preserved in MOZ 6146P. The posteroventral end of the quadratojugal extends posteriorly towards the condylar region of the quadrate. The lateral surface of this region is not as smooth as the ascending process, although it lacks a developed pattern of ornamentation. Its posterior end is rounded and would have overlapped laterally the distal body of the quadrate. Its posteroventral margin is subcircular and slightly projected ventrally, although it does not seem to form an articular condyle as in some crocodyliforms (e.g. *Sebecus icaeorhinus*; *Araripesuchus gomesii*; *Trematochampsa taqueti*: Buffetaut 1974; Ortega *et al.* 2000). Furthermore, due to its disarticulation with the quadrate, it cannot be determined if the posteroventral end of the quadratojugal reached the quadrate lateral condyle or if it was located dorsal to it.

The right quadrate of MOZ 6146P is almost completely preserved, although it is slightly displaced and partially occluded by the axis. Unfortunately, the left quadrate has not been preserved in this specimen. The distal body of the quadrate is well developed, lateromedially wide and anteroposteriorly narrow. The quadrate has robust articular condyles anteroposteriorly expanded with respect to the thin shaft of the quadrate's distal body (Fig. 9). Proximally, the quadrate contacts the ventrolateral flange of the exoccipital and their contact extends dorsally towards the large notch for the cranioquadrate passage.

The anterodorsal process of the quadrate is smooth and faces posteriorly (Fig. 10), as in other metriorhynchids (e.g. *Metriorhynchus superciliosus* (Wenz 1968); *Geosaurus araucanensis* MACN-N 95; *Pelagosaurus typus* BSP 1890.I.5; *Steneosaurus bollensis* BSP 1945.XV.1). This condition contrasts with that of most crocodyliforms in which this process is orientated posterolaterally or laterally. The anterodorsal branch of the quadrate forms the floor of the reduced otic notch, which, consequently, opens posteriorly rather than laterally (Figs 10, 11). The quadrate is slightly displaced from its contact with the quadratojugal. The dorsal end of this branch of the quadrate is poorly preserved although it probably contacted the postorbital and squamosal at the anterolateral margin of the otic recess. Details of the anatomy of the otic notch cannot be observed in MOZ 6146P.

The palatines of MOZ 6146P are exposed ventrally and the left element is slightly disarticulated from its natural contact with the pterygoids. The palatines are medially sutured to each other (Fig. 12), extending posteriorly the secondary palate characteristic of mesoeucrocodylians. These elements are notably wide and probably restricted the development of the suborbital fenestrae (not visible in MOZ 6146P). The anterior end of the palatines is obscured by matrix but probably met the palatal branches of the maxillae. The posterior edge of the palatal surface of the palatines is V-shaped and delimits the anterior margin of the choanal opening. The acute posterolateral ends of each palatine form the lateral border of the choana and overlap ventrally the pterygoids (Fig. 12).

The pterygoids are completely fused and exclusively exposed on their ventral surface in MOZ 6146P. Most of the exposed surface is occupied by the depression that forms the choanal opening. This surface is large, rounded, deeply concave and lacks a choanal septum (Fig. 12). Posterior to its contact with the palatines, the pterygoids form a well-developed rim that borders the choanal depression on its lateral and posterior edges. Lateral to this region, the pterygoid

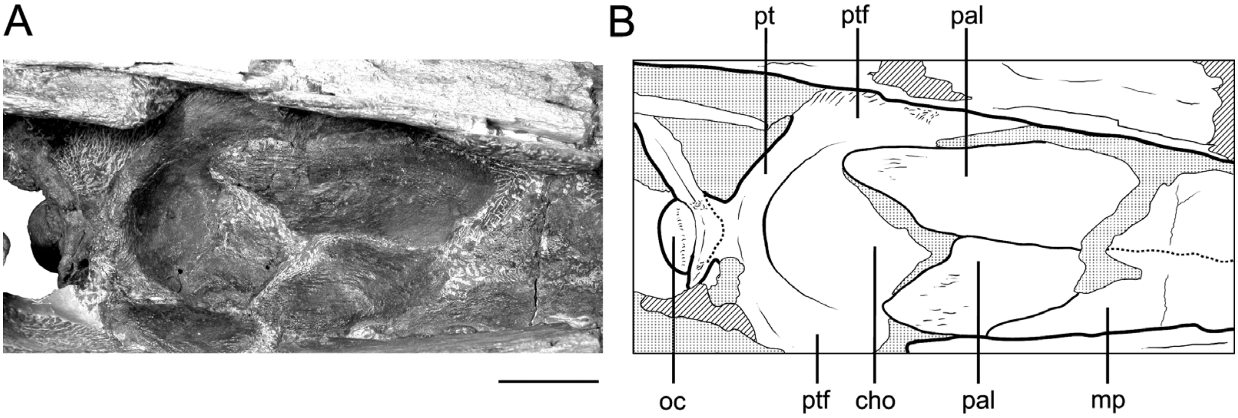


Figure 12 **A**, Palatal region of *Dakosaurus andiniensis* (MOZ 6146P) in ventral view, **B**, reconstruction. Abbreviations: **cho**, choana; **mp**, palatal branches of maxilla; **oc**, occipital condyle; **pal**, palatine; **pt**, pterygoid; **ptf**, pterygoid flange. Scale bar = 5 cm.

flanges project ventrolaterally, although most of the flanges and their contact with the ectopterygoids are obscured by the lower jaw and surrounding matrix. These flanges are poorly developed and seem to lack pneumatic spaces within them. The base of the quadrate processes of the pterygoids is markedly narrow as in most mesoeucrocodylians and is sutured to a reduced ventral surface of the basisphenoid. Its contact with the quadrate has not been preserved in MOZ 6146P.

The basisphenoid is poorly preserved in MOZ 6146P. Its ventral surface is markedly narrow, slightly concave and triangular. The lateral margins of the basisphenoid are bordered by the elevated ridges of the quadrate processes of the pterygoids.

The basioccipital is modestly exposed on the occipital surface below the occipital condyle. Its lateral margins are concave and are sutured to the exoccipitals and its ventral margin is deeply notched along the midline and bears two basioccipital tubera (Fig. 9). These tubera are poorly developed in comparison with those of other thalattosuchians in which these are notably prominent. This difference could be related to the short-snouted condition of MOZ 6146P, since these structures are exclusively present in longirostrine forms (Langston 1973; Brochu 2001; Busbey 1995; Clark 1994). The dorsal region of the basioccipital forms a large, hemispherical occipital condyle that is separated from the occipital surface by a well-developed neck. Although this region is slightly crushed, it seems that the exoccipitals do not contribute to the formation of the condyle in MOZ 6146P.

The exoccipitals of MOZ 6146P are extensively exposed on the occipital surface of the skull. These elements have two major components, the paroccipital process and the ventrolateral flange. The latter is notably enlarged, a condition also present in other thalattosuchians and protosuchids (Clark 1994). This flange extends ventrolateral to the cranioquadrate passage and is slightly recessed from the level of the paroccipital process (Fig. 9). It is sutured ventrolaterally to the quadrate and ventromedially to the basioccipital. The ventrolateral flange of the exoccipital of MOZ 6146P is pierced by three foramina. The two dorsalmost foramina are located at the level of the occipital condyle and are probably for the exit of cranial nerves IX–XI and XII. The third foramen is located ventrolateral to the occipital condyle and is interpreted to be for the internal carotid artery (Fig. 9). This opening is remarkably large in comparison with most crocodyliforms, except for metriorhynchids in which this opening is similarly enlarged (e.g. *Metriorhynchus superciliosus* (Wenz 1968); *Geosaurus araucanensis* MLP 72-IV-7-1).

The supraoccipital is a large subtriangular element bordered ventrally by the exoccipitals and dorsally by the squamosal and, probably, the parietals. Its external surface is flat, although most of it is damaged and its precise contact with the other bones cannot be determined in MOZ 6146P. Unfortunately, it cannot be determined if this element extends onto the dorsal skull roof surface.

Mandible

The right lower jaw of MOZ 6146P is complete, while the left mandibular ramus is only partially preserved. In addition, MOZ 6140P includes the anterior end of the left dentary (Fig. 13). The mandibular rami slightly diverge posteriorly following the narrow outline of the skull. The external mandibular fenestra is absent, as in all metriorhynchids (e.g. *Geosaurus araucanensis* MLP 72-IV-7-1; *Metriorhynchus superciliosus* SMNS 10116). However, the mandibular ramus is notably high and robust (Fig. 2), instead of being low and gracile as in the above-mentioned forms. The mandibular symphysis is moderately short and low, and seems to be formed exclusively by the dentaries. The anterior end of the lower jaw tapers anteriorly, having a straight dorsal margin and convex ventral margin (Fig. 13).

The left dentary of MOZ 6146P is completely preserved, while the right element has its anterior end poorly preserved. The external surface of the dentaries is slightly convex, dorsoventrally high and lacks any ornamentation pattern. Its dorsal margin is straight, lacking the festooning pattern present in neosuchian crocodyliforms. Its ventral margin is also straight, except for its anteriormost part. Posteriorly, the dentaries are strongly sutured to the surangular and angular, denoting the absence of an external mandibular fenestra. The dentaries bear a broad and deep sulcus on their posterodorsal region that is continuous with the large groove present in the surangular (Fig. 13; see below). This sulcus ends anteriorly in a large foramen (approximately 14 mm of dorsoventral diameter) that opens posteriorly.

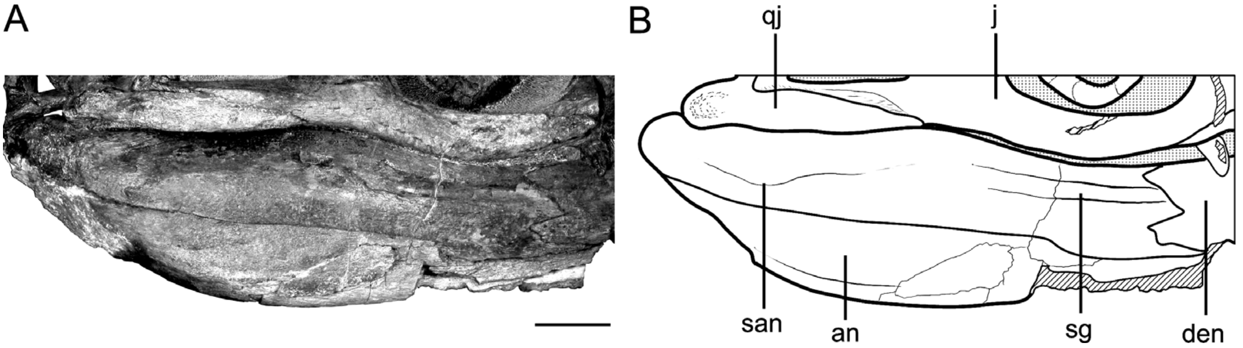


Figure 13 **A**, Posterior region of the mandible of *Dakosaurus andiniensis* (MOZ 6146P) in lateral view, **B**, reconstruction. Abbreviations: **an**, angular; **den**, dentary; **j**, jugal; **qj**, quadratojugal; **san**, surangular; **sg**, surangular groove. Scale bar = 5 cm.

The angular forms the ventral half of the posterior region of the mandibular ramus. Its ventral margin is straight and curves dorsally towards the articular region, where the angular tapers ending in an acute tip. Its dorsal margin is strongly sutured to the surangular, extending parallel to the surangular groove (Fig. 13).

The surangular covers the dorsal half of the posterior region of the mandibular ramus. Its anterior end has three large processes that interlock with the posterior margin of the dentary forming a strong suture. The dorsalmost process runs dorsally to the dentary near the alveolar edge. The middle process is less developed than the other two and runs ventral to the surangular groove (Fig. 13). The ventralmost process is the most extensive and wedges between the angular and dentary, reaching the level of the last maxillary tooth. The anterior region of the lateral surface of the surangular is pierced by a large surangular foramen, similar to the opening found in extant crocodyliforms. This foramen opens into a notably broad and deep groove that extends anteriorly along the lateral surface of the surangular, running parallel to the longitudinal axis of the skull (Fig. 13). This sulcus continues on the dentary and reaches the large foramen described above. Interestingly, a large surangular groove is also present in *Dakosaurus maximus* (SMNS 8203). Other metriorhynchids and *Pelagosaurus typus* also have a similarly located groove on the surangular and dentary. Although in these forms, the sulcus is much less developed, being shallow and dorsoventrally low (e.g. *Geosaurus araucanensis* MLP 72-IV-7-1; *Metriorhynchus superciliosus* BMNH R2025; *Metriorhynchus casamiquelai* IIG.1.080573; *Pelagosaurus typus* BSP 1925.I.34). Posteriorly, the surangular is bowed dorsally and forms the lateral wall of the craniomandibular articulation.

Dentition

The dentition of MOZ 6146P is remarkable. Only the posterior maxillary and mandibular teeth are completely preserved; the anterior teeth have most of their external surface damaged. However, several features of anterior dentary and maxillary teeth can be observed in the molds of the lingual surface of eroded teeth preserved in the matrix. The premaxillary dentition is composed of three elements. The maxilla bears 10 (or 11) teeth that interlock with the mandibular elements. The lower jaws preserve 12 teeth, but only the posterior teeth are well preserved. This number of teeth is unusually low for a thalattosuchian, which usually have between 25 and 40 teeth (Vignaud 1997).

All preserved teeth are notably large (crown height of posterior maxillary teeth approximately 5 cm), robust and only slightly curved (Fig. 14A). The dentition of MOZ 6146P, reduced in tooth number and notably enlarged in tooth size, markedly contrasts with that of most thalattosuchians (e.g. *Geosaurus araucanensis* MLP 72-IV-7-1; *Metriorhynchus* AMNH 997; *Steneosaurus bollensis* SMNS 15951; *Pelagosaurus typus* BMNH R32599). In these forms, the dentition is generally composed of numerous, small and acute teeth (see Vignaud 1997). Interestingly, *Dakosaurus maximus* (Fraas 1902) from the Tithonian of Europe shares with *Dakosaurus andiniensis* a reduced tooth number and enlarged tooth size. However, *D. maximus* bear at least 20 elements in the upper tooth row (Vignaud 1995).

All the tooth crowns are buccolingually compressed and have large denticles on the mesial and distal margins (Fig. 14B) formed by both the enamel and the dentine (i.e. true ziphodont condition *sensu* Prasad & de Broin 2002). This condition is found only in *D. andiniensis* (MOZ 6146P) and *D. maximus* (Vignaud 1995; BSP AS.VI.1) among marine crocodyliforms. Unfortunately, this condition cannot be confirmed in the type specimen of *Dakosaurus andiniensis* (MHNSR PV 344) due to the poor preservation of the tooth crowns.

