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An Unusual Marine Crocodyliform from the Jurassic-Cretaceous Boundary of Patagonia

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Remains of the marine crocodyliform *Dakosaurus andiniensis* from western South America reveal a lineage that drastically deviated from the skull morphology that characterizes marine crocodyliforms. The snout and lower jaw are extremely robust, short, and high and only bear a few large teeth with serrated edges (resembling those of some terrestrial carnivorous archosaurs). This unusual morphology contrasts with the long and gracile snout and lower jaws bearing numerous teeth present in its closest relatives (interpreted as feeding on small fish or mollusks). Thus the morphological diversity of pelagic marine crocodyliforms was wider than had been thought.

The fossil record of crocodyliformes (crocodiles and extinct relatives) shows a wide morphological and ecological diversity. One of the most remarkable examples is Thalattosuchia, the only group of archosaurs completely adapted to the marine environment (*1*). This group is characterized by numerous features including an extremely long and tubular hyperdentate snout (*1–2*). Here, we describe a fossil crocodyliform from Patagonia that expands this variation further.

In the Southern Hemisphere most Mesozoic marine crocodyliforms have come from the Vaca Muerta Formation (*3–5*) in the Neuquén Basin (western Argentina; fig. S1). An extremely fragmentary crocodyliform specimen was previously discovered in this unit and named *Dakosaurus andiniensis* (*6*), due to some similarities with *D. maximus* (*7*) from the Jurassic of Europe. However, the fragmentary nature of this enigmatic material offered few answers about the habits and relationships of this large marine crocodyliform. Two new specimens of *D. andiniensis* were recently found in Pampa Tril (fig. S1), a rich fossiliferous locality of the Vaca Muerta Formation, and are referred to this taxon due to the presence of autapomorphic characters for a marine crocodyliform (*8*). One of these includes of a lower jaw (MOZ 6140P) and the other (MOZ 6146P) consists of an almost complete skull and lower jaws (Fig. 1 and fig. S2). The new skull is almost complete and reveals an unusual skull and dental morphology. The skull and mandible are approximately 80 cm long from the anterior end to the cranio-mandibular articulation. The snout is high with respect to its anteroposterior length (Fig. 1 and fig. S2) in comparison with all other marine crocodyliforms (*2– 9*), being 42 cm long and 15.3 cm high (measured at the anteroposterior midpoint of the rostrum). The lateromedial width of the rostrum is subequal to its dorsoventral depth. Anteriorly, the rostrum tapers rapidly, producing an unusual bullet-shaped skull. Most of the dorsal surface of the snout is convex and level with the dorsal surface of the frontal and supratemporal region. The subcircular orbit faces laterally and is large, constituting approximately 18% of the skull length. A large scleral ring is preserved in this opening. The elongated antorbital fossa is obliquely oriented and the lacrimal, nasal, maxilla, and jugal bones form its margins, as in metriorhynchid thalattosuchians (*2–10*).

The premaxilla is only preserved on the left side and encloses a large narial opening, although the dorsomedial region of this element is unknown for this taxon. The maxilla is notably short and high, and extends dorsally contacting its counterpart and separating the nasals from the premaxilla. This element contributes to 65% of the rostral length. The nasals are short and broad but they project posteroventrally as a long and acute process onto the lateral surface of the snout. The lacrimals are only exposed on the lateral surface of the rostrum and are dorsally sutured to the extensive prefrontal and nasals. The enlarged prefrontal extends onto the lateral surface of the snout and overhangs the orbit, a synapomorphic character of metriorhynchids (*2*).

The frontals and parietals are completely fused into single elements, as in all mesoeucrocodylians (*10*). The straight frontal-nasal suture runs at a 45-degree angle with the sagittal plane, resembling the condition of *D. maximus* (*7*). The squamosal has a short anterior branch and the postorbital extends ventrally on the lateral surface of the postorbital bar, being continuous with the lateral surface of the jugal as in all thalattosuchians (*10*). The quadrate is well developed, with robust articular condyles, and contacts the ventrolateral flange of the exoccipital as in all crocodyliforms (*10*). The basioccipital is low and bears small basioccipital tubera, contrasting with the developed condition of marine crocodyliforms. The exoccipital bears a large foramen for the internal carotid artery on its ventrolateral flange. The palatines form an extended secondary palate and enclose with pterygoids a wide choanal opening.

The mandible is high, robust, and slightly diverges posteriorly following the narrow outline of the skull, contrasting with the low and gracile morphology of other marine crocodyliforms (*1*, *2*, *11*). The mandibular symphysis is short and its external surface is slightly convex and dorsoventrally high (MOZ 6140P; fig. S2). A broad and deep sulcus extends on the lateral surface of the dentaries and surangular, ending in a large foramen at both ends (as in *D. maximus*). The external mandibular fenestra is completely obliterated.

