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New material of *Dolichochampsa minima* (Archosauria: Crocodylia) from the Cretaceous–Palaeogene El Molino Formation of Bolivia sheds light on the early evolution of Gavialinae

Kevin I. Vélez-Rosado^{a,b*}, Olga I. Zalles-Grebetskaya^c, Jeffrey A. Wilson Mantilla^{a,b}, Blaire Schoene^d, Adam Maloof^d and Bolton Howes^{d,e}

^aMuseum of Paleontology, University of Michigan, 1105 N. University Avenue, Ann Arbor, Michigan 48109-1085, USA; ^bDepartment of Earth and Environmental Sciences, University of Michigan, 1100 N. University Avenue, Ann Arbor, Michigan 48109-1005, USA; ^cUniversidad Mayor de San Andrés, Campus de Cota Cota, calle 27, La Paz, Bolivia; ^dDepartment of Geosciences, Princeton University, Princeton, New Jersey 08544, USA; ^eRosenstiel School of Marine, Atmospheric, & Earth Science, Miami, FL 33149, USA

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Four Late Cretaceous taxa have been suggested to be amongst the oldest gavialoids: 'thoracosaurs' from North America; *Ocepesuchus eoafricanus* from Africa; *Portugalosuchus azenhae* from Portugal; and *Dolichochampsa minima* from South America. The evolutionary relationships of these taxa to definitive gavialoids remain contentious. Resolving the evolutionary relationships of early gavialoids is important for understanding the timing of the origin of the clade and its potential distribution across landmasses. Here, we report new material of *Dolichochampsa minima* from the Late Cretaceous–early Paleocene (73–64 Ma) El Molino Formation of Bolivia that provides key anatomical information elucidating the evolutionary relationships of early gavialines. A phylogenetic analysis based on a revised and expanded morphological character data set recovers *D. minima* nested within Gavialinae. The other putative gavialoids, however, were resolved outside of Gavialoidea: *Ocepesuchus* was recovered within alligatorids; 'thoracosaurs' were recovered outside crown-group Crocodylia; and *Portugalosuchus* was recovered within 'thoracosaurs'. This phylogenetic hypothesis implies that several characters associated with longirostry evolved independently in gavialines and 'thoracosaurs'. The phylogenetic relationships and geographical distribution of early gavialines suggest a plausible centre of origination in Gondwana for the group, followed by multiple trans-oceanic dispersals during the Late Cretaceous to other landmasses and possible dispersals to South America from the peri-Tethys during the late Palaeogene.

Keywords: Gavialinae; Dolichochampsa; systematics; palaeobiogeography; Bolivia

Introduction

Gavialid crocodylians today are represented by just two species, both of which are restricted to freshwater habitats in Asia (Bezuijen et al., 2010; Stevenson, 2015) – the Indian gharial (*Gavialis gangeticus*) and the Indonesian false gharial (*Tomistoma schlegelii*). The relatively restricted habitat, low diversity and geographical distribution of living gharial species belies the deeper history of the group, which was more diverse, and achieved a nearly global distribution during most of the Cenozoic, perhaps due to different dispersal capabilities. Unravelling the history of the earliest gavialids is essential for understanding when and where the group originated, which has important implications for their biogeographical history and palaeobiology.

The phylogenetic names used herein follow phylogenetic definitions proposed by Brochu (2003). Eusuchia (eusuchians) includes the last common ancestor of Hylaeochampsa vectiana, Crocodylus niloticus, Gavialis gangeticus and Alligator mississippiensis. Crocodylia is defined by the last common ancestor of Gavialis gangeticus, Alligator mississippiensis, and Crocodylus niloticus and all of its descendants. Gavialoidea (gavialoids) is defined by a group including G. gangeticus and all crocodylians more closely related to it than to A. mississippiensis or C. niloticus. Gavialidae (gavialids) includes the last common ancestor of G. gangeticus and Tomistoma schlegelii and all of its descendants. Gavialinae (gavialines) is a subgroup of Gavialidae that includes G. gangeticus and all crocodylians more closely related to it than to T. schlegelii.

Corresponding author. Email: kvelez@umich.edu

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Several Late Cretaceous taxa have been suggested to be amongst the earliest fossil gavialoids: the 'thoracosaurs' from the circum-Atlantic; Ocepesuchus eoafricanus from Africa: Portugalosuchus azenhae from Portugal; and Dolichochampsa minima from South America (Brochu, 2004, 2007; Carpenter, 1983; Gasparini & Buffetaut, 1980; Jouve et al., 2008; Mateus et al., 2019; Rio & Mannion, 2021). The evolutionary relationships of these four taxa to gavialoids are either ambiguously resolved ('thoracosaurs', O. eoafricanus) or have not been tested in a phylogenetic framework (D. 'Thoracosaurs' comprise several North minima). American (Eothoracosaurus mississippiensis, Eosuchus minor and Thoracosaurus neocesariensis) and European (Eosuchus lerichei) taxa, some reaching body lengt hs of up to 6 m (Brochu, 2004; Carpenter, 1983; Delfino et al., 2005; Rio & Mannion, 2021). They are generally associated with sediments and fauna from coastal to shallow marine environments, an indication that perhaps they were capable of tolerating marine waters (Brochu, 2004; Carpenter, 1983; Delfino et al., 2005; Erickson, 1998; Gallagher et al., 1986; Schwimmer, 1986; Troxell, 1925). 'Thoracosaurs' share a suite of morphological attributes with crown-group gharials, some of which are associated with longirostry (Brochu, 2004, 2006; Delfino et al., 2005; Rio & Mannion, 2021; Vélez-Juarbe et al., 2007). As a consequence, 'thoracosaurs' have been resolved consistently within Gavialoidea in osteological phylogenetic analyses (Brochu, 2004, 2006; Salas-Gismondi et al., 2016, 2019; Vélez-Juarbe et al., 2007).

Total evidence approaches to resolve the apparent disagreement between molecular and morphological data have produced an entirely new hypothesis of relationships for 'thoracosaurs'. Analysis of a data set combining DNA and morphology recovered 'thoracosaurs' outside of Crocodylia (alligators and caimans, crocodiles, and gharials), on the stem lineage leading to the group (Lee & Yates, 2018, fig. 2). Because 'thoracosaurs' were resolved outside of Crocodylia, Gavialidae was hypothesized to originate more recently in the Cenozoic, consistent with molecular-based analyses (Densmore & Dessauer, 1984; Hass et al., 1992; Janke et al., 2005; Meredith et al., 2011; Oaks, 2011; Pan et al., 2021; Willis et al., 2007). Gatesy et al. (2003) and Lee and Yates (2018) offered an explanation for why 'thoracosaurs' and gharials previously had been recovered together in most phylogenetic studies, referring to a 'perfect storm' of morphological similarities due to shared feeding behaviour (i.e. fish-eating) and atavisms in gavialids. It is important to state that although the results of their total evidence approach resolve 'thoracosaurs' outside Crocodylia, analysis of the morphological data alone still supports a sister-clade relationship to crown gharials (Lee & Yates, 2018, fig. 1) as proposed by other morphology-based studies (Brochu, 1997, 2003, 2004; Brochu & Storrs 2012; Salas-Gismondi et al., 2016, 2019; Vélez-Juarbe et al., 2007).