The denticles have a proportionately large basal length (varying between 0.33 and 0.5 mm) with respect to their height (varying between 0.15 and 0.2 mm). The denticles vary slightly in size and small denticles tend to be clustered in pairs whereas larger denticles tend to be well separated from their adjacent serrations (Fig. 14F, G). The serration density measured at the midpoint of the crown varies between 9.5 and 13 denticles per 5 mm (depending on the tooth) and the fore–aft basal length (FABL) of posterior crowns varies between 7 and 8 mm (measurements taken following Farlow *et al.* 1991). The profile of the denticles is rounded in buccal view, but the serrations bear a sharp cutting edge on the mesial and distal margins (Fig. 14H). The denticles of *D. andiniensis* are well separated from each other by wide cella and interdenticular slits and, in most denticles, the diaphysis occupies only 50% of the denticular height (Fig. 14F, G).

This morphology contrasts with the denticles of other ziphodont crocodyliforms that are 'chisel-shaped', with shorter basal length (ranging between 0.14 and 0.35 mm), larger diaphyseal height (occupying between 60 and 80% of

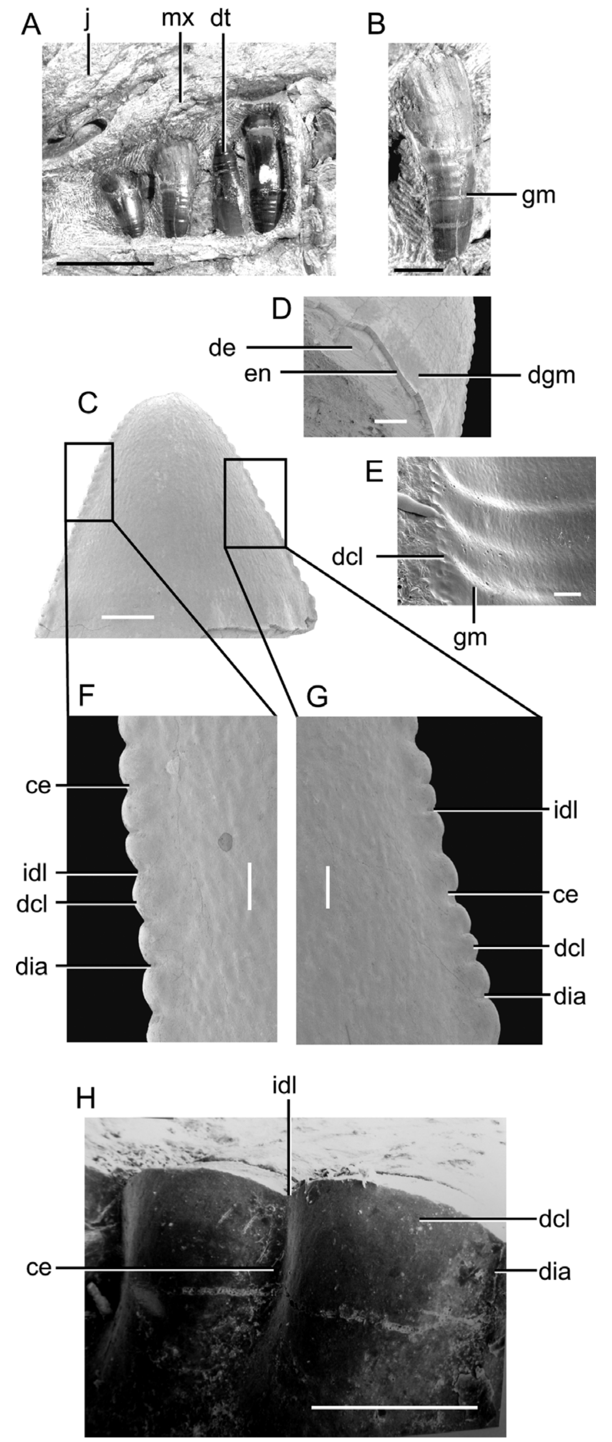


Figure 14 Dentition of *Dakosaurus andiniensis* (MOZ 6146P). **A**, posterior maxillary and mandibular teeth in buccal view. **B**, posterior maxillary tooth in posterobuccal view. **C**, apex of isolated mandibular tooth in buccal view (boxes indicates position of the details shown in **F** and **G**). **D**, apical growth mark of isolated mandibular tooth. **E**, silicon mold of posterior maxillary tooth showing three basal growth marks and serrations. **F**, distal serrations of isolated mandibular tooth. **G**, mesial serrations of isolated mandibular tooth. **H**, two denticles of isolated mandibular tooth in mesiobuccal view. Abbreviations: **ce**, cella; **dcl**, denticle; **de**, dentine; **dgm**, depression of apical growth mark; **dt**, dentary tooth; **dia**, diaphysis; **en**, enamel; **gm**, growth marks; **idl**, interdenticular slit; **j**, jugal; **mt**, maxillary tooth; **mx**, maxilla. Scale bars = 4 cm (**A**), 1 cm (**B**, **D**, **E**), 2 cm (**C**), and 500 μm (**F–H**).

the denticular height), and narrower slits and cella (Farlow *et al*. 1991; Legasa *et al*. 1994; Riff & Kellner 2001; Prasad & de Broin 2002; Company *et al*. 2005). The differences in denticle dimensions and proportions of *D. andiniensis* and other ziphodont crocodyliforms reflect more than just size differences in their teeth, since the ratio of serration density and FABL is lower in *D. andiniensis* than in other ziphodonts.

The outer enamel surface of the posterior (distal) teeth has a thick enamel layer that is divided into a basal smooth zone and a wrinkled apical region. The apical region of most tooth crowns bears three well-developed growth marks, ring-like grooves orientated perpendicularly to the major axis of the tooth crown (Fig. 14E). In addition, each crown has an extra groove located close to the apex. This is slightly more developed than the others and is not evenly continuous along the buccal surface of the crown, being composed of individual mesiodistally aligned sub-circular depressions (Fig. 14D).

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of *D. andiniensis* are discussed here on the basis of the results of a cladistic analysis within the context of all major crocodyliform lineages. This analysis is based on the dataset of Gasparini *et al*. (2006), with minor modifications (see "Supplementary data" available on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477201908002605). The taxon-sampling scheme of this analysis was designed to simultaneously test two major aspects of crocodyliform phylogeny.

First, we were interested in testing the relationships of the usually overlooked Jurassic metriorhynchids from South America. Therefore, this analysis has increased the taxon and character sampling with respect to previously published datasets, which usually included between one and three supraspecific thalattosuchian terminal taxa (Clark 1994; Wu *et al*. 1997, 2001; Buckley *et al*. 2000; Ortega *et al*. 2000; Sereno *et al*. 2001; Pol & Norell 2004b). The analysis included nine thalattosuchian terminal taxa scored at the species level. The sampling of terminal taxa was mainly focused within Metriorhynchidae (seven out of the nine included thalattosuchians). This taxon-sampling scheme included all previously known South American thalattosuchians (Gasparini & Dellapé 1976; Gasparini & Chong Díaz 1977; Vignaud & Gasparini 1996), in order to test their taxonomic assignments and their biogeographical implications (Gasparini 1985, 1992). The two other thalattosuchian species, *Pelagosaurus typus* and *Steneosaurus bollensis*, were chosen on the basis of specimen availability (see Supplementary data: Appendix 3) and on their phylogenetic position in previous studies within Thalattosuchia. *Steneosaurus bollensis* from the Toarcian of Europe was included in the analysis as a representative of Teleosauridae, the other large group of Thalattosuchia (Buffetaut 1981; Vignaud 1995). This taxon was chosen because of the large number of specimens that were examined for this study. Certainly, a comprehensive phylogeny of Thalattosuchia will require testing the monophyly of Teleosauridae (which has not been thoroughly tested so far) including a denser taxon sampling on 'teleosaurids' from the Jurassic of Europe and Asia, but this exceeded the scope of this study. *Pelagosaurus typus* was included in the analysis due to the presence of a large number of plesiomorphic characters, which have led to it being considered as the sister taxon of all other thalattosuchians (Clark 1986, 1994; Buckley *et al.* 2000; Wu *et al.* 2001; Brochu *et al.* 2002; Pol 2003) or Metriorhynchidae (Buffetaut 1981; Vignaud 1995).

The second point of interest in this study was to test the phylogenetic position of Thalattosuchia within Crocodyliformes. This issue has been a recurring point of debate in phylogenetic studies of Crocodyliformes. Previous cladistic hypotheses have considered three main positions for Thalattosuchia: as the possible sister taxon of all other crocodyliforms (Benton & Clark 1988; as a plausible although less parsimonious topology), as the sister clade of most mesoeucrocodylians (Clark 1986; Buckley *et al.* 2000; Sereno *et al.* 2001, 2003; Tykoski *et al.* 2002), or as closely related to other longirostrine crocodyliforms, such as pholidosaurids and dyrosaurids (Clark 1994; Wu *et al.* 1997, 2001; Buckley & Brochu 1999; Larsson & Gado 2000; Brochu *et al.* 2002; Pol & Apesteguía 2005; Jouve *et al.* 2006). In particular, the latter option was considered problematic since it contradicted most pre-cladistic studies, which depicted Thalattosuchia in a more basal position within Crocodyliformes (e.g. Buffetaut 1981; Gasparini 1996). Recent contributions to crocodyliform phylogenetics adding new characters and previously ignored longirostrine taxa (e.g. *Sarcosuchus*, *Terminonaris*, *Hyposaurus*), provided additional support for the close relationships between dyrosaurids and pholidosaurids (Sereno *et al.* 2001; Wu *et al.* 2001). We attempt, with this analysis, to address the 'longirostrine problem', combining an improved taxon sampling of Thalattosuchia (described above) with the new evidence published by those authors, based on a first hand revision of the relevant material. Thus, the analysis presented here improves the taxon and character sampling of longirostrine forms. As mentioned above, the taxon-sampling scheme of this phylogenetic analysis is far from being complete and the inclusion of other members of these clades will be critical to further test the results presented here.

The analysed dataset consists of 257 characters scored for 60 crocodylomorph taxa and the outgroup *Gracilisuchus stipanicicorum* (Romer 1972). The data matrix and character list are available as Supplementary Data (see Appendices 1 and 2). This dataset was analysed with equally weighted parsimony using TNT v.1.0 (Goloboff *et al.* 2003*a*). A heuristic tree search strategy was conducted by performing 1000 replicates of Wagner trees (using random addition sequences) followed by tree bisection-reconnection (TBR) branch swapping (holding 10 trees per replicate). A final round of TBR branch swapping was employed on the best trees retained during the replicates. 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 a single most parsimonious tree (MPT) of 856 steps (Consistency Index (CI) = 0.367, Retention Index (RI) = 0.71) found in 951 out of the 1000 replicates. If a less strict collapsing criterion is used (i.e. rule 3 of Coddington & Scharff 1994), the analysis yields 27 MPTs. The strict consensus of these topologies, however, is identical to the single MPT shown in Fig. 15.

The most parsimonious hypothesis of this analysis (Fig. 15) depicts Thalattosuchia as a monophyletic group closely related to dyrosaurids and pholidosaurids (i.e. the longirostrine clade *sensu* Clark 1994). Within Thalattosuchia, Metriorhynchidae forms a monophyletic group, in which the Late Jurassic–Early Cretaceous forms of South America are depicted as closely related to various taxa from the Late Jurassic–Early Cretaceous of Europe.

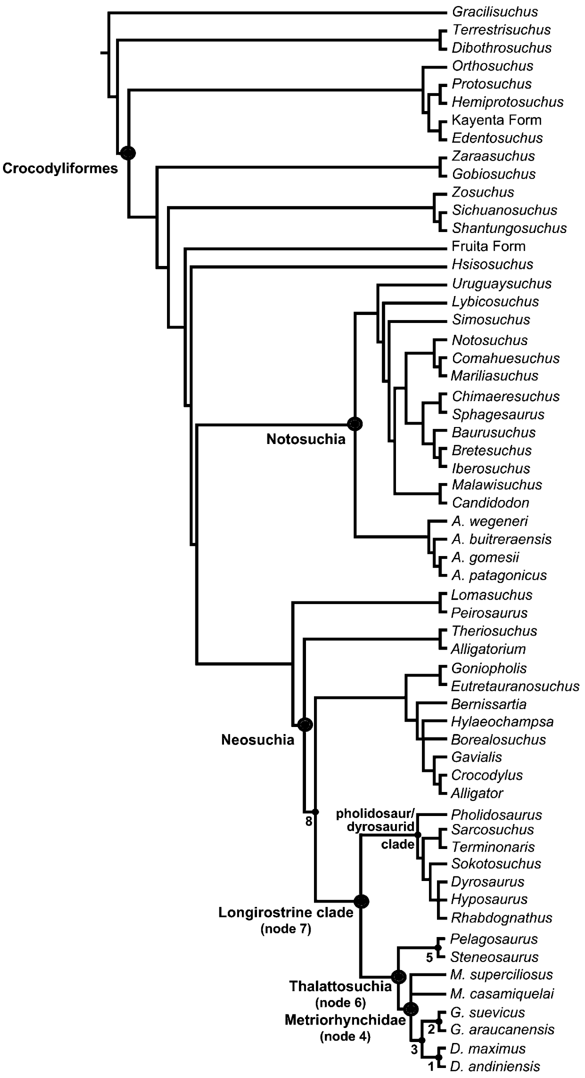


Figure 15 Most parsimonious hypothesis obtained in the phylogenetic analysis (see online Supplementary Data for a complete list of characters, data matrix and taxa used in the analysis). The synapomorphic features of the numbered nodes are discussed in the text.

The specimens described here provide evidence sufficient to unambiguously depict *Dakosaurus andiniensis* as the sister taxon of *Dakosaurus maximus*, justifying their taxonomic assignment (node 1; see Fig. 15). The *Dakosaurus* clade is supported by several characters since its members are the only metriorhynchids with a short and high rostrum (character 3), lateromedially compressed posterior teeth (character 140) with serrated margins (character 120) and broad U-shaped suture between premaxillae and maxillae (character 242).

The two species of *Geosaurus* included in this analysis, *G. suevicus* and *G. araucanensis*, also form a monophyletic group (node 2; see Fig. 15). *Geosaurus* monophyly is supported by the presence of external nares slightly retracted (character 6) and completely divided by a premaxillary bony septum (character 66). In addition, the margins of the antorbital fenestra in *Geosaurus araucanensis* are enclosed by the lacrimals posteriorly and the nasals anteriorly, whereas in all other crocodylomorphs the maxilla forms part of the antorbital fenestra margin. Due to preservational artifacts, we were not able to determine this condition in the studied specimens of *G. suevicus*. Therefore, we cannot establish if this peculiar character diagnoses the *Geosaurus* clade or if it is an autapomorphic character of *G. araucanensis*.

