

A new fossil from the Jurassic of Patagonia reveals the early basicranial evolution and the origins of Crocodyliformes

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ABSTRACT

Extant crocodylians have a limited taxonomic and ecological diversity but they belong to a lineage (Crocodylomorpha) that includes basal and rather generalized species and a highly diverse clade, Crocodyliformes. The latter was among the most successful groups of Mesozoic tetrapods, both in terms of taxonomic and ecological diversity. Crocodyliforms thrived in terrestrial, semiaquatic, and marine environments, and their fossil diversity includes carnivorous, piscivorous, insectivorous, and herbivorous species. This remarkable ecological and trophic diversity is thought only to occur in forms with a completely akinetic skull, characterized by a functionally integrated and tightly sutured braincase–quadrate–palate complex. However, the patterns of evolutionary change that led to the highly modified skull of crocodyliforms and that likely enabled their diversification remain poorly understood. Herein, a new basal crocodylomorph from the Late Jurassic of Patagonia is described, *Almadasuchus figarii* gen. et sp. nov. The new taxon is known from a well-preserved posterior region of the skull as well as other craniomandibular and postcranial remains. *Almadasuchus figarii* differs from all other crocodylomorphs in the presence of six autapomorphic features, including the presence of a large lateral notch on the upper temporal bar, an otic shelf of the squamosal that is wider than long, a deep subtriangular concavity on the posterolateral surface of the squamosal, and an elongated pneumatopore on the ventral surface of the quadrate. Phylogenetic analysis focused on the origin of Crocodyliformes places *Almadasuchus* as the sister group of Crocodyliformes, supported by synapomorphic features of the skull (e.g. subtriangular basisphenoid, absence of basiptyergoid process, absence of a sagittal ridge on the frontal, and a flat anterior skull roof with an ornamented dorsal surface). New braincase information provided by *Almadasuchus* and other crocodylomorphs indicates that most of the modifications on the posterior region of the skull of crocodyliforms, including the strongly sutured braincase, quadrate, and the extensive secondary palate appeared in a stepwise manner, and pre-dated the evolutionary changes in the snout, jaws, and dentition. This indicates that the progressively increased rigidity of the skull provided the structural framework that allowed the great ecological diversification of crocodyliforms during the course of the Mesozoic. The phylogenetic pattern of character acquisition inferred for the strongly sutured (akinetic) skull and the appearance of more diverse feeding behaviours that create high mechanical loads on the skull provides another interesting parallel between the evolution of Mesozoic crocodyliforms and the evolutionary origins of mammals.

Key words: Crocodyliformes, braincase, evolution, Jurassic, Patagonia, *Almadasuchus figarii*.

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I. INTRODUCTION

Crocodylomorphs first appeared in the Late Triassic, to become one of the most ecologically diverse groups of tetrapods during the Jurassic and Cretaceous (Langston, 1973; Clark *et al.*, 1989; Wu *et al.*, 1995; Buckley *et al.*, 2000; Carvalho *et al.*, 2005; Pol & Gasparini, 2007, 2009; Sereno & Larsson, 2009; O'Connor *et al.*, 2010; Nesbitt, 2011). Only during the late Cenozoic did they become limited to the semiaquatic forms that we are familiar with today. The most basal crocodylomorphs, traditionally known as 'sphenosuchians' (a paraphyletic array of basal crocodylomorphs), thrived from the Late Triassic to the Early Jurassic and were small (<20 kg), cursorial, terrestrial predators (Clark *et al.*, 2000, 2004) that did not differ significantly in skull structure from more primitive archosaurs. Of this initial radiation, only one lineage, *Crocodyliformes*, led to the great diversification recorded during the Jurassic and Cretaceous. The hallmarks of the crocodyliform skull are the total absence of cranial kinesis (Langston, 1973; Clark *et al.*, 2004) by firmly suturing both the palate and the quadrate to the braincase, and a great diversity of shapes in the snouts and dentitions indicative of a broad range of dietary habits. However, the sequence of transformations leading from the typical basal archosaurian skulls of 'sphenosuchians' to the tightly sutured braincase-quadrate-palate complex of crocodyliforms is still poorly understood, with only the late Middle Jurassic Chinese form *Junggarsuchus* providing some information (Clark *et al.*, 2004). Here we present a new crocodylomorph and a phylogenetic study on the origins of *Crocodyliformes* that depicts the new taxon as the closest relative of this clade and reveals the progressive nature of the pattern of character acquisition that resulted in the functionally integrated and akinetic skull of crocodyliforms.

II. SYSTEMATIC PALAEONTOLOGY

Archosauria Cope, 1869

Crocodylomorpha Walker, 1970

Almadasuchus figarii gen. et sp. nov.

(1) Etymology

From the type locality, Puesto Almada, and *suchus*, Greek for crocodile. The species epithet honors Argentinean geologist Eduardo G. Figari, for his contributions to the knowledge of the geology of the Jurassic sequences in the Cañadón Asfalto Basin.

(2) Holotype

Museo Paleontológico Egidio Feruglio (MPEF) PV 3838, undistorted posterior half of the skull, further isolated elements of skull and lower jaws, fragmentary postcranium. The posterior region of the skull and the isolated cranial, mandibular, and postcranial elements were found closely associated to each other in a thinly-bedded sandstone layer, and no other remains of any kind were found at this locality. All elements match in size and morphology and are interpreted as belonging to a single individual.