The upper dentition is composed of three premaxillary and 10 (or 11) large maxillary teeth, an unusually low number of teeth for a marine crocodyliform. Most thalattosuchians have between 25-40 small teeth, except for *D. maximus*, which has a minimum of 20 teeth in the upper tooth row (*2*). All preserved teeth of *D. andiniensis* are large, robust, poorly curved, and interlock extensively with the lower dentition (Fig. 1E). The crowns are lateromedially compressed and have serrated margins, resembling only those of *D. maximus* (*7*) among marine crocodyliforms. The denticles have a proportionately large basal length with respect to their height and are well separated from each other by broad cella and interdenticular slits (Fig. 1, F and G). 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. 1F). The outer enamel surface of all preserved teeth is divided into a basal smooth zone and a wrinkled apical region with distinct ring-like depressions.

This dental morphology is unique among marine reptiles; only some mosasaurs have serrated teeth, but they have remarkably small denticles (*12*). In contrast, the presence of denticles is common among terrestrial carnivorous archosaurs, including some crocodyliforms [e.g., *Baurusuchus, Iberosuchus*, *Sebecus*, *Pristichampsus* (*1*, *9*, *13*, *14*)]. However, the serrated teeth of terrestrial crocodyliforms are chisel-shaped, with a shorter basal length, larger diaphyseal height, and narrow interdenticular slits (*12*, *14*–*16*). These differences are consistent with the independent origin of ziphodont dentition in *Dakosaurus* inferred from the phylogenetic results.

A phylogenetic dataset was gathered considering representatives of all major clades of Crocodyliformes (*17*, *18*). The cladistic analysis places *D. andiniensis* as closely related to *D. maximus* (Fig. 2), as indicated by the presence of a proportionately higher rostrum and lateromedially compressed and serrated teeth. This group is deeply nested within Metriorhynchidae, the clade of crocodyliforms with the most remarkable adaptations to the marine environment [e.g., paddle-like forelimbs, hypocercal tail, osteoporotic-like bone (*19*), hypertrophied nasal salt glands (*20*)]. This group is well supported by the data and diagnosed by numerous cranial synapomorphies present in *D. andiniensis* (*17*). The available postcranial material of *D. andiniensis* is too scarce to assess if the swimming capabilities of this crocodyliform were similar to those of other metriorhynchids.

The phylogenetic hypothesis implies that the *Dakosaurus* lineage evolved from the ancestral gracile condition present in most thalattosuchians (Fig. 2). Within this framework, the European *D. maximus* represents an initial stage in the evolution of a lineage that departs from the above mentioned conditions, showing the acquisition of relatively enlarged teeth with serrated margins, and a moderately high snout, but preserving many plesiomorphies of other metriorhynchids (e.g., large number of teeth, elongated symphysis, snout length occupying more than 60% of the skull). However, the unusual morphology of *D. andiniensis* creates a large morphological gap between this taxon and all other marine crocodyliforms.

One of the most striking differences is the extremely high and robust rostrum in *D. andiniensis*. We considered the variation in rostral height and length through the optimization of their ratio across the phylogenetic tree of Crocodyliformes using the maximum parsimony criterion (Fig. 3). As optimized in the tree, this analysis illustrates the differences between *D. andiniensis* and other marine taxa, while revealing the major trends in rostral change along the evolutionary history of Crocodyliformes.

The large diversity of rostral shapes among basal terrestrial crocodyliforms (*21*) is reflected in the disparity of rostral height/length ratios among these small forms (left of Fig. 3). However, this graph shows a clear phylogenetic trend in neosuchian crocodyliforms toward longer rostra that are proportionately low dorsoventrally (right of Fig. 3). These morphological changes coincide with a shift toward the aquatic habits inferred for most neosuchian taxa and have been explained as adaptations to this environment, related changes in feeding strategies, and to increase mechanical resistance in their rostra (*1*, *9*, *22*).

Although different rostral morphologies are present in living crocodylians (*23*) and moderate cases of rostral shortening have been reported in some longirostrine groups (*17*, *24*, *25*), the general trend toward long and low snouts is present in most neosuchian groups (Fig. 3). This trend reaches an extreme condition in thalattosuchian crocodyliforms, depicting the characteristic elongated and gracile snouts of these marine crocodyliforms. The hyperdentate tubular rostrum in this group has long been considered as an adaptation to feeding on small agile prey, such as mollusks (*26*) or fishes (based on the diet of extant crocodylians with similar rostral morphology (e.g., *Gavialis*) (*1*, *9*, *22*). The feeding strategy of these taxa is usually inferred to be based on rapid lateral movements, facilitated by the large angular speed and low hydrodynamic resistance of their elongated and low rostra (*1*, *9*, *22*).