Geosaurus and *Dakosaurus* are sister clades (node 3; see Fig. 15) due to the presence of the following derived characters: choanal groove lacking a pterygoid septum (character 69), maxilla–lacrimal contact completely included within the antorbital fossa (character 131), surangular–dentary groove ends anteriorly within a large foramen in the dentary (character 245), angle between anterior and medial margins of supratemporal fossa close to 45° (character 253).

Metriorhynchidae (node 4; see Fig. 5) is a well supported group diagnosed by the presence of the following derived characters: elongate and low antorbital fenestra orientated obliquely (character 246), nasals descending on lateral surface of skull with extensive participation in antorbital fossa and fenestra (character 172), jugal participating in the antorbital fossa (character 102), broad prefrontals orientated transversely (character 111) and overhanging the orbit (character 247), posteromedial branch of squamosal dorsally concave (character 251) and directed posterolaterally, oblique to the longitudinal axis of the skull (character 250), enlarged foramen for the internal carotid artery (character 248), large and deep groove on surangular and posterior region of dentary and closed mandibular fenestra (character 75). In addition, several metriorhynchids share the lack of sculpturing on the surface of the skull roof bones (character 1), although this character varies in other thalattosuchian taxa (both metriorhynchids and teleosaurids).

Metriorhynchus casamiquelai Gasparini & Chong Díaz, 1977 has an ambiguous phylogenetic placement in this analysis due to the lack of characters to adequately resolve its relationships. Further study, remains and the inclusion of more species of metriorhynchids may help to test this issue in future analyses.

In the present analysis, *Pelagosaurus typus* is depicted as the sister taxon of *Steneosaurus bollensis* (node 5; see Fig. 15), the only included teleosaurid. Such phylogenetic placement is congruent with the most traditional classification of *P. typus* (e.g. Eudes-Deslongchamps 1863; Westphal 1962; Antunes 1967; Steel 1970; Duffin 1979). However, it contradicts other hypotheses that considered this taxon as a primitive metriorhynchid (Mercier 1933; Buffetaut 1981; Vignaud 1995) or as the sister taxon of a clade formed by Teleosauridae and Metriorhynchidae (e.g. Clark 1994; Wu *et al*. 2001; Pol 2003). The grouping of *Steneosaurus bollensis* with *Pelagosaurus typus* has minimal Bremer support values and is supported by only two characters: the presence of the external nares at the anterior edge of the snout, instead of being slightly retracted as in *Metriorhynchus* or exposed dorsally as in *Geosaurus*, *Dakosaurus* and most neosuchians (character 6), and the lack of well-developed prefrontal pillars strongly sutured to the palate (character 15). Although this hypothesis is the most parsimonious interpretation of all the available evidence, we consider that a thorough evaluation of the teleosaurid affinities of *Pelagosaurus* will require a more extensive character sampling and the consideration of other 'teleosaurids' and more plesiomorphic forms of Metriorhynchidae, as has been noted recently by Pierce & Benton (2006). Furthermore, the only two synapomorphies of the clade proposed here are reversions to the plesiomorphic condition found in basal crocodyliforms, denoting the interdependence of understanding the phylogenetic placement of Thalattosuchia and understanding its internal relationships.

The monophyly of Thalattosuchia (node 6; see Fig. 15) is well supported in this analysis and this clade is diagnosed by 24 synapomorphies. Some of them are unique characters that were traditionally recognised as differentiating thalattosuchians from other crocodyliforms: nasals not contacting premaxilla (character 14; paralleled in *Gavialis*), descending process of the postorbital overlapping laterally the ascending process of the jugal (character 16), cranioquadrate passage located near lateral surface of the skull (character 49), putative absence of palpebral bones (character 65), extremely large supratemporal fenestra covering most of the dorsal surface of the skull (character 68), squamosal anterior branch reduced and postorbital posterior process forming most of the dorsal temporal arcade (character 166), and anteriorly elongated coronoid (character 175). An additional set of characters that distinguishes thalattosuchians are: pterygoid flanges narrow, bar-like and poorly developed (character 179), posterolateral region of nasals deflected ventrally, forming part of the lateral surface of the snout (character 228), postorbital bar mostly formed by the descending process of the postorbital with poor participation of the reduced ascending process of the jugal (character 244), posterolateral region of squamosal bearing a large, subrounded and concave surface (character 249), and presence of longitudinal depressions on the palatal surfaces of the maxillae and palatines (character 253). The latter character was usually considered as a distinctive character of metriorhynchids (Wenz 1968), but as pointed out by Vignaud (1995) this feature is actually present in several specimens of *Pelagosaurus* and *Steneosaurus*.

Other synapomorphies diagnose this clade but show numerous convergences with other crocodyliforms (e.g. quadratojugal not reaching the quadrate condyles (character 141), cranial table as wide as ventral region of the skull (character 206)). Finally, as noted by Clark (1994), many of the thalattosuchian synapomorphies (10 out of the 24) optimised in the MPT are reversals to the plesiomorphic condition found in basal Crocodyliformes. Therefore, this set of characters provide support for this clade only if it is located deeply nested within Crocodyliformes (e.g. anterior region jugal as deep as infratemporal region (character 17), absence of supratemporal skull table (character 24), dorsal end of postorbital bar broadens gradually (character 30), narrow dorsal surface of parietal between supratemporal openings (character 33), posterior edge of quadrate gently concave and broad (character 46), dorsal head of quadrate articulates with squamosal, otoccipital and prootic (character 47), large ventrolateral flange of exoccipital ventral to paroccipital process (character 60), elongated anterior process of ilium (character 84), pubis and ischium contacting the pubic peduncle of ilium (character 86), postorbital bar continuous with the lateral surface of jugal (character 167)). As in several of the previous cladistic studies (Clark 1994; Wu *et al*. 2001), despite the consideration of this long list of plesiomorphic conditions, thalattosuchians are most parsimoniously depicted as deeply nested within longirostrine neosuchian crocodyliforms (see discussion below).

The longirostrine clade clusters thalattosuchians, pholidosaurids and dyrosaurids (node 7; see Fig. 15) and is diagnosed by six synapomorphies: absence of a notch at the premaxilla–maxilla contact (character 9; reversed in *Sokotosuchus*), transversally flattened postorbital bar (character 26), mastoid antrum not entering into supraoccipital (character 63), posteriorly elongated and triangular retroarticular process facing dorsally (character 71), splenial extensively involved in the mandibular symphysis (character 77), absence of enlarged teeth in dentary and maxillary tooth rows (characters 79 and 81).

The sister group of Thalattosuchia is a clade formed by taxa traditionally grouped in Pholidosauridae and Dyrosauridae. The MPT agrees with recent studies (Wu *et al.* 2001; Sereno *et al.* 2001) in postulating pholidosaurids as paraphyletic with respect to dyrosaurids. We refer to this clade as the pholidosaur/dyrosaurid clade (Fig. 15), although future studies expanding the character and taxon sampling of these forms may evaluate a formal taxonomic decision if this clade remains stable. The pholidosaur/dyrosaurid clade is supported by the presence of an elongated and narrow posterolateral process of the squamosal that extends posteriorly and is not ventrally deflected (character 36), the participation of pterygoids in part of the anterior margin of the choanal opening (character 43), and the rostral ramus of the frontal exceeding anteriorly the prefrontal (character 238).

Relationships of South American thalattosuchians

One of the main objectives of the phylogenetic analysis presented here was to test the relationships of South American metriorhynchids. With regard to this point, the results of the cladistic analysis provide support for the close relationships between the species of *Geosaurus* and *Dakosaurus* from western South America with those of the Jurassic of Europe. These results not only provide clear support to the previously proposed taxonomic assignments but also to the biogeographical connection of these distant marine regions. As proposed by Gasparini (1985, 1992) a plausible explanation for this would be the seaway connection of these areas through the Caribbean or Spanish Corridor. Further studies, considering the recently found *Geosaurus* remains from the Oxfordian of Cuba (Gasparini & Iturralde-Vinent 2001, 2006), *Geosaurus vignaudi* and *Geosaurus saltillense* from the Tithonian of central-east México (Frey *et al.* 2002; Buchy *et al.* 2006), as well as a re-evaluation of the thalattosuchian remains from North America (e.g. Buffetaut 1979*a*) will be critical to further test this biogeographical connection between Europe and western South America.

Thalattosuchia and the 'longirostrine problem'

The phylogenetic position of Thalattosuchia has been a controversial issue since the first cladistic approaches to the evolution of Crocodyliformes (Clark 1986). The traditional interpretation considered that Thalattosuchia was basal to most other crocodyliforms and that its long-snouted morphology and marine habits were acquired independently from other longirostrine forms (e.g. pholidosaurs, dyrosaurids, gavialoids: Langston 1973; Buffetaut 1981). This view was mainly based on three different lines of evidence. First, most thalattosuchians show the plesiomorphic crocodyliform (or crocodylomorph) condition in several characters (Benton & Clark 1988; see above). Second, it was traditionally assumed that similar longirostrine snout shapes had appeared convergently multiple times in the evolutionary history of 'neosuchian' (e.g. Kälin 1955; Langston 1973; Busbey 1995) and eusuchian crocodyliforms (see Brochu (2001) for a phylogenetic perspective on this issue within Eusuchia). Therefore, the similarities between thalattosuchians and other long-snouted forms were regarded as yet another case of convergent evolution. Third, thalattosuchians appear early in the Jurassic, well before other longirostrine crocodyliforms (e.g. the Late Cretaceous dyrosaurids and gavialoids).

The latter point has no strict relevance to the formulation and evaluation of phylogenetic hypotheses since temporal disparity between first appearances of sister groups in the fossil record does not provide adequate information to test their cladistic relationships (Rieppel 1997; Smith 2000, 2002), especially in cases in which the fossil record is as sparse as that of Mesozoic crocodyliforms. Furthermore, an updated calibration of the phylogeny of Crocodyliformes against geological time reveals that the evolutionary origin of most neosuchian lineages must be extended well before their first appearance datum (FAD) in the fossil record, as previously noted by Tykoski *et al.* (2002). This inference is based on the extension of lineages prior to the FAD of a clade on the basis of the age of its sister group (ghost lineage *sensu* Norell 1992) and the age of the recently described goniopholid *Calsoyasuchus valliceps* from the Early Jurassic Kayenta Fromation (Tykoski *et al.* 2002). This early record of Gonipholidae, an undisputed neosuchian group, implies a similar minimum age for the origin of other neosuchian lineages, including the one leading to the pholidosaur/dyrosaurid clade and the one leading to advanced neosuchians (i.e. *Bernissartia* and Eusuchia). Based on this scenario, placing dyrosaurids or pholidosaurs as closely related to thalattosuchians or other neosuchian groups (e.g. goniopholids) would require a nearly identical temporal extension of their ghost lineages (Fig. 16). Therefore, the chronological disparity of the first appearances of Thalattosuchia and other longirostrine forms cannot be postulated as an argument against the neosuchian affinities of the former clade. The inclusion or exclusion of Thalattosuchia within Neosuchia does not increase the amount or extension of ghost lineages of other neosuchian groups (Fig. 16).

In contrast, the first two arguments supporting a basal position for Thalattosuchia are potentially relevant to this phylogenetic problem since they concern the reliability and independence of several morphological characters. Parsimony analyses of most previous studies of the phylogenetic relationships of Crocodyliformes reject the traditional interpretation of Thalattosuchia as a basal, non-neosuchian, member of Crocodyliformes. These analyses (Benton & Clark 1988; Clark 1994; Wu *et al.* 1997, 2001; Buckley & Brochu 1999; Larsson & Gado 2000; Ortega *et al.* 2000; Brochu *et al.* 2002; Pol & Norell 2004*a*, *b*; Jouve *et al.* 2006) depicted Thalattosuchia as nested in the longirostrine neosuchian

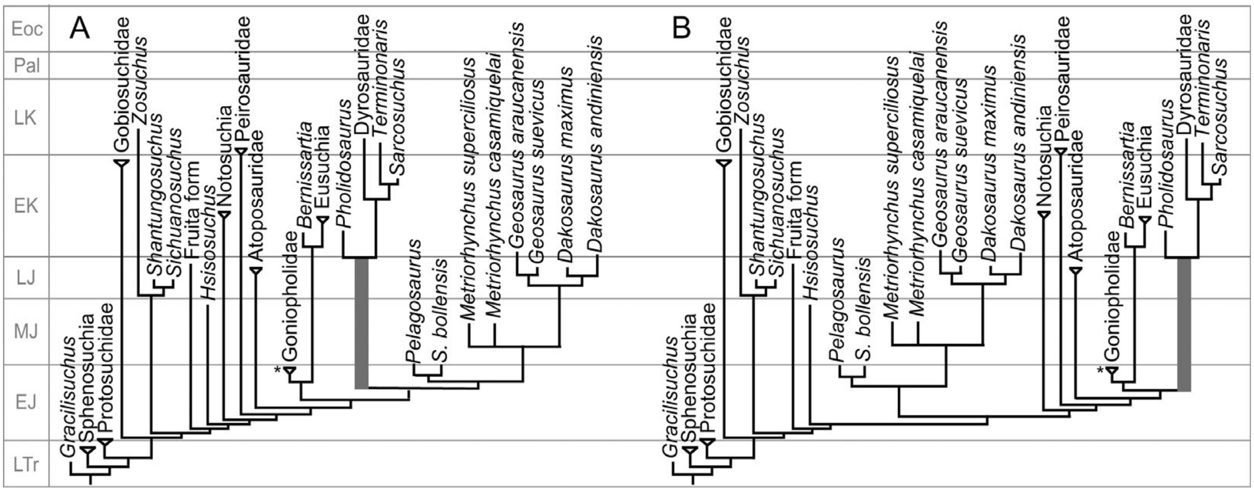


Figure 16 Alternative phylogenetic hypotheses of Crocodyliformes calibrated against geological time. **A**, summary of phylogenetic relationships based on the phylogenetic proposal presented herein. **B**, alternative phylogenetic hypothesis depicting Thalattosuchia as the sister group of all mesoeucrocodylians. Thick grey branch highlights the extensive ghost lineage leading towards the pholidosaur/dyrosaurid clade. The similar extension of this implied gap in each tree is caused by the Early Jurassic age of the first record for Goniopholidae, marked with a star (i.e. *Calsoyasuchus valliceps*; Tykoski *et al.* 2002). E, Early; Eoc, Eocene; J, Jurassic; K, Cretaceous; L, Late; M, Middle; Pal, Paleocene; Tr, Triassic.

clade (along with pholidosaurs and dyrosaurids; see Fig. 15). Some cladistic analyses, however, retrieved a more traditional and basal position for Thalattosuchia (Sereno *et al.* 2001, 2003; Buckley *et al.* 2000; Tykoski *et al.* 2002; Turner & Calvo 2005) but they did not include some taxa critical for testing the monophyly of the neosuchian longirostrine clade (either pholidosaurs, dyrosaurids or thalattosuchians). Several researchers considered the derived longirostrine group as suspicious since it was partially supported by the presence of several characters traditionally thought to be correlated with the presence of an elongated rostrum among Crocodyliformes (Langston 1973; Buffetaut 1981; Clark 1986, 1994; Benton & Clark 1988; Buckley & Brochu 1999; Jouve *et al.* 2006) and other groups of marine amniotes (e.g. mosasaurs: Langston 1973). The dependency of these characters with the longirostrine condition was commonly explained as an adaptive, functional, or structural character complex (e.g. Langston 1973; Busbey 1995).