Portugalosuchus azenhae is a relatively large (2.5-3.0 m body length) eusuchian from the Late Cretaceous of Portugal (Mateus et al., 2019; Puértolas-Pascual et al., 2023). The holotype of P. azenhae was first described as one of the earliest members of Crocodylia, being recovered as the sister taxon to non-gavialoid crocodylians (Mateus et al., 2019, fig. 11). Later, Rio and Mannion (2021), in their extensive study using an expanded morphological data set of crocodylians, recognized P. azenhae as a gavialoid. In their analysis, it forms a clade with Eothoracosaurus and Thoracosaurus based on skull characters. More recently, Darlim et al. (2022) recovered P. azenhae outside of Crocodylia in a tip-dated Bayesian analysis that used DNA and morphology. Uncertainty still surrounds the phylogenetic position of P. azenhae but its significance as an early gavialoid deserves consideration in the present study.

The two putative gavialoid species from the Late Cretaceous of Gondwana, Ocepesuchus eoafricanus and Dolichochampsa minima, may have important implications for the spatiotemporal origin of the clade. Ocepesuchus is from the latest Cretaceous of the Oulad Basin of Morocco and is represented by a partial skull (Jouve et al., 2008). A morphology-based phylogenetic analysis recovered both O. eoafricanus and 'thoracosaurs' in a polytomy within crown gharials, a result that seems to agree with morphology-based studies (Brochu, 1997, 2003, 2004, Brochu & Storrs 2012; Jouve et al., 2008; Salas-Gismondi-et al., 2016, 2019; Vélez-Juarbe et al., 2007). Dolichochampsa, in turn, is a small (1 m estimated total body length) longirostrine crocodylian from South America (Buffetaut, 1987; Gasparini & Buffetaut, 1980: Jouve et al., 2021). The holotype of D. minima is a partial dentary from the Cretaceous of the Yacoraite Formation of Salta Province in Argentina (Gasparini & Buffetaut, 1980). Referred materials from the same locality and from Bolivia include portions of the skull, axial column, pelvis and hindlimb. Dolichochampsa was proposed to be a gavialid based on features present only found in the basally diverging gharials Eogavialis africanus and Argochampsa krebsi: (1) a long and flat symphysis; (2) an estimated tooth count of approximately 20 teeth, separated by deep lateral sulci; (3) alveoli of similar size and located lower than the medial margin of the symphysis; and (4) the presence of a basioccipital tuber (Buffetaut, 1987; Gasparini & Buffetaut, 1980; Jouve



Figure 1. Map of South America showing where the new specimen of *Dolichochampsa minima* FCGV-8178 was collected in southern Bolivia. The inset map details the syncline of Maragua and identifies the locality (yellow star) within an exposed section of the Upper El Molino Formation.

et al., 2021). Although *D. minima* shares a set of morphological characters with crown-group gharials (Gavialinae), the taxon has never been included in phylogenetic studies. Evaluating *D. minima* in a cladistic context is important because if it is indeed a member of Gavialinae, it will suggest a Cretaceous origin for the group, as opposed to a much younger, Miocene origin for the clade as proposed by molecular-based hypotheses (Densmore & Dessauer, 1984; Hass et al., 1992; Janke et al., 2005; Willis et al., 2007).

The evolutionary relationships of 'thoracosaurs', *Portugalosuchus azenhae, Ocepesuchus eoafricanus* and *Dolichochampsa minima* have important implications for the temporal (Cretaceous vs Cenozoic) and geographical (Laurasia vs Gondwana) origin of early gavialines, as well as their past dispersal history. Here, we report new material of a small-sized eusuchian from the Cretaceous–Paleocene El Molino Formation of Bolivia. We present a detailed morphological description of the new specimen,

which appears to be referable to *D. minima*, and compare it with contemporaneous and related crocodylian taxa. We examine the evolutionary relationships of *D. minima* for the first time and reevaluate the gavialoid affinities of 'thoracosaurs' and *Ocepesuchus eoafricanus* within a parsimony framework using an expanded morphological data set. We discuss the implications of this phylogenetic hypothesis and the palaeobiogeography of Cretaceous gavialines in South America.

Institutional abbreviations

FCGV, Collection of Vertebrates, Universidad Mayor de San Andrés, Facultad de Ciencias Geológicas, La Paz, Bolivia; MLP, Collection of the División Paleontología Vertebrados, Museo La Plata; MUSM, Vertebrate Palaeontology Collection of the Natural History Museum of San Marcos University; UM, University of Michigan, Ann Arbor, Michigan, USA.

Geological and palaeoenvironmental setting

The new specimen of Dolichochampsa minima (FCGV-8178) described herein was found in 2019 during a field survey of exposures of the Middle and Upper Members of the El Molino Formation of the Potosí Basin near the village of Maragua, approximately 18 km west of Sucre, Bolivia (Howes, 2023, fig. 1). The Potosí Basin is a back-arc flexural basin formed in response to the emergence of the Andes that accumulated up to 450 m of sediment from the Cenomanian to middle Paleocene (Lamb et al., 1997; Sempere, 1994; Sempere et al., 1997). The El Molino Formation is exposed throughout Bolivia, particularly in the Eastern Cordillera and on the Altiplano, and it may be penecontemporaneous with the Yacoraite Formation of Argentina, where the holotype of D. minima was collected (Gasparini & Buffetaut, 1980; Marquillas et al., 2011; Sempere et al., 1997).

During the Late Cretaceous, the deepest portion of the basin, the foredeep, was in what is now the Altiplano in western Bolivia. The shallower portion of the basin, potentially the forebulge or backbulge, is preserved in the Eastern Cordillera, which includes Maragua (Sempere, 1994). The latest Cretaceous–Early Paleocene sediments of the Potosí Basin record a tropical-to-subtropical $(23-25^{\circ}S)$ lacustrine environment roughly the size of the modern Caspian Sea $(370,000 \text{ km}^2; \text{ Matthews et al., 2016})$. This environment experienced fluctuating water levels and occasional marine influence (Camoin et al., 1997; Gayet et al., 1993; Rouchy et al., 1993; Tasistro-Hart et al., 2020).

The cause of fluctuating water levels and the degree to which the basin was connected to the ocean has been a source of debate. Gayet et al. (1993) and Sempere (1994) argued that eustasy was the primary control on water levels in the Potosí Basin, based on a correlation between the transgressions at the base of the Lower, Middle and Upper members of the El Molino Formation and the global marine transgressions of the Haq et al. (1987) sealevel curve. However, Rouchy et al. (1993) and Camoin et al. (1997) suggested that fossil (vertebrate, invertebrate and pollen) assemblages of the El Molino are almost entirely terrestrial and that some previously identified fossils were incorrectly attributed to marine environments. Rouchy et al. (1993) and Camoin et al. (1997) also argued that sulfur isotopes from evaporitic gypsum from the Chaunaca and Santa Lucia Formations are lighter than would be expected from evaporating marine waters and, therefore, it is most likely that the El Molino also is predominantly terrestrial.