(3) Locality and horizon

Puesto Almada locality, 15 km north of the village of Cerro Cónдор, Chubut province, Argentina. The specimen was found approximately 30m above the Almada fish fauna (López-Arbarello *et al.*, 2008), in sediments alternatively referred by Rauhut (2006a) and Cúneo *et al.* (2013) to the Cañadón Calcáreo Formation (Proserpio, 1987) or by Cabaleri *et al.* (2010a) to the Puesto Almada Member of the Cañadón Asfalto Formation. Regardless of the referral to a particular geological unit, an early Upper Jurassic age (Oxfordian) has recently been established for this section by

radiometric dating (Cabaleri *et al.*, 2010b; Cúneo *et al.*, 2013). See Figari (2005) for a discussion of these units and online Supporting Information Appendix S1 for further geological data.

(4) Diagnosis

Basal crocodylomorph with the following autapomorphies: deep lateral notch on the upper temporal bar; postorbital forms 75% of the lateral margin of the supratemporal fenestra; squamosal otic shelf wider than long; deep vertical and subtriangular concavity on posterolateral part of the squamosal; large ovoid quadrate fenestra close to the quadratojugal suture; elongated pneumatopore on the ventral surface of the quadrate confluent with the lateral Eustachian openings; posttemporal fenestra transversely elongated and located close to the lateral margin of the supraoccipital.

III. DESCRIPTION

The temporal region of the skull is approximately twice as wide as high. The orbits are dorsolaterally directed and the supratemporal fossae are proportionately large, triangular, separated medially by a thin sagittal crest that broadens anteriorly, and have an expanded floor in their posterior and medial parts (Fig. 1). The infratemporal fenestra has a marked posterodorsal projection (Fig. 2B) and the posttemporal fenestrae are transversely elongated and enclosed between the squamosal and exoccipital.

The isolated premaxilla (Fig. 2) has an overlapping contact with the maxilla, as in 'sphenosuchians', but unlike the firm suture of crocodyliformes. The premaxillary teeth are moderately compressed labiolingually and lack serrations mesially, but their sigmoid distal carinae bear small denticles that lack interdenticular slits. The frontals are paired and their dorsal surface is ornamented with small and shallow pits and grooves, as in crocodyliforms. The postorbital dorsal surface is flat and ornamented, forming an incipiently developed flat skull table that resembles the apomorphic condition of Crocodyliformes (Fig. 1A). The parietals are fused and taper posteriorly to form a narrow sagittal crest along their posterior half. Posteriorly they expand transversely and contribute to a low, transversely oriented nuchal crest. The dorsal surface of the squamosal is partly ornamented and forms a broad, ventrally deflected otic shelf. The lateral margin of skull roof is markedly concave between the jugal process of the postorbital and the squamosal otic shelf. The squamosal has a deep posterolateral concavity bound posteriorly by the distal end of the paroccipital process and anteriorly by the otic shelf (Fig. 1). Ventral to this concavity, the squamosal is sutured to the quadrate posteriorly, closing the otic aperture of *Almadasuchus*, as in derived crocodyliforms (i.e. Mesoeucrocodylia). This contrasts with the condition in basal crocodylomorphs (i.e. 'sphenosuchians') and basal crocodyliforms (e.g. *Protosuchus*)

in which the squamosal fails to contact the quadrate posterior to the otic region.

The quadrate is strongly sutured with the posterior skull region, having interdigitated sutures with the squamosal, laterosphenoid and prootic dorsally. The quadrate of *Almadasuchus* is also tightly sutured with the exoccipital [as in *Junggarsuchus* (Clark *et al.*, 2004) and crocodyliforms] and contacts the basisphenoid along its ventromedial surface (Fig. 1), an apomorphic condition only shared with crocodyliforms. The distal body of the quadrate is highly pneumatized and inflated, and its internal cavity connects the tympanic area and basisphenoid recess *via* a remarkably large quadrate foramen and opens ventrally through an elongated pneumatopore on the ventral surface of the quadrate, being confluent with the lateral Eustachian opening (Fig. 1F).

The paroccipital processes are robust and distally flared. The exoccipital is pierced by the foramina for the cranioquadrate passage, vagal nerve and cranial nerve IX, and cranial nerve XII. Furthermore, the entrance of the internal carotid artery is completely enclosed within the exoccipital on the occipital surface of the skull. The basisphenoid is remarkably similar to the condition of basal crocodyliforms (e.g. *Protosuchus*), with an expanded triangular ventral surface that is laterally bounded by the quadrate but fails to contact the exoccipitals (Fig. 1F). In contrast to all 'sphenosuchians' (including *Junggarsuchus*; see Section V) the anterolateral margins of the basisphenoid completely lack basiptyergoid processes, as in crocodyliforms. The ventral surface of the basioccipital (at its contact with the basisphenoid) bears a deep median recess pierced by the foramen intertympanicum (Fig. 1F), as in crocodyliforms and the 'sphenosuchians' *Sphenosuchus* and *Dibothrosuchus* (Nesbitt, 2011). The basioccipitobasisphenoid suture, however, is transversely narrow and does not extend lateral to this recess, contrasting with the derived condition of crocodyliforms, in which these bones are tightly sutured along their entire lateromedial extent.