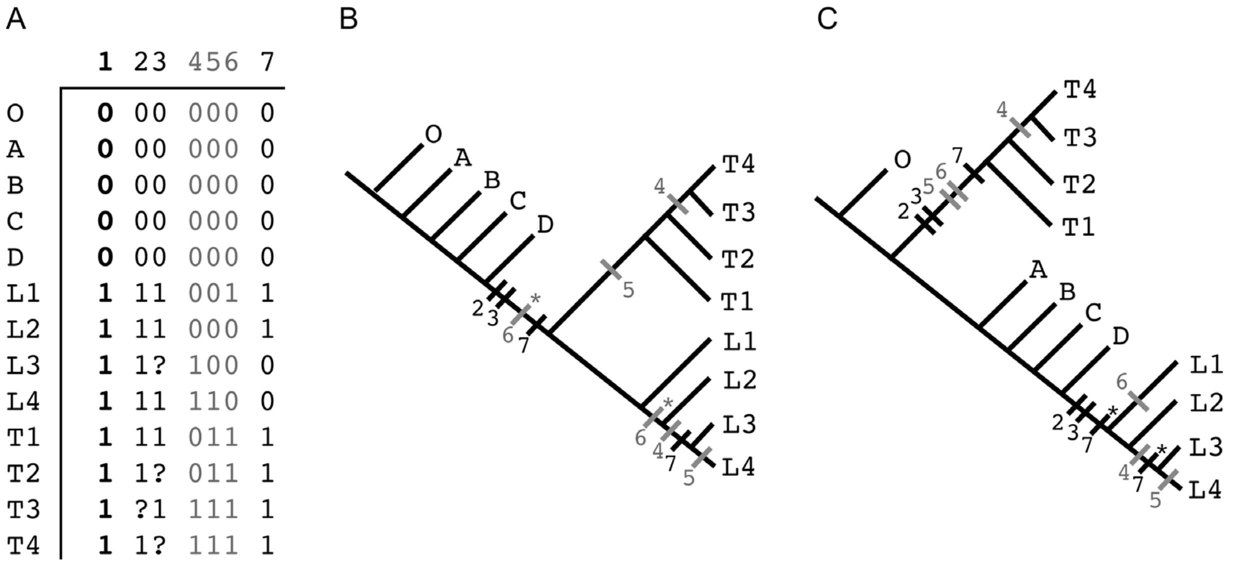
Character dependency, correlation and cladistic analysis

Character independence is one of the assumptions of most methods of phylogenetic reconstruction, including cladistic analysis (Kluge & Farris 1969). Two main classes of dependent characters have been traditionally recognised in the literature, those based on logical grounds and those based on functional/biological dependencies. Logically dependent characters are clearly identified and routinely excluded in the primary stages of character formulation (Sneath & Sokal 1973). However, biologically or functionally dependent characters are harder to identify (Kluge 1989), in particular for fossil taxa (O'Keefe & Wagner 2001). In the following discussion we employ some terms that have been used in the literature with a variety of meanings. Thus, for the sake of clarity we define our usage of three terms used herein: compatibility, biologically dependent characters and biologically correlated characters.

Compatibility of characters refers to the character state distribution of two or more characters. Compatible characters are those that do not show homoplasy in, at least, one phylogenetic tree (Le Quesne 1969). The character state distributions of these features may be identical or not, but they cannot have conflict in their distributions.

In our discussion, we consider biologically dependent characters in a strict sense. Two characters can be postulated as biologically dependent only when they meet two different conditions. Firstly, a dependency between them must be postulated on a theoretical basis. A wide variety of causes can be used for postulating these dependencies, such as belonging to a functional or adaptive complex (e.g. Bock 1981; Szalay & Bock 1991; Szalay 2000), structural or biomechanical requirements, or any other biological reason (e.g. physiological, developmental, genetic). These causes cluster all dependencies not based on logical or definitional causes. Secondly, this type of association between characters is only accepted as existing if they have a compatible character state distribution. Note that these characters do not need to have identical distributions as they can show a nested pattern of derived character state distributions. In addition, differences in the state distribution of these characters can include the distribution of missing data.

Character correlation is used here only in a statistical sense. The character state distribution of these characters can be correlated in most, but not all, cases and, therefore, they can have some incompatibilities. If this correlation is predicted or explained by a biological argument, these characters can be considered as biologically correlated characters. Biologically dependent characters are a special case of correlated characters in which the correlated characters are compatible. Our use of biological correlation is consistent with procedures seeking to find statistical correlation in the evolutionary history of two characters such as the comparative method (Felsenstein 1985; Maddison 1990; Harvey & Pagel 1991). These procedures measure if there is



	1	23	456	7
O	**0**	00	000	0
A	**0**	00	000	0
B	**0**	00	000	0
C	**0**	00	000	0
D	**0**	00	000	0
L1	**1**	11	001	1
L2	**1**	11	000	1
L3	**1**	1?	100	0
L4	**1**	11	110	0
T1	**1**	11	011	1
T2	**1**	1?	011	1
T3	**1**	?1	111	1
T4	**1**	1?	111	1

Figure 17 Hypothetical example of the influence of characters postulated as being biologically dependent upon a given feature (character 1), constructed on the basis of the longirostrine problem. **A**, character state distribution of features postulated as being biologically dependent. Characters 2–7 have a compatible distribution with respect to character 1 (bold font). Characters 2 and 3 have equivalent distributions with respect to character 1. Characters 4–7 have non-equivalent distributions with respect to character 1. **B**, tree postulating a sister group relationship between the L and T clades (analogous to the longirostrine clade). **C**, tree postulating a basal position for clade T (analogous to trees depicting Thalattosuchia in a basal position). The optimisation of the character state changes are mapped on both trees. Black changes for characters imply more steps in topology **C**, while grey changes for characters imply the same number of steps in both topologies. Ambiguous optimisations are marked with an asterisk (only 1 of the 2 most parsimonious reconstructions is shown).

significant correlation between two characters and therefore provide evidence for the influence of one character on the evolution of the other (Maddison 1990), irrespective of their compatibility. Therefore, they do not target strict character independence as defined here.

Biological dependency and cladistic analysis

The suspicion of biological dependence between some characters and the longirostrine condition needs to be thoroughly tested before including/excluding the putatively dependent characters from a phylogenetic analysis. The evaluation of compatibility can be performed *a priori* of the parsimony analysis, as it only depends on the distribution of character states. Failure to meet the compatibility condition is interpreted here as a rejection of biological dependency of the analysed characters. This occurs, for instance, when one of the character states suspected of being dependent on the longirostrine condition is found in non-longirostrine forms and, at the same time, there are longirostrine taxa that lack the supposedly dependent character. In such cases, the incompatibility of the characters under scrutiny shows that they must have had independent evolutionary histories and the presence of one feature did not condition the development of the other. Note that such characters can still be statistically correlated, but provide different (and incompatible) grouping information. Therefore, we consider that they can be taken as independent evidence of phylogenetic affinity for the purpose of a cladistic analysis. This case highlights the distinction between biological dependency and biological correlation (as used in this paper).

When the supposedly dependent character and the longirostrine condition are compatible, their biological dependency cannot be *a priori* rejected. In such cases, this character may be problematic or not and its influence should be examined *a posteriori* from the parsimony analysis (see below). Therefore, the fact that it has a compatible character state distribution does not necessarily mean it must be automatically excluded from a cladistic analysis. Compatible characters can show two main classes of character state distribution patterns: equivalent or non-equivalent. Let us suppose state *n* of one character is postulated as biologically dependent with the presence of state *m* of another character. Equivalent character state distributions are identical to each other except for the distribution of missing entries (if character state *m* is present in one character for taxon *x*, the other character can only be scored as *n* (or missing data) for the same taxon; see character pairs 1–2, 1–3 and 2–3 in Fig. 17A). Characters that are compatible but non-equivalent show a nested pattern of character state distribution (if character state *m* is present in one character for a set of taxa *X*, the other character can only be scored as *n* in a subset of *X*; character pairs 1–4, 1–5, 1–6 and 1–7 in Fig. 17A).

Features showing an equivalent character state distribution with the longirostrine condition are the most problematic for two reasons. Firstly, they provide direct support for the monophyly of the suspected clade (i.e. the longirostrine clade) and alternative hypotheses that break the monophyly of this group will imply more steps for these characters. Secondly, the equivalent character state distribution shows us that all the available evidence suggests these characters indeed had the same evolutionary history and changes in both characters may be representing the same evolutionary event. Clearly, if these characters are not independent, their information in the parsimony analysis will be overweighted during the evaluation of competing hypotheses (biasing the choice toward trees that cluster longirostrine forms). A sample case of this kind of character is presented in the hypothetical example in Fig. 17 (character 1 [independent feature] and characters 2 and 3 [with optimised changes as black bars]). The tree that postulates the monophyly of the group formed by the L-clade and the T-clade implies one step for each of these characters, whereas the alternative tree that depicts T in a basal position implies two steps for each of these characters. Therefore, if the biological argument that postulates their dependency is solid, this is the first kind of character that should be considered for exclusion (at least in exploratory analyses conducted to assess the sensitivity of the results to the inclusion/exclusion of this information).

Features showing a compatible but non-equivalent character state distribution with the longirostrine condition can be less problematic in cladistic analyses, although their distribution should be carefully examined *a posteriori* to understand their possible influence on the outcome of the analysis. The non-equivalent character state distribution implies that this character varies, at least partially, independently from the longirostrine condition. This can occur when the character state suspected of being dependent on the longirostrine condition occurs in some, but not all, of the longirostrine taxa (and is not observed in non-longirostrine forms). Note that this kind of character may indeed be functionally/biologically related in some way to the presence of a long snout (in some taxa), its presence might be conditioned to appear only on long snouted forms and their relative presence may be considered as statistically correlated by the comparative method (e.g. Maddison 1990). However, the character state distributions of such a character and the longirostrine condition show that they are not necessarily linked and may have appeared at different times during the evolutionary history of a group (e.g. in a stepwise manner). These characters, therefore, provide different (but compatible) grouping information and may be considered as independent units for the purpose of a cladistic analysis. It could be argued that this kind of character should be represented as an ordered multistate character (considering the presence of the 'dependent' character as a third state), or as a more complex Sankoff character associated with a step-matrix (Sankoff & Rousseau 1975). However, these alternatives would be identical in terms of character optimisation and the obtained results (if changes among contiguous states are defined with equal costs). Furthermore, treating them as independent characters allows an independent assignment of missing entries to the different characters based on the preserved information of each taxon.

Given that these kinds of characters are only present in some longirostrine taxa and, therefore, contain different phylogenetic information with respect to the longirostrine condition, what consequences would their inclusion in a cladistic analysis produce? This depends on the particular character state distribution of the supposedly dependent character and its optimisation in competing cladograms. We discuss here the hypothetical example shown in Fig. 17, which matches some of the aspects of the longirostrine problem. Clade T can be positioned as the sister group of clade L (Fig. 17B) or as a basal member of the tree (Fig. 17C). For the purpose of this example we assume that these two trees are equally optimal on the basis of a number of characters that support their relationships. The data matrix shown in the figure (Fig. 17A) represents an additional set of characters postulated as biologically dependent. Character 1 represents the 'independent' character (e.g. longirostrine condition) and characters 2 through 7 represent the characters postulated as biologically dependent. As mentioned above, characters 2 and 3 are compatible and equivalent to character 1 and, therefore, will directly influence the analysis toward one of the topologies (Fig. 17B). Characters 4 through 7, instead, are compatible with, but non-equivalent to, character 1.

In this example some of the compatible non-equivalent characters are irrelevant for choosing amongst the two (otherwise equally optimal) competing hypotheses. This is the case for characters 4 through 6 (changes optimised as grey bars). Note that these characters imply two steps in both competing hypotheses and, therefore, cannot be interpreted as biasing the choice toward the monophyly of the longirostrine clade (i.e. clade L + clade T in Fig. 17). Moreover, note that this kind of character may be critical to resolving the relationships within these clades. If these characters were completely deleted from a parsimony analysis, unambiguous character support for clades T3+T4 and L3+L4 (character 4) and clade T1+T2+T3+T4 (character 5) would be eliminated. In some cases, characters like these may be the only evidence available for solving the relationships of these taxa and their elimination may result in a less complete understanding of the evolution of these subsets of longirostrine taxa. Given this scenario, it does not seem appropriate to ignore the information of this kind of character since they are not redundant and provide useful phylogenetic information.

However, other compatible non-equivalent characters can have a character state distribution that may prove decisive in the choice amongst two (otherwise equally optimal) competing hypotheses. This is the case of character 7 in the hypothetical example of Fig. 17 (changes optimised as black bars). The character state distribution of this character is unique and different from that of character 1 (or any other character). However, the derived state of character 7 is present in the basal members of clades L and T. When these two groups are depicted as sister clades, character 7 is optimised as having an unambiguous synapomorphy with the suspicious clade L+T (Fig. 17B). In this tree, the condition is subsequently reversed in the clade L3+L4 and, therefore, the character implies two steps. When the T-clade is placed basally on the tree (Fig. 17C), character 7 requires three steps. This situation will happen for all compatible non-equivalent characters that are optimised as unambiguous synapomorphies of the suspicious clade L+T (providing the rooting of each of these clades does not change in competing hypotheses). In these cases, testing the effect of considering this information or not is recommended for assessing whether the results are actually dependent on this possibly dependent feature (at least as exploratory analyses).

In summary, we consider here the *a priori* examination of character compatibility as the first step in testing the biological dependency postulated on the basis of biological theories. Incompatibility is interpreted as a rejection of the dependency hypothesis. If these characters are compatible they should be examined *a posteriori* to assess their effect on the topological results. Compatible and equivalent characters provide direct support that may result in overweighting of the evidence if characters are indeed non-independent. Compatible and non-equivalent characters may or may not influence the results depending on their distribution and optimisation patterns in competing trees. Exploratory analyses of these cases can provide valuable insights for understanding their effects on the phylogenetic analysis.

So far we have discussed only compatible non-equivalent characters in which the supposedly dependent character state occurs in a subset of the taxa scored with the 'independent' character (e.g. longirostrine condition). The inverse relationship can be observed, in which the longirostrine condition occurs in a subset of the taxa showing the supposedly dependent character state. These characters are also compatible and non-equivalent but the nesting pattern is inverted from what was expected on the basis of the biological theory that postulated them as dependent. Therefore, we also consider this case as an empirical rejection of the hypothesis of character dependency.