A recent cyclostratigraphic study of the El Molino Formation seems to reconcile the marine and lacustrine viewpoints by demonstrating that regional hydrology and global sea level were both primary

drivers of lake levels and sediment composition, but at different times (Tasistro-Hart et al., 2020). The sediments at the bottom of the Lower El Molino preserve periodicities consistent with semi-precession, precession and eccentricity (which modulates precession), potentially reflecting the orbitally driven changes in the position of the intertropical convergence zone (ITCZ). The sensitivity to the position of the ITCZ implies that regional hydrology was the driver of lake levels and sediment flux during the deposition of the lower portion of the Lower Member of the El Molino Formation. In the upper portion of the Lower Member of the El Molino Formation, the precession signal disappears, and an obliquity signal becomes statistically significant, which Tasistro-Hart et al. (2020) attributed to a strengthened connection with the ocean. It appears that at that time, the ocean was experiencing obliquity-driven glacioeustasy (according to the sea-level curve from Miller et al., 2005), which is recorded by the El Molino Formation.

In addition to clarifying the depositional history of the El Molino, the cyclostratigraphic study of the Potosí Basin provided new age estimates for the El Molino Formation. Previous palaeontological work had determined that the Maastrichtian-Danian boundary is within the El Molino Formation, but had not precisely located the position of the K-Pg boundary. The U-Pb ages and astrochronology from Tasistro-Hart et al. (2020) determined that the K-Pg boundary is near the contact between Middle and Upper Members of the El Molino Formation at Maragua. The sample in this study was collected in the uppermost portion of the Middle Member of the El Molino Formation, and so our best estimate of the age places the sample in the late Maastrichtian, but uncertainty in the U-Pb ages and astrochronology do not preclude an early Danian age for this sample.

Phylogenetic methods

The new Bolivian crocodylian specimen (FCGV-8178) possesses features that place it within Eusuchia (e.g. choana within pterygoids, procoelous vertebral centra). We incorporated FCGV-8178 into a data set of a subset of Neosuchia that includes Crocodylia (crown-group crocodylomorphs, uniting Alligatoridae, Crocodylidae and Gavialidae), its immediate relatives (e.g. *Hylaeochampsa*), and three putative gavialoid taxa (i.e. 'thoracosaurs', *Ocepesuchus eoafricanus, Dolichochampsa minima*). Below, we outline the methods we implemented for the parsimony analysis.

Character-taxon matrix

The taxonomic scope of our analysis (Crocodylia and immediate relatives) is similar to that of many previous phylogenetic studies. We chose the Salas-Gismondi et al. (2022) data set as a starting point because it is the most recent iteration of a character list that has been in development for more than two decades (Brochu, 1997, 2003, 2004; Salas-Gismondi et al., 2016; 2019; Vélez-Juarbe et al., 2007), and because it includes a large number of gavialoid operational taxonomic units (OTUs). The Salas-Gismondi et al. (2022) data set contained 233 discrete morphological characters that include 185 cranial (79%), 22 axial (9%), 14 appendicular (6%), 8 osteodermal/ shield (3%), and 4 soft tissue (2%) features.

We reevaluated the character list of Salas-Gismondi et al. (2022) and modified the states of 24 characters to better reflect the morphological variation in the OTUs included in this analysis using two data sets and firsthand observation of specimens (see Supplemental Material Appendix S1, S2.1, and S2.2). In addition, we incorporated 26 characters from the Ristevski et al. (2018) data set. We removed 17 characters from the Salas-Gismondi et al. (2022) data set, 15 of which were uninformative (ch. 15, 20, 21, 30, 80, 83, 98, 99, 107, 110, 136, 170, 193, 199, and 214), and two of which (ch. 191, 209) were redundant with characters incorporated from Ristevski et al. (2018) that included additional character states. To this revised data set, we added six new discrete characters. The complete matrix includes 265 osteological characters listed and described in Supplemental Material Appendix S2.1. In addition to the complete data set, we included a .tnt file containing only the 248 characters and 68 OTUs used in the phylogenetic analysis as a supplementary file. Descriptions of morphological characters in the following sections follow the complete data set, which can be found in Supplemental Material Appendix S2.1.

The original matrix of Salas-Gismondi et al. (2022) included 69 OTUs, but we pruned three taxa by safe taxonomic reduction (Wilkinson, 1995): Charactosuchus fieldsi, Crocodylus falconensis and Gavialosuchus eggenburgensis. We also removed the Siwalik Gavialis from the analysis because it requires further taxonomic revision (Martin, 2019), as well as an undescribed taxon (MUSM 1513) for which we were not able to verify scorings. We added Isisfordia duncani and Ocepesuchus eoafricanus. Portugalosuchus azenhae was scored in our matrix using the available data set by Narváez et al. (2016), which is mainly based on the Brochu (1999) matrix and similar to the present study. Portugalosuchus was scored only for 53 (21%) characters, 44 cranial and 9 mandibular. Specimen FCGV-8178 is a single individual that we refer to Dolichochampsa minima, based on its morphological

similarities to the holotype and other individuals associated with the same taxon, as discussed below (Buffetaut, 1987; Gasparini & Buffetaut, 1980; Jouve et al., 2021). We scored *D. minima* based on first-hand observations from FCGV-8178, photographs and descriptions of the holotype, and referred material from Bolivia available in the published literature (Buffetaut, 1987; Gasparini & Buffetaut, 1980; Jouve et al., 2021). We were able to score *D. minima* for 35 of the 248 characters (86% missing) used in the analysis (see .tnt file under Supplemental Material for more details), including 24 cranial, 10 mandibular, and 1 girdle features.

Parsimony analysis

We performed a maximum parsimony analysis in TNT 1.6 (Goloboff & Morales, 2023). Characters were equally weighted, unordered and non-additive. Bernissartia fagesii was designated as the outgroup taxon. The settings were changed to hold a maximum of 99,999 trees. A traditional heuristic tree search was executed using 1000 Wagner replicates and random addition sequences, and a tree bisection-reconnection (TBR) algorithm was implemented. Nodal support values were calculated using the BREMER.RUN script included in the TNT package, and standard bootstrap and jackknife analyses were performed under a traditional search using 1000 replicates with absolute frequencies activated. Unstable taxa were identified post-analysis by the iterative positional congruence (reduced) (PCR) protocol (Pol & Escapa, 2009) as implemented in TNT 1.6.