The palate of *Almadasuchus* is only represented by a left palatine (Fig. 2C). The element shows the plesiomorphic morphology of 'sphenosuchians' (e.g. *Sphenosuchus*, *Dibothrosuchus*), having a rhomboid shape and a deeply incised anterior notch that delimits the posterior end of the choana. A deep ventral fossa is present on its ventral surface posterolaterally to the postchoanal ridge, as in 'sphenosuchians' (Walker, 1990). The medial end of this bone is anteroposteriorly elongated for its contact with the vomer and pterygoid. The lateral end is also expanded and has a notch along its posterior half that represents the anteromedial margin of the suborbital fossa. The morphology of the palatine and its participation on the posterior margin of the choana differs from the flat and extensive palatines that participate on the bony secondary palate in derived crocodyliforms (i.e. mesoeucrocodylians), which indicates the absence of a participation of the palatine in the bony secondary palate in *Almadasuchus*.

The informative remains of the lower jaw include a triangular posteroventrally directed retroarticular process

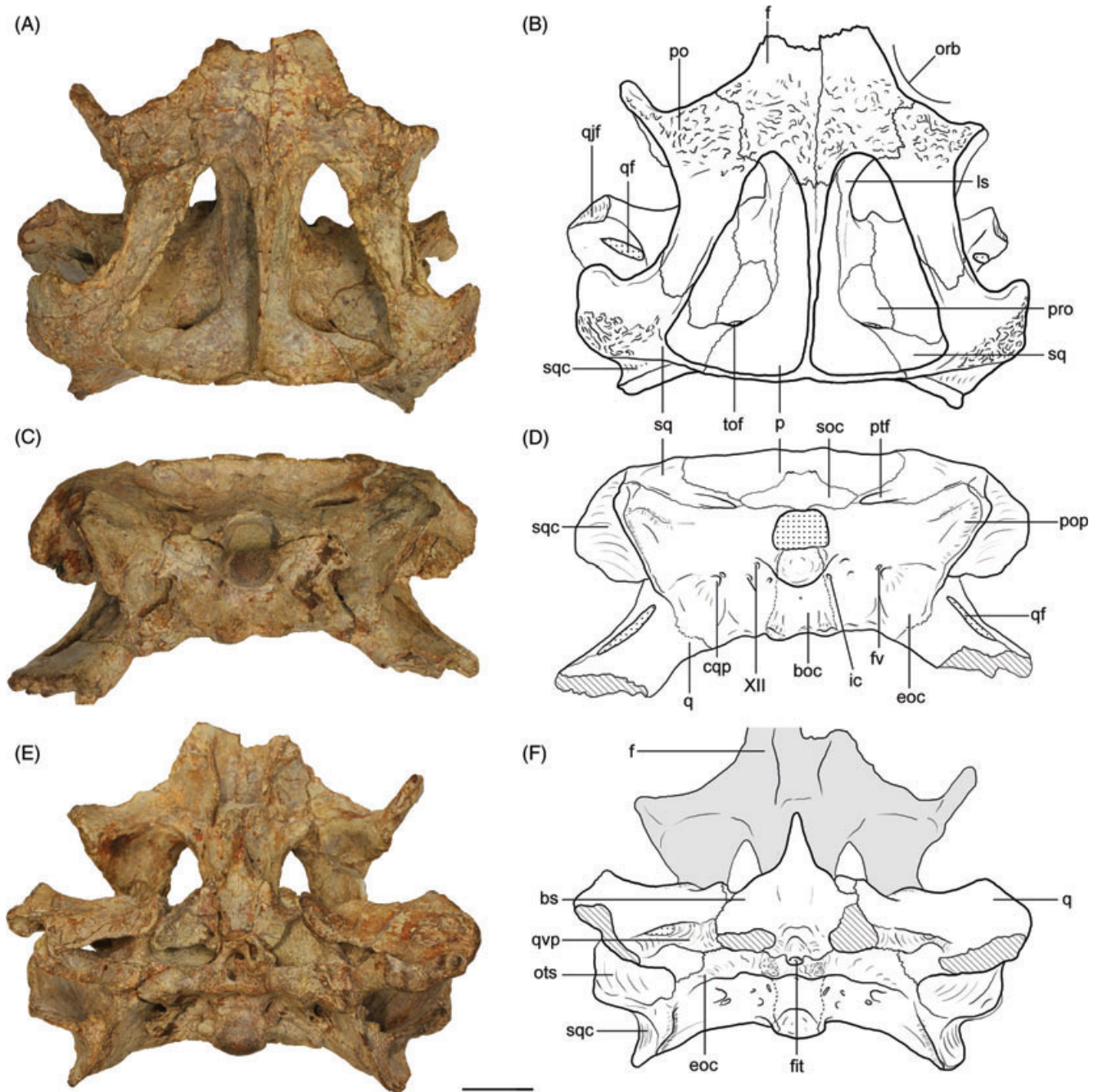


Fig. 1. Skull of *Almadasuchus figarii* (MPEF-PV 3838). (A–F) posterior skull region in dorsal (A, B), occipital (C, D), and ventral (E, F) views. Dotted pattern, sediment; hatched pattern, broken surfaces; grey areas, background surfaces. XII, openings for cranial nerves XII; boc, basioccipital; bs, basisphenoid; cqp, cranioquadrate passage; eoc, exoccipital; fit, foramen intertympanicum; f, frontal; fv, foramen vagi; ic, internal carotid foramen; ls, laterosphenoid; orb, orbital margin; ots, otic shelf of squamosal; p, parietal; po, postorbital; pop, paroccipital process; pro, prootic; ptf, posttemporal fenestra; q, quadrate; qf, quadrate foramen; qjf, facet for quadratojugal; qvp, quadrate ventral pneumatopore; soc, supraoccipital; sq, squamosal; sqc, posterolateral concavity of squamosal; tof, temporo-orbital foramen. Scale bar: 2 cm.