Re-evaluation of character dependency with longirostry

The unusual short-snouted thalattosuchian described here, as well as the expanded taxon sampling of this analysis and several relevant recently published taxa, prompted us to re-evaluate characters previously considered to be dependent with the longirostrine condition. This set of characters is of particular interest to us given that their appropiateness for cladistic analysis has been questioned in the past (e.g. Langston 1973; Benton & Clark 1988; Clark 1994; Jouve *et al.* 2006). A close examination of their character state distribution shows that most of these cannot be considered as biologically dependent with the longirostrine condition among Crocodyliformes (within and outside the longirostrine clade). In this section we first discuss the distribution of the longirostrine condition and then evaluate the characters most frequently suggested to be dependent on this morphology.

Longirostrine condition

This condition has been applied to the description of the snout shape of a wide variety of crocodyliforms. In its broadest sense, this term is applied to taxa with a long and slender rostrum. Busbey (1995) categorised long rostra as those occupying more than 70% of the basal skull length and also defined the tubular and narrow rostral categories for those taxa having subequal rostral height and width (tubular) or a rostral width/height between 1.2 and 1.9 (narrow). According to these categories, most crocodyliforms traditionally considered as longirostrine taxa have a tubular rostrum that is medium to long in length (greater than 60% of the basal skull length). As previously recognised (Busbey 1995; Brochu 2001) these categories do not represent discrete morphometric divisions and their boundaries are somewhat arbitrary. Nevertheless, they are used here as they serve to quantify more precisely the condition traditionally described as longirostrine in Crocodyliformes. This morphology has been considered as an adaptation to piscivory by various authors (Iordansky 1973; Langston 1973; Busbey 1995; Jouve *et al.* 2006; Pierce & Benton 2006). Part of this inference is based on diet and behaviour of *Gavialis* that catch these prey items by rapid lateral movements of the head under the water surface (Thorbjarnarson 1990; Salisbury & Willis 1996). Other authors have linked the rostral shape of longirostrines to a similar behaviour since the low profile of their snout is thought to reduce drag (Frey 1982; Busbey 1995). The degree to which this feeding habit can be inferred for extinct longirostrine taxa is difficult to test and fossil findings relevant to this subject are scarce, although some suggest metriorhynchids included other prey items in addition to fish (Martill 1986; Forrest 2003; Pierce & Benton 2006).

Within the Eusuchia, the longirostrine condition is found, at least, in three crown-group taxa: Gavialoidea, Tomistominae and *Euthecodon* (Brochu 2001). In addition, several species of *Crocodylus* and *Mecistops cataphractus* have long and slender rostra, but not as narrow or elongated as those of *Gavialis* or *Tomistoma* and, therefore, they are not commonly included in the longirostrine condition. Despite their categorisation, most of these eusuchian taxa are not closely related to each other and, therefore, the longirostrine morphology seems to have been convergently acquired multiple times within Eusuchia (see Brochu 2001). Other lineages within Eusuchia have also developed an elongated rostrum (e.g. nettosuchids), although these forms cannot be considered as longirostrines given their remarkably flat and broad snout ('duck-faced' crocodylians: Brochu 2001).

Outside Eusuchia, all the studied taxa showing this condition are clustered in the 'longirostrine clade' (see Fig. 15). Within this group, however, some exceptions occur. Firstly, *Sarcosuchus imperator* has a long rostrum (74–77% of skull length) but approaches a narrow/broad condition in the largest known specimens (see Sereno *et al.* 2001). Secondly, *Dakosaurus* is the taxon that deviates the most from the longirostrine condition, having a proportionately short snout (approximately 50% of skull length). Thus, the longirostrine clade is not entirely homogeneous with respect to snout shape, although the cases cited above can be interpreted as derived (secondary) modifications from an ancestral longirostrine condition because of their position in the phylogenetic tree.

Nasal not reaching the external nares (character 13)

This condition, cited as one of the characters possibly dependent with longirostry by Benton & Clark (1988), is actually present in many neosuchian taxa that lack a particularly elongated rostrum (e.g. *Borealosuchus* (Brochu 1999); *Diplocynodon* (Salisbury & Willis 1996); *Goniopholis simus* BMNH 41098). In addition, some long-snouted forms (e.g. *Stolokrosuchus lapparenti*) that are presumably not related to the longirostrine clade (Larsson & Gado 2000) have the nasals anteriorly extended and reaching the external nares. The same condition was noted to occur in the long-snouted eusuchians *Crocodylus johnstoni*, *Harpacochampsa camfieldensis* (Salisbury & Willis 1996) and some basal tomistomines (e.g. *Maroccosuchus*). Furthermore, the short-snouted *D. andiniensis* also have nasals failing to reach the external nares. It could be argued that the condition in the short-snouted *Dakosaurus andiniensis* is explained by inheritance from a longirostrine ancestral condition. This argument, however, is actually based on the independent variation of the long-snouted condition and this character, demonstrating that they are different units of phylogenetic evidence. The presence of this character state in non-longirostrine forms and its absence in other long-snouted taxa indicate the incompatibility of this character with the longirostrine condition. Therefore, we consider there is no strong basis to consider it as directly dependent with longirostry (as also noted by Salisbury & Willis 1996). Moreover, in the phylogenetic analysis, this condition is not synapomorphic of the longirostrine clade, but a diagnostic character of a large clade of neosuchians (node 8: see Fig. 15) reverted in some taxa such as *Bernissartia* and several eusuchians.

External nares confluent (character 66)

This condition was also cited as possibly correlated with longirostry by Benton & Clark (1988). As in the previous character, external nares lacking a bony septum are actually present in many non-longirostrine taxa, including *D. andiniensis*, numerous neosuchians (*Borealosuchus formidabilis* (Erickson, 1976); *Goniopholis simus* BMNH 41098; *Crocodylus niloticus* FMNH 17157) and several short-snouted basal mesoeucrocodylians (*Notosuchus terrestris* MACN-RN 1037; *Comahuesuchus brachybuccalis* MOZ 6131P; *Mariliasuchus amarali* MZSP-PV 50). Moreover, the improved taxon sampling analysed in this study includes some longirostrine thalattosuchians with a bony septum that completely divides the external nares (e.g. *Geosaurus araucanensis* MACN-N 64). Therefore, the character distribution of this feature is not compatible with that of the longirostrine condition and changes in this character do not seem to be particularly conditioned by snout shape.

Nasals not contacting the premaxillae (character 14)

This character was considered as probably correlated with the longirostrine condition (Benton & Clark 1988; Clark 1994) and is actually present in some longirostrine forms (e.g. *Gavialis gangeticus*) and almost all thalattosuchians. The only exception among the latter group seems to be *Enaliosuchus macrospondylus*, a metriorhynchid thalattosuchian that was recently described as having the nasals sutured to the premaxilla (Hua *et al.* 2000). Other non-thalattosuchian longirostrine forms also have the nasals contacting the posterior end of the premaxilla, including dyrosaurids (e.g. *Sokotosuchus ianwilsoni*, *Dyrosaurus phosphaticus*) and most gavialoids (e.g. *Eothoracosaurus*; Brochu 2004). Furthermore, the short-snouted *D. andiniensis* lacks a contact between the nasals and the premaxillae. As in previous cases, the distribution of this character is not compatible with that of the longirostrine condition and their dependency is rejected when all the available evidence is considered.

Absence of notch at the premaxilla–maxilla contact (character 9)

This condition was mentioned as putatively correlated with longirostry by Benton & Clark (1988). The character optimisation of this character on the MPT presented here (or in any of the previously published studies) indicates that this condition is highly labile. It is usually considered that thalattosuchians, pholidosaurs and dyrosaurids lack a well-developed notch at the premaxilla–maxilla contact. However, the actual distribution of this character is more complex and not strictly coupled with the longirostrine condition; several longirostrine forms have a very small and incipient notch. In fact, the basal dyrosaurid *Sokotosuchus ianwilsoni* was noted to have this notch present (Buffetaut 1979*b*). Furthermore, the absence of this notch is actually a rather widespread condition among Crocodyliformes, found in several short-snouted neosuchians (e.g. *Alligator mississippiensis* FMNH 8201), basal mesoeucrocodylians (e.g. *Notosuchus terrestris* MACN-RN 1037; *Simosuchus clarki* UA 8679), and crocodylomorph outgroups (e.g. *Gracilisuchus stipanicicorum* PVL 4597). The distribution of this character is therefore not compatible with the longirostrine condition and their dependency is rejected by the available data. It must be noted, however, that this character is optimised as a synapomorphic feature of the longirostrine clade and, therefore, will imply more steps if Thalattosuchia occupies a more basal position in the tree.

Jugal infratemporal bar rod-like (character 18)

This character was considered as possibly correlated with longirostry (Benton & Clark 1988; Clark 1994; Salisbury & Willis 1996). As noted by Clark (1994), crocodyliforms have a mediolaterally flattened infratemporal bar of the jugal, except for several long snouted forms (e.g. *Gavialis gangeticus*, *Pholidosaurus*, most thalattosuchians), which have a cylindrical, rod-like bar of the jugal. Interestingly, the short-snouted *D. andiniensis* has a mediolaterally flattened infratemporal bar. However, several longirostrine neosuchian taxa show a transversally flattened infratemporal bar of the jugal, including the thalattosuchian *Teleosaurus cadomensis* (S. Jouve, pers. comm., May, 2005), *Sarcosuchus imperator* (MNN 604) and dyrosaurids (e.g. *Rhabdognathus* (Brochu *et al.* 2002; CNRST-SUNY 190); *Dyrosaurus phosphaticus* (Jouve 2005*b*); *Chenanisuchus lateroculi* (Jouve 2005*a*)). The presence of a rod-like infratemporal bar of the jugal seems to be present only in longirostrine forms, although not in all of them. The distribution of this character state is, thus, compatible with that of the longirostrine condition, although non-equivalent (since it occurs in a subset of the longirostrine taxa). The optimisation of this character in the most parsimonious topology reveals this morphology as convergently acquired in *Gavialis* and the longirostrine clade (Fig. 18A). In the latter group, however, the rod-like infratemporal bar is optimised as an ambiguous synapomorphy, being either originated in the ancestral node of the clade (and subsequently lost in *Dakosaurus* and dyrosaurids+*Sarcosuchus*) or convergently acquired in

Figure 18 Character optimisation for four characters previously proposed to be dependent on the longirostrine condition. These characters are optimised on the most parsimonious tree (MPT) obtained in the complete analysis (only their distribution within Neosuchia (node marked by filled circle) is shown in this Fig.). The character state supposedly dependent upon the longirostrine condition is optimised in grey. The alternative character state is optimised in black. Branches coloured in grey and black denote ambiguous optimisations. The scoring of each taxon is shown by means of rectangles located at the tip of the terminal branches (the absence of a rectangle indicates taxon was scored with missing entries). **A,** optimisation of jugal shape beneath infratemporal fenestra (character 18: lateromedially flattened (black) or rod-like (grey)). **B,** optimisation of frontal width between the orbits (character 20: as broad as nasals (black) or broader than nasals (grey)). **C,** optimisation of development of basioccipital tubera (character 57: reduced (black) or long pendulous tubera (grey)). **D,** optimisation of splenial participation in mandibular symphysis (character 77: no participation (thick black), slight participation (black), or extensive participation (grey)).

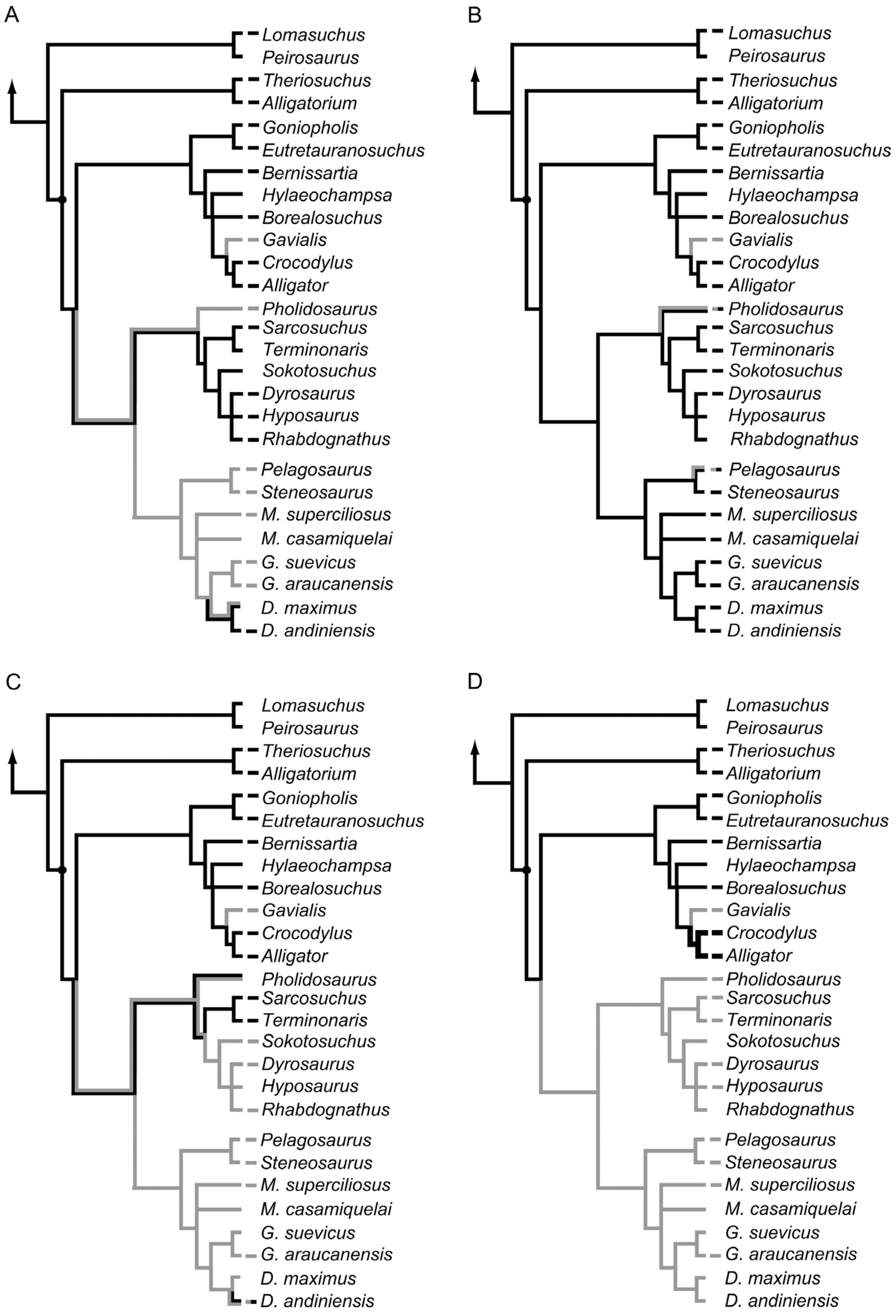


Figure 18 See legend on facing page.

thalattosuchians and the dyrosaurids+*Sarcosuchus* clade (Fig. 18A). Thus, this character only provides equivocal support for the neosuchian position of Thalattosuchia and would imply the same number of steps if thalattosuchians were depicted in their current position or outside Neosuchia. Therefore, we interpret this character as providing an independent source of phylogenetic information that is not biasing the analysis towards topologies with a monophyletic longirostrine clade.