Systematic palaeontology

Suborder Eusuchia Huxley, 1875 Crocodylia Gmelin, 1789

Superfamily **Gavialoidea** Hay, 1930 (*sensu* Brochu, 1999) Family **Gavialidae** Adams, 1854 (*sensu* Brochu, 2003) Subfamily **Gavialinae** Nopcsa, 1923 (*sensu* Brochu, 2003) Species *Dolichochampsa minima* (Gasparini & Buffetaut, 1980)

(Fig. 2)

Diagnosis (emended from Gasparini & Buffetaut, 1980; Jouve et al., 2021). *Dolichochampsa minima* is a smallsized gavialine crocodylian diagnosed by the following unique combination of character states: the posterior margin of the choana is not defined, being flush within the pterygoids; the 'secondary wings' of the pterygoid are large and contribute to the posterior floor of the choana; and the interchoanal septum is a narrow bony sheet that does not fully divide the opening. We identified a new autapomorphy based on the skull of FCGV-



Figure 2. Photograph of the block containing all elements of the new specimen of *Dolichochampsa minima* (FCGV-8178). Abbreviations: al, alveoli; ch, choana; dv, dorsal vertebra; j, jugal; mt I, metatarsal I; mx, maxilla; ns, neural spine; pfe, proximal part of femur; pl, palatine; pt, pterygoid; sc, scapula; sof, suborbital fenestra; ti, tibia.

8178, a flat pterygoid wing. *Dolichochampsa* differs from all other gavialines by having a septum that remains recessed within the choana (ch. 125 [1]), which is the primitive condition in basal eusuchians such as *Isisfordia duncani* (Salisbury et al., 2006, fig. 4).

Referred material. The new material of *Dolichochampsa minima* (FCGV-8178) includes both cranial and postcranial remains. The skull includes part of the braincase, palate (pterygoid, palatine) and rostrum (maxilla). Postcranial elements include the right scapula, a dorsal vertebra, the right ischium, the right femur, a right tibia, and a metatarsal.

Locality, horizon and age. The new specimen was retrieved near Maragua, Oropeza Province, Bolivia, some 18 km W of Sucre. It was preserved in a brown-to-reddish mudstone unit from the upper portion of the Middle El Molino Formation, which has been dated at *c*. 73–64 Ma (Tasistro-Hart et al., 2020, table 3).

Comments. We refer FCGV-8178 to *Dolichochampsa minima* based on morphological similarities to the holotype from Argentina and referred specimens from Bolivia. These include a tubular snout with well-defined notches that form an interdigitating jaw closure, procoelous dorsal vertebrae with a well-developed condyle, and the overall resemblance of the femur to specimen MLP 73-II-28-1 from Argentina (Gasparini & Buffetaut, 1980, fig. 4). The new material described here is stratigraphically older than previously referred material of *D. minima* from the Upper El Molino of Bolivia (Buffetaut, 1987; Jouve et al., 2021).

Preservation. Specimen FCGV-8178 consists of a skull and postcranial elements found in tight association in a block measuring $15 \times 7 \times 3$ cm. The skull is exposed in ventral view and lacks most of the rostrum and elements of the skull table. The occipital region is also damaged, impeding a detailed anatomical description of that region. Portions of the ventral surface of the palate are missing, exposing the tubular nasopharyngeal duct. The left pterygoid flange is damaged, and the anteriormost margins of the suborbital fenestrae are incomplete. All hindlimb elements pertain to the right side; the side of the metatarsal is uncertain. Most postcranial bones are complete, except for the ischium, which lacks the shaft and the proximal region; the femur, which lacks its distal end; and the dorsal vertebra, which lacks most of its neural arch processes.

Description. An elongate element preserved along one side of the block probably represents the maxilla, based on its tight association with the skull and absence of features associated with the mandible, such as a symphysis, external mandibular fenestra, sutures, articular

facets and retroarticular process. The maxilla is preserved as a thin slice that approximates a sagittal section along the tooth row. The maxilla has been completely detached from the skull, but it remains in relative proximity to it and may be in its natural position. It is exposed in medial view, showing the interior surfaces of some maxillary alveoli. All maxillary sutures (e.g. premaxilla-maxilla) are indistinguishable due to preservation. The maxilla is anteroposteriorly linear and is 68.9 mm long as preserved. Although not complete, it lacks lateral or dorsoventral expansions (festooning), which gives the impression of a long snout (also known as the longirostrine condition). The tooth row is located at the lateral margin of the maxilla, and the alveoli are equally spaced. We cannot distinguish the entirety of the alveolar size and shape across the maxilla due to incompleteness; however, occlusal notches to accommodate the dentary teeth are well developed. Based on the similar space between the alveoli and the length of the notches, we estimate the maxillary tooth count was 15-18 teeth. There is a short portion at the anterior part of the maxilla that has been slightly bent ventrally and does not follow the linear profile of the rest of the rostrum. We suggest that this bend is taphonomic (e.g. compaction) and does not represent the actual morphology of the specimen. Longirostrine crocodylians (e.g. Gavialis) tend to have an anteroposteriorly planar maxillary palate that extends from the tip of the rostrum to the back of the last alveoli.

The palatine is exposed in ventral view, revealing the tubular nasopharyngeal duct. It is more distinct along the medial margins of the suborbital fenestra and posteriorly at the pterygoid-palatine suture. The palatine meets its opposite at the ventral midline of the skull, where it forms the floor and lateral walls of the nasopharyngeal duct. FCGV-8178 lacks palatine bullae, although we cannot rule out their loss during burial and diagenesis. The posteriormost part of the palatine meets the pterygoid along a transverse suture at the same level as the posterior edge of the suborbital fenestra. Anterior to this contact, the palate continues, contributing to the medial margin of the suborbital fenestra. The incompleteness of the anterior portion of the palate makes it difficult to distinguish the extent of its contribution to the suborbital fenestra and its sutural relationship with the posterior process of the maxilla.

FCGV-8178 preserves both pterygoids, with the left side missing a considerable portion of the pterygoid process (flange). Both pterygoids lack the posterolateral contact with the ectopterygoids. The pterygoid is located in the posteriormost region of the skull, where it encloses the secondary palate. It meets its opposite at the midline anterior to the choana, along an







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anteroposteriorly oriented suture. Most of its ventral surface is flat and smooth. Posterolaterally, the pterygoid expands to form the well-developed transverse process (pterygoid wing) that is inclined at a low angle in occipital view. Extending posterior to the skull are two triangular, robust processes that contribute to the roof of the choana. These are relatively closely placed processes that meet at the midline of the choana, where the septum is visible. We refer to these processes as 'secondary wings' to differentiate them from the transverse processes of the pterygoids. The pterygoid contributes to the posterior and lateral margins of the suborbital fenestra, although its lateral extent is uncertain due to preservation. Its anteromedial extension terminates where it meets the posterior margin of the palatine along a transverse suture. The pterygoid wings of Dolichochampsa minima differ from those of all eusuchians in being mostly flat. In crown gharials, the pterygoids are relatively small and weakly inclined $(<30^\circ)$ in occipital view. In other taxa within Crocodylia (e.g. Crocodylus, Tomistoma), these are large and much more inclined (>45°). The choana pierces the pterygoid at its posteriormost border, as in eusuchians. The choanal opening is wider than long (10 mm wide and 5.2 mm long) and posteroventrally oriented. The anterior and lateral margins of the choana are well defined, but the posterior portion lacks a dividing margin and is continuous within the secondary wings of the pterygoids. An interchoanal septum projects from the dorsal surface of the choana (Supplemental Material Appendix S3), as in Isisfordia duncani and alligatorids (Salisbury et al., 2006, fig. 4).