(Fig. 2D, E). The retroarticular process of *Almadasuchus* lacks the medially directed process that is present in protosuchids (Clark, 1986) and some basal crocodylomorphs (e.g. *Dibothrosuchus*). The left radiale (Fig. 3C) is an elongated element, as in all crocodylomorphs, but to a greater degree

than in other basal crocodylomorphs (being 30% of the total length of the femur). This proximal carpal elongation is a condition shared with *Junggarsuchus*. The radiale is expanded at both its proximal and distal ends. The proximal end is L-shaped in proximal view, and bears an anteroposteriorly

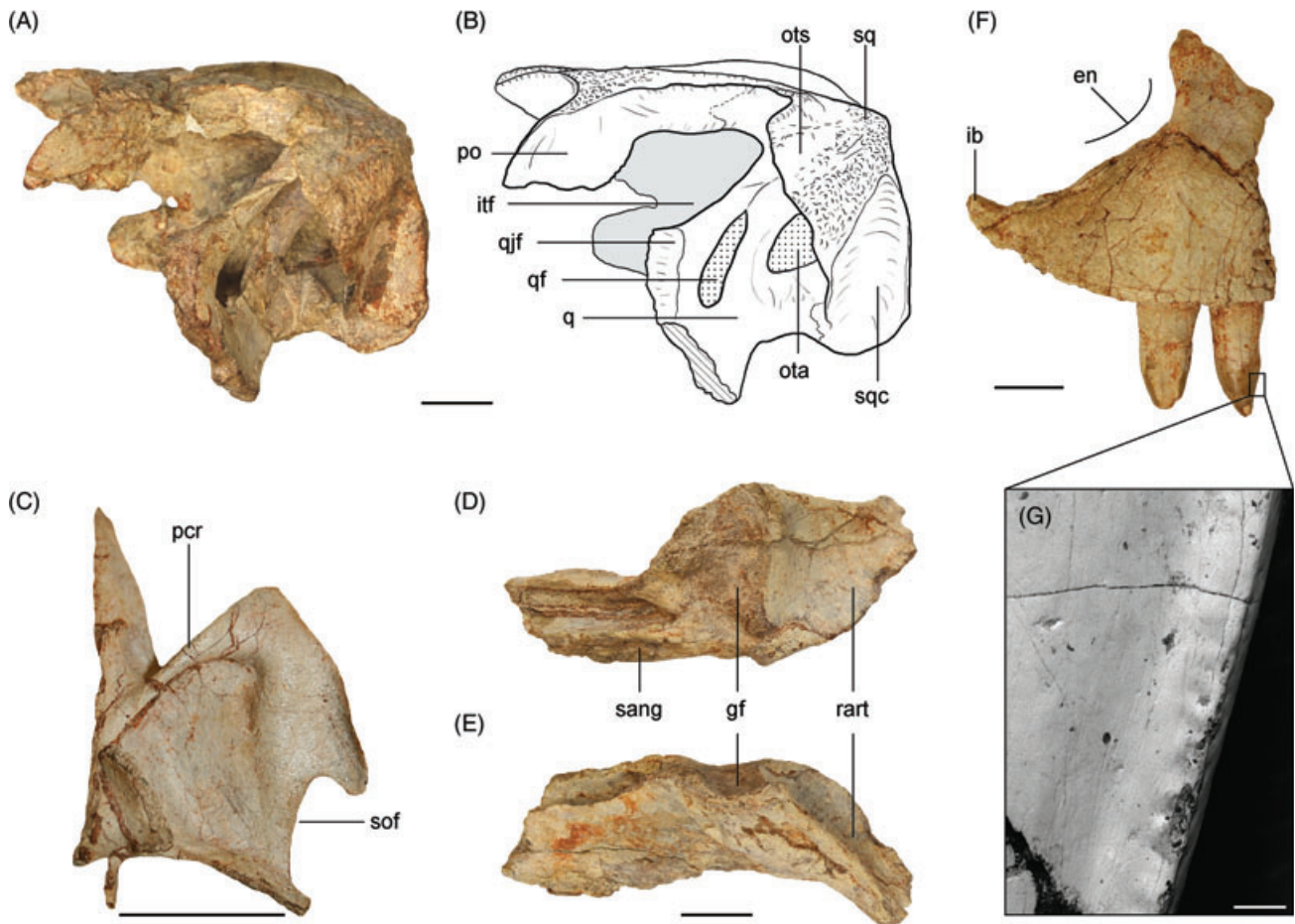


Fig. 2. Additional craniomandibular remains of *Almadasuchus figarii* (MPEF-PV 3838). Skull in (A, B) lateral view. (C) Left palatine in ventral view. Articular region of the mandible in (D) dorsal and (E) medial views. Left premaxilla (F) in lateral view and (G) scanning electronmicrograph (SEM) image of distal margin of premaxillary tooth. Dotted pattern, sediment; hatched pattern, broken surfaces; grey areas, background surfaces. en, external nares; gf, glenoid articular facet; ib, internarial bar; itf, infratemporal fenestra; ota, otic aperture; ots, otic shelf of squamosal; pcr, postchoanal ridge; po, postorbital; q, quadrate; qf, quadrate foramen; qjf, facet for quadratojugal; rart, retroarticular process; sang, surangular; sof, margin of suborbital fossa; sq, squamosal; sqc, posterolateral concavity of squamosal. Scale bars: 2 cm (A–F) and 200 μ m (G).

elongated articular surface for the radius that is separated from the medial articulation for the ulna by a convex knob. The shaft of the radiale is elliptical in cross section, with the main axis oriented anteroposteriorly. The distal articular surface is damaged, but is oriented obliquely with the anterior apex oriented anterolaterally.