Frontal width between orbits twice as broad as nasals (character 20)

This character was suggested as being correlated with longirostry by Clark (1994), who noted that broad frontals were present in *Gavialis*, *Pholidosaurus*, *Pelagosaurus* and Metriorhynchidae. However, as also noted by that author, other longirostrine forms (e.g. *Dyrosaurus phosphaticus*, *Sokotosuchus ianwilsoni*, *Steneosaurus bollensis*) have rather narrow frontals, as in the rest of the Crocodyliformes. To this list, we can now add more longirostrine taxa, such as *Sarcosuchus imperator* (MNN 604) and *Terminonaris robusta* (Wu *et al.* 2001). The condition within Metriorhynchidae is difficult to score: because of their notably wide nasals, all metriorhynchids have their frontal as wide as the nasals (or even narrower as in *D. andiniensis*). Based on this character definition metriorhynchids were scored as having a frontal as broad as the nasals. The condition of *Pholidosaurus* and *Pelagosaurus* was considered to be uncertain in our dataset as the frontal in these taxa seems to be slightly broader than the nasals, but not as much as in *Gavialis* (Salisbury 2002; Pierce & Benton 2006). Therefore, the only definitive derived character state in our dataset was scored for *Gavialis*. As in the previous character, a frontal wider than the nasal seems to be present only in longirostrine forms (but certainly not in all of them). Thus, the distribution of this character state is compatible but non-equivalent to that of the longirostrine condition. The optimisation of this character in the MPT depicts the derived state in *Gavialis* and possibly a convergent feature in *Pelagosaurus* and *Pholidosaurus* (Fig. 18B). Again, as scored in our analysis, this character does not provide support for the neosuchian position of Thalattosuchia. Alternative trees with Thalattosuchia placed in a more basal position imply the same number of steps for this character. Therefore, this character seems to provide an independent source of phylogenetic information that does not bias the result towards a monophyletic longirostrine clade.

Large supratemporal fenestra (character 68)

Langston (1973) stated that there is a clear relationship between the size of the supratemporal fenestra and the rostral length in extinct and living forms and, more recently, Benton & Clark (1988) considered this character as possibly correlated with longirostry. The presence of large supratemporal fenestrae was traditionally linked to the longirostrine condition since these openings locate important components of the jaw adductor musculature (*M. pseudotemporalis*). It would be reasonable to suppose that long-snouted crocodyliforms require large bundles of these muscles and, therefore, the fenestrae would be bound to be large in these forms. However, recent comparative studies of the *M. pseudotemporalis* in extant crocodyliforms showed that its degree of development differs markedly among longirostrine eusuchians (Endo *et al.* 2002). It seems that in extant taxa, the presence of an elongated rostrum and mandible does not equate with an enlarged supratemporal opening or an increase in the development of the *M. pseudotemporalis*. For instance, in *Tomistoma schlegelii* this muscle is poorly developed, is formed from thin bundles and the supratemporal opening is relatively small. In contrast, the *M. pseudotemporalis* of *Gavialis gangeticus* is well-developed and is the main component in the jaw adductor musculature (Endo *et al.* 2002). Although the condition of *T. schlegelii* may be derived, given the relatively larger supratemporal opening of basal tomistomines (e.g. *Gavialosuchus*, *Dollosuchus*), it seems that functional modifications related to longirostry have been differently established in different lineages within Eusuchia.

The distribution of this condition among Crocodyliformes shows that thalattosuchians and dyrosaurids have extremely large supratemporal fenestrae. As noted by Langston (1973) and Clark (1994), several long-snouted forms (e.g. *Gavialis*, *Pholidosaurus*, *Stomatosuchus*, *Mourasuchus*) have smaller openings in comparison with thalattosuchians or dyrosaurids. Similarly, the long-snouted *Sarcosuchus imperator* (MNN 604) has reduced supratemporal fenestrae with respect to the condition of thalattosuchians and dyrosaurids. Furthermore, long-snouted crocodyliforms (presumably not related to the longirostrine clade) also have supratemporal openings significantly smaller than those of thalattosuchians (e.g. *Stolokrosuchus lapparenti* (Larsson & Gado 2000); *Calsoyasuchus valliceps* (Tykoski *et al.* 2002)). It must be noted that some of these forms have a slightly enlarged supratemporal fenestra (e.g. *Gavialis*, *Pholidosaurus*) in comparison with others (e.g. *Tomistoma*). However, these differences are minor in comparison to differences in the markedly enlarged condition of thalattosuchians and dyrosaurids. Therefore, the presence of a large supratemporal fenestra is scored here as only present in thalattosuchians and dyrosaurids.

Dakosaurus andiniensis has notably large supratemporal fenestrae as all other thalattosuchians, but provides the only case of a short-snouted crocodyliform with enlarged supratemporal openings. It seems evident that enlarged supratemporal fenestrae do not occur in all longirostrine taxa and its presence in *D. andiniensis* demonstrates the incompatibility of the distribution of this character with that of the longirostrine condition. The dependency of this character is therefore rejected by the available data. Evaluating the optimisation of this character in the MPT reveals that the presence of enlarged supratemporal openings is interpreted as convergently acquired in thalattosuchians and dyrosaurids. Thus, this character does not provide direct support for the monophyly of the longirostrine clade. Moreover, because of the presence of enlarged supratemporal fenestrae in crocodyliform outgroups (*Gracilisuchus* and sphenosuchians), this condition is optimised as arising three times over the entire tree. Interestingly, if Thalattosuchia were the most basal clade of Crocodyliformes, this character would imply only two steps. Thus, rather than providing support for the neosuchian position of Thalattosuchia, in this dataset this character provides evidence against it.

Enlarged basioccipital tubera (character 57)

This character was traditionally considered as being correlated to the presence of a long snout. Langston (1973) noted that the enlarged basioccipital tubera of *Gavialis* and teleosaurids probably reflected convergent modifications of the *M. basioccipitovertebralis* and *M. occipitotransversalis*. In most previous analyses, due to the reduced taxon sampling of long-snouted forms, this character seemed to be perfectly correlated with longirostry. However, as already noted by Sereno *et al.* (2001) and Wu *et al.* (2001), the long-snouted *Sarcosuchus imperator* and *Terminonaris robusta* lack the enlarged, pendulous basioccipital tubera present in other longirostrine forms. Other cases of long-snouted crocodyliforms that lack pendulous tubera have been noted within Eusuchia (Brochu 2006). In this case, the short-snouted *D. andiniensis* seems to lack the enlarged basioccipital tubera present in other thalattosuchians. The distribution of this character is, therefore, compatible with that of the longirostrine condition but non-equivalent since it occurs in a subset of these forms. The optimisation of this character on the MPT shows the enlarged basioccipital tubera as convergently acquired in the longirostrine clade and *Gavialis* (Fig. 18C). Within the longirostrine clade, however, the presence of large basioccipital tubera is optimised as an ambiguous synapomorphy, being either convergently acquired in Thalattosuchia and dyrosaurids, or originated at the base of the clade and subsequently lost in the *Sarcosuchus*+*Terminonaris* clade (Fig. 18C). Therefore, this character only provides ambiguous support for the longirostrine clade and requires the same number of steps if thalattosuchians are placed outside Neosuchia. Therefore, this character is considered to provide independent phylogenetic information and its inclusion does not bias the results towards monophyly of the longirostrine clade.

Position of jaw joint (character 105)

Langston (1973) suggested this character was correlated with jaw and snout shape. Three character states are considered here for this character: located at the level of the basioccipital condyle, below the basioccipital condyle but above the level of the lower toothrow, or below the level of the toothrow. As defined in our dataset, this character does not show a correlation with snout or mandibular shape. The most generalised condition among crocodyliforms is the presence of the craniomandibular joint located at an intermediate level between the occipital condyle and the lower tooth row. This condition is actually found in longirostrine forms such as thalattosuchians, pholidosaurs and dyrosaurids. However, the same morphology is observed in numerous crocodyliforms, including many short-snouted forms (e.g. basal crocodyliforms and basal mesoeucrocodylians). Only some notosuchians have a mandibular joint located below the level of the toothrow. Finally, goniopholids and more derived neosuchians (including eusuchians) have a dorsally located craniomandibular joint (at the level of the basioccipital condyle). Interestingly, a dorsally located craniomandibular joint is also present in the longirostrine *Gavialis gangeticus*. Therefore, because of the presence of the thalattosuchian condition in non-longirostrine taxa and its absence in *G. gangeticus*, the distribution of this character is not compatible with that of the longirostrine condition. Based on the available data we can reject the proposed dependency between snout shape and position of jaw joint. Furthermore, given the generalised distribution of the thalattosuchian jaw joint position, this character would not exclusively support a neosuchian position for Thalattosuchia.

Splenial extensively involved in mandibular symphysis (character 77)

With the exception of the derived exclusion of the splenial from the mandibular symphysis in several crown-group clades (e.g. most crocodylids, caimanines, *Alligator mississippiensis*), this bone participates in the symphysis in most mesoeucrocodylians. In these forms the splenials contact each other at the midline and form the posterior region of their mandibular symphyisis. The degree of extension of the splenials into the symphysis varies among mesoeucrocodylians and has been divided into two different character states (following Clark 1994 and Brochu 1997). Most mesoeucrocodylians have a reduced splenial participation that only extends along the length of less than five alveoli, although the most generalised condition is restricted to the length of two or three alveoli. In contrast, the derived long splenial symphysis of some forms extends along five or more alveoli, as defined by Brochu (1997). Benton & Clark (1988) and Clark (1994) noted this character was correlated with the longirostrine condition and, indeed, all of the taxa considered in our dataset corroborate this correlation. Langston (1973) noted that an extensive splenial participation in the symphysis would have strengthened the mandible, but noted two exceptional longirostrine forms that did not show the extensive participation of the splenial in the mandibular symphysis: *Stomatosuchus* and *Mourasuchus*. The latter form is a bizarre Caimaninae from the Tertiary of South America in which the splenial does not participate in the extremely short mandibular symphysis (Price 1964; Langston 1965, 1966; Brochu 1999). *Stomatosuchus inermis* is an enigmatic eusuchian from the Cenomanian of Egypt (Stromer 1925) reported to have an edentulous mandible that may have had no symphysis between the dentaries (Langston 1973). Although these two taxa possess a remarkably long rostrum that comprises more than 80% of the skull length (Busbey 1995), they have an unusually broad and flat duckbill-like rostrum. This is a very different rostral shape than that of all other taxa that form part of the problematic 'longirostrine' clade and adaptive/functional arguments may not apply to these forms. More recently, Salisbury & Willis (1996) noted that narrow-snouted species of *Crocodylus* also lack a participation of the splenial in the mandibular symphysis and Brochu (1999) scored a restricted participation of the splenials in *Euthecodon arambourgii*. In contrast to *Stomatosuchus* and *Mourasuchus*, the latter form is usually considered to be a longirostrine crocodylian because of its narrow and extremely elongated snout (see Brochu 2001).

In summary, with the exception of the above-mentioned taxa, all of the long-snouted taxa included in this analysis have an extensive participation of the splenial in the symphysis. The distribution of this character is, therefore, compatible with that of the longirostrine condition. Despite the fact that in our dataset this character has an equivalent distribution with respect to the longirostrine condition, future studies considering other longirostrine eusuchians may consider this character as non-equivalent and providing different phylogenetic information (as noted by Salisbury & Willis 1996). In contrast to previous characters, however, the extensive participation of the splenials in the symphysis is optimised as an unambiguous synapomorphy of the longirostrine clade (convergently acquired in *Gavialis*: Fig. 18D). Therefore, trees in which Thalattosuchia is depicted more basally require additional steps for this character. Thus, the inclusion of this character can be regarded as potentially problematic since it influences the analysis towards topologies in which the longirostrine clade is monophyletic.

Absence of wave variation in maxillary and posterior dentary tooth size (characters 79, 81)

Several authors have suggested the possible dependence of homodoncy and longirostry as most of these forms have this condition in the maxillary and posterior dentary toothrows (Benton & Clark 1988; Jouve *et al.* 2006). However, the primitive dyrosaurid *Sokotosuchus ianwilsoni* has tooth size variation in the maxillary toothrow, as previously noted by Buffetaut (1979*b*) and Clark (1994). Other longirostrine taxa (e.g. *Sarcosuchus imperator* MNN 604) seem to have an intermediate condition, showing a relatively enlarged maxillary tooth close to the anteroposterior midpoint of the upper toothrow (Sereno *et al.* 2001). In addition, many non-longirostrine crocodylomorphs also lack a wave variation in their maxillary tooth-size. Therefore the distribution of this character appears to be incompatible with that of the longirostrine condition and we interpret this evidence as rejecting the dependency between longirostry and homodoncy. The optimisation of these characters reveals that the absence of wave variation in maxillary and dentary tooth size is actually optimised as unambiguous synapomorphies of the longirostrine clade (as they are the only neosuchians that lack this character). However, this condition is also present in most basal members of Mesoeucrocodylia (character 81) and almost all basal members of Crocodyliformes (characters 79 and 81). Therefore, these characters may not be decisive when evaluating trees in which Thalattosuchia is depicted as close to basal crocodyliforms and trees in which it clusters with pholidosaurs and dyrosaurids.

Summary

As seen above, a revision of the distribution of characters previously suggested as being dependent with the longirostrine condition (Langston 1973; Benton & Clark 1988; Clark 1994) shows, on the basis of a denser taxon sampling, that 8 out of 12 have an incompatible distribution with the longirostrine condition. This contradictory variation is interpreted here as rejecting their dependency and allowing the treatment of them as independent units of phylogenetic evidence.

Instead, four of the 12 characters show a distribution that is compatible with that of the longirostrine condition and their absence in short-snouted forms suggest that there might be a functional/structural relationship between these and the presence of elongated snouts. However, three of these (characters 18, 20 and 57) occur only in a subset of longirostrine crocodyliforms, showing a non-equivalent character state distribution with respect to the longirostrine condition. This suggests that these characters contain different phylogenetic information and have had a different evolutionary history. Furthermore, despite their possible relationship with the longirostrine condition, these three characters cannot be interpreted as biasing the analysis toward the monophyly of the longirostrine clade (Fig. 18). They are not optimised as unambiguous synapomorphies of this clade and they imply the same number of steps when Thalattosuchia is placed outside Neosuchia. Finally, these three characters have a different character state distribution in comparison to each other (i.e. different grouping information) and can be safely treated as independent units of phylogenetic evidence in the context of our dataset.