The *Dakosaurus* lineage appears to have reversed this trend in a drastic morphological change, with *D. maximus* an incipient representative of this condition and *D. andiniensis* the most extreme case of rostral modification (Fig. 3). The relatively short and high rostrum and ziphodont dentition probably reflects a modified feeding strategy, as the hydrodynamic advantages allowing rapid lateral movements would not be present in *D. andiniensis*. Although the snout height/length ratios depict similar values for *D. andiniensis* and some terrestrial crocodyliforms (e.g., *Baurusuchus*), there are remarkable differences in other aspects of their rostral shape, such as the reduced width of the snout and the vertically orientated maxillae of these terrestrial forms.

References and Notes

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18. The phylogenetic dataset included 257 characters scored across 58 crocodylomorph taxa at the species level, expanding previously published datasets (*27*), and was analayzed using using parsimony in TNT v.1.0 (*28*). See supporting online material for further details (*17*).
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30. The specimens reported here were found by S. Cocca and R. Cocca from the Museo Olsacher (Dirección de Minería, Neuquén Province, Argentina) and prepared by J. Moly (Museo de La Plata). SEM images were taken by D. Urréjola. Drawings for Figs. 1 to 3 were executed by Jorge González. We thank S. Hwang and G. Erickson for

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Supporting Online Material
www.sciencemag.org/cgi/content/full/1120803/DC1
Materials and Methods
Figs. S1 and S2
References

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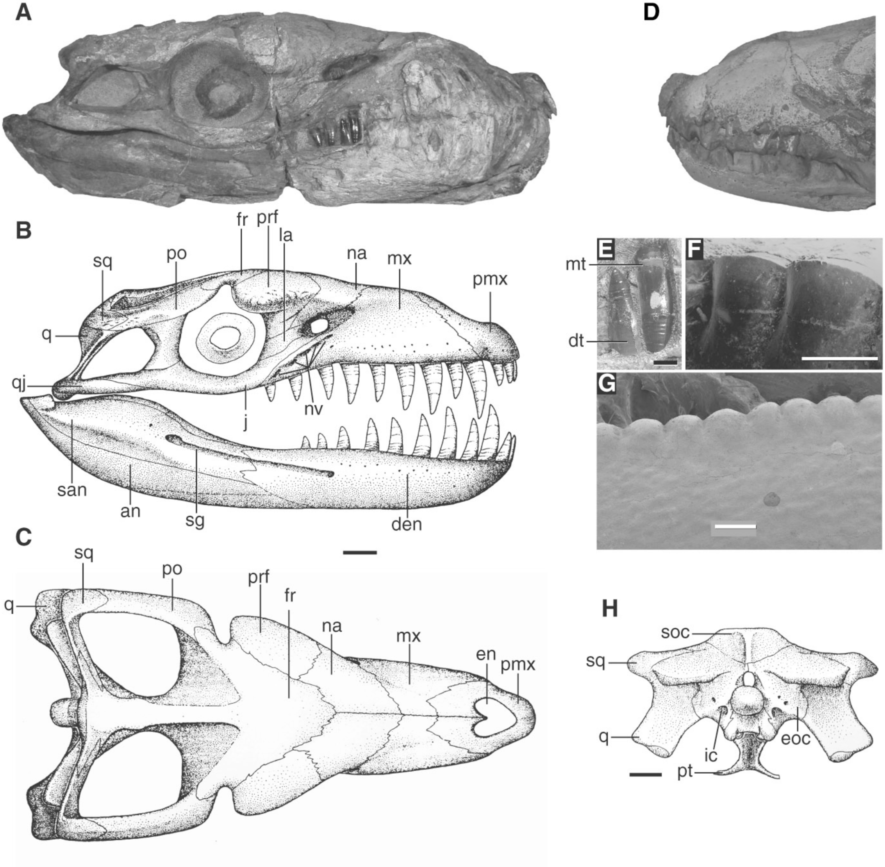
Fig. 1. *Dakosaurus andiniensis* MOZ 6146P in (**A**) right lateral view. Skull reconstruction in lateral (**B**), dorsal (**C**), and occipital (**H**) views (based on left and right sides). (**D**) Rostrum of in left dorsolateral view. (**E**) Posterior maxillary and dentary teeth. (**F** to **G)** Mesial denticles in mesial (F) and buccal (G) views. Scale bars: 5 cm [(A) to (E) and (H)], 500 μm [(F) to (G)]. Abbreviations: an, angular; den, dentary; dt, dentary tooth; eoc, exoccipital; fr, frontal; ic, internal carotid foramen; j, jugal; la, lacrimal; mt, maxillary tooth; mx, maxilla; na, nasal; pmx, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; san, surangular; sg, surangular groove; soc, supraoccipital; sq, squamosal.

Fig. 2. Phylogenetic relationships of Crocodyliformes obtained in the cladistic analysis, plotted against geochronologic epochs (strict consensus of most parsimonious trees; some taxa distantly related to *D. andiniensis* collapsed into triangular clades). Only skulls figures of Thalattosuchia were drawn to the same scale (*17*). Numbered nodes: 1: Crocodyliformes, 2: Neosuchia, 3: Thalattosuchia, 4: Metriorhynchidae. Further phylogenetic information is available on *Science* Online (*17*).

Fig. 3. Phylogenetic tree of Crocodyliformes displaying the evolution of rostral shape, as measured by the rostral height / rostral length ratio optimized using TNT (*28*, *29*). Root of the tree located on the left side of the figure (marked in gray) and derived forms toward the right. Vertical location of the nodes determined by the ratio values following the ordinate axis (solid circles = measured species (*17*), empty circles = inferred ancestral values, error bars = ranges of possible ancestral values). Circle size represents the absolute value of rostral length measured in terminal taxa and inferred for ancestral nodes (scale for circle size and rostral length in cm in top right corner) (*17*). Abbreviations: Gra, *Gracilisuchus*; Dib, *Dibothrosuchus*; Orth, *Orthosuchus*; Prot, *Protosuchus*; Gobio, *Gobiosuchus*; Sich, *Sichuanosuchus*; Simo, *Simosuchus*; Noto, *Notosuchus*; Baur, *Baurusuchus*; Ara, *Araripesuchus*; Loma, *Lomasuchus*; Gonio, *Goniopholis*; Gav, *Gavialis*; Croc, *Crocodylus niloticus*; Allig, *Alligator*; Sarco, *Sarcosuchus*; Dyros, *Dyrosaurus*; Steneo, *Steneosaurus*; Pelago, *Pelagosaurus*; M.sup, *Metriorhynchus superciliosus*; M.cas, *Metriorhynchus casamiquelai*; Geo, *Geosaurus araucanensis*.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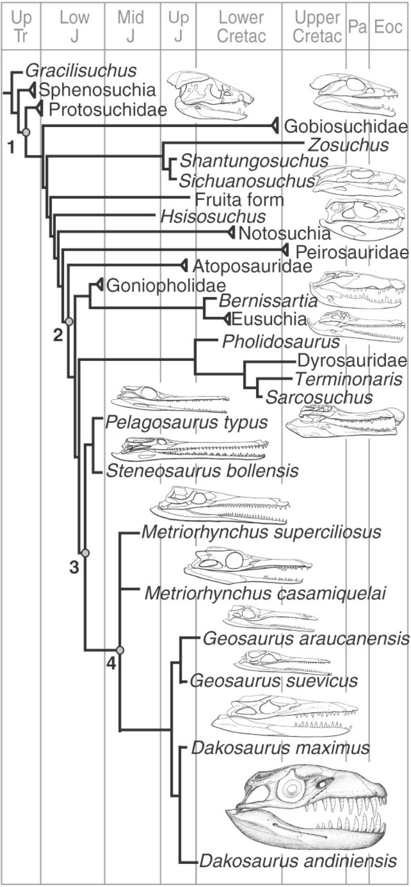
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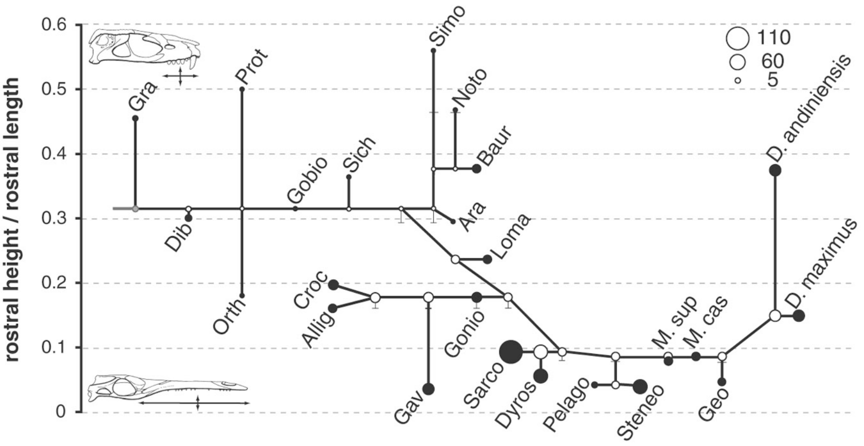
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