The femur (Fig. 3A, B) is slender with a head that projects medially and that is parallel to the lateromedial axis of the distal end, as in many sphenosuchians, but not in crocodyliforms. The lateral region of the anterior proximal surface has a long and sharp trochanter, a feature interpreted as the lesser trochanter (trochanteric crest) in other 'sphenosuchians' [e.g. *Hallopus* (Walker, 1970), *Macelognathus* (Göhlich *et al.*, 2005), and *Kayentasuchus* (Clark & Sues, 2002)]. The posterolateral edge of the proximal femur bears a low but distinct ridge (Fig. 3), interpreted as the 'pseudointernal trochanter' (sensu Walker, 1970), as in the femora of *Macelognathus*, *Dromicosuchus*, and *Kayentasuchus*.

The femoral shaft has a low, broad, proximally placed fourth trochanter and the fibular condyle extends further distally than the tibial condyle. The posterior lateral surface bears a well-developed lateral condyle, which is narrow, high, and posteriorly directed. On the posterior surface the condyles are separated by a wide and deep intercondylar groove (Fig. 3).

IV. PHYLOGENETIC ANALYSIS

(1) Taxon and character sampling

The phylogenetic analysis was conducted using an expansion of the published dataset of Clark *et al.* (2004). Fifteen taxa were added to this dataset, including two non-crocodyliform crocodylomorphs (through the addition of *Macelognathus* and *Almadasuchus*) and 13 representatives

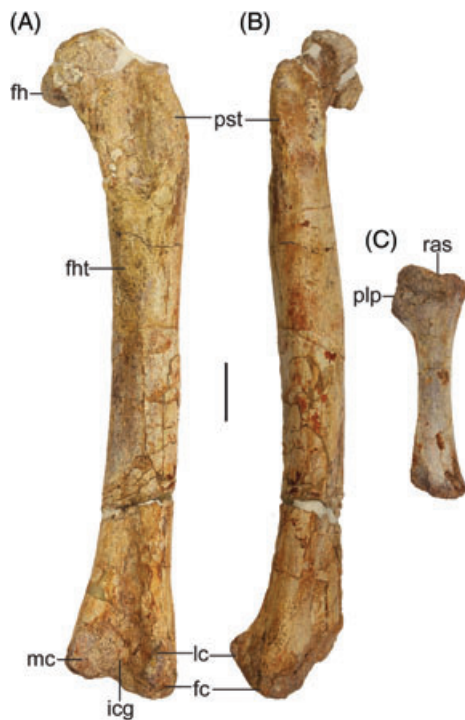


Fig. 3. Postcranial remains of *Almadasuchus figarii* (MPEF-PV 3838). Femur in (A) posterior and (B) lateral views. Radiale in (C) anterior view. fc, fibular condyle; fh, femoral head; fht, fourth trochanter; icg, intercondylar groove; lc, lateral condyle; mc, medial condyle; plp, posterolateral process; pst, pseudointernal trochanter; ras, radial articular surface. Scale bar: 2 cm.

of the major groups of crocodyliforms, including basal crocodyliforms (*Orthosuchus*, *Sichuanosuchus*, *Zosuchus*, *Hsisosuchus*), notosuchians (*Simosuchus*, *Baurusuchus*, *Notosuchus*), Thalattosuchians (*Dakosaurus*, *Cricosaurus*, *Metriorhynchus*), and neosuchians (*Goniopholis*, *Gavialis*, *Crocodylus*). The extended taxon sampling of this dataset (32 taxa) includes members of the major lineages of crocodyliforms that display a broad range of modes of life, dietary habits, and body plans. The character sampling was expanded with respect to the original data matrix (Clark *et al.*, 2004) through the inclusion of 41 characters that are relevant to the phylogenetic relationships of basal crocodylomorphs and to resolve the affinities of the crocodyliforms added in this study (yielding a total of 96 characters). Character scorings were modified for some taxa after personal observation of relevant specimens, including new character scorings on the braincase anatomy of *Junggarsuchus* conducted after the full preparation of its holotype (IVPP V14010) has revealed the presence of basiptyergoid processes in the basisphenoid, the plesiomorphic condition for crocodylomorphs that contrasts with the condition of *Almadasuchus* and Crocodyliformes.

(2) Heuristic tree searches

The phylogenetic data matrix was analyzed in TNT v.1.1 (Goloboff *et al.*, 2008) using equally weighted parsimony. A heuristic tree search of 1000 replicates of Wagner trees

with random addition sequences was performed followed by tree-bisection-reconnection (TBR) branch-swapping (see online Supporting Information Appendix S2).

(3) Phylogenetic results

Phylogenetic analysis places *Almadasuchus* as the sister group to Crocodyliformes, closer to this clade than the advanced late Middle Jurassic ‘sphenosuchian’ *Junggarsuchus* (Fig. 4). Shared derived features of *Almadasuchus* and Crocodyliformes include the suture of the quadrate to the exoccipital and enclosure of the carotid and cranial nerves IX–X, pneumatized and broadly expanded basisphenoid, fenestrated quadrate, and posttemporal fenestra located close to the lateral margin of the supraoccipital (see online Supporting Information Appendix S2). The sister-group relationship of *Almadasuchus* and Crocodyliformes is supported by the subtriangular basisphenoid lacking a basiptyergoid process, the absence of a sagittal ridge on the frontal, and a flat anterior skull roof that has an ornamented dorsal surface. Major synapomorphic features of Crocodyliformes absent in *Almadasuchus* include the quadratojugopostorbital contact, a lateral groove on the squamosal, a flat parietal between the supratemporal fossae, a poorly expanded paroccipital process, a contact between the quadrate and laterosphenoid that covers the prootic, and the exoccipitobasisphenoid sutural contact (see online Supporting Information Appendix S2).