The only character in our dataset that shows a compatible and equivalent distribution with respect to the longirostrine condition in the data matrix is the presence of extensive participation of the splenial in the mandibular symphysis (character 77, see above). Consequently, this is optimised as an unambiguous synapomorphy of the longirostrine clade (Fig. 18). If this character is, indeed, biologically dependent upon the longirostrine condition, it may be overweighting the support for the monophyly of the longirostrine clade. When this character is excluded from the analysis (and/or the three other compatible characters), the resulting MPTs still depict Thalattosuchians in the same position: deeply nested within the longirostrine clade. Thus, its influence in the analysis is not decisive in our dataset (although this may change in other/future studies).

Finally we note this re-examination of the character data distribution does not confirm the notion that the monophyly of the longirostrine clade of Clark (1994) was caused by poor taxon or character sampling in his original study. In fact, the present analysis (which doubles the number of characters and almost doubles the number of taxa) not only corroborates his, then unorthodox, results, it also rejects the strict linkage of most characters that had correlated distributions with the longirostrine condition in Clark's dataset (due to a broader taxon sampling).

Robustness of the phylogenetic position of Thalattosuchia

To further explore the longirostrine problem and the robustness of the phylogenetic position of Thalattosuchia, we have performed several exploratory analyses based on data elimination and examination of suboptimal trees. The latter analysis is frequently used in phylogenetic analysis as a support measure (Bremer 1988) or to test particular alternative hypotheses. Data elimination procedures are valuable tools for assessing the robustness or sensitivity of phylogenetic results (Lanyon 1985; Farris *et al.* 1996; Goloboff *et al.* 2003*b*), although are not appropriate if the most corroborated phylogenetic hypothesis is being sought (unless the data at hand is suspected of being based on erroneous observations, is biased, or is redundant). Therefore, we explored different types of data elimination in order to test whether the phylogenetic position of Thalattosuchia hinges, or not, on the data under suspicion. Previous workers have suggested various strategies to deal with these cases, including taxon elimination, character elimination and character downweighting.

Taxon elimination

This is probably the most drastic procedure that can be applied. The major drawback of this method is that the empirical content of the analysis (and the competing hypotheses) is reduced (Grant & Kluge 2003). As has been repeatedly noted in the literature, dense taxon sampling schemes are critical to phylogenetic reconstruction (Gauthier *et al.* 1988; Donoghue *et al.* 1989; Wheeler 1992; Nixon 1996; Hillis 1996, 1998; Graybeal 1998; Lee 1998*a*; Poe 1998; Pollock *et al.* 2002; Zwickl & Hillis 2002; Hillis *et al.* 2003). In particular, the exclusion of relevant taxa (i.e. all of their scorings) may alter the relationships of the non-excluded taxa relative to each other. This results from disregarding a large amount of potentially relevant phylogenetic information that may influence topology outside the clade of interest and may not be related to the suspected character complex (i.e. the set of dependent or functionally related characters). The only appropriate justification for this procedure would be in cases in which all of the characters scored for the problematic taxa are suspected of being similarly biased. For instance, this procedure may be an adequate exploratory test for problems associated with long branched taxa in the analysis of DNA sequences (Siddall & Whiting 1999). In these cases, a biasing process is thought to affect homogeneously the entire set of scorings of the long branched taxa (Felsenstein 1978; Huelsenbeck 1997). However, in the particular case of the crocodyliform longirostrine problem, taxon elimination does not seem to be an appropriate approach since the characters thought to be functionally or biologically dependent are a strong minority in the phylogenetic dataset. These are focused in some aspects of rostral morphology and areas of jaw adductor musculature. Therefore, it would be risky to exclude the entire set of scorings of (some) longirostrine crocodyliforms, as they may provide potentially relevant combinations of character states that can affect phylogenetic inferences on the position of both longirostrine and non-longirostrine crocodyliforms.

Buckley & Brochu (1999) tested the elimination of some longirostrine taxa (pholidosaurs and dyrosaurids) and noted in the exploratory analysis of their dataset that Thalattosuchia was depicted as a basal clade of Mesoeucrocodylia (instead of allied to pholidosaurs and dyrosaurids as the complete analysis suggested). A similar result was obtained in two subsequent analyses based on expansions of the same dataset (Buckley *et al.* 2000; Tykoski *et al.* 2002). More recently, Jouve *et al.* (2006) attempted different taxon elimination procedures obtaining different results (e.g. when only dyrosaurids were eliminated, the neosuchian affinities of Thalattosuchia were maintained). When a taxon elimination procedure is employed in our dataset (excluding *Rhabdognathus*, *Sokotosuchus*, *Dyrosaurus*, *Hyposaurus*, *Pholidosaurus*, *Sarcosuchus* and *Terminonaris robusta*), thalattosuchians are depicted in the most parsimonious topologies as the sister group of all other crocodyliforms. The most parsimonious topologies, however, differ from those from the complete analysis in the relative relationships of many non-longirostrine crocodyliform taxa (Fig. 19). Firstly, in addition to Thalattosuchia, three main crocodyliform clades are retrieved as monophyletic: a large clade of protosuchians (including the Fruita form as the most basal member), a large clade of notosuchians (including *Hsisosuchus* as the most basal member) and a large clade of neosuchians. The position of the Fruita form and *Hsisosuchus* are rather unorthodox and differ from their position in the complete analysis (as well as the monophyly of Protosuchia). However, a more surprising result is the relative relationship of these three clades (depicted as a polytomy in the strict consensus): two of the four MPTs depict the large notosuchian clade as the sister taxon of the inclusive protosuchian clade, leaving Thalattosuchia and the neosuchian clade as the two successive most basal clades of Crocodyliformes. This exemplifies the problems noted above with the taxon elimination procedure: ignoring the entire set of scorings of pholidosaurs and dyrosaurids severely affects not only the position of longirostrine taxa but also our understanding of the relationships of non-longirostrine taxa (e.g. notosuchians and protosuchians).

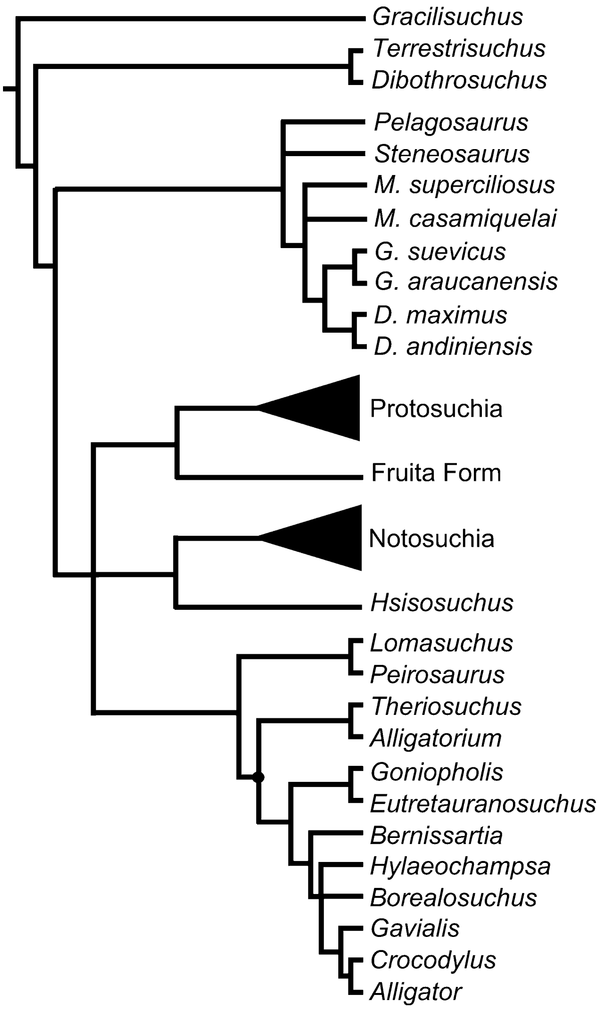


Figure 19 Strict consensus of the most parsimonious trees (MPTs) obtained when the taxon elimination procedure was employed in the analysis (excluding members of the pholidosaur/dyrosaurid clade). Protosuchia and Notosuchia have been collapsed into a single terminal in the figure for the sake of simplicity. Neosuchia is marked by a solid circle at the node.

The potential benefit of taxon elimination procedures lies, however, in providing clues regarding areas of the tree that are strongly sensitive to taxon sampling schemes. This pattern, in turn, can lead researchers to conduct a more thorough taxon and character sampling effort for the unstable clades (Grant & Kluge 2003), as interpreted by Buckley & Brochu (1999) from the results of their taxon elimination procedure. In the dataset used here, this procedure also indicates that the phylogenetic position of Thalattosuchia as neosuchians is sensitive to the taxon sampling of longirostrine forms. This only suggests that more data is needed to provide a more robust assessment of the phylogenetic position of these forms. In particular, a denser taxon sampling of basal longirostrine forms could be critical to further test their relationships. The inclusion of some basal thalattosuchians, such as *Peipehsuchus teleorhinus* (Young 1948; Li 1993) from the Lower Jurassic of China, could be highly desirable.

Peipehsuchus is one of the earliest records of Thalattosuchia and has been considered a plesiomorphic form (Vignaud 1995) that interestingly shares some character states with pholidosaurs (e.g. premaxilla wider than rostrum). Taxon sampling of other neosuchian groups could also be enhanced and may be influential to the longirostrine problem. For instance, several long-snouted taxa such as the Early Jurassic *Calsoyasuchus valliceps* (Tykoski *et al.* 2002) or the Early Cretaceous *Vectisuchus leptognathus* (Buffetaut & Hutt 1980) should be integrated into comprehensive phylogenetic analyses (Brochu *et al.* 2002; Jouve *et al.* 2006).

Character data elimination

As noted above, the longirostrine problem is suspected as being based on a set of rostral and jaw adductor characters. Therefore, character data elimination seems a more appropriate choice to explore alternative signals in our dataset and to test the effect of the suspected characters on the phylogenetic position of Thalattosuchia. This procedure is not viewed as a way to reject the most parsimonious hypotheses obtained in a simultaneous analysis of all the available evidence, as also recognised earlier by Clark (1994). The evidence discussed above suggests that the suspected characters contain unique phylogenetic information (not redundant with the longirostrine condition).

Among character data elimination procedures, the most drastic measure is the exclusion of all supposedly dependent characters. Clark (1994) tested this procedure in his dataset and obtained Thalattosuchia in the same phylogenetic position (i.e. in the longirostrine clade), whereas Jouve *et al.* (2006) obtained Thalattosuchia in a basal position within Mesoeucrocodylia. When this procedure is performed in our dataset, the analysis yields MPTs that locate Thalattosuchia as the most basal crocodyliform clade (Fig. 20). As in the taxon elimination procedure, three main crocodyliform clades are retrieved as monophyletic: a large clade of protosuchians (including the Fruita form as the most basal member), a large clade of notosuchians (including peirosaurids and *Hsisosuchus* as the two successive most basal members) and a large clade of neosuchians (in which pholidosaurs and dyrosaurids are more closely related to eusuchians than goniopholids). These modifications in the topology of non-longirostrine crocodyliform clades indicate the major drawback of completely excluding the suspected characters. As noted above, these characters contain different phylogenetic information, which may include critical data for testing the relationships of non-longirostrine crocodyliforms. Completely eliminating their scorings for these characters prevents their participation in evaluating the relative position of non-longirostrine taxa (in which this character would not be subject to the 'evolutionary constraint' imposed by the longirostrine condition). This can explain some of the topological modifications noted above for these crocodyliforms (e.g. position of peirosaurids as closely related to notosuchians).

It has been argued that rather than eliminating the suspected characters, a more appropriate procedure would be to downweight them in the parsimony analysis, either to a downweight inversely proportional to their number (Emerson & Hastings 1998) or to an arbitrary low value (Lee 1998*a*, *b*). This approach attempts to rescue some of the phylogenetic information of these characters, since it might still be useful for other clades (e.g. in non-longirostrine crocodyliforms in which these characters can vary independently). Performing an inversely proportional downweighting (suspected character weight equals 1/12 of other character's weight) in our dataset yields identical results to the elimination of the suspected characters (Fig. 20). Note that this procedure is not ideal either, since the grouping information of any of these characters (e.g. presence of external nares septum, position of jaw joint) would be severely diminished against other characters uniformly on the entire tree, even in non-longirostrine taxa. Therefore, this procedure suffers from a similar problem to that of the elimination of characters (see above).

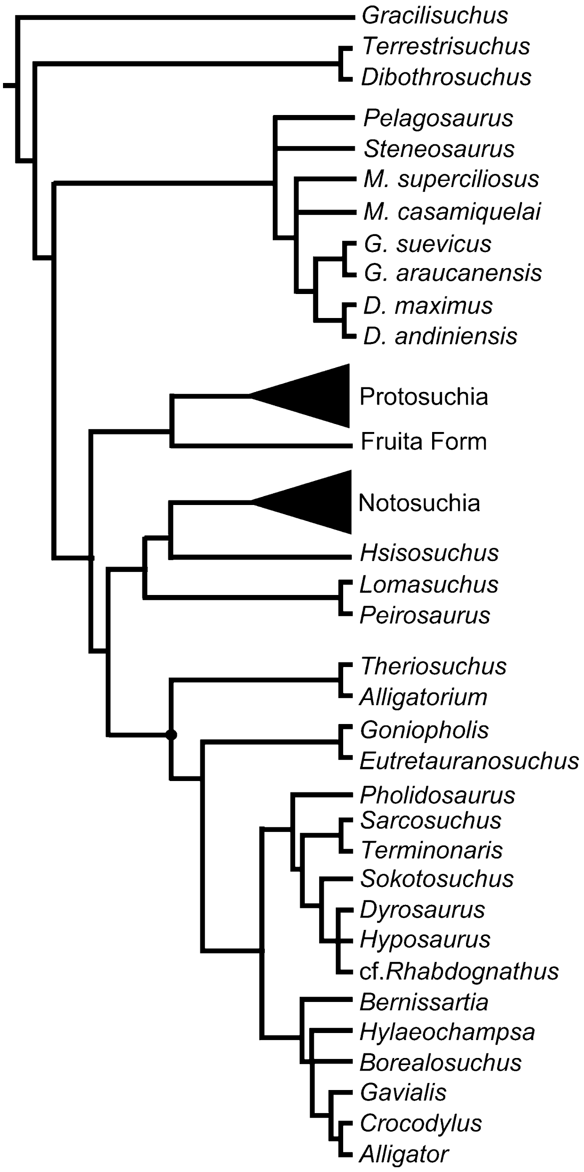


Figure 20 Strict consensus of the most parsimonious trees (MPTs) obtained when the character elimination procedure was employed in the analysis (excluding all characters previously suggested as being dependent upon the longirostrine condtion). Protosuchia and Notosuchia have been collapsed into a single terminal in the figure for the sake of simplicity. Neosuchia is marked by a solid circle at the node.

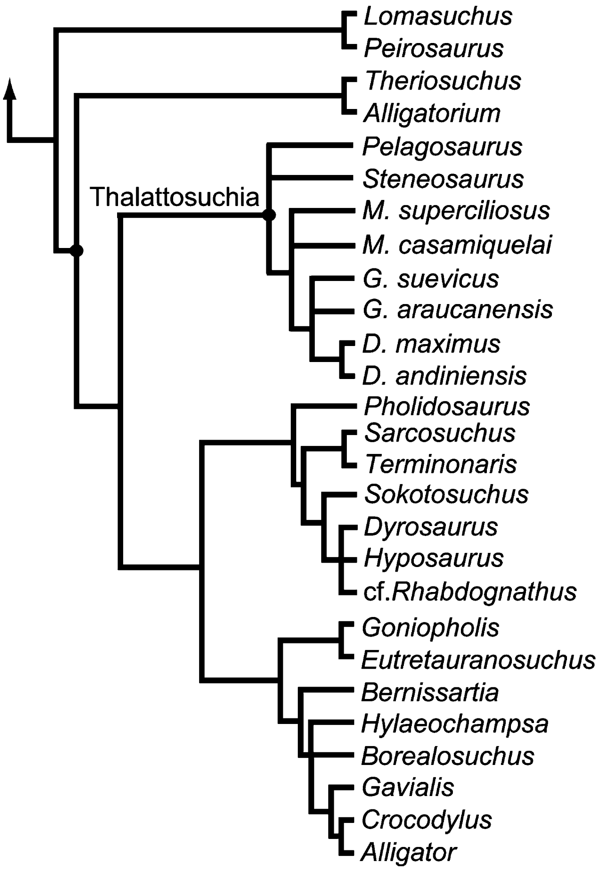


Figure 21 Strict consensus of the most parsimonious trees (MPTs) obtained when the missing entry replacement procedure was employed in the analysis (scoring missing data in all thalattosuchians for all characters previously suggested as being dependent upon the longirostrine condition). Only the relationships within Neosuchia (circled node) are shown in this figure for the sake of simplicity (non-neosuchian crocodyliforms have the same topology as shown in Fig. 15).

Among the character data elimination procedures, the less disruptive approach would be to replace the scorings of the suspicious characters with missing entries only in the taxa that are supposedly misplaced (i.e. the scorings of longirostrine-related characters in thalattosuchians). The main advantage of this approach is that the supposedly biased information is eliminated from the analysis, but the phylogenetic information of these characters is left unaltered outside the longirostrine clade. This is particularly relevant for this problem since some of the characters under scrutiny are relevant for establishing the relationships of non-thalattosuchian crocodyliforms. When the scorings of the 12 characters discussed above are replaced with missing data for all thalattosuchian taxa, the resulting tree depicts this clade within Neosuchia (Fig. 21). In this case, however, Thalattosuchia is not the sister group of the pholidosaur/dyrosaurid clade but it is located as the sister taxon of a group formed by the pholidosaur/dyrosaurid clade and derived neosuchians (goniopholids, *Bernissartia* and Eusuchia). Note that the only difference in the results of this procedure and those of the complete analysis is the phylogenetic placement of Thalattosuchia (i.e. the topology of all other taxa remains identical), since this exploratory analysis only aims to test the influence of these characters in the placement of Thalattosuchia.

Two conclusions can be drawn from these results. Firstly, although these characters seem to be independent, they are indeed decisive for selecting the sister group relationship of thalattosuchians and the pholidosaur/dyrosaurid clade and show the neosuchian affinities of Thalattosuchia. Secondly, we find it particularly interesting that thalattosuchians are depicted in the last exploratory analysis as basal neosuchians despite not being closely related to the longirostrine clade of pholidosaurs and dyrosaurids. This suggests that the neosuchian affinities of Thalattosuchia must also be based on other character data (see below).

Suboptimal topologies

Bremer support values (Bremer 1988) for the complete analysis (i.e. including all the taxon and character evidence) shows that several clades are minimally supported and collapsed with only one or two extra steps. In particular, the longirostrine clade has a Bremer support of 2, as well as most thalattosuchian nodes and most nodes within the pholidosaur/dyrosaurid clade. However, the fact that these values are low does not necessarily mean that the traditional placements of Thalattosuchia are nearly optimal in the complete dataset (several factors can affect the values of branch support: see Wilkinson *et al.* 2000).

The strength of character support for the inclusion of Thalattosuchia in Neosuchia in this dataset is evidenced when the former group is forced to take a basal position within Mesoeucrocodylia (the most widely accepted alternative position): the MPTs require 10 extra steps to explain the data. If thalattosuchians are forced to be the sister group of all Crocodyliformes (as suggested by Benton & Clark 1988), the MPT requires only four extra steps. Interestingly, assuming thalattosuchians take this phylogenetic position also forces us to reinterpret our understanding of the evolution of Crocodyliformes. In this dataset, several of the MPTs obtained under these constraints depict notosuchians and protosuchians forming a monophyletic group of terrestrial forms, locating Thalattosuchia and the neosuchian clade as the two successive most basal clades of Crocodyliformes (similar, in this respect, to the results of the taxon elimination procedure; see above).

Finally, when Thalattosuchia is allowed to occupy any position in the tree, except being the sister group of the pholidosaur/dyrosaurid clade (performed through negative constraints in TNT), the resulting MPT still depicts Thalattosuchia within Neosuchia. This tree requires three steps more than the unconstrained analysis and locates Thalattosuchia as the sister taxon of a large clade of advanced neosuchians (formed by the pholidosaur/dyrosaurid clade, goniopholids, *Bernissartia fagesii* and Eusuchia). These results are similar to those of the missing entry replacement procedure (see Fig. 21), indicating again the neosuchian affinities of Thalattosuchia (irrespective of the similarities with the longirostrine pholidosaur/dyrosaurid clade).

Neosuchian affinities of Thalattosuchia

One of the most interesting outcomes of these exploratory procedures is that the neosuchian affinities of Thalattosuchia do not seem to be exclusively based on those supposedly convergent characters of longirostrine crocodyliforms. Thus, a final question arises from these exploratory analyses: what characters are actually supporting the neosuchian affinities of Thalattosuchia? Comparing the optimisation of different characters in the competing phylogenetic hypotheses, several cranial and postcranial characters appear as relevant to explaining the neosuchian affinities of Thalattosuchia.

The absence of a posterior palpebral (character 65) is only recorded in neosuchians within Crocodylomorpha. Thalattosuchians seem to have lost both the anterior and the posterior palpebrals early in their evolutionary history. The ventral surface of the basioccipital and the basisphenoid is vertically orientated and faces posteriorly in *Lomasuchus* and neosuchians (character 112). Thalattosuchians also show this character state but in notosuchians and basal crocodyliforms these elements face posteroventrally. The quadrate of thalattosuchians, pholidosaurs (e.g. *Sarcosuchus*), dyrosaurids (e.g. *Rhabdognathus*), and some advanced neosuchians (e.g. *Bernissartia* (Norell & Clark 1990)) lack a preotic siphonium foramen (anterior foramen aërum (Iordansky 1973; Hecht & Tarsitano 1983)) or any other accessory fenestra in addition to the otic aperture (character 45). More basal forms, have a preotic siphonium foramen instead, as well as additional openings on the laterodorsal surface of the quadrate (within the otic recess). Within Crocodylia, however, the preotic siphonium foramen is also present in several members of Brevirostres (Salisbury & Willis 1996). The quadrate body (distal to the otoccipital–quadrate contact) of thalattosuchians is ventrolaterally directed (in posterior view). This condition is otherwise only found in pholidosaurs, dyrosaurids, goniopholids, *Bernissartia* and eusuchians (character 212). In addition, some sebecosuchians (e.g. *Iberosuchus*) and some basal crocodyliforms (e.g. *Protosuchus*, *Orthosuchus*) have this condition (interpreted as convergently acquired). Other crocodyliforms, instead, have the distal region of the quadrate ventrally directed in posterior view.

Among the postcranial characters, thalattosuchians share with neosuchians the presence of reduced and poorly curved postzygapophyses in the axis (character 153). Non-neosuchian crocodyliforms show, instead, much more developed and curved axial postzygapophyses (although the large number of missing entries for this character may reveal a different optimisation pattern in the future). The coracoid in thalattosuchians is well developed, being approximately equal in proximodistal length to the scapula (character 83). This condition is similarly found in goniopholids, eusuchians, and some dyrosaurids (Wu *et al.* 2001; Jouve & Schwarz 2004). In addition, this condition was also noted to be present in *Pholidosaurus* (Clark 1994) and *Terminonaris* (Wu *et al.* 2001). Non-neosuchian taxa have instead a much more reduced coracoid (with the exception of a few notosuchians and sebecosuchians). Finally, the radiale of thalattosuchians is symmetrically expanded in its proximal end, to a similar degree as the distal end (character 117). This condition is also found in *Terminonaris robusta* and eusuchians but contrasts with the hatchet-shaped radiale of more basal crocodyliforms (markedly expanded proximomedially). It must be noted, however, that some basal crocodyliforms (*Protosuchus*) and sphenosuchians also have a symmetrically expanded proximal end of the radiale.

None of these characters seem to be related to the longirostrine condition and, therefore, are interpreted as evidence supporting the neosuchian affinities of Thalattosuchia.

The evolution of aquatic habits in Crocodyliformes

Extant crocodiles are characterised by their semi-aquatic habits and display a large number of characters commonly regarded as adaptations to this environment in their skull morphology (Langston 1973), feeding behaviour (Busbey 1995), sensory organs (Soares 2002) and 'semi-erect' locomotion (Brinkman 1980; Gatesy 1991; Reilly & Elias 1998). However, it is now widely recognised that the ancestral condition of crocodylomorphs was of cursorial and probably terrestrial habits (Carrier 1987; Parrish 1987; Carrier & Farmer 2000; Clark *et al.* 2004). An increasing number of recently discovered non-neosuchian crocodylomorphs indicate that all known basal crocodylomorphs (Clark & Sues 2002; Clark *et al.* 2004), all known basal crocodyliforms (Wu *et al.* 1997; Pol & Norell 2004*a*, *b*; Pol *et al.* 2004) and non-neosuchian mesoeucrocodylians (Buffetaut & Taquet 1978; Nobre 2004; Pol 2005) lack the recognised aquatic adaptations of extant crocodylians. Moreover, the postcranial anatomy of some of these forms has characteristics that denote a markedly cursorial locomotion (Whetstone & Whybrow 1983; Hecht & Tarsitano 1984; Clark *et al.* 2004; Pol 2005). Thus, all of the supposed aquatic adaptations and the absence of cursorial characters seem to occur exclusively in derived neosuchians (node 8 in Fig. 15). This suggests that the transition to an amphibious mode of life (seen in extant crocodylians) may have occurred late in the phylogeny of Crocodylomorpha, since all of the modifications purportedly related to aquatic/terrestrial habits are optimised at (or close to) this node of derived neosuchians (node 8 in Fig. 15). The phylogenetic results obtained here, depicting Thalattosuchia within the neosuchian longirostrine clade, imply that the switch from a terrestrial to an aquatic mode of life would have occurred only once in the evolution of Crocodylomorpha. The alternative (more traditional) placements of Thalattosuchia discussed above would imply that there were at least two independent invasions to the aquatic realm during the evolutionary history of Crocodyliformes.

The evolution of aquatic living habits within Neosuchia is, however, much more complicated when differences in freshwater versus marine habits are considered. Some neosuchian clades are exclusively found in marine deposits (e.g. Thalattosuchia), others are known only from freshwater deposits (e.g. goniopholids), while others include taxa from both freshwater and marine environments (e.g. pholidosaur/dyrosaurid clade). Within extant crocodylians some forms are much more aquatic and better suited for hyperosmotic environments than others (Mazzoti & Dunson 1984; Jackson *et al.* 1996). Even within Thalattosuchia a progressive marine adaptation has been postulated, from the early appearing teleosaurids to the derived pelagic metriorhynchids (Fernández & Gasparini 2008). The lack of correlation between phylogenetic relatedness and modes of life indicates the evolutionary complexity of habitat preference among neosuchians, even if broad and simplistic categories are used (e.g. marine, freshwater, terrestrial). In particular, the marine habits of thalattosuchians and other longirostrine forms (e.g. dyrosaurids) have been convergently acquired.

CONCLUSIONS

The skull anatomy of *Dakosaurus andiniensis* from the Jurassic/Cretaceous boundary of Argentina is described in detail and depicted as closely related to *Dakosaurus maximus* from the Jurassic of Europe. This repeats the phylogenetic pattern seen in other marine crocodyliforms from South America (e.g. *Geosaurus*), demonstrating the close faunal relationship between these two distant areas of the globe.

The phylogenetic analysis performed here results in most parsimonious hypotheses that depict Thalattosuchia in the 'problematic' longirostrine clade, despite the increased taxon and character sampling of longirostrine crocodyliforms. Within the context of this dataset, alternative positions of Thalattosuchia are moderately to markedly suboptimal. The character evidence that has led previous authors to reject or cast doubts on the monophyly of the longirostrine clade indicates that there is no valid justification to consider the neosuchian affinities of Thalattosuchia as biased by non-independent character evidence (in the context of the present analysis). Despite these results, we consider that the phylogenetic position of Thalattosuchia is still dependent on rostral data and is one of the most critical open questions in crocodyliform phylogeny. Certainly, this problem requires further study, such as considering more taxa (and characters) in future approaches to crocodyliform phylogenetics (e.g. other 'teleosaurids' and goniopholids).

Finally, the new information from *D. andiniensis* is significant beyond its phylogenetic implications. This taxon shows an unusual morphology for a marine crocodyliform, such as a snout that is remarkably short and high with ziphodont dentition. Interestingly, as optimised in the phylogenetic hypothesis, this suite of characters seems to have evolved from the ancestral condition seen in gracile longirostrine forms (Gasparini *et al.* 2006). Once again, a crocodylomorph shows unexpected morphologies, adding evidence to a number of recent discoveries that are transforming our knowledge and understanding on the breadth of the adaptive radiation that this group underwent during the Mesozoic (Clark *et al.* 1989, 2004; Wu *et al.* 1995; Buckley *et al.* 2000; Pol *et al.* 2004). These findings indicate that Crocodylomorpha was probably one of the most morphologically and ecologically diverse clades of archosaurs, thriving in terrestrial, fluviolacustral and marine environments during the Mesozoic.

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