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INSUFFICIENT EVIDENCE FOR SPINOSAURID SURVIVAL INTO THE LATEST CRETACEOUS: A COMMENT ON OLMEDO-ROMAÑA *ET AL.* (2025)

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Abstract. The recent description of putative spinosaurid teeth from the latest Cretaceous (Campanian–Maastrichtian) of Peru by Olmedo-Romaña *et al.* (2025) has interesting implications for our understanding of these atypical dinosaur predators. Such a late occurrence of the clade would require a temporal range extension of some 15 million years, suggesting they survived the currently enigmatic faunal turnover events experienced during the "mid"-Cretaceous and persisted for some time beyond the Cenomanian. This commentary reviews the taxonomic affinities of these specimens. We demonstrate that their morphology is inconsistent with spinosaurid dentition and that they lack key characters exhibited by the clade, with our revised interpretation instead favouring crocodylomorph affinities for these specimens. Accordingly, we urge caution in the interpretation of conidont tooth morphologies given that multiple semi-aquatic and aquatic amniote lineages independently converged on this dental morphotype. Spinosaurids did not, therefore, survive into the latest Cretaceous and instead appear to go extinct around the Cenomanian–Turonian boundary, the drivers of which remain unclear.

Key words. Crocodylomorph. Spinosaurid. Teeth. Late Cretaceous. Taxonomy. Morphological convergence.

Resumen. EVIDENCIA INSUFICIENTE DE LA SUPERVIVENCIA DE LOS ESPINOSÁURIDOS EN EL CRETÁCICO TERMINAL: UN COMENTARIO SOBRE OLMEDO-ROMAÑA *ET AL.* (2025). La descripción reciente de supuestos dientes de espinosáuridos del Cretácico terminal (Campaniano–Maastrichtiano) de Perú, por Olmedo-Romaña *et al.* (2025), tiene interesantes implicancias para nuestro entendimiento de estos atípicos dinosaurios depredadores. Esta ocurrencia tardía del clado requeriría una extensión del rango temporal de 15 millones de años, sugiriendo que ellos sobrevivieron a los eventos faunísticos de recambio experimentados durante el Cretácico "medio" y que persistieron por algún tiempo más allá del Cenomaniano. Este trabajo revisa las afinidades taxonómicas de esos especímenes. Nosotros demostramos que su morfología es inconsistente con la dentición de los espinosáuridos y que carecen de caracteres exhibidos por el clado, y que, en cambio, nuestra interpretación es a favor de afinidades con crocodylimorfos. Por consiguiente, nosotros pedimos precaución en la interpretación de dientes de morfología conidonte, dado que múltiples linajes de amniotas acuáticos y semiacuáticos han convergido independientemente en esta morfología. Entonces, los espinosáuridos no sobrevivieron hasta el Cretácico terminal y en lugar de ello parecen haberse extinguido alrededor del límite Cenomaniano–Turoniano, siendo las causas de este suceso aún poco claras.

Palabras clave. Crocodylomorfos. Espinosáuridos. Dientes. Cretácico Tardío. Taxonomía. Convergencia morfológica.

OLMEDO-ROMAÑA *ET AL.* (2025) recently described a collection of dinosaur fossils from the Upper Cretaceous (Campanian–Maastrichtian) Fundo El Triunfo Formation (Bagua Basin, Peru). Among these are three isolated dental specimens (MUSM 4269, 5121 and 5122) referred by these authors to Spinosauridae, an unusual clade of theropod dinosaur well known for their atypical craniodental (and, in some taxa, postcranial) morphology and semi-aquatic ecology (Stromer, 1915; Taquet, 1984; Charig & Milner, 1997; Holtz, 1998; Amiot *et al.*, 2010; Hone & Faulkes, 2014; Ibrahim *et al.*, 2014; Hone & Holtz Jr, 2017; Hassler *et al.*, 2018; Hone & Holtz, 2021; Sereno *et al.*, 2022). A latest Cretaceous occurrence for spinosaurid material is surprising and necessitates a c.15-million-year extension to the currently accepted geological range of this clade; unambiguous spinosaurid remains are from the Berriasian/Valanginian to Cenomanian interval of Europe, Asia, Africa and South America (Stromer, 1915; Charig & Milner, 1997; Bertin, 2010; Hone & Holtz Jr, 2017; Ibrahim *et al.*, 2020; Malafaia *et al.*, 2020; Lacerda *et al.*, 2023; Barker *et al.*, 2024; Samathi & Puntanon, 2025) and hence all previous indications are that the group did not persist close to the end of the Cretaceous.

Inaccurate referral of isolated teeth to Spinosauridae has previously extended the clade's temporal range beyond the well-supported Berriasian/Valanginian–Cenomanian

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interval (Fig. 1): the probable nomen dubium *Ostrafikasaurus* (Buffetaut, 2012), together with isolated teeth from Niger and France (Vullo *et al.*, 2014; Serrano-Martínez *et al.*, 2015, 2016), were initially considered Jurassic representatives of the clade displaying transitional dental morphologies from a ziphodont ancestor. Though Spinosauridae likely originated in the Jurassic (Carrano *et al.*, 2012; Barker *et al.*, 2021), these specimens are instead better interpreted as ceratosaurian and megalosaurid theropods (Rauhut, 2011; Hendrickx *et al.*, 2019; Soto *et al.*, 2020). An intriguing report of a possible spinosaurid pedal ungual is also known from the Bathonian of India (Sharma *et al.*, 2023), though we note the dinosaurian sample used in the quantitative analyses was limited and lacked specimens pertaining to any other sauropsid clades, suggesting the affinities of this specimen should be revisited. Putative post-Cenomanian spinosaurids have also been reported from Patagonia (Salgado *et al.*, 2009), Brazil (Candeiro *et al.*, 2004), and China (Hone *et al.*, 2010), although such referrals are similarly erroneous (Candeiro *et al.*, 2006; Katsuhiro & Yoshikazu, 2017; Buffetaut *et al.*, 2019; Soto *et al.*, 2020; Barker *et al.*, 2023), as correctly highlighted by Olmedo-Romaña *et al.* (2025). Here, we explain why the Fundo El Triunfo specimens examined by Olmedo-Romaña *et al.* (2025) do not represent late-surviving spinosaurids, and are instead best interpreted as belonging to a crocodylomorph lineage.

Institutional abbreviations. BEXHM, Bexhill Museum, Bexhill, UK; **HASMG,** Hastings Museum and Art Gallery, Hastings, UK; **IWCMS,** Dinosaur Isle Museum (Isle of Wight County Museum Service), Sandown, Isle of Wight, UK; **MSNM,** Museo di Storia Naturale di Milano, Milan, Italy; **MUSM,** Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **NHMUK,** Natural History Museum, London, UK.

RESULTS AND DISCUSSION

Olmedo-Romaña *et al.* (2025) used both qualitative morphological comparisons and a linear discriminant analysis (LDA) on a pan-theropodan dataset to support referral of the Fundo El Triunfo Formation specimens to Spinosauridae. Spinosaurids have highly apomorphic dentition relative to other theropods (Hendrickx & Mateus, 2014; Hendrickx *et al.*, 2019), although many of the traits concerned (*e.g.*, conidont crown shapes and fluted enamel surfaces) evolved convergently among various semi-aquatic and aquatic amniote lineages (Larsson & Sues, 2007; McCurry *et al.*, 2019; Pochat-Cottilloux *et al.*, 2023; D'Amore *et al.*, 2025). Indeed, spinosaurid teeth have sometimes been confused for those of crocodylomorphs, plesiosaurs, and ichthyosaurs (Buffetaut, 2010), and careful analysis is required to confidently determine spinosaurid affinities when dealing with isolated dental material.

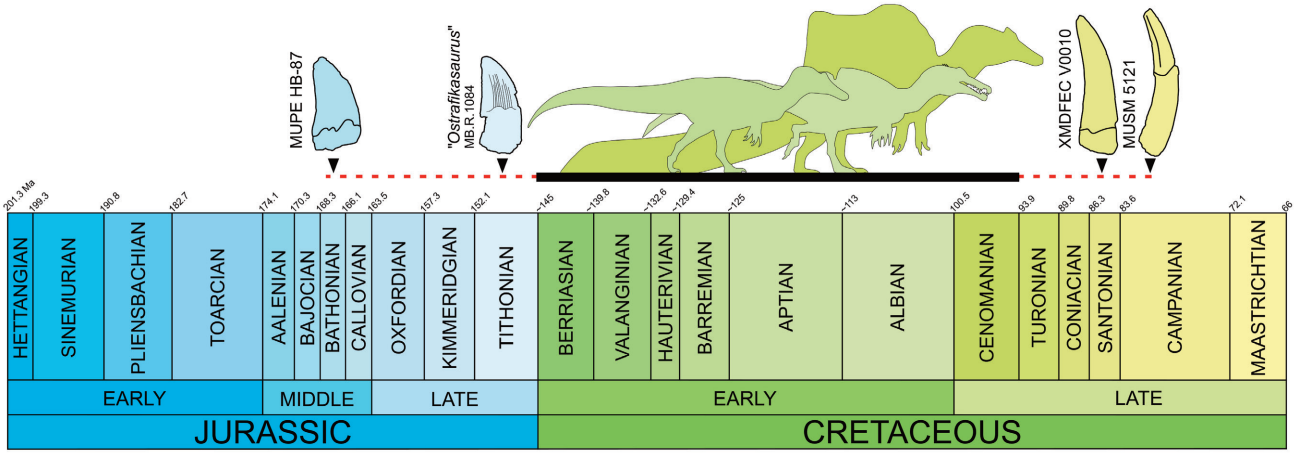


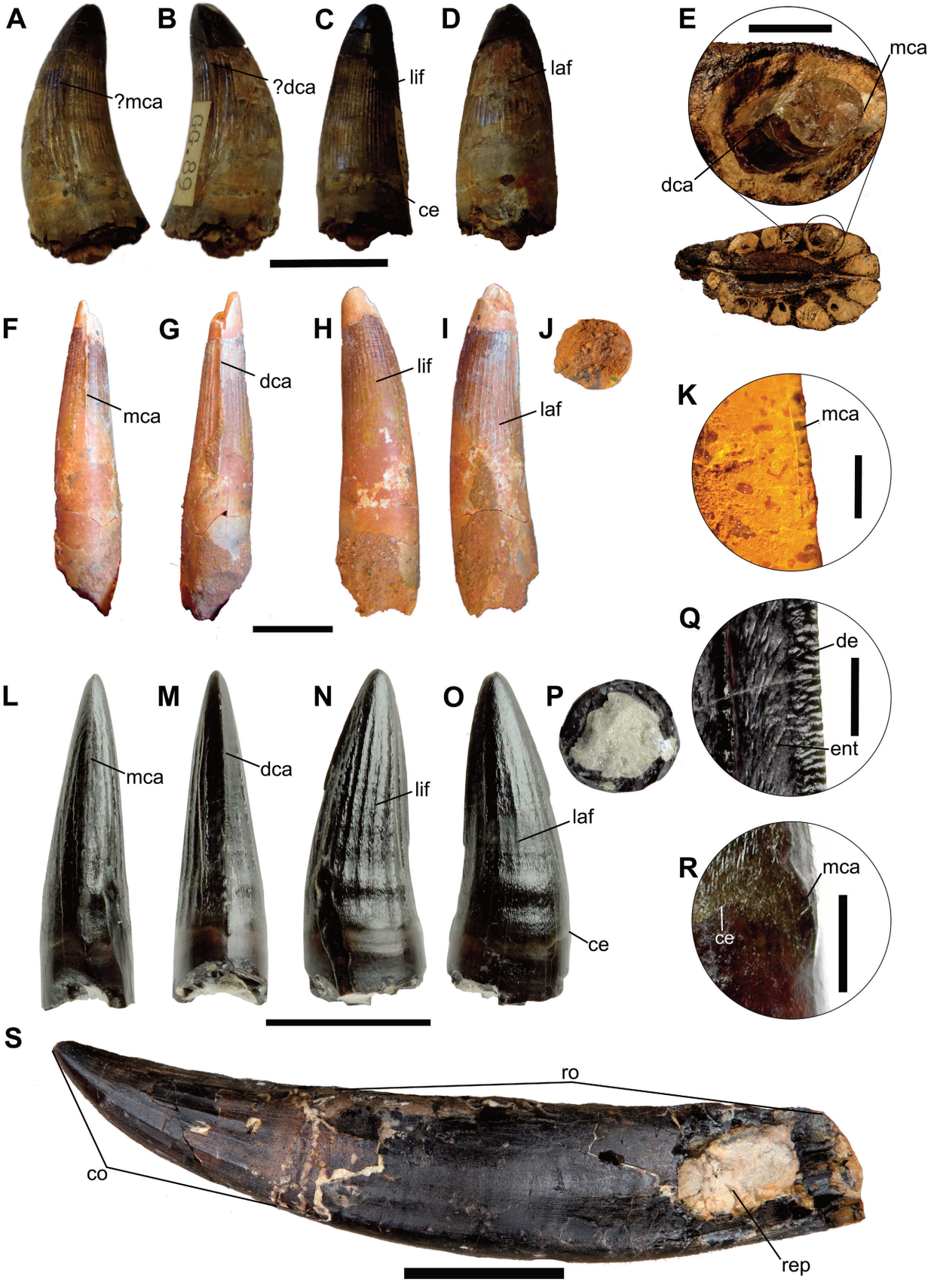
Figure 1. The temporal range of Spinosauridae. Unambiguous specimens have been recovered from the Berriasian/Valanginian–Cenomanian of Africa, Asia, Europe, and South America. Additional finds have also been reported from Jurassic and post-Cenomanian strata (*e.g.*, MUPE HB-87, MB. R.1084, XMDFEC V0010, MUSM 5121), but their referral to Spinosauridae is erroneous (see main text). Stratigraphic column based on Walker and Geissman (2022). Phylopic silhouette credits: *Baryonyx* — Ivan Iofrida (CC BY 4.0, https://creativecommons.org/licenses/by/4.0/); *Ichthyovenator* — Pranav Iyer (CC BY 1.0); *Spinosaurus* — Alessio Ciaffi (CC BY 4.0, https://creativecommons.org/licenses/by/4.0/).

LDAs have well documented limitations when applied to the identification of isolated teeth (Buckley *et al.*, 2010; Hendrickx *et al.*, 2015a, 2020, 2024; Wills *et al.*, 2021; Marques *et al.*, 2025). It is true, however, that the distinctive morphology of spinosaurid dentition (Fig. 2) can render LDA useful in some tooth identification studies (Hendrickx *et al.*, 2015a, 2024) and discriminant analyses of spinosaurid-only samples have reported high reclassification rates (Barker *et al.*, 2023). Nevertheless, the taxon- and clade-level classifications of MUSM 5121 to *Suchomimus* and Spinosauridae reported by Olmedo-Romaña *et al.* (2025) returned reclassification values of 59.18% and 60.58%, respectively, confidences well below the 90% minimum hit rate usually recommended for a noteworthy result (Hammer & Harper, 2006). Furthermore, the use of LDAs to identify isolated archosaur tooth crowns appears limited given the method's low discernment of taxa with similar crown morphologies (Hendrickx *et al.*, 2015a, 2020), with previous works demonstrating that crocodylomorph and spinosaurid crowns may occupy overlapping morphospace due to their convergent crown morphologies (Sanguino, 2020). Importantly, though other computational methods (*e.g.*, cladistics, machine learning [ML]) have proven informative for the identification of isolated teeth (Hendrickx *et al.*, 2020, 2024; Wills *et al.*, 2021), their underlying datasets must be carefully constructed to prevent such morphological convergence impacting results. Indeed, the classification of the Peruvian sample (or any conidont specimen) using cladistic or ML methods on theropod-only datasets would likely return similar results as the LDA, and the sample should ideally be analysed using data from a wider variety of clades.

Specimens MUSM 4269 and 5121 appear to pertain to the same morphotype given the overlap in morphological characters tabulated by Olmedo-Romaña *et al.* (2025: table 1). In contrast, the third specimen (MUSM 5122) differs in its purported presence of distal, rather than lingual, curvature. Its fragmentary nature and poor preservation render it difficult to confidently determine the specimen's original position, though we note a pronounced carina-like feature is clearly visible in fig. 3.3 and 3.4 of Olmedo-Romaña *et al.* (2025). If genuine, the carina would thus be perpendicular to the main direction of the curvature, and MUSM 5122 would closely resemble MUSM 4269 and 5121.

Olmedo-Romaña *et al.* (2025: p22–23) highlighted the limited distal recurvature, slender crown proportions, and "granular, vein-like" enamel texture in support of their referral of MUSM 4269, 5121 and 5122 to Spinosauridae, additionallyarguing that the specimens differ in these traits from crocodylomorphs and marine reptiles. They further cited the temporal range of the Peruvian material as evidence against referral to Thalattosuchia, Pliosauridae, or Ichthyosauria, though we note that the same argument could also be applied to a spinosaurid identification given the above-mentioned temporal range of this group. We agree that a "marine reptile" (*i.e.*, sauropterygian, ichthyosaurian, thalattosuchian or mosasaurid) identity for the Peruvian teeth is unlikely: temporal range aside, plesiosaurian crowns typically lack basally extending carinae and their replacement teeth typically develop within discrete bony crypts (=alveolar spaces), while ichthyosaur teeth are usually simple, straight cones that may be associated with fluted roots (Massare, 1987; Kear *et al.*, 2017). Similarly, metriorhynchid thalattosuchian crowns are more labiolingually compressed, and a mosasaurid origin is unlikely given the crown proportions (Massare, 1987) and absence of a mineralised periodontal ligament (LeBlanc *et al.*, 2017). We also agree that these teeth can be distinguished from the ziphodont condition observed in sebecid and barausuchid notosuchians (Prasad & de Broin, 2002; Ruiz *et al.*, 2021; Leardi *et al.*, 2024), though we note some ziphodont notosuchians may also present conidont crowns for various tooth positions (*e.g.*, *Hamadasuchus*) (Larsson & Sues, 2007).

Figure 2. Crocodylomorph (**A–D**) and spinosaurid (**E–S**) teeth compared. **A–D,** ***Goniopholis crassidens*** tooth (HASMG GG.89) in **A,** ?mesial; **B,** ?distal; **C,** lingual; and **D,** labial views. E, ***Ceratosuchops inferodios*** holotype premaxillae (IWCMS 2014.95.5) in ventral view. **F–J,** indeterminate spinosaurine tooth (MSNM V6424) in **F,** mesial; **G,** distal; **H,** lingual; **I,** labial; and **J,** basal views. **K,** Close of the mesial carina of an isolated spinosaurine crown (SMA 0173) in ?lingual view. **L–R,** Isolated baryonychine tooth (BEXHM 1995.485) in **L,** mesial; **M,** distal; **N, Q,** lingual; **O, R,** labial; and **P,** basal views. **S,** baryonychine tooth (IWCMS 2014.95) in lingual view. Abbreviations: **ce,** cervix; **co,** crown; **dca,** distal carina; **de,** denticle; **ent,** enamel texture; **laf,** labial flute; **lif,** lingual flute; **mca,** mesial carina; **rep,** resorption pit; **ro,** root. Scale bars: **A–D, F–J, S,** 20 mm; **E, L–P,** 10 mm; **K,** 2 mm; **Q–R,** 1mm.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Importantly, several morphological characters are inconsistent with a spinosaurid identity and are more suggestive of a non-ziphodont crocodylomorph. Direction of crown curvature is considered a useful morphological character to help distinguish spinosaurids from crocodylomorphs (Buffetaut *et al.*, 2019), and MUSM 4269, 5121 and 5122 (assuming our above-described reinterpretation of the latter's carina is correct) display pronounced lingual curvature that is unusual for spinosaurids. Consequently, the carinae in the Peruvian teeth are grossly perpendicular to the main direction of curvature that, together, recall a range of crocodylomorph taxa (*e.g.*, Fig. 2A–D). In contrast, curvature in spinosaurids is either largely absent (*e.g.*, spinosaurines) or primarily mesiodistal (*e.g.*, baryonychines), with the carinae oriented in line with the direction of any curvature (Fig. 2E–P) (Buffetaut *et al.*, 2008; Canudo *et al.*, 2008; Richter *et al.*, 2013; Alonso *et al.*, 2017; Barker *et al.*, 2023, 2024; Cabrera-Argudo *et al.*, 2024). We additionally note that MUSM 5122 appears to lack a carina on the opposite (and better preserved) side, deviating substantially from the bicarinate condition reported in spinosaurids (*e.g.*, Stromer, 1915; Charig & Milner, 1997; Hendrickx *et al.*, 2019), including those forms where the mesial carina is only present in the apical half-to-two-thirds of the crown (Canudo *et al.*, 2008; Isasmendi *et al.*, 2020).

Olmedo-Romaña *et al.* (2025) also reported a "granular" or "sculptured" enamel texture in the Peruvian teeth. As an aside, this terminology is inconsistent with that typically used for theropod dentition: spinosaurids commonly possess what are termed "veined" or "anastomosed" enamel textures (*e.g.*, Fig. 2Q—R) (Hendrickx *et al.*, 2015b, 2019), and we believe the consistent use of standardised anatomical and morphological terminology is paramount in the study of fossil tooth specimens. Olmedo-Romaña *et al.* (2025) also referred to a "granular, vein-like" (Olmedo-Romaña *et al.*, 2025: p. 22) texture for all three specimens, although this is only clearly visible in their fig. 2.7. With numerous crocodylomorphs also exhibiting similarly rugose or "wrinkled" enamel textures (Sander, 1999; Larsson & Sues, 2007; Pol *et al.*, 2014), further work is required to describe and categorise crocodylomorph enamel surfaces to allow more detailed comparisons. Notably, MUSM 5121 differs from spinosaurid teeth (Fig. 2Q) in lacking areas where the veined enamel texture curves towards the carinae (Olmedo-Romaña *et al.*, 2025: table 1) (Hendrickx *et al.*, 2019), and we regard this as another strike against the proposed spinosaurid identification.

The extent of the carinae relative to the cervix was not described for the Peruvian material but, in contrast to those of many spinosaurids (Fig. 2R) (Hendrickx & Mateus, 2014; Hendrickx *et al.*, 2019), the carina of MUSM 5121 does not appear to extend below the cervix (Olmedo-Romaña *et al.*, 2025: fig. 4). Both the mesial and distal carinae of MUSM 4269 are 5122 are described as lingually deflected (Olmedo-Romaña *et al.*, 2025: p. 8, 12); this is also in contradiction to the spinosaurid condition where the carina is more centrally positioned (Fig. 2E–G, L–M) (Buffetaut *et al.*, 2008; Canudo *et al.*, 2008; Richter *et al.*, 2013; Alonso *et al.*, 2017; Barker *et al.*, 2023, 2024; Cabrera-Argudo *et al.*, 2024). Slight variation in the position and extent of spinosaurid carinae is known (*e.g.*, Isasmendi *et al.*, 2020; Chowchuvech *et al.*, 2025), but we are unaware of specimens where both carinae display lingual deflection; this instead recalls the morphology reported in crocodylomorphs (*e.g.*, allodaposuchids) (Martin *et al.*, 2016). Lingual deflection of the mesial carina, such that both carinae face lingually to some degree and impart a D- or U-shaped cross-section to the crown, is present in the mesialmost dentition of some theropods, but it is not present in spinosaurids (Hendrickx *et al.*, 2015b, 2019). *In situ* premaxillary teeth of *Ceratosuchops* (IWCMS 2014.95.5), for example, have mesiodistally aligned carinae (Fig. 2E), as does *Baryonyx* (NHMUK PV R9951) (Charig & Milner, 1997).

Denticles are largely absent from the Peruvian specimens where the carina is preserved, although some are present along the distal carina of MUSM 5121 (Olmedo-Romaña *et al.*, 2025). Amongst spinosaurids, denticulated carinae are mostly found in baryonychine-type taxa, whereas spinosaurines typically lack such features (though some specimens appear to possess incipient or vestigial denticles; Fig. 2K, Q) (Sereno *et al.*, 1998; Carrano *et al.*, 2012; Hendrickx *et al.*, 2019, 2024; Rauhut & Pol, 2019; Barker *et al.*, 2021). Confounding matters is the fact that several crocodylomorphs, including elosuchids, thalattosuchians, and notosuchians, also possess serrated carinae (Gasparini *et al.*, 1991; de Broin, 2002; Prasad & de Broin, 2002; Andrade & Bertini, 2008; Young *et al.*, 2013, 2017). Olmedo-Romaña *et al.* (2025) provided limited information

on the morphology of these features in MUSM 5121: 5 denticles per millimetre may be present, a value seen in such spinosaurids as *Baryonyx* and *Suchomimus* (Charig & Milner, 1997; Hendrickx *et al.*, 2019), but are also reported for sebecid and notosuchid notosuchians (Lecuona & Pol, 2008; Viñola López *et al.*, 2025). Importantly, given that derived Cenomanian spinosaurines typically lack denticles, and that the latest reported occurrence of serrated, baryonychine-type teeth (as far as we are aware) are Albian in age (Fanti *et al.*, 2014), the presence of denticulated carinae in MUSM 5121 would be unexpected for a putative spinosaurid taxon surviving into the latest Cretaceous.

Elsewhere, MUSM 5121 also preserves a long and slender root that lacks the apical tapering synapomorphic for Spinosauridae (Fig. 2S) (Carrano *et al.*, 2012; Hendrickx *et al.*, 2019; Barker *et al.*, 2021). Instead, the root in MUSM 5121 maintains sub-equal proportions along its length (Olmedo-Romaña *et al.*, 2025: table 2). Further, its elongate proportions, lingual curvature, and convex labial surface all recall those of various neosuchians (Martin *et al.*, 2020).

It is therefore apparent that these Peruvian specimens do not represent late-surviving spinosaurids, but instead likely belong to one or more conidont crocodylomorph taxon (possibly a notosuchian). Post-Cenomanian spinosaurids are thus absent from the fossil record, and their apparent extinction around the Cenomanian–Turonian boundary remains poorly understood (Candeiro *et al.*, 2017; Barker *et al.*, 2023). Suggestions that the increased sea levels experienced at the time affected available spinosaurid habitat may be inconsistent with their ability to also exploit habitats inland (Sales *et al.*, 2016). Though environmental perturbations (*i.e.*, the Oceanic Anoxic Event 2, the Plenus Cold Event and the onset of the Cretaceous thermal Maximum) occurred at around this time (Mannion, 2024; Navarro *et al.*, 2025), coinciding with changes in "mid"-Cretaceous vertebrate faunas in several regions (Coria & Salgado, 2005; Novas *et al.*, 2005; Krause *et al.*, 2020), the dinosaur fossil record during this interval is undersampled and there is currently no evidence for a geologically instantaneous or globally widespread turnover event among dinosaur communities (Mannion (2024) and references therein). It is interesting to note, however, that carcharodontosaurid allosauroids also go extinct by the Turonian–Coniacian boundary (Coria & Salgado, 2005; Novas *et al.*, 2005, 2013; Delcourt & Grillo, 2018; Krause *et al.*, 2020; Meso *et al.*, 2021; Canale *et al.*, 2022), tentatively suggesting that shared drivers experienced during the Turonian impacted large terrestrial predator guilds. Nevertheless, given the issues associated with the study of "mid"-Cretaceous dinosaurian faunas, particularly around the Cenomanian–Turonian boundary (Novas *et al.*, 2005; Krause *et al.*, 2020; Mannion, 2024), the study of spinosaurid extinction remains frustratingly opaque.

CONCLUSIONS

The claimed presence of spinosaurid theropods in western South America near the end of the Cretaceous is an exciting proposal and one with the potential to usurp prior hypotheses on spinosaurid extinction and longevity. We applaud Olmedo-Romaña *et al.* (2025) in putting new material from the Campanian–Maastrichtian Fundo El Triunfo Formation of Peru on record and documenting it in appropriate detail. However, history has taught us to be cautious when dealing with surprising claims based on isolated theropod teeth, and the qualitative and quantitative evidence proffered in support of a spinosaurid identity for the specimens concerned (MUSM 4269, 5121, and 5122) is weak. Specifically, the conidont morphologies, fluted enamel surfaces, and labiolingual curvature present in the teeth recall traits seen elsewhere in crocodylomorphs. In addition, the specimens lack spinosaurid synapomorphies, including the presence of curved enamel texture located adjacent to the carinae and apically tapering roots. As highlighted by previous authors, multiple methods should be employed to identify isolated teeth with confidence, and referrals based on application of a singular methodology may produce erroneous results (Hendrickx *et al.*, 2020, 2024; Wills *et al.*, 2021). The identification of conidont archosaur teeth thus requires a combined approach centred on phylogenetic and machine learning methods (Hendrickx *et al.*, 2020, 2024; Wills *et al.*, 2021), using datasets that take into account the great diversity of Mesozoic crocodylomorphs (and, ideally, other archosaur taxa) in order to counter issues imposed by morphological convergence. Unambiguous spinosaurid material thus remains limited to the Berriasian/Valanginian–Cenomanian interval, and the drivers behind their apparent extinction in the early Late Cretaceous remain unclear.

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