A potentially important taxon for crocodyliform origins is *Kayentasuchus walkeri*. A recent analysis placed it as sister taxon to the Crocodyliformes (Nesbitt, 2011), but the braincase and palatal features shared by *Almadasuchus* and crocodyliforms cannot be determined in *Kayentasuchus* due to the incompleteness of its holotype, and other characters support a more basal position of this taxon in our analysis. A groove on the lateral edge of the squamosal in *Kayentasuchus* and crocodyliforms, for the origination of external ear musculature, may have been obscured in *Almadasuchus* with the extreme modification of its dorsal temporal bar.

V. BRAINCASE EVOLUTION OF CROCODYLOMORPHA

The skull of *Almadasuchus* and the phylogenetic analysis presented here allows an improved understanding of the pattern of character acquisition that led to the highly modified crocodyliform skull (Fig. 5). The skull of the most basal crocodylomorphs lacks the sutural connection between the ventral part of the quadrate and the braincase that in crocodyliforms precludes any movement and provides greater resistance to forces incurred by mandibular adduction on prey. The earliest changes in the braincase, present in *Junggarsuchus* and more derived forms, involve the development of strong and extensive sutures of the quadrate with the posterior skull through the exoccipital and the expansion of the internal pneumatization of the basisphenoid

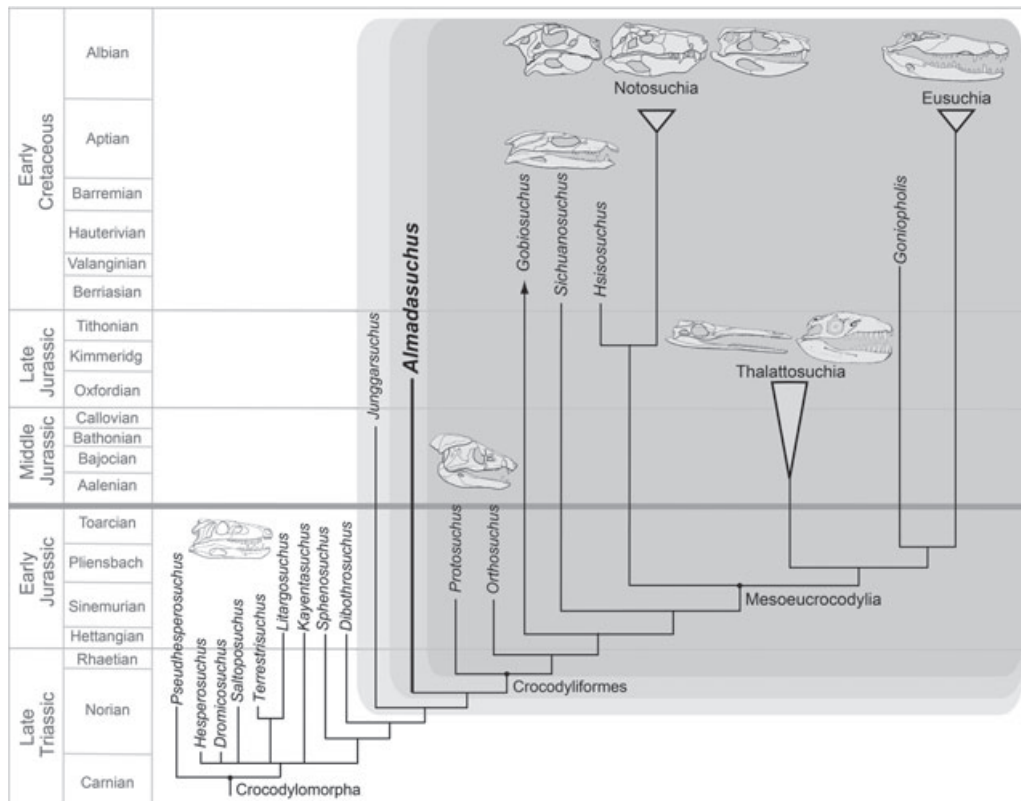


Fig. 4. Summarized phylogenetic tree of Crocodylomorpha. Derived clades are collapsed and examples of extreme skull morphologies are shown (modified from Buckley *et al.*, 2000; Carvalho *et al.*, 2005; Pol & Gasparini, 2009). See online Appendix S2 for further details of the phylogenetic analysis.

(Clark *et al.*, 2004), with a reduction of the basiptyergoid process (Fig. 5). *Almadasuchus* reveals a further step in the strengthening of the skull, with the quadrate strongly sutured to the exoccipital and also contacting the basisphenoid along its lateroventral margins, and a basisphenoid that is not only expanded and highly pneumatic, but also triangular in shape and completely lacking basiptyergoid processes (Fig. 5), a set of features previously known only in Crocodyliformes (e.g. *Protosuchus*). This morphology indicates the achievement of a tightly sutured exoccipitoquadratobasisphenoid complex that differs markedly from the presumably moveable synovial joints between the quadrate and the braincase, present in basal crocodylomorphs (Fig. 5) (Walker, 1990) and most diapsids (Holliday & Witmer, 2008). Although it is uncertain how much movement was actually possible in the skulls of basal crocodylomorphs, it is certain that the cranium was fully akinetic in *Almadasuchus* and all known crocodyliforms. Subsequent changes in the evolutionary history of this group further strengthened the skull, with the development of the exoccipitobasisphenoid suture in crocodyliforms and the anterior extension of the quadrate to contact the laterosphenoid (Fig. 5). The final phase in the evolution of the tightly sutured crocodyliform skull is present in the morphologically diverse Mesoeucrocodylia, which have a solid palate (with fused pterygoids and an extensive participation of the palatine in the bony secondary

palate) that is strongly sutured to the basisphenoid and quadrates, as well as the squamosal suture to the posterior surface of the quadrate (the latter convergently acquired in *Almadasuchus*; Fig. 5). This analysis reveals that the tightly sutured skull that has long distinguished crocodyliforms from other archosaurs originated through the progressive and stepwise appearance of strong sutures between different elements of the braincase, quadrate, and palate along the basal nodes of Crocodyliformes and their successive outgroups *Almadasuchus* and *Junggarsuchus* (Fig. 5).

Most modern crocodylians have a powerful bite (Erickson *et al.*, 2012) and kill prey with rapid whole-body rolling movements in the water (Cott, 1961; Busbey, 1994; Cleuren & Vree, 2000; Erickson *et al.*, 2002), which creates high vertical and torsional loads on the skull (McHenry *et al.*, 2006). Modifications of the snout and palate have been identified as critical for tolerating these stresses in modern crocodiles (Busbey, 1994; McHenry *et al.*, 2006; Pierce *et al.*, 2008), but the tightly sutured braincase-quadrate-palate complex is also necessary for allowing such feeding behaviour. The functional integration of the entire posterior region of the skull (braincase, quadrate, and palate), that progressively increased during the evolution of crocodylomorphs (Fig. 5), allowed not only the evolution of the particular rolling-feeding behaviour of the semi-aquatic modern crocodiles (and likely other semi-aquatic

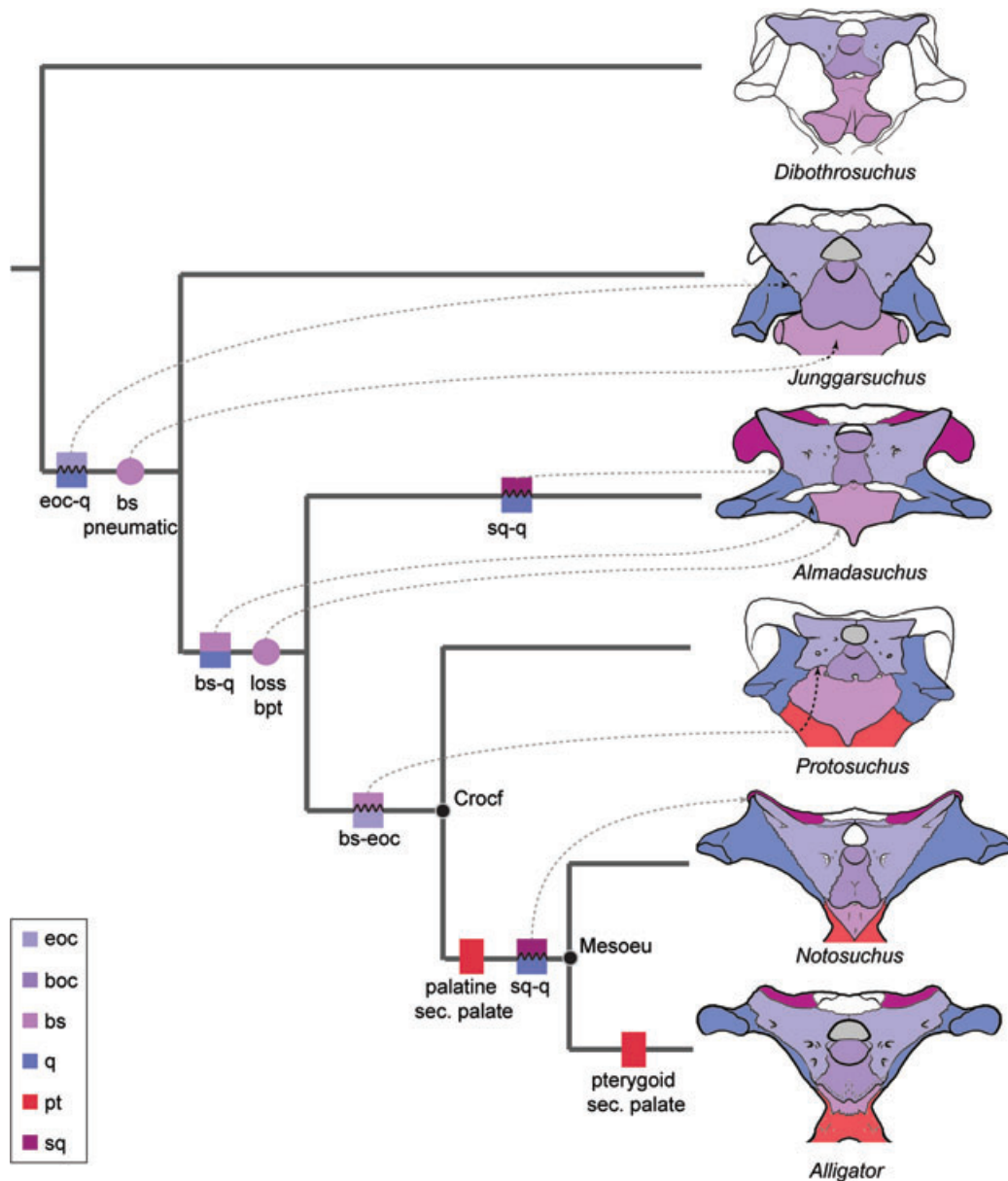


Fig. 5. Major stages in the early braincase evolution of crocodylomorphs, exemplified by six skulls in ventrooccipital view (the partially preserved braincase of *Junggarsuchus* has been reconstructed based on information from the left and right side; *Protosuchus* was modified from Clark, 1986). Major evolutionary events related to the solidification of the skull are mapped on the branches of the tree: coloured rectangles represent appearance of sutural contacts (firm interdigitated sutures are marked with zigzag lines) and circles represent increased pneumaticity. Only bones that are firmly sutured to the braincase are coloured in the figured skulls. boc, basioccipital; bpt, basipterygoid process; bs, basisphenoid; eoc, exoccipital; pt, pterygoid; q, quadrate; sec., secondary; sq, squamosal. Crocf, Crocodyliformes; Mesoeu, Mesoeucrocodylia.

platyrostral taxa, such as advanced neosuchians) but might also have been crucial for the appearance of the remarkable diversity in skull shapes and other feeding strategies in other fossil groups of Mesoeucrocodylia (Figs 4, 5). Examples of this diversity include the marine thalattosuchians in which stress peaks are inferred at the posterior region of the skull during biting (Pierce *et al.*, 2009) or the terrestrial notosuchian crocodyliforms, which evolved into large carnivores (Gasparini, 1984; Carvalho *et al.*, 2005;

Riff & Kellner, 2011) and aberrant, small-sized herbivores with extensive intraoral food processing (Clark *et al.*, 1989; Wu *et al.*, 1995; Buckley *et al.*, 2000; Pol, 2003; O'Connor *et al.*, 2010) (Fig. 4). The relationship of acquisition of a completely akinetic skull and the mechanical requirements of feeding in the morphologically diverse mesoeucrocodylians has an interesting parallel in mammalian evolution, in which the acquisition of an akinetic skull was associated with remarkable ecological diversification, including various

snout and tooth morphologies indicative of intraoral food processing, and the formation of a bony secondary palate (Davis, 1961; Maier, 1999; Liem *et al.*, 2001; Kemp, 2005).

Another implication of the phylogenetic analysis is that, although the initial radiation of 'sphenosuchians' and crocodyliforms already began in the Late Triassic, the only lineages that survived the Early Jurassic were the crocodyliforms and their close relatives *Almadasuchus* and *Junggarsuchus* (Fig. 4) and the poorly known Late Jurassic *Macelognathus* (see online Supporting Information Appendix S2). The derived features that distinguish the surviving lineages from the basal 'sphenosuchians' that went extinct at the end of the Early Jurassic are those related to the initial development of a strongly sutured posterior region of the skull, further underlining the importance of these evolutionary changes.

VI. CONCLUSIONS

(1) A new basal crocodylomorph, *Almadasuchus figari*, from the early Late Jurassic of Patagonia is described. The holotype and only known specimen is represented by a well-preserved posterior region of the skull and associated remains of the premaxillary rostrum, palate, lower jaw, and postcranial elements. *Almadasuchus* differs from all other basal crocodylomorphs in the presence of numerous autapomorphic traits, such as an unusually deep lateral notch on the upper temporal bar, a squamosal with an otic shelf that is wider than long and a deep subtriangular concavity on its posterolateral surface, and an elongated pneumatopore on the ventral surface of the quadrate.

(2) A phylogenetic analysis focused on basal crocodylomorphs and basal crocodyliformes places *Almadasuchus* as the most derived non-crocodyliform crocodylomorph, being the sister group to Crocodyliformes. This phylogenetic position is supported by the shared presence in *Almadasuchus* and Crocodyliformes of derived features of the posterior region of the skull related to the highly modified morphology of the basisphenoid and the skull roof that have long distinguished crocodyliforms from more basal crocodylomorphs.

(3) From a phylogenetic point of view, the braincase anatomy of *Almadasuchus*, coupled with new information on the crocodylomorph *Junggarsuchus* from the late Middle Jurassic of China, reveals a stepwise pattern of character acquisition that finally resulted in the highly modified condition of mesoeucrocodylian crocodyliforms, which have a completely akinetic skull, in which the braincase, quadrate, and an extensive secondary palate are firmly sutured to each other. This integration of the braincase, quadrate, and palate might have been influential for the evolution of the high morphological and ecological disparity of Mesoeucrocodylia.

(4) *Almadasuchus* represents one of the few lineages of non-crocodyliform crocodylomorphs that survived the Early/Middle Jurassic boundary, together with *Junggarsuchus sloani* from China (Clark *et al.*, 2004) and *Macelognathus vagans* and *Hallopus victor* from North America (Marsh, 1877, 1884;

Göhlich *et al.*, 2005). The presence of *Almadasuchus* in the early Late Jurassic of Patagonia demonstrates that basal crocodylomorphs were also part of the continental faunal assemblages in the Middle/Late Jurassic of the southern hemisphere.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Geological and palaeontological context.

Appendix S2. Phylogenetic analysis.

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