A centrum and neural spine of a dorsal vertebra are preserved. The elements are not articulated, but we consider them to belong together because of the matching size of the partially preserved neural spine and centrum. The serial position of the vertebra within the dorsal series is uncertain. The centrum is c. 21 mm long and procoelous, with a well-developed convex condyle protruding 3 mm from the main body. The condyle is circumferentially inset on the centrum, leaving a small, flattened band around the perimeter of the articular surface. The left transverse process projects laterally from the neural arch and is 6 mm wide. The associated neural spine is exposed in a right-lateral view and is c. 29 mm long as preserved. Although the maxilla covers the anterior edge of the neural spine, its posterior edge indicates its border

was linear from the apex to the mid-section, gradually expanding at its base before meeting the postzygapophysis. The neurocentral suture is visible in dorsal view of the centrum aspect since the neural spine is detached from the main body. It is entirely fused in the specimen FCGV-8178, indicating that the individual was at least close to its final stages of maturity. The procoelous condition of the specimen of FCGV-8178 is similar to the dorsal vertebra of the referred specimens of Dolichochampsa minima from Gasparini and Buffetaut (1980, fig. 3H) and Jouve et al. (2021, fig. 3). The condyles are well developed as in modern eusuchians, which is unlike the incipiently developed condyle of basal eusuchians (e.g. Isisfordia duncani; Salisbury et al., 2006).

The right scapula is partially preserved. It is exposed in lateral view, and its medial side is currently embedded in matrix. The scapula is dorsoventrally short (28 mm). The dorsal edge of the scapular blade is nearly linear, being slightly concave in lateral view. Both anterior and posterior edges are weakly flared from the mid-shaft, showing concave profiles. These edges gradually thicken from the shaft to the tip, making the surface of the scapular blade concave. The distal scapular blade is twice as broad anteroposteriorly (12.2 mm) as it is at mid-length (6.2 mm), which is similar to the breadth of the proximal end (12.7 mm). The blade is dorsoventrally linear, lacking any curvature on the anterior and posterior edges. The area of the acromion process, which is the origin site of the deltoideus muscle (m. deltoideus clavicularis), is incompletely preserved.

The distal portion of the right ischial blade and shaft are preserved (Supplemental Material Appendix S3). As preserved, the ischial blade is long posteriorly (28.1 mm). The anterior part of the edge of the blade is broken, and its proximal portion seems to be restricted to the anterior end of the blade, giving the impression of an L-shaped bone. A shallow depression at the centre of the blade divides the anterior and posterior parts, probably formed by taphonomic processes (e.g. burial compression).

The right femur is mostly complete, missing a section of the distal end of the shaft and a portion of the distal condyle. The detailed description and measurements of the femur are based on micro-computed tomography (μ CT) scan observations, because the proximal end and shaft are buried in the block, mainly below the tibia. The μ CT scan of the specimen of FCGV-8178 is available in the Supporting Information (Supplemental

Figure 3. Results of parsimony analysis and iterPCR. A, 50% majority-rule consensus of 987 most parsimonious trees. *Dolichochampsa minima* is recovered within Gavialinae, 'thoracosaurs' are placed as the sister clade to *Borealosuchus formidabilis*, and *Ocepesuchus eoafricanus* is nested within Alligatoridae. B, Result of the iterPCR analysis showing the alternative placements of the unstable taxa (*D. minima*, *Dadagavialis gunai* and *O. eoafricanus*). Abbreviation: OTU, operational taxonomic unit.

Material Appendix S6). The femur is long (91 mm) and sigmoid (S-shaped) to a minor degree. It is subcircular in cross-section at mid-shaft (diameter = 9 mm), becoming mediolaterally compressed at the head (20 mm), which forms a convex surface for articulation with the acetabular area of the ilium. The head bends anteriorly to a minor degree and is twisted relative to the shaft. Additional information is provided by µCT scan imaging of the block containing the fossil. The femur resembles that of *Dolichochampsa minima* in possessing a weekly sigmoidal shaft, which is the condition of most crocodyliforms. It is unclear whether the femfourth trochanter of FCGV-8178 is oral "less pronounced" than that of modern eusuchians, as was described for a referred specimen of Dolichochampsa (Gasparini & Buffetaut, 1980, fig. 4B).

The right tibia is preserved in near-articulation with the femur. It is exposed in medial view, and the inaccessibility in other views precludes the description of additional aspects of the bone. The tibia is linear with broad proximal and distal ends. It is a long and robust bone (57.8 mm long) that is 64% of the total length of the femur. Observations from the μ CT scan show that the shaft is circular in cross-section at mid-shaft (diameter = 7 mm) and becomes gradually elliptical at both ends. The proximal head and distal extremity are almost twice as wide (12.7 proximal and 13.2 mm distal) as the minimum shaft width. The distal edges bulge to form well-defined crests with ridges, and they flatten to form a spoonshaped medial surface of the tibia.

The metatarsal is completely preserved and is visible on the surface of the block. A small section of the shaft has been damaged, which is covered by the proximal end of the scapula. The metatarsal is long (40.4 mm), comprising 70% of the length of the tibia. The proximal end is flat and slightly wider transversely (8.4 mm) than both the shaft (5 mm) and the distal end (7.1 mm). The metatarsal shaft is sub-circular in cross-section. The close association of this element with the right hind foot suggests that it might pertain to that side and may represent the first metatarsal.

Phylogenetic and iterPCR results

Phylogenetic analysis of Crocodylia and closely related taxa recovered 991 most parsimonious trees of 461 steps (consistency index (CI): 0.375, retention index (RI): 0.762) after removing uninformative characters (Fig. 3A). Despite the relatively large number of most parsimonious trees, much of the topology is fully resolved, with uncertainty localized within Gavialinae. Crocodylia is recovered as a monophyletic group, as are crown-group alligatorids (Alligator, Caiman, Melanosuchus and Paleosuchus) and their fossil allies (Fig. 3A).

Crocodylids (Crocodylus, Mecistops, Voav, Osteolaemus) form a clade that is the sister taxon to Gavialoidea. The node containing the genus *Crocodylus* is resolved with the exception of C. moreletii and C. intermedius (see Supplemental Material Appendix S4). Tomistoma and morphologically similar taxa (e.g. Kentisuchus. *Paratomistoma*) form a paraphyletic group at the stem of Gavialidae; their placement within the clade is weakly supported (see Supplemental Material Appendix S4). Gavialinae is resolved as a monophyletic clade with high support values, although the interrelationships of most taxa are unresolved. Our analysis resolves 'thoracosaurs' as a clade outside Crocodylia, as the sister clade to Borealosuchus formidabilis (Fig. 3A).

Dadagavialis gunai, Dolichochampsa minima and Ocepesuchus eoafricanus were identified as unstable OTUs by the iterPCR analysis. When the uncertainty surrounding their relationships was accounted for, the strict consensus tree was improved (Fig. 3B). The putative gavialoid O. eoafricanus (Jouve et al., 2008) was deeply nested within Alligatoridae. recovered Dadagavialis is placed within Aktiogavialis spp. and in multiple places within the two gryposuchine clades (Fig. 3B). Dolichochampsa was deeply nested within Gavialinae, but its position within the clade was not resolved; equally parsimonious trees place it close to species of Aktiogavialis, Gavialis and Gryposuchus.

Discussion

The new specimen of *Dolichochampsa minima* has important implications for the taxonomy, palaeobiology and palaeobiogeography of early gavialines. In the following sections, we provide evidence supporting its referral to *D. minima*. We then make detailed comparisons with other Cretaceous–Palaeogene crocodyliforms from South America and elsewhere. We discuss the phylogenetic placement of 'thoracosaurs', *Ocepesuchus eoafricanus*, and *Portugalosuchus azenhae*. Last, based on the phylogenetic results, we explore the palaeobiogeography of South American gavialines.

Referral of FCGV-8178 to Dolichochampsa minima

Specimen FCGV-8178 is clearly a eusuchian, based on the position of the choana at the posteriormost edge of the pterygoids and the possession of well-developed procoelous vertebrae. We refer it to *Dolichochampsa minima* (Gasparini & Buffetaut, 1980) based on several key pieces of information. First, the femur of FCGV-8178 is identical to that of the holotype of *D. minima* in having a straight shaft and poorly developed proximal head (see μ CT scan at https://doi.org/10.7302/65y9bf75; Gasparini & Buffetaut, 1980; Vélez-Rosado et al., 2025). These features contrast with the sigmoidal (S-shaped) femoral shaft and well-developed proximal head present in other eusuchians (see Morgan et al., 2018). Second, both FCGV-8178 and *D. minima* are small-bodied. We estimated FCGV-8178 to be 1 m long based on the length of its femur, which matches the estimated size of the holotype of *D. minima* (Gasparini & Buffetaut, 1980). Referred specimens of *D. minima* described by Buffetaut (1987) and Jouve et al. (2021) are from individuals of similar size. Third, FCGV-8178 and other specimens of *D. minima* are longirostrine forms, with homodont dentition (Buffetaut, 1987; Gasparini & Buffetaut, 1980). The combination of these features supports referral of FCGV-8178 to *D. minima*.

Comparison of *Dolichochampsa minima* to other Cretaceous–Palaeogene crocodyliforms

Dolichochampsa minima is a gavialine crocodylian with similar spatial and temporal distributions to other longirostrine dyrosaurs from South America. Dyrosauridae is a clade of Cretaceous-Eocene crocodyliforms, some of which independently evolved a long snout as in gavialoids (Jouve et al., 2021). In Bolivia, the longirostrine dyrosaurs Rodeosuchus machukiru, Dorbignysuchus niatu and Luciasuchus lurusinga are found in Torotoro, Charcas Province, which is located some ~ 105 km north of the site where the specimen of this study (FCGV-8178) was found and some 22 km SW of putative material of D. minima presented by Jouve et al. (2021). In Brazil (Guarinisuchus munizi) and Colombia (Acherontisuchus guajiraensis), longirostrine dyrosaurs are also found in strata slightly younger (Paleocene) than the El Molino Formation in Bolivia (Barbosa et al., 2008; Hastings et al., 2010). Although these taxa overlap to some degree with D. minima, there are key anatomical differences. For instance, the dentary alveoli of the holotype of D. minima are nearly the same size, whereas in R. machukiru there is evident size variation across the dentary alveoli (Jouve et al., 2021, fig. 5A, B). The specimen presented herein (FCGV-8178) shows a septum that does not completely separate the choana (Fig. 2): in contrast, the choana in the dyrosaur G. munizi is fully separated (Barbosa et al., 2008, fig. 2d). Also, the choana in D. minima is located in the posteriormost region of the pterygoid, a condition that it shares with all crocodylians, whereas in G. munizi and D. niatu the choana pierces the pterygoid more anteriorly (Barbosa et al., 2008; Jouve et al., 2021). Associated postcranial remains present in FCGV-8178 and those found in the El Molino Formation (Jouve et al 2021, fig. 3) show that the taxon had a well-developed procoelous dorsal vertebra, which differs from the

amphicoelous condition in Dyrosauridae. Although procoely had appeared independently in various crocodyliform groups, it is a condition that became fixed in the most recent common ancestor of Crocodylia (Buscalioni et al., 2001; Turner & Pritchard, 2015).

Another Cretaceous taxon that has been recently considered a gavialoid crocodylian is Portugalosuchus azenhae (Rio & Mannion, 2021), which was first described as a basal eusuchian by Mateus et al. (2019). Both P. azenhae and Dolichochampsa minima are represented by partially preserved skulls, which limits comparison between these taxa. However, there are at least three key anatomical features that can be used to distinguish them. First, the pterygoids in *P. azenhae*, although incomplete, appear to be inclined to some degree (Mateus et al., 2019, fig. 3C), whereas in D. minima they are mostly flat in occipital view (Fig. 2; see Supplemental Material Appendix S3). Second, the lateral borders of the choana differ in the two taxa. Portugalosuchus has a choana with well-defined lateral borders (Mateus et al., 2019, fig. 3B), in contrast to D. minima in which the choana is flush with the pterygoid surface (Fig. 2). Third, P. azenhae lacks the interchoanal septum, a condition that it shares with most crocodylians. This septum is present in D. minima, which is the plesiomorphic condition in eusuchians such as Isisfordia duncani (Salisbury et al., 2006, fig. 4b).

Although we recognize that the study conducted by Rio and Mannion (2021) was the first to recover Portugalosuchus azenhae as a gavialoid crocodylian, in the present study there are no shared characters that unite the taxon with the clade or even within Gavialinae. For instance, P. azenhae is missing key gavialine synapomorphies due to preservation such as longirostry, homodont dentition, a pendulous basioccipital tuber and a long dentary symphysis. The supratemporal fenestrae in P. azenhae are large, which is comparable to most gavialoids (e.g. Tomistoma, Gavialis); still, this condition also appears in other Cretaceous longirostrine forms (e.g. Eothoracosaurus). Owing to the lack of pterygoids in the holotype of P. azenhae due to preservation, we could not compare it with Gavialinae (Mateus et al., 2019, fig. 3B, C). Thus, we consider P. azenhae to be a basal eusuchian - as the analysis of Mateus et al. (2019) showed – until evidence emerges that demonstrates a different evolutionary relationship.

Dolichochampsa minima also differs considerably from the Cretaceous 'thoracosaurs' from the circum-Atlantic, *Eothoracosaurus mississippiensis* and *Thoracosaurus neocesariensis*. First, the space between the teeth in *D. minima* remains constant across the dentary (Buffetaut, 1987; Gasparini & Buffetaut, 1980). In contrast, the third and fourth dentary teeth of *E*. *mississippiensis* are confluent, a condition that shares with *Borealosuchus* (Brochu, 2004, fig. 8; Gilmore, 1910). Last, the femur of *T. neocesariensis* resembles the typical eusuchian type with an S-shaped shaft and a welldeveloped proximal head, whereas the femoral shaft in *D. minima* is straight and has a poorly developed proximal head (Gasparini and Buffetaut, 1980, fig. 4A; Fig. 2).

Phylogenetic placement of *Dolichochampsa* minima

Our phylogenetic analysis resolves Dolichochampsa minima within Gavialinae (Fig. 3A), consistent with previous morphological studies (Gasparini & Buffetaut, 1980). The placement of D. minima within Gavialinae could not be resolved unambiguously, but iterPCR narrows its possible positions to the sister taxon of Gavialis, within or immediately outside Aktiogavialis, or within Gryposuchus (Fig. 3B). Characters from the skull and mandible support the inclusion of D. minima within Gavialinae. Its uncertain lower-level interrelationships are the result of high levels of missing data in D. minima and variation in scorings within Gavialinae. For example, D. minima shares character state 23[0] with Gavialis gangeticus, but the optimization of that character is ambiguous for other gavialine taxa. Dolichochampsa shares the following character states with most gavialines that can be scored: no differentiation of dentary alveoli caudal to fourth alveolus (ch. 51[2]); contribution of splenial in mandibular symphysis (ch. 54[0]); a pterygoid surface surrounding internal choana slightly depressed or flush with the choanal margins (ch. 123[0]); ectopterygoid does not extend to the posterior tip of the lateral pterygoid flange at maturity (ch. 127[1]); a choana wider than long (ch. 252[0]); and a pterygoid poorly to mildly inclined, no more than 45° (ch. 253[0]). Dolichochampsa also shares a frontal plate well ornamented with deep pits and furrows (ch. 202[0]) and a subcircular choana (ch. 251[0]) with Gavialis and Aktiogavialis, but the scorings within Gryposuchus differ. Within Gavialinae, D. minima, Gryposuchus and Aktiogavialis share a narrow frontal plate between orbits (247[0]).

Although the exact placement of *D. minima* within Gavialinae remains unknown, its unambiguous placement within the clade is strongly supported (see Supplemental Material Appendix S4), which has important implications. The age of *D. minima* pushes back the origin of Gavialinae to the Late Cretaceous (73–64 Ma) and opens the possibility that the clade originated in South America. The results of our study are consistent with elements of both molecular- and morphology-based analyses. Like molecular-based hypotheses, we recover a sister-clade relationship between morphological

tomistomines and Gavialinae (Iijima et al., 2022; Lee & Yates, 2018; Meredith et al., 2011; Oaks, 2011; Pan et al., 2021; Willis et al., 2007). Like morphology-based studies, our results imply an early, Gondwanan origin for Gavialinae (Brochu, 1997, 2003, 2004; Rio & Mannion, 2021; Salas-Gismondi et al., 2016, 2019; Vélez-Juarbe et al., 2007).

Phylogenetic placement of 'thoracosaurs', Ocepesuchus eoafricanus, and Portugalosuchus azenhae

'Thoracosaurs' have long been considered basally diverging gavialids based on morphological characters, which we included in our data set (Brochu, 2004: Salas-Gismondi et al., 2016, 2019; Vélez-Juarbe et al., 2007). Our analysis resolves 'thoracosaurs' outside Crocodylia, as the sister clade to the Genus Borealosuchus, whose two species are rendered paraphyletic (see Supplemental Material Appendix S2.1, 2.2, and S5). Borealosuchus species range from the Late Cretaceous to the Eocene of North America, a spatiotemporal distribution that coincides with that of 'thoracosaurs'. Although the relationship of 'thoracosaurs' with Borealosuchus is only weakly supported (see Supplemental Material Appendix S4), their placement outside Crocodylia in our parsimony analysis is consistent with previous studies (Lee & Yates, 2018; Rio & Mannion, 2021; Salas-Gismondi et al., 2022). Characters supporting the placement of 'thoracosaurs' with Borealosuchus include: dorsal osteoderms not keeled (ch. 38[0]); an external naris that opens flush with the dorsal surface of premaxillae (ch. 85[0]); and an incisive foramen equal to or more than 2 times the diameter of the first premaxillary alveolus (ch. 88[2]). Eothoracosaurus shares with Borealosuchus a short dorsal premaxillary process that does not extend beyond the third maxillary alveolus (ch. 90[0]); a pseudo-homodont dentition, with some variation (ch. 93[8]); dorsal surface of rostrum generally linear, fitting the skull table (ch. 95 [2]); a palatine that sends two processes that converge anteriorly, forming a V-shaped suture with the maxilla, process does not extend beyond the third maxillary alveolus that is anterior to the suborbital fenestra (ch. 116[2]); quadratojugal greatly reduced (ch. 140[1]), a condition shared between Borealosuchus and Eosuchus; a frontoparietal suture deeply within the supratemporal fenestra, frontal prevents broad contact between postorbital and parietal (ch. 150[0]); ventral premaxillary-maxillary suture is mainly transversal to W-shaped (ch. 185[0]); process of frontal extends well anterior, frontal process significantly long, more than the length of the frontal plate (ch. 188[1]); a maxilla with a convergent profile posteriorly, at midrostrum it becomes subparallel (ch. 237[3]); a circular supratemporal fossa (ch. 245[3]); and space between alveoli is similar in length to alveolar diameter and constant across the dentary, but the third and fourth alveoli are well separated from the neighbouring teeth by a diastema and are nearly confluent (ch. 261[5]). Given the phylogenetic placement of 'thoracosaurs' outside Crocodylia in the present study - along with their age and geographical occurrence - we suggest these Late Cretaceous taxa could have been adapted to a similar lifestyle as early gharials from South America (i.e. Dolichochampsa minima). Considering that some 'thoracosaurs' have been found in marginal to coastal marine deposits (Brochu, 2004; Carpenter, 1983), it is possible that the group was exploiting marine habitats, hence adapting to a fish-eating diet, as has been proposed (Lee & Yates, 2018).

Ocepesuchus eoafricanus was first recognized by Jouve et al. (2008) as a basally diverging gavialoid phylogenetically closer to 'thoracosaurs' than to gavialids. Characters supporting the inclusion of O. eoafricanus within Gavialoidea were mainly cranial, including a slender-snouted morphology, an occipital surface dorsally inclined and largely visible in dorsal view, and a supraoccipital located posteriorly to the rear margin of the skull table (Jouve et al., 2008). Our parsimony analysis, however, recovered O. eoafricanus within crown alligatorids, in one of five different positions (Fig. 3A, B). Characters in our study supporting the placement of O. eoafricanus within Alligatoridae include the dorsal surface of the rostrum curves smoothly (ch. 95[0]), prefrontals separated by the frontal and nasals, anterior process of frontal around the same level or posterior to the anterior margin of the orbit (ch. 129[1]), and the quadrate foramen aërum on the dorsal surface of the quadrate (ch. 177[1]). Ocepesuchus shares character states with crown-group gharials as well, including the presence of homodont maxillary dentition (ch. 93[5]), supraoccipital exposure on dorsal skull table points posteriorly to the caudal margin of the parietal (ch. 160[1]), and the edge of maxillary tooth alveoli higher than the space between toothrows (ch. 182[1]). *Ocepesuchus* also shares with Borealosuchus formidabilis and Eosuchus minor a circular supratemporal fossa (ch. 245[3]). Thus, the combination of alligatorid, gavialine and 'thoracosaur' characters underscores the complex nature of this taxon. Moreover, O. eoafricanus has a large number of missing characters in our data set (91%), which we recognize has an impact on its phylogenetic position in the present study. Scoring more characters of O. eoafricanus will be crucial to resolving its evolutionary relationship within Eusuchia. Until more material of O. eoafricanus is found, the taxon should continue to be considered a putative eusuchian.

Portugalosuchus azenhae is a Late Cretaceous eusuchian from Portugal first recognized as an early crocodylian, phylogenetically closer to Borealosuchidae (Mateus et al., 2019). More recently, Rio and Mannion (2021, fig. 10), in their extensive study on Crocodylia, recovered P. azenhae within Gavialidae, forming a separate clade with Eothoracosaurus mississippiensis and Thoracosaurus neocesariensis. Not surprisingly, our phylogenetic analysis had a similar result to those of these previous studies (Mateus et al., 2019; Rio & Mannion, 2021), with P. azenhae recovered within 'thoracosaurs' as the sister taxon to T. neocesariensis. Character states supporting the placement of P. azenhae within 'thoracosaurs' include an ectopterygoid that extends to the posterior tip of the lateral pterygoid flange at maturity (ch. 127 [0]); the ventral margin of postorbital bar flush with lateral jugal surface (ch. 135[0]), although the character state is present in some gavialines (Dadagavialis, Ikanogavialis); the dorsal margin of orbit flush with skull surface (ch. 137[0]); and a frontoparietal suture deeply within the supratemporal fenestra and frontal prevents broad contact between postorbital and parietal (ch. 150[0]). The result of our phylogenetic analysis is consistent with previous studies, which recognized P. azenhae as an early diverging eusuchian and, most likely, a 'thoracosaur'. The phylogenetic placement of P. azenhae within 'thoracosaurs' is also consistent with their spatiotemporal distribution. 'Thoracosaurs' have been found in coastal to marine deposits in North America. In addition, North America was relatively close to Western Europe during the Late Cretaceous, and many shallow marine areas extended across these landmasses (Scotese, 2001), thus facilitating the geographical expansion of large semi-aquatic reptiles such as 'thoracosaurs' around the circum-Atlantic.

Palaeobiogeography of Cretaceous gavialines

The temporal and geographical distributions of numerous gavialine taxa associated with marine environments (i.e. Dadagavialis, Piscogavialis, Argochampsa, Aktiogavialis) and their close phylogenetic relationships imply that the group likely underwent multiple transoceanic dispersals events between the Gondwanan and Laurasian landmasses (Brochu & Rincón, 2004; Jouve et al., 2006; Salas-Gismondi et al., 2016, 2019, 2022; Vélez-Juarbe et al., 2007). This hypothesis requires that gavialines have the physiological capabilities to tolerate saltwater conditions, which are not present in the modern, freshwater-restricted forms (Gavialis and Tomistoma) (Salas-Gismondi et al., 2016, 2019; Vélez-Juarbe et al., 2007).

The ancestral range for gavialines has been suggested to be the northern peri-Tethyan coasts (northern Africa + southern Europe), based on statistical dispersal-vicariance analysis (Salas-Gismondi et al., 2022, fig. 3). In that analysis, the Paleocene taxon *Argochampsa krebsi* from Morocco (Jouve et al., 2006) represented the oldest gavialine, because 'thoracosaurs' were resolved outside Crocodylia. Such statistical analyses are sensitive to changes in topology (Yu et al., 2010), and so recovering *Dolichochampsa minima* deeply nested within gavialines in our analysis may add more complexity to the proposed hypothesis of a peri-Tethyan origin.

The results of our phylogenetic analysis provide equal support for Dolichochampsa minima as the sister taxon to Gavialis, to Aktiogavialis, and to Grvposuchus. The latter two genera are predominantly South American (with the exception of A. puertoricencis from the Caribbean), implying these clades diversified from a South American ancestor and do not represent a dispersal from the peri-Tethys. In contrast, if D. minima is phylogenetically closer to Gavialis than to the other gavialines, then a more complex palaeobiogeographical distribution is implied, with multiple trans-oceanic dispersals between Laurasian and Gondwanan landmasses (Salas-Gismondi et al., 2019, 2022; Vélez-Juarbe et al., 2007). We recognize the current uncertainty in the phylogenetic position of D. minima within Gavialinae, but its placement within this lineage provides insights into the dispersal capabilities of the group. The gavialines hypothesized to be closest to D. minima are Argochampsa krebsi and Eogavialis africanum, from the Paleocene and Eocene of Africa, respectively (Hua & Jouve, 2004; Jouve et al., 2006; Salas-Gismondi et al., 2022). Even if the evolutionary relationships of D. minima within Gavialinae remain unknown, its age and geographical distribution with respect to the other gavialines suggests a possible transoceanic dispersal during the Cretaceous-Palaeogene, lending support to the hypothesis that early gavialines were able to tolerate and cross marine waters (Brochu & Rincón, 2004; Vélez-Juarbe et al., 2007).

Conclusions

We describe new material of a small-bodied (\sim 1 m), longsnouted crocodylian collected from the Cretaceous– Palaeogene (c. 73–64 Ma) El Molino Formation in Bolivia. We refer the new specimen to *Dolichochampsa minima*. We incorporated the new specimen into an expanded and modified osteological data matrix, along with other putative oldest gavialid crocodylians from North America and Europe ('thoracosaurs'), Africa (*Ocepesuchus eoafricanus*) and Portugal (*Portugalosuchus* azenhae), to test their evolutionary relationships in a phylogenetic context. Our results reveal that *D. minima* is a gavialine, whereas 'thoracosaurs' and *P. azenhae* are recovered outside of Crocodylia. *Ocepesuchus eoafricanus* is recovered within alligatorids, but there are reasons to question the result for the latter taxon. First, *O. eoafricanus* shares characters with alligatorids, gavialoids, and 'thoracosaurs'. Second, *O. eoafricanus* is missing 91% of characters in our data set, which we recognize can impact its phylogenetic resolution within Eusuchia.

The current position of 'thoracosaurs' and differences in character states from gavialines imply that longirostry evolved independently in the two clades. The age and provenance of *D. minima* has important implications for gavialine origins and palaeobiogeography. The Late Cretaceous to early Palaeogene age of D. minima pulls the origin of Gavialinae down into the Mesozoic (73-64 Ma). These results contradict molecular studies that posit a younger, Cenozoic origin for gavialines. Its South American provenance opens the possibility of an origin for Gavialinae on that landmass or elsewhere in Gondwana. Importantly, the occurrence of а Cretaceous-Palaeogene gavialine in South America suggests a possible dispersal to Africa and Asia, lending support to the hypothesis that salinity tolerance appeared in early gavialine history, as previously proposed (Brochu & Rincón, 2004; Vélez-Juarbe et al., 2007).

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No potential conflict of interest was reported by the author(s).

Supplemental